

# Variability of Mediterranean Stone pine cone production: Yield loss as response to climate change

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## Abstract

Cones are harvested from Mediterranean Stone pine *Pinus pinea* L. for their edible kernels, pine nuts, which have been used as a food item in the region since Palaeolithic times. At present, cone yields render higher incomes to the owners of these pine forests than any other forest product. The large annual variation of cone yields is an important issue for forest management planning, which requires further research in order to establish its causes. One of the simplest explanations given for masting habits in polycarpic plants is that of weather tracking. Many plant ecologists, however, consider that this theory is insufficient and that further causes should be investigated. In this context, the present study analyses historical weather and yield registers over 41 years in one of the world's main Stone pine areas, the Northern Inland Plateau of Spain. Significant relationships found between rainfall and temperatures at certain key periods during the 4-year cone development period allowed for a multiple linear regression model for the log-transformed annual cone yield to be set up. This also included a negative autocorrelation with the ripening cone load during strobili induction. The model accounts for 75% of total variance between years. The observed trend of cone-yield reduction from 180 to less than 100 kg ha<sup>-1</sup> in the last 40 years was slightly overestimated by the predicted effects of the covariables that show significant tendencies to a warmer and drier climate.

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## 1. Introduction

In Mediterranean climate, growth and timber production of forest trees are subject to many climatic constraints, most notably the availability of water (cf. Gracia et al., 1999), while non-wood forest products (NWFPs) such as cork, mushrooms or dry fruits often present a special relevance and a greater economic value than timber (Scarascia-Mugnozza et al., 2000). An example of these NWFPs from Mediterranean woodlands are the cone crops gathered from the

singular umbrella-shaped Stone pine (*Pinus pinea* L.), whose edible seeds, pine nuts, have been used in the Mediterranean region for human consumption since Palaeolithic times because of their high nutritional value (50% fats and 35% proteins) (Gil, 1999; Badal, 2001). Pine nuts are currently highly prized in international markets meaning that their cones have become the most important product of Stone pine forests providing higher incomes to their owners than any other forest resource (timber, grazing, hunting rights, etc.). In spite of this, the Stone pine remains a genuine forest species and unlike most other nut trees in the region, which were domesticated during the neolithic period, it never was used in cultivated plantations. Only in the last 50 years have certain Mediterranean countries made efforts to install grafted

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experiment plantations. But at present, virtually total commercial cone yield is still harvested from natural or naturalised forests (Mutke et al., 2000).

The large variations in cone production mean that the average forest-owner's income for cone crops can vary as much as from €0.67 to 72 ha<sup>-1</sup> from one year to another and from €4 to 168 ha<sup>-1</sup> between forests in the same growth region. Thus, data taken over several consecutive years from each stand are required in order to accurately estimate average cone production for the purposes of forest planning (Gordo et al., 2000). Furthermore, over recent decades, natural regeneration techniques (e.g. the exclusion of stands near rotation age from cone harvesting in order to guarantee abundant seed rain) have gained importance in Forest Policy, thus generating a need for better information about seed yields.

In conclusion, a better understanding of cone-yield variation patterns would facilitate many aspects of management. Moreover, the average annual cone production (200–600 kg ha<sup>-1</sup>) of these trees means a biomass allocation similar to their bole volume growth which is often less than 1 m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup> in these woodlands on poor, excessively well drained soils (Cabanettes and Rapp, 1981; Mutke et al., 2003; Montero et al., 2004). This huge reproductive effort is unique among European pines species (cf. Helmisaari et al., 2002).

It is possible that masting and strong resource allocation to reproduction might both be explained by the Stone pine's singular life history, particularly by its dependence on animal predators to disperse its large, wingless seeds (Lanner, 1998). The causes of masting have aroused the interest of the biological research community since the annual seed production of populations of polycarpic plants fluctuates considerably around the average value, often with synchrony at regional or even geographic scale (cf. Sork, 1993; Kelly, 1994; Herrera et al., 1998; Koenig and Knops, 1998, 2000; Kelly and Sork, 2002). Species-specific studies have determined proximate causes for mast seeding such as climatic factors (*weather tracking*), both by resource-constraining or as purely synchronising cue (Forcella, 1981; Sork et al., 1993; Wright et al., 1999; García et al., 2000; Schaubert et al., 2002; Sarker et al., 2003), or correlations with insect pests', avian seed dispersers' or predators' population dynamics (Christensen and Whitham, 1991; Koenig et al., 1994; Despland and Houle, 1997; García, 2001). The reduction of flower numbers induced in mast years as result of resource depletion was also proposed as another mechanism for masting (flower masting)

particularly in species with relatively high nutrient and carbon costs of fruit production (Davis, 1957; Sork et al., 1993; Tapper, 1996; Koenig and Knops, 2000), e.g. agricultural fruit crops in which an additional phytohormonal control by ripening seeds is known to inhibit new flower initiation (Lee, 1979; Baldini, 1986).

On the other hand, several evolutionary causes of masting habit as a demographic strategy in plants' life histories have been proposed and contrasted widely with meta-database analyses and with theoretical models focussing on resource balance and on economies of scale considerations, e.g. wind pollination efficiency, predator swamping or animal disperser attraction (Foster, 1986; Isagi et al., 1997; Herrera et al., 1998; García, 2001; Kelly et al., 2001; Obeso, 2002). The weather tracking theory has in fact been considered lacking as a sole explanation of masting habits of many species in which seed production, apart from showing clear bimodality, also displays a much higher variability (coefficients of variation  $\gg$  150%) than any climatic variables (Herrera et al., 1998; Koenig and Knops, 2000). Nevertheless, weather and resource matching remain the simplest explanations for annual crop variations within most plant species (Kelly and Sork, 2002). Take, for example, the higher coefficients of variation in seed production found at higher altitudes and latitudes within a given species, presumably related to unfavourable growth conditions, they are often due to either one single, critically limiting weather factor (e.g. chilling, heat sums or water availability), or several such factors producing multiplicative effects which may even include erratic interruptions in the reproductive cycle (e.g. pollination failure due to heavy rains, flower abscission after late frosts) (Despland and Houle, 1997; Kelly et al., 2001; Sutton et al., 2002; Mutke et al., 2003). If this were indeed the case, the implied Poisson processes would cause bimodality and even frequent nil yields as a direct result of weather. Hence, we postulate that neither bimodality nor greater variability of seed production is a priori incompatible with weather tracking as the likely main cause of masting (nor the latter with ultimate evolutionary causes).

In agriculture, yield models for rain-fed crops commonly include meteorological factors as predictive variables for crop output (Sarker et al., 2003). Moreover, in the last decade, modelling of weather-dependent biological traits, such as phenology or economic crop yield, has attracted new attention in the light of discussion about the impact of climatic change on ecosystems and agriculture (Wright et al., 1999; Saxe et al., 2001; Mutke et al., 2003; Badeck et al., 2004).

In this context, the present paper studies cone-yield series of Mediterranean Stone forests over 41 years (1960–2000) in the Northern Plateau of Inner Spain, the coldest and one of the driest provenance regions of the natural range of the species, sited at its Northern and altitudinal limit. Stone pine strobili are wind pollinated and need 3 years to ripen (Francini, 1958). The different development stages of the seeds are therefore clearly differentiated in time, whereas in many other plant species ripening occurs in little more than a single year; thus, in such species, the effects of environment factors cannot be unequivocally associated with one or another stage of development from primordium to seed.

Thus, the Stone pine seems to present interesting features (meeting all previously mentioned premises for masting habit, both by resource balance and by evolutionary ecology) which allow for the study of those possible key factors involved in annual yield variations during seed development, particularly in the chosen study area of inland Spain where weather tracking can also be expected. The present paper aims to evaluate the degree of masting in Stone pine and to explain the roll of rainfall and temperature as proximate factors of observed yield variations.

## 2. Materials and methods

### 2.1. Area description

The stone pine forests of Spain cover some 450,000 ha and constitute two-thirds of the world's total area of the species. The country's principal growing areas are Western Andalusia and the Northern Inland Plateau; however, pure or mixed Stone pine stands also spread over Catalonia, Castile La Mancha, Madrid and Extremadura. The present study covers the province of Valladolid, situated on the Northern Inland Plateau, a sedimentary plain at 600–900 m. Due to surrounding high mountain ranges, the climate of the Inland Plateau is not genuine mild Mediterranean, but it has a continental tendency with hot, dry summers and long, harsh winters. Average annual temperatures in the province range from 10.1 to 13.5 °C, with absolutes from –22 to 44 °C. Occasional frosts may occur from September until May or June. Yearly rainfall ranges from 350 to 600 mm, though it has a very irregular distribution not only between years, but also from one season to another. Stone pine is the most important tree species of the province covering 45% of its forest area constituting approximately 40,000 ha of pure or Stone pine-dominated mixed stands and totalling about 6% of the species' global range. The importance of cone

harvest and processing in the local culture and economy has been well documented since the Middle Ages (Prada et al., 1997; Gil, 1999), the area being one of the world's most important producers of pine nuts. Most pine forests are located on sandy regosol in a flat area extending about 80 km East–West by 40 km North–South. Since the climate is homogeneous over this limited zone, the only first-order meteorological observatory of the area (Valladolid, 04°46'27"W; 41°38'40" N; 735 m) was used to obtain monthly temperature and rainfall data since 1957.

### 2.2. Yield data

The analysed data are the cone yields harvested each year for sale and registered in the annual management plans of public forests, documents conserved in the archives of the provincial Forest Service since 1960 (crop 1959/60: cones are harvested in winter from November to April). No historical yield registers from private forests exist, but both property types are ecologically similar and mixed in space; thus, analysed data are considered representative for the region. There are nearly 16,000 ha of public Stone pine forest grouped in 58 management units each one with its individual cone-yield series. Cropped yield does not include worthless cones destroyed or damaged by cone-boring insects. Moreover, in certain years and forests, very low per-hectare yields made it uneconomic to harvest cones; thus, these cases were registered as nil crops. The biological reproductive effort was therefore slightly underestimated and crop-failure frequency overestimated.

### 2.3. Stone pine reproductive phenology

Like most European pines, Stone pine has a monopodial, cyclic growth pattern. Annual shoots, preformed in buds on the apex of last year's shoots and elongated from April to June, bear a subapical whorl of lateral buds and female strobili (Francini, 1958). In June  $i - 4$  (nearly 4 years before the cone harvest or seed rain takes place), the new terminal buds are formed containing primordia for the following year's subapical organs (both lateral shoot buds and female strobili). In the next year  $i - 3$ , these shoot buds elongate and female strobili develop until anthesis and pollination occurs in June. Strobili undergo little growth during the next 20 months (final cone length: year  $i - 3$ , 10–15 mm; year  $i - 2$ , 20–40 mm). Fertilisation takes place in June of year  $i - 1$  and seed maturation until autumn with the main growth spurt to final cone size occurring from April to mid-July (final length 8–15 cm;

Table 1  
Phenostages of Stone pine cone development and relevant weather factors

Event	Year	Month
Primordia initiation inside the preformed terminal buds	$i - 4$	June
Female strobili on new shoot apices	$i - 3$	May, June
Pollination	$i - 3$	June
Main cone growth	$i - 1$	April–July
Cone ripeness, start of cone harvest	$i - 1$	November (until April)
Seed rain from unharvested cones	$i$	April–September
Main growth of the cones three cohorts before ( $Y_{i-3}$ )	$i - 4$	April–July
$P_5$ (winter/spring rainfall before primordia formation)	$i - 4$	January–May
$P_{\text{oct}}$ (rainfall in October before pollination)	$i - 4$	October
$P_5$ (winter/spring rainfall before pollination)	$i - 3$	January–May
$T_{ij}$ (average midsummer temperature after pollination)	$i - 3$	June, July
$P$ (annual rainfall before cone ripening)	$i - 2/i - 1$	September–August

fresh weight 200–500 g). Cone-opening, pre-dispersal seed predation and seed rain occur during the following spring (year  $i$ ) provided cones are not harvested the winter before (Table 1).

#### 2.4. Data analysis

In order to obtain per-hectare values, the yield registers of each forest have been referred to its area with Stone pine stands, an information updated in the management registers at 5-year intervals. Firstly, exploratory frequency analyses for each individual time series were performed (population level). To estimate the extent of masting, coefficients of variation of each raw data and log-transformed series were calculated. However, given that the Stone pine area estimations of each forest had been re-adjusted only in the 5-year revisions of the management plan, they did not take into account the yearly area changes (e.g. by clear-cuttings, etc.). This error, along with the presupposed crop-failure frequency overestimation, is presumably randomised by averaging all 58 series; hence, further analyses of the temporal variation, frequency distribution fitting, autocorrelations, correlations and finally regression for annual cone yield against meteorological factors and autocorrelations were performed only on meta-population scale (total annual cone yield divided by total Stone pine area). Average temperatures and rainfall sums of all months, bimesters, trimesters, etc., up to full year intervals from cone induction until seed maturity were calculated as independent variables for the correlation and regression analyses. The confidence intervals for regression parameters were obtained by jackknife estimations of the parameters' deviations both across all years and all individual forests' series (Efron and Gong, 1983).

Finally, the presence of significant trends was analysed in the significant variables with the aim of evaluating the possible tendencies and the consequences of the ongoing climate change on cone production, both as the main economic output and as key factor for natural regeneration of the Stone pine forests.

### 3. Results

The analysed annual cone crop of public forests in the province of Valladolid varied during the 41 years in an apparently erratic manner between a minimum of 278 Mg (17 kg ha<sup>-1</sup>) in 1985 and the record yield which in 1980 reached 14,237 Mg (909 kg ha<sup>-1</sup>) (Table 2). The annual mean was 3096 Mg, i.e. 193 kg ha<sup>-1</sup> (standard deviation 175 kg ha<sup>-1</sup>). Cone-yield frequency distribution between years was right-skewed, with 6 meager crops with less than 50 kg ha<sup>-1</sup> at regional scale, 15 regular crops of 50–150 kg ha<sup>-1</sup>, 14 good crops of 150–350 kg ha<sup>-1</sup> and 6 bumper crops above 350 kg ha<sup>-1</sup>. The observed temporal distribution of annual mean cone yield at regional scale fitted neatly an exponential distribution, and the natural logarithmic transformation achieved normality (Shapiro–Wilks'  $W = 0.989$ ,  $p = 0.95$ ). Coefficient of variation (Cv) was 94% for the raw data and 18% for the log-transformed regional series.

Individual forests gave 41-year averages between 55 and 591 kg ha<sup>-1</sup>, with Cv between 77 and 199%. Cv of log-transformed individual series (adding 1 kg ha<sup>-1</sup> in order to avoid zero values before log transformation) ranged from 19 to 99%. Among the transformed series, two different types of frequency distributions were observed: 51 of 58 series (83% of the area) showed a non-normality due to bimodality with a secondary mode

Table 2  
Regional average cone yields and meteorological covariables

	$Y$ [kg/ha]	$\ln(P)$	$P_5$ [mm]	$P_{\text{oct}}$ [mm]	$P$ [mm]	$T_{jj}$ [°C]
1960	138.0	4.928	293	160	602	19.7
1961	347.0	5.849	160	54	600	19.6
1962	144.7	4.975	225	17	555	19.6
1963	260.3	5.562	231	30	383	19.4
1964	244.9	5.501	190	12	497	20.0
1965	50.5	3.922	144	41	256	19.6
1966	63.6	4.153	304	105	582	18.6
1967	89.6	4.496	215	23	417	19.6
1968	154.2	5.038	212	36	383	19.7
1969	355.3	5.873	286	27	540	19.4
1970	593.1	6.385	269	13	506	20.4
1971	101.3	4.618	311	19	519	18.5
1972	102.6	4.630	245	79	379	18.9
1973	72.1	4.278	195	38	508	18.8
1974	423.3	6.048	230	6	455	19.3
1975	198.2	5.289	171	14	349	19.9
1976	353.2	5.867	146	38	390	21.0
1977	98.6	4.591	251	68	590	16.4
1978	165.1	5.106	275	18	518	17.9
1979	25.2	3.227	306	99	548	20.4
1980	908.8	6.812	214	38	447	18.1
1981	444.3	6.097	138	25	334	20.0
1982	301.6	5.709	123	24	335	21.1
1983	130.8	4.874	125	7	426	20.5
1984	26.6	3.279	182	63	384	19.6
1985	17.4	2.859	201	3	479	20.6
1986	152.3	5.026	173	31	299	20.5
1987	123.4	4.816	235	45	459	19.9
1988	330.8	5.802	243	27	537	18.1
1989	85.5	4.449	169	24	287	21.5
1990	153.5	5.034	132	42	504	21.8
1991	230.6	5.441	157	25	301	21.0
1992	34.4	3.537	100	108	253	19.4
1993	42.7	3.755	152	142	402	19.9
1994	73.2	4.293	199	56	457	21.6
1995	44.1	3.786	106	20	314	21.5
1996	81.0	4.395	275	16	570	21.2
1997	228.7	5.433	192	44	557	18.7
1998	214.7	5.369	224	11	615	20.9
1999	202.6	5.311	122	107	314	21.4
2000	88.2	4.479	201	53	493	20.5

$Y$ : cone yield;  $P_5$ : rainfall from January to May;  $P_{\text{oct}}$ : October rainfall;  $P$ : annual rainfall (from September the year before until August);  $T_{jj}$ : average temperature of June/July.

at zero ('zero inflated normal distribution', including the previously mentioned unharvested next-to-nil crops); only 7 series (17% of the area) had normally distributed crops with an absence of crop failures. The deviation of the yield series of each forest was negatively correlated with its mean in the first group and not correlated in the second group. The highest

coefficients of variation (>69%) were obtained in eight forests (3% of the area) where crops failed frequently (more than 10 nil crops in 41 years) (Fig. 1).

The regression model for the log-transformed cone crop of year  $i$  includes the only significant autocorrelation ( $R = -0.39$ ) with a time lag of 3 years and significant effects of several weather factors during the cone development (Table 1):

$$\begin{aligned} \ln(Y_i) = & 9.74(\pm 0.89) - 0.487(\pm 0.031)\ln(Y_{i-3}) \\ & + 0.0025(\pm 0.0005)a + 0.0076(\pm 0.0007)b \\ & + 0.0053(\pm 0.0007)c - 0.277(\pm 0.035)d \\ & + 0.0024(\pm 0.0003)e \end{aligned} \quad (1)$$

where  $\ln(Y_i)$ : log-transformed average cone yield of year  $i$  at regional scale [ $\text{kg ha}^{-1}$ ];  $\ln(Y_{i-3})$ : the same variable 3 years before [ $\text{kg ha}^{-1}$ ];  $a$ :  $P_{5,i-4}$ , rainfall from January to May 4 years before [mm];  $b$ :  $P_{\text{oct},i-4}$ , rainfall in October 4 years before [mm];  $c$ :  $P_{5,i-3}$ , rainfall from January to May 3 years before [mm];  $d$ :  $T_{jj,i-3}$ , average temperature of bimester June/July 3 years before [°C];  $e$ :  $P_{i-1}$ , annual rainfall from September to August the year before [mm].

All intervals of confidence given in Eq. (1) correspond to  $\pm 1.96$ -fold standard deviations of jack-knife estimations between years, whereas deviations between forests were consistently smaller than those between years for all parameters (0.2–0.3-fold).

The independent variables of the equation showed no multicollinearity (absolute values of all correlations below 0.5, all Variance Inflation Factors below 1.4), and the model achieved  $R^2 = 0.755$  (adjusted to the degrees

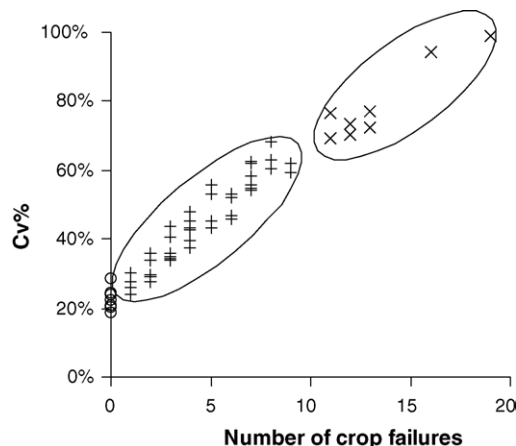


Fig. 1. Coefficient of variation Cv% vs. number of nil yields in 41 years from 58 forests (o: no nil yield; +: 1–10 nil yields, x: more than 10 nil yields).

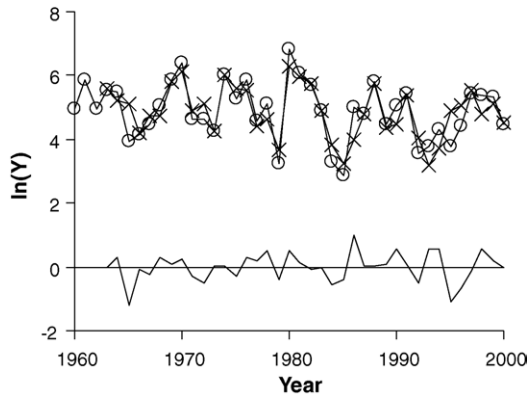


Fig. 2. Observed (open circles), predicted (crosses) and residual values (no symbols) of log-transformed annual cone yield at regional scale  $\ln(Y)$  ( $Y$  in  $\text{kg ha}^{-1}$ ).

of freedom  $R^2 = 0.708$ ). Residual analyses as time series showed no significant difference from white noise, most notably no trend in time was observed (Fig. 2). The degree of determination attributed to each factor (Type I Sum of Squares divided by the total Sum of Squares, entering the factors in order of their temporal occurrence during cone development, Table 1) ranged from 7 to 26%. This greatest value corresponded to the spring rainfall (January–May) before pollination ( $P_{5,i-3}$ ) (Table 3).

The observed log-transformed cone yield and all regression factors with the exception of the October

Table 3

Analysis of variance for log-transformed annual mean cone yield,  $\ln(Y_i)$

Factor	Sum of Squares Type I	Degrees of freedom	Mean squares	F-value	p	$\Delta R^2$ (%)
$\ln(Y_{i-3})$	4.19	1	4.19	17.0	0.0003	13
$P_{5,i-4}$	3.84	1	3.84	15.5	0.0004	12
$P_{\text{Oct},i-4}$	2.57	1	2.57	10.4	0.0030	8
$P_{5,i-3}$	8.11	1	8.11	32.8	0.0000	26
$T_{jj,i-3}$	2.68	1	2.68	10.9	0.0025	9
$P_{i-1}$	2.22	1	2.22	9.0	0.0054	7
Residuals	7.66	31	0.25			
Total	31.27	37				75

$\ln(Y_{i-3})$ : autocorrelation with time lag 3 years;  $P_{5,i-4}$ : rainfall sum from January to May before primordia formation;  $P_{\text{Oct},i-4}$ : rainfall in October before pollination;  $P_{5,i-3}$ : rainfall sum from January to May before pollination;  $T_{jj,i-3}$ : average temperature of bimester June/July after pollination;  $P_{i-1}$ : amount of rainfall from September to August before yield.

rainfall showed significant linear trends in the studied period (Fig. 3). The (retransformed exponential) yield trend diminished from  $180 \text{ kg ha}^{-1}$  in 1960 to less than  $100 \text{ kg ha}^{-1}$  in 2000. During the same time interval, the midsummer temperature  $T_{jj}$  trend increased  $0.04 \text{ }^\circ\text{C year}^{-1}$  (from  $19.0$  to  $20.7 \text{ }^\circ\text{C}$ ). Both annual rainfall  $P$  and winter/spring rainfall  $P_5$  showed a parallel tendency to decrease about  $1.8 \text{ mm year}^{-1}$ , thus reducing the 1960 trend value ( $480$  and  $240 \text{ mm}$ , respectively) to  $410$  and  $170 \text{ mm}$  in 2000. If these

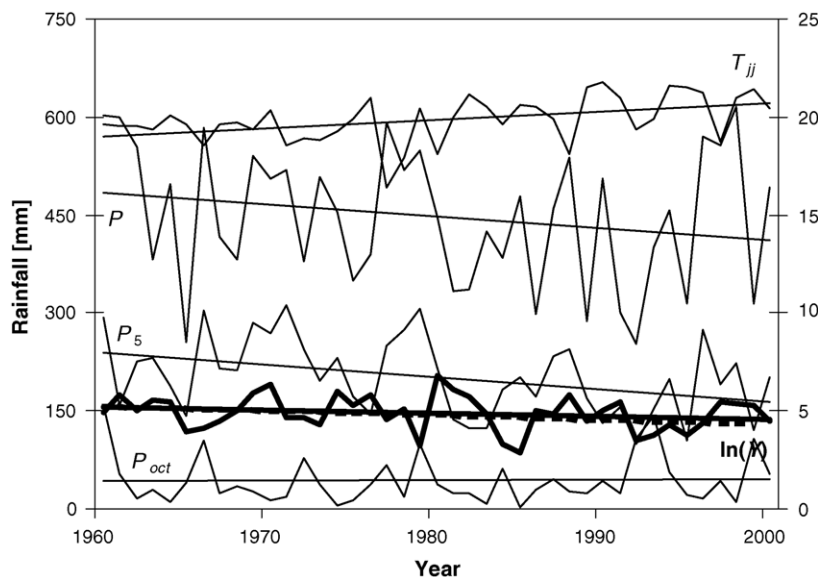


Fig. 3. Observed log-transformed cone yield  $\ln(Y)$ , its linear trend (bold lines, right scale) and its estimation  $\ln(Y)_{\text{est}}$  (dotted line, right scale) predicted by introducing in the model (Eq. (1)) the linear trends of the climate factors between 1960 and 2000 ( $T_{jj}$ : average temperature June/July, right scale ( $^\circ\text{C}$ );  $P$ : annual rainfall;  $P_5$ : rainfall from January to May;  $P_{\text{Oct}}$ : rainfall in October, rainfall variables left scale).

tendencies were to continue, mean annual crops will have decreased to less than  $80 \text{ kg ha}^{-1}$  by the year 2015.

#### 4. Discussion

During the studied 41-year series, both consecutive bumper crops and consecutive poor crops occurred; hence, no evidence of resource depletion on a year-by-year basis exists which would support any putative stored resource matching or resource budget considerations. On the other hand, the only significant autocorrelation with the time lag of 3 years does match both postulated hypotheses about resource tracking (depletion) and/or hormonal inhibition caused by the (three cohorts older) cone that ripen at the moment of flower primordia formation.

The marginal 3% of Stone pine area where crops failed more than 10 years out of 41 and individual forests' coefficients of variation were highest (Fig. 1) includes eight forests with the worst site qualities, e.g. on eroded slopes of chalky marls with gypsum layers, or in shallow soils over endorheic saline groundwater levels. This indicates that their stronger annual cone-yield variation is less a result of some evolutionary advantage of masting than a direct consequence of the limiting environment.

Also, the observed (log-scaled) normal distributed regional crop variation of Stone pine in Inland Spain seems to be caused mainly by weather and resource tracking during flower and cone development. Indeed, cone-yield correlation with rainfall in the spring before pollination has previously been described in the species (Pozzera, 1959). The additive multiple linear regression model for the log-transformed annual cone yield corresponds to a multiplicative model at real scale; thus, the combined effects of the predictor variables explain a higher coefficient of variation (Cv) of the re-transformed response variable (71%) than those of the predictors themselves (all  $Cv < 30\%$ ). Except  $P_{\text{Oct},i-4}$ , all independent factors included in the model make clear biological sense with respect to the previously mentioned critical periods of reproductive phenology (Mutke et al., 2003). In accordance with the results of the regression analysis, cone yield was favoured by: higher water availability and a smaller load of ripening cones at the time of primordia formation (in June of the 4th previous year); by higher water availability during pollination (in June of the 3rd previous year); by milder midsummers just after pollination (less conelet abscission); by higher water availability during the most important growth spurt and final ripening of the cones (annual rainfall during the

last year). Only the October rainfall before pollination ( $P_{\text{Oct},i-4}$ ) does not match any already known phenological event but there might be a connection with the differentiation of primordia inside the terminal bud between reproductive and vegetative structures that is known to occur at some moment between June and December of year  $i - 4$ , when vegetative and reproductive structures are already distinguishable under a microscope (Abellanas and Pardos, 1989).

On the other hand, linear regression analyses are not able to include threshold factors or erratic events such as late frosts around pollination which in certain years have been known to drastically reduce the strobili setting in Stone pines (Mutke et al., 2003). This in turn means that the 'stochastic' residual variation in the resulting cone yield does include such additional meteorological causes.

As a matter of fact, Herrera et al. (1998) questioned the meaning of the very concept of "mast seeding" as a putatively well-defined, genuinely interesting biological phenomenon after revising 296 datasets from 144 woody species, because virtually any supra-annual fruiting schedule implies a certain degree of variability. In this sense, the population coefficients of variation (Cv) observed in Stone pines were similar to the Cv range estimated for other pine species (42–168%) (revised in Herrera et al., 1998). Most notably, yield data from another zoochorous species, Pinyon pine (*P. edulis*), had a Cv of 70%, yet Forcella (1981) considered its cone production 'erratic' and found it to depend exponentially on late summer temperature (putative moment of flower primordia differentiation). Moreover, in three North American oak species with different maturation spans from flower primordia to mature acorns (2 or 3 years), high correlations of current acorn production with past yield (negative autocorrelations) and meteorological factors at critical moments of fruit development were shown to depend on specific events of floral biology such as primordia initiation, pollination, etc. (Sork et al., 1993). This underlines the necessity to contrast possible environmental correlations with the reproductive biology and phenology of each studied species in order to elucidate accurate causal mechanisms, while discarding spurious correlations.

In the present study, 68% of the total cone-yield variation was determined by the Sums of Squares attributed to the factors acting from flower primordia formation until strobili setting after pollination. These results are in accordance with the flower masting that produces a strong correlation ( $>0.85$ ) in different Stone pine clone banks between the annual conelet number after pollination and the corresponding cone yield 3

years later (Mutke, 2005). Also, the observed 3-year-lag autocorrelation (possibly due to the important biomass sink of ripening cones at the moment of flower induction) is supported by previous analyses at tree and shoot scale in Stone pines, which have shown that both vegetative shoot vigour (length, number of lateral shoot buds) and female conelet number (ripening 2 years later) suffer from insufficient water availability (previous rainfall) and from the number of ripening cones produced the year before (bud formation) (Mutke et al., 2003, 2005). It would therefore seem likely that resource shortcoming is the more probable hypothesis and that phytohormonal inhibition should not, in itself, affect shoot vigour. To sum up, the present results indicate that at (meta)population scale, proximate causes for masting due to environmental factors and autocorrelations do not, as such, constitute ‘resource matching’ in the very last year of cone main growth and ripening as this would imply a ‘forward’ matching of flower masting to future environmental limitations 2 years later, but rather a (backward) ‘resource tracking’, i.e. flower masting as a physiological consequence of constraints at the moment of their induction and setting (climate factors, resource depletion, etc.).

The observed temperature increase ( $+0.04\text{ }^{\circ}\text{C year}^{-1}$  from 1960 to 2000) matches the general rise in air temperature caused by the climate change observed in the Iberian Peninsula in this period (Hulme and Sheard, 1999) and estimated for the 21st century in  $+3$  to  $+7\text{ }^{\circ}\text{C}$  (Santos et al., 2001; Saxe et al., 2001). Furthermore, the observed tendency to drier springs is in accordance with the considerable reduction in rainfall predicted for Inland Spain within the next 50 years (Hulme and Sheard, 1999). The observed reduction in rainfall has been particularly apparent in early spring (bimester February–March) causing decidedly acute problems for the Stone pine as, even at present, a significant reduction in shoot length is apparent after dry springs indicating that the species has, in inland Spain, already reached its water stress limit (Mutke et al., 2003, 2005). If the current trends to stronger aridity continue, the consequences would affect not only cone production and natural regeneration, but also the very stability of the existing pine forests in the region.

Although these simple linear trends of a four-decade time series from a single weather station are similar to cited general climate tendencies, this does not necessarily mean that, in as far as middle and long term variations are concerned, they will supersede the uncertain circumstances suffered in any climate scenario, i.e. fluctuations, particularly rainfall fluctuation. Their inclusion in the

present paper only aims to illustrate their accordance with the observed yield loss. In fact, introducing the annual values of the linear trends of climatic covariables in the model would result in a certain overestimation of the yield-decrease rate, i.e. tendencies displayed by climatic factors would even lead to a slightly more pronounced decrease in cone yields than that actually observed (Fig. 3). One reason might be the fact that temperature is known to influence many other features of plant biology, namely phenology (Badeck et al., 2004). In the Spanish Northern Inland Plateau, an empirical model for spring phenology predicted earlier Stone pine conelet pollination by nearly 1 week/ $1\text{ }^{\circ}\text{C}$  warming (Mutke et al., 2003) which is in accordance with the general advance of tree growth onset in spring, estimated as 8 days/ $1\text{ }^{\circ}\text{C}$  (Chmielewski et al., 2001). Hence, under a shifting phenology calendar, it might be more appropriate to calculate the regression factors for thermal time intervals rather than for fixed calendar months. However, even if the Stone pine to some extent manages to ‘escape’ the negative effects of midsummer droughts by switching to earlier dates for phenostages (bud onset, flowering, etc.), it will still be vulnerable to other, considerably heightened risks such as frost damage. Just as in the case of other fruit trees or field crops, changes in the timing of phenology in Stone pines could become of vital importance economically because of the direct impact this would have on yield formation processes and, therefore, on the final crop yield (Chmielewski et al., 2004).

## 5. Conclusions

The results show that annual Stone pine cone-yield variation is mainly a direct response to weather factors and resource depletion. The most notable limiting factor seems to be water stress, as seen both in an exponential yield response to rainfall amounts during different cone development stages and in the negative effect of hot midsummers on cone setting. The observed trend to yield loss over the last 40 years (from 180 to less than  $100\text{ kg ha}^{-1}$ ) is smaller than that predicted through the model as the consequence of ongoing climate change. Therefore, in the future, further efforts are required in order to accurately estimate the impacts of temperature rise and changes in rainfall patterns on cone development and final cone yield in Stone pines.

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