

Seed and Cone Production Patterns from Seventy-Nine Provenances of *Pinus halepensis* Mill. Across Tunisia Forests

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Abstract: *Pinus halepensis* Mill. is an important tree species in the Mediterranean Basin. In Tunisia, there is an increasing interest in its seed production due to their impact on the socio-economical life of the Tunisian population, forest regeneration (seedling production) and biodiversity maintenance. Adaptive strategies were developed to fire recurrence by early cone production and seed storage in the serotinous cones. Tunisia's native forests were investigated to examine the impact of four bioclimatic zones on Aleppo pine cone and seed production. Stand characteristics and average tree size measurements were studied with simple and multiple regression analyses for explaining their influences in seed and cone production and characteristics. Results showed a positive relationship between the accumulated rainfall and the geographical variables to the number of cones and its seeds content. Density had a strong adverse effect on the average tree's cone crop and seed yield. The cone production and the total seed mass were positively correlated with tree dimensions, but diameter at breast height and crown height were the most explanatory variables. Several environmental factors substantially increased the production of cones and seeds. The results could help foresters to decide better locations of cone and seed production according to density in Aleppo pine forests.

Keywords: Tree dimensions, bioclimatic gradient, cone and seed production, Aleppo pine, stands characteristics, Tunisia.

INTRODUCTION

Aleppo pine (*Pinus halepensis* Mill.) is the main studied Mediterranean coniferous tree species for several reasons, i.e., fire disturbance and drought stress adaptation [1, 2]. In addition, a further topic relating the seed and cone production to the effect of several environmental factors is under discussed in many Mediterranean countries [3]. The northern Mediterranean countries distribution of Aleppo pine is often related to reduced reproductive capacity (low cone crop and seed quantity), whereas, the southern coast area is related to good fructification [3, 4]. This variability is due to the trade-off between several environmental factors such as growing season rainfall, temperature, resource allocation and plant adaptation [5, 6]. Moreover, cold temperature kills flowers and produces a general damage on coning phenomena [7, 8]. Nonetheless, there is no data concerning the global environmental effects on the species cone crop and seed yield, except a small number of studies in Algeria and Morocco [9, 10]. In Tunisia, similar few studies at Aleppo pine forests [5, 11, 12] were conducted to quantify its cone and seed production under several variables. These studies showed that cone and seed

production are usually influenced by tree density and age for each studied stratum, whereas, the cone crop and seed yield varied respectively, between 258.5 to 555.75 kg for total mature cones harvested and 5.11 to 11.16 kg for total seeds extracted [12]. Surprisingly, the average Aleppo pine's seed weight noted a general increasing pattern varying from 14.2 to 17.5 mg from the wettest forest area to the driest one. Moreover, this later variable was positively linked to altitude and negatively with longitude [11]. Recently, they also showed that coning was usually influenced by nutrient allocation for growth instead of Aleppo pine fructification. Besides, some of the obtained results dealing with pine cone production proved that it is affected by tree age and height [13].

This species show an early age of reproduction (reproductive saplings of 3-6 years old) and annual fructification [14, 15]. Cones of Aleppo pine ripe in early spring of the second year, changing the color of cones from green to reddish brown and end the maturation period in the summer of the third year, turning to grayish [15]. Recently Spanish research team found ecotype specialization for the cone production, where resource-poor ecotypes favored early reproduction while resource-rich ecotypes favored vegetative growth. Moreover, medium-sized trees produced the highest cone yield [4, 13]. Aleppo pine trees produce non-serotinous and serotinous cones allowing both,

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longtime seed conservation and an important regeneration capability [16, 17]. Several authors showed that, production of cones and seeds in this species are strongly affected by the influence of various environmental factors, such as climate, tree size and site quality [18, 19, 20, 21]. Actually, Aleppo pine seed is the most important food sub-sector of several others forest products in Tunisia offering the best goods and services and that are often undervalued [22]. Similarly, the species seed production represents a real employment and income source for local and rural population. Recent published report illustrate that Tunisian national incomes of Aleppo seed production have exceeding ten times better that its wood production. Tunisian Aleppo pine forests have several others benefits such as pharmaceutical and cosmetic products.

This study aimed to a better understanding of Aleppo pine cone crop and seed yield and to document the environmental factors which affecting its cone and seed production. Therefore, we investigated the reproductive performance of the species grown in native forests along a longitudinal, latitudinal and altitudinal gradient. We tested the hypotheses that large native forests distribution in the driest zones is linked to good cone crop and seed yields. This means

to move southwards for latitudinal gradient and westwards for longitudinal gradient. In addition, constructed models under simple and multiple regressions would help researchers to know the effect of many environmental factors on Aleppo pine forest's reproductive traits in Tunisia. Thus, the main objectives were to test if (i) the reproductive traits of Aleppo pine were influenced by the combined effect of environmental factors or by each parameter separately and, (ii) to determine the most explanatory variables on fructification for this coniferous tree species.

MATERIALS AND METHODS

Study Region and Sampling Procedure

The study region covered most of Tunisia's natural forests of Aleppo pine that were scattered over four different bioclimatic zones ranging from the sub-humid (the wettest) to the lower semiarid (the driest), as previously delimited by [23], (Figure 1). The surface of Aleppo pine forests located in the humid and arid bioclimatic zones of Tunisia were very small so they were overlooked [24]. Thus, in the upper semiarid area we included some plots where Aleppo pine forests just constituted from 1.1 to 12.7% of the district's total land cover. These forests were scattered over the northern mountain ranges, which are broken elevations oriented

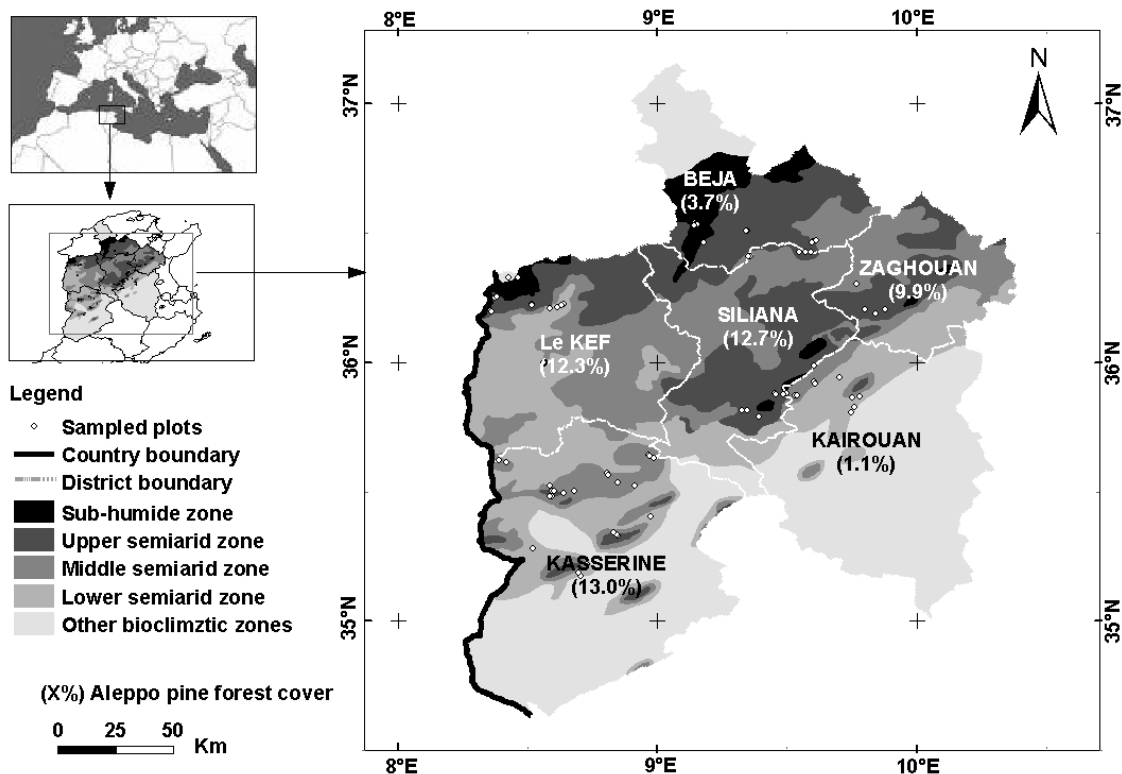


Figure 1: Map showing the geographic location of all 79 plots of *Pinus halepensis* Mill. Across Tunisia forests.

from the southwest to the northeast, with altitudes ranging between 250 and 1185 m above sea level (asl). The latitudes of this study varied between 35.17 and 36.53° N, whereas the longitudes varied between 8.33 and 9.85° E (Figure 1).

The study region is a typical Mediterranean climate, with two distinct wet seasons (autumn and spring) and an intense dry season (summer droughts), and the aridity gradient increases southwards. During the period from 1997 to 2006, the study area received an average annual rainfall of 457 mm and the maximum and minimum annual averaged temperatures were 33.1 °C in July and 4.1 °C in January, respectively, which was similar to the studied three years of the reproductive cycle of cones being concentrated almost all precipitation (96%) between September and May. Furthermore, the studied region showed a rainfall gradient decreasing southwards, going from 625 mm in the sub-humid areas (the wettest) to 423 mm in the lower semiarid ones (the driest) meanwhile in the upper and middle semiarid zones, the mean annual precipitations were 502 and 476 mm respectively (Table 1). Using the bioclimatic classification of Emberger [25], the Q-ratios obtained in the study area ranged from 32 to 97. Furthermore, the sub-humid offered the highest Q-values varying from 64 to 97, whereas the lowest Q-values were recorded in the lower semiarid zones and ranging between 32 and 38 (Table 1). However, it was not possible to calculate the Emberger's Aridity Index for each plot or forest stand because the climate data were coming from nearest meteorological station provided by the National Institute of Meteorology.

The richest and most developed soil substrates were found in the sub-humid areas, often represented by yellow to brown calcareous soil or red soils. These

are typically Mediterranean soils and resemble those where preferred by *Pistacia lentiscus* L., *Olea europaea* L. var. *olaster*, and *Cistus monspelliensis* L. They presented medium to fine textures with thick litter layers and high organic matter contents, resulting in a high water retention capacity in the deeper horizons. The red soil types usually are dominated by *Tetraclinis articulata* Benth, *Quercus ilex* L., *Rosmarinus officinalis* L., and *Calycotome villosa* (Poir) Link, in addition to *P. halepensis*. They are characterized by coarse textures and low organic matter contents, in addition to the presence of ferrous oxides.

In the semiarid zones, two major types of soils were distinguished, although both have evolved from calcareous bedrocks. Both are composed with medium to fine sedimentary deposits which horizon depth depends on slopes and run-off intensities [26]. Their porosity remains dependent upon the depth and texture of the water deposited sediments. On deeper deposits, vegetation is usually dominated by *P. halepensis*, *Juniperus phoenicea* L., *Ceratonia siliqua* L. and *Erica scoparia* L. On shallow deposits, the natural vegetation is often represented by *P. halepensis*, *J. oxycedrus* L., *Cistus libanotis* L. and *Ampelodesma mauritanicum* (Poir.) Dur. et Schinz. The second soil, commonly encountered in the lower and middle semiarid areas, are the least developed and the shallowest with a rendzinic profile, resulting in coarse textures and an abundant presence of gravel and stones at the soil surface. They host a variety of plant associations dominated by one or more of the following species: *P. halepensis*, *C. siliqua*, *J. oxycedrus*, *Phillyrea angustifolia* L. and *Stipa tenacissima* L.

According [2], we selected rectangular plots to sample the study area. A total of 79 rectangular plots (40x25 m) were defined to include the higher variability

Table 1: Site Description and Main Characteristics of the Major Study Region Hosting most of the Tunisian Aleppo Pine Forests (n=79)

Mean values	Bio-climatic zones			
	Sub-humid	Upper semiarid	Middle semiarid	Lower semiarid
<i>Climatic parameters</i>				
Annual rainfall (mm)	625	502	476	423
Maximum Temperature (°C)	32.2	32.3	33.1	32.1
Minimum Temperature (°C)	3.5	3.5	4.4	4.1
Emberger's quotient (Q)	64<Q<97	44<Q<64	38<Q<44	32<Q<97
<i>Site characteristics</i>				
Density (tree/ha)	869 ± 270*	1054 ± 487	890 ± 418	973 ± 435
Basal area (m ² /ha)	16.96 ± 4.66	12.42 ± 4.99	11.13 ± 5.25	11.96 ± 4.69

*Standard deviation.

of the studied stands [27]. The allocation of the sampling plots among the bioclimatic zones was made according to the importance of the species forest cover within each one of these geographic entities. Plot selection and delimitation were based on the requirement of the total absence of anthropogenic disturbance, as well as on the need of covering a wide array of tree densities and canopy covers within each bioclimatic zone. The forest stand characteristics were determined by measuring the total and specific tree density, the basal area and the canopy coverage in each plot (Table 1). The height and the diameter breast height (DBH) were recorded in all the Aleppo pine trees (7686) contained in the monitored plots to calculate their means and the average tree size. We selected and marked in each plot an average pine which had the average DBH and height calculated by the mean of all the trees measured in the plot. We harvested all mature cones [17, 20], from this average tree and carried them to the laboratory. Only mature and damage free cone were harvested, leaving on the tree the pre-ripe green or yellowish (immature cones) and decaying cones showing partially or fully opened scales were ignored. Sampling and measurements were carried out in summer 2006 to obtain cones which completed the maturing process of 3 years and to take advantage of the summer stop in vegetative growth.

In the laboratory, all harvested cones (8890) were separated into sets according the bioclimatic provenance and their lengths and widths were measured. Thereafter, we recorded their air-dry weight after 21 days of exposure in a well aerated and dry room. All cones were subsequently introduced in an oven set at 55° C where they stayed for 5 days in order to induce the opening of their scales [28]. Afterwards, all seeds were carefully removed from underneath the scales using a hand-held knife which also served to open any remaining closed scales and extract the hidden seeds, all of which were counted and weighed for each cone separately.

Statistical Analysis

We performed descriptive statistics but also simple and multiple regression analyses to check relationships linking the selected factor or their combination (bioclimatic zones, geographical parameters, forest stand characteristics and tree size) on the studied variables to characterize reproductive parameters: cone parameters (number, weight and size) and seed parameters (number, mass per cone and mass per average tree). In all cases, the regression models were only taken if they were significant at the critical probability P of 0.05. Under simple regression, mathematical transformations of the initial values were performed for all variables involved. The transformation maximizing the determination coefficient (R^2) was chosen, and then the correlation coefficient was calculated. Under multiple regression analysis, a stepwise forward procedure was carried out using the initial values without mathematical transformation. The model was kept only when a minimum P -value of 0.05 was recorded. To control multi-collinearity during construction of the new multivariate model, a variance inflation factor (VIF) test was used and only explanatory variables with $VIF < 5$ were accepted for the final model. In addition, we tested for differences in onset of cone characteristics, cone crops and seed yield among bioclimatic zones using one-way ANOVA and Tukey's Studentized Range test. The statistical software package SAS version 9.1 (SAS Institute, Cary, North Carolina, USA [29]) was used to perform all the aforementioned procedures.

RESULTS

Influence of Bioclimatic Zones

Mean annual rainfall; mean annual, minimum and maximum temperatures characterizing the different bioclimatic zones had no significant ($P > 0.05$) effect on the cone and seed characteristics or on the cone and seed yield. However, the accumulated rainfall during

Table 2: Relationships between the Accumulated Rainfall (Rain) during Coning Cycle with Cone Production and Seed yield Produced by the Average Tree of Aleppo Pine in Tunisian Forests

Predicted variables (y)	Prediction models	r	P-value
<i>I - Cone crop</i>			
Cone number/tree (n)	$y=0.129 \text{ Rain} -88.539$	0.947	0.043
Cone average weight (g)	$y=0.000058 (\text{Rain})^2-0.181743 \text{ Rain} +163$	0.998	0.018
<i>II- Seed yield</i>			
Seed number/Cone (n)	$y=0.00015(\text{Rain})^2-0.48110 \text{ Rain} +460$	0.995	0.022
Seed number/tree (n)	$y=0.015x-11.822$	0.984	0.031
Seed weight/tree (g)	$y=0.257 \text{ Rain} -252.460$	0.949	0.037

cone growing season was found to be significantly related to cone and seed characteristics (Table 2). Accumulated rainfall was significantly related to the number of cones produced by the average Aleppo pine tree ($r = 0.947$, $P < 0.043$), the seed weight per tree ($r = 0.949$, $P < 0.037$) and the number of seeds per tree ($r = 0.984$, $P < 0.037$), as a simple linear regression. In addition, second grade equations were found to relate the accumulated rainfall of this period to the average weight of the individual cone ($r = 0.998$, $P < 0.018$) and the number of seeds contained in a cone ($r = 0.995$, $P < 0.022$).

Among-bioclimatic zones variability, cone characteristics showed significant differences ($p < 0.05$) for the individual cone average weight and the sub-humid area having the higher values (Table 3). Furthermore, Aleppo pine cone size was similar between bioclimatic zones. The values recorded at average tree level showed similar tendency. Total cone number and total cone weight per tree increased significantly according to the increasing precipitation (Table 3). Their values were growing from lower semiarid to the sub-humid area with a represented gain of about 90 additional cones per tree in the considered

period. Across bioclimatic zones, this gain corresponds to 5 cones year⁻¹ for each 100 mm annual rainfall increment. When these values were calculated for the stand level (related to the unit of surface), all the values were distributing across a climatic gradient, decreasing according to lower rainfall or Emberger quotient. So, we found that the sub-humid had the highest values in cone number and weight per hectare while the lower semiarid areas showed the lowest values (Table 3). A similar tendency was found for the seed yield. At cone level the sub-humid area showed the highest values of seed number and seed weight while the lowest values were recorded in the upper semiarid area (Table 3). Similar pattern was followed by the weight of an individual seed, decreasing from the sub-humid area to upper semiarid area. The tree and stand seed production were confirming to related climatic gradient while the highest values were found in the sub-humid and the lowest values were obtained in the semiarid area (Table 3).

Influence of Geo-Positional Parameters

Longitude was highly ($P < 0.001$) linked to the mean values of the cone and seed characteristics, such as

Table 3: Descriptive Statistics (Mean \pm Standard Deviation) and Significant Differences in Different Bioclimatic Zones of Tunisia Aleppo Pine's Cone Characteristics

Bio-climatic zone	Sub-humid	Upper semiarid	Middle semiarid	Lower semiarid
<u>I - Cone characteristics</u>				
Length (mm)	74.2 \pm 4.0 a*	63.3 \pm 8.5 a	64.9 \pm 6.5 a	69.2 \pm 9.3 a
Width (mm)	28.5 \pm 3.9 a	30.3 \pm 2.7 a	30.8 \pm 1.8 a	30.0 \pm 1.8 a
Weight (g)	27.2 \pm 6.0 a	19.0 \pm 6.6 b	19.6 \pm 4.8 b	22.9 \pm 5.4 b
<u>II - Cone crops</u>				
a) At Tree level				
Cone number (n)	160 \pm 96 a	115 \pm 77 ab	119 \pm 103 ab	70 \pm 24 b
Cone weight (kg)	3.956 \pm 1.909 a	2.04 \pm 1.38 ab	2.2 \pm 1.955ab	1.63 \pm 0.679b
b) Stand level (per ha)				
Cone number (n x 10 ³)	117.04 \pm 45.22a	105.91 \pm 56.50 a	89.62 \pm 40.6 ab	54.38 \pm 31.81b
Cone weight (kg)	3026 \pm 899 a	1892 \pm 945 ab	1816 \pm 835 b	1301 \pm 885 b
<u>III - Seed yield</u>				
a) At cone level				
Seed number	97 \pm 15 a	77 \pm 17 b	78 \pm 19 ab	88 \pm 19 ab
Seed weight (g)	1.724 \pm 0.304 a	1.116 \pm 0.377 b	1.165 \pm 0.382 b	1.526 \pm 0.482 b
Individual seed weight (mg)	18.8 \pm 2.9 a	14.5 \pm 3.8 c	15.7 \pm 3.5 bc	17.3 \pm 2.9 ab
b) At Tree level				
Seed number (n)	14740 \pm 8642 a	8574 \pm 5439 b	8952 \pm 7976 b	6052 \pm 2196 b
Seed weight (g)	261.6 \pm 131.3 a	118.4 \pm 71.8 b	129.5 \pm 120.6 b	106.2 \pm 45.0 b
c) Stand level (per ha)				
Seed number (n x 10 ⁶)	10.99 \pm 4.75 a	8.01 \pm 4.25 b	0.14 \pm 0.12 b	0.11 \pm 0.05 b
Seed weight (kg)	199 \pm 72.96 a	110.73 \pm 55.55 b	110.7 \pm 52.63 b	88.11 \pm 63.54 b

*Different letters mean differences between bio-climatic zones.

Table 4. Correlation (r) and P-value between Altitude, Latitude and Longitude and Reproductive Features (Cones and Seeds) of Tunisian Aleppo Pine's Native Forests Stands

Traits	Altitude (m, asl*)		Latitude (°N)		Longitude (°E)	
	r	P-value	r	P-value	r	P-value
Cone weight (g)	0.377	<0.001	-0.111	0.328	-0.529	<0.001
Cone length (mm)	0.251	0.023	0.022	0.851	-0.474	<0.001
Cone width (mm)	0.356	<0.001	0.257	0.160	-0.552	<0.001
Seed weight (mg)	0.355	0.007	0.029	0.133	0.644	<0.001
Seed number per cone (n)	-0.206	0.061	0.305	0.008	0.010	0.890
Seed number per hectare (n)	-0.166	0.094	0.447	0.006	0.240	0.140
Seed weight per hectare (kg)	-0.058	0.612	0.224	0.043	-0.084	0.470

*asl : above sea level.

individual cone weight, length and width or individual seed weight (Table 4). The linear regressions obtained showed that displacements eastwards result in smaller cones and lighter seed mass. The prediction values presented that each 100 km eastwards would suffer a drastic reduction of 29.9% for cone weight, 12.8% for cone length, 10.3% for cone width and 28.9% for the individual seed weight.

Latitude was significantly ($P < 0.05$) linked to seed characteristics but not to cone production per hectare neither in number nor in weight ($P > 0.05$). The linear regression tests showed that the seed number per cone has a positive correlation with northwards movements (Table 4). Seed number and their weight per hectare were positively correlated northwards. The predicted values obtained indicate that each 100 km northwards the experimental latitudinal gradient could increase about 23.1% for seeds per cone, 89.7% for seed number per hectare and 32.5% for the total seed weight per hectare. The average number and weight of seeds per single cone and the yield of the average Aleppo pine tree in either cone number or total seed mass were not significantly ($P > 0.05$) affected by altitude. However, the mean cone weight and its average size (cone length and cone width) were positively linked to increasing terrain elevation (Table 4) showing high correlation coefficient values. In addition, the mean weight of the individual seed was correlated to altitude. Accordingly to the predicted values coming from the equations calculated, a rise in terrain elevation would theoretically result in greater cone weight and size with heavier seeds. The increases predicted values were of about 3.2% for cone weight, 1.1% for cone length, 1.2% for cone width and 2.7% for the individual seed weight for each 100 m altitudinal rise.

Effects of the Forest Stand Characteristics

Canopy cover measurements taken from the sampled forest stands had no significant ($P > 0.05$) relationship on all cone and seed characteristics under simple regression. By contrast, tree density and basal area were found to be significantly ($P < 0.001$) linked to the cone and seed production. The stand basal area had a positive linear effect on cone and seed production per tree and per hectare. We found a negative linear relationship between tree density log

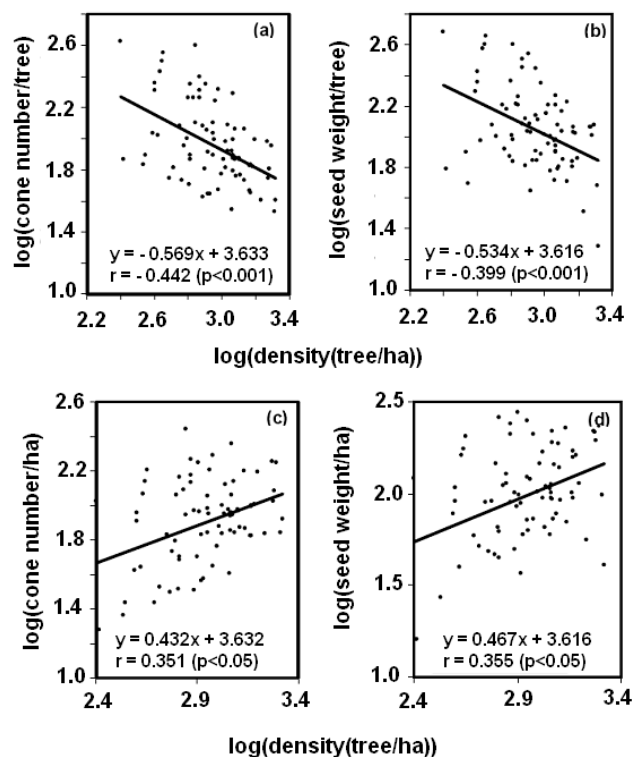


Figure 2: Relationships of Aleppo pine tree density in Tunisia forests on the cone and seed production: (a) cone number per tree, (b) seed weight per tree, (c) cone number per hectare and (d) seed weight per hectare.

transformed and cone number and seed weight per tree. According to the predicted values, they decreased from about 212 to 43 cones per tree, corresponding to a decrease in nearly 9 cones for every 100 trees ha^{-1} (Figure 2a). Similarly, the total seed weight yielded per tree would drop from 253 to 57 g, representing a reduction of about 11 g for every additional 100 trees ha^{-1} in Aleppo pine stand density (Figure 2b). In addition density (log transformed) had a positive linear relationship with cone number and seed weight per hectare (Figure 2d), respectively. In this case (using a range for Aleppo pine tree density of 250 to 2090 trees ha^{-1}) the cone production was increasing fast until a medium density of about 1000 trees ha^{-1} , but after that density, the increase is getting slower.

Effect of the Average Tree's Measurements

When the bioclimatic zones were not taken into account, the tree size measurements (crown height and DBH) were found positively correlated with the total cone number ($P < 0.01$) and the total seed weight contained in these cones ($P < 0.05$) (Figure 3). These

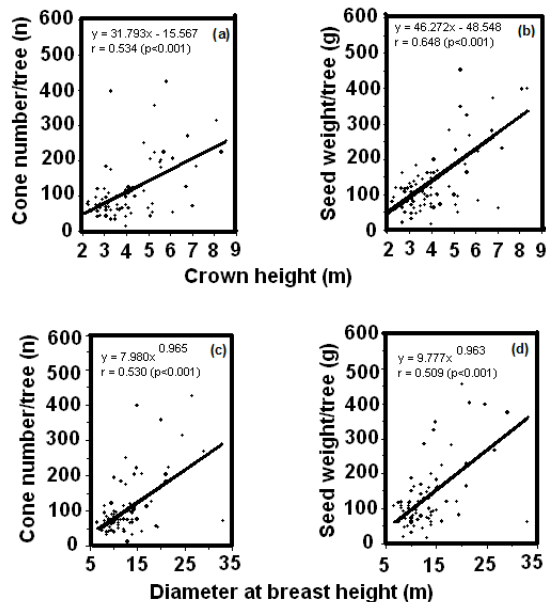


Figure 3: Influence of the tree crown height (a) and (b) and the DBH (c) and (d), on the total cone number and on the total weight of seeds per average tree produced by *Pinus halepensis* Mill. in Tunisia forests.

increases corresponded to an increase of about 48 to 248 cones and 44 to 336 g of seeds produced per tree representing 32 additional cones and 46 g of seeds for every 1m rise in the tree's crown height (Figures 3a and 3b, respectively). Similarly, using DBH as an explanatory variable, the number of cones harvested

per tree would grow from nearly 37 to 269 (Figure 3c), while its seed yield would rise from approximately 43 to 334 g (Figure 3d). These results indicated that expected gain would attain 9 additional cones and 11 g of supplementary seed mass for every 1 cm increment in the DBH.

The multiple regression analyses showed that the crown height and DBH were influencing highly ($p < 0.001$) the cone number and seed weight (Figure 3). Among DBH, total height, age and crown measurements, the Aleppo pine tree age showed the lowest significant correlation coefficient with cone number and total seed yield per tree (Table 5). By contrast, the highest correlation coefficient values were obtained when the crown diameter of the tree was used to explain the variability in cone number, as well as when the crown height was used to predict the total seed weight per tree.

Table 5: Simple Regression Equation Predicting the Total Cone Number and Seed Mass Produced by the Average Aleppo Pine Tree in Tunisian Native Forests Stands using Age and Various Tree Size Measurements

Predicted variables	Prediction equations	Correlation coefficient (r)	P-value
Cone number per tree (n)	$y = 1.402 \text{ age}^* + 50.266$	0.313	0.030
	$y = 37.427 \text{ crown diameter} - 32.018$	0.579	0.001
	$y = 20.493 \text{ total height} - 29.220$	0.462	0.001
Seed weight per tree (g)	$y = 1.752 \text{ age} + 60.068$	0.326	0.011
	$y = 40.045 \text{ crown diameter} - 16.775$	0.516	0.001
	$y = 29.515 \text{ total height} - 66.271$	0.555	0.001

*Age (year), Crown diameter (cm), Total height (m)

Modelling of Reproductive Characteristics

The combined effects of the various weather factors characterizing the different bioclimatic zones under multiple regression analyses showed that no significant ($P > 0.05$) multi-variable model could be obtained. On the contrary we found that altitude and longitude affected cone weight as well as cone dimensions (Table 6). Similarly, the combination of tree density-basal area and crown height-DBH were describing the cone number and seed weight variations (Table 6). For the combined effects of stand characteristics, the canopy cover was found to be non-significant ($P > 0.05$) under all circumstances, whilst both Aleppo pine tree density and basal area remained significant ($P <$

0.01), for explaining the variability in the number of cones borne by the average Aleppo pine tree, and its seed yield. Concerning the various tree measurements, only crown height and DBH were found to be significant ($P < 0.001$), determining the number of cones borne by the average tree and the total seed weight contained.

Table 6: Multiple Regression Models Predicting Cone Characteristics and Cone Number Produced by the Average Aleppo Pine Tree and its Seed Weight yield using Geo-Positional Parameters, Stand and Tree Characteristics

Predicted Variables	Prediction models	Correlation coefficient (r)	P-value
I - Geo-positional parameters			
Cone weight (g)	$Y = + 0.028 \text{ altitude} - 0.068 \text{ longitude} + 47.540$	0.462	0.001
Cone length (mm)	$Y = - 0.001 \text{ altitude} - 0.098 \text{ longitude} + 108.465$	0.476	0.001
Cone width (mm)	$Y = + 0.001 \text{ altitude} - 0.031 \text{ longitude} + 42.841$	0.556	0.001
II - Stand characteristics			
Cone number (n)	$Y = 0.056 \text{ basal area} - 0.073 \text{ density} + 117.58$	0.563	0.001
Seed weight (g)	$Y = 0.079 \text{ basal area} - 0.082 \text{ density} + 123.573$	0.590	0.001
III - Tree characteristics			
Cone number (n)	$Y = 0.502 \text{ crown height} + 0.108 \text{ diameter at breast height} - 1.206$	0.719	0.001
Seed weight (g)	$Y = 31.801 \text{ crown height} + 5.448 \text{ diameter at breast height} - 62.957$	0.679	0.001

DISCUSSION

The cumulative rainfall accumulated in the previous 3 years to the harvest was the most influential weather factor. It was positively related to the cone and seed production. These results were in agreement with results on cone and seed production obtained in loblolly pine [6], where the effective cumulative rainfall received during the second half of the growing season was the main influencing factor. According to [18], site quality and climate were determining the production of cones and seeds but also their characteristics such as cone size and weight or seed weight. In our study, the bioclimatic effect was embedded within the subdivision made by [23]. So, the cumulative precipitation received during coning cycle was useful to explain the variability observed at cone level, where the wetter areas offered substantially heavier cones with higher seed fills. However, the accumulated rainfall during the 33-month period prior to harvesting failed to the minimum values observed in the intermediate bioclimatic zones in the

weight of cones, as well as in the number of seeds and weight contained. We found that this reduction was caused by the higher Aleppo pine tree density observed in the upper and lower semiarid areas, indicating that increased tree competition resulted in the hindrance of fructification. This inference was previously advocated in Spain by [18], based on the positive correlations they found between growth increase and reproductive characteristics linked to the levels of the essential nutrients, N, P, and K, contained in the needles [30]. Similarly, [17] linked the number of conelets borne by an individual tree and their development to the nutrient availability. In the present study, the level of cone crop and seed yield suffered severe reductions attaining nearly one third at 750 trees ha^{-1} , and one half at 1000 trees ha^{-1} , per comparison to a stand density of only 250 stems ha^{-1} . Beyond, the critical pine tree density level of 1000 trees ha^{-1} , the decrease rate in cone counts and seed weight per average tree was softening. Similar results were achieved by [21], the low pine tree density stands were yielding more cones than high density stands. Both argued that thinning was reducing the pine tree densities promoting a greater resource availability, light exposition and higher photosynthetic surface areas. Indeed if the canopy receives more light, it stimulates the differentiation of buds from the vegetative to the reproductive stage.

The adverse effect of increased tree density on fructification and cone size was also explained by the fact that the individual tree is lower sized what induces to a lower numbers of fully developed cones and increases the cone abortion because the pine trees invest nutrients primarily in growth and secondarily in fructification [17]. This effect has been checked for the individual pine tree but at the stand level the result is the opposite due to the higher number of pine trees contributing to the total cone crop and seed yield. The optimum density should be those that promote individual production but maximize the cone crop and the aerial seed bank. Similar studies dealing with the effect of density and weather variables on cone characteristics and seed yields of coniferous trees remain badly lacking in the literature.

Concerning the geo-positional parameters, longitude had the most marked effect, firstly by its drastic reduction in the mean weight of a single cone and its total seed weight. In addition, the longitude caused another substantial reduction in cone length and width. A similar negative effect due to West-East longitudinal changes on the specific seed weight of *P.*

halepensis was previously documented by [11] and [24] in Tunisia. The fact that greater proximity to the sea coastline has an adverse effect on the fructification processes implies that an increasing continental gradient is beneficial to cone and seed production [9]. It was supported with the latitude results because in northern areas the total seed count per cone increased. Also this result was supporting the relationship linking it to the cumulative precipitation received in the different bioclimatic zones during the 33-month period prior to harvesting since in the northern locations (sub-humid areas) the fructification is promoted. The similitude between these two results lies in the fact that latitudinal changes are widely known to cause a rapid north to south aridity gradient in North Africa [9]. Thus, the effect of latitude in Tunisia, as well as in North Africa, is embedded with that of the prevailing climatic conditions, promoting plant growth and reproduction in the north, and slowing them in the south result to limited resources [31]. The improvements coming from the altitude effect on the characteristics of a single cone confirmed the previous results obtained by [10] showing the existence of similar relationships in Morocco's forests of Aleppo pine. But in neighbouring Algeria, no significant altitudinal effect was observed on the cone dimensions of the same tree species, a result which could be explained by the fact that only eight locations were investigated [9]. In another Moroccan study dealing with *P. pinaster* Ait., increased elevation promoted only the width of the cone [32]. In temperate regions, the favourable influence of altitude on the cone's weight and dimensions has been, often, attributed to better moisture conditions and lower temperatures inducing better cone development and higher plant photosynthetic rates in other conifers [10]. In cold regions, opposite results showing a negative altitudinal effect on pine cone production [13] were explained by slower growth and weaker reproduction rates because of reduced light intensities and durations, in addition to excessively low temperatures. Cold temperatures are known to cause cone abortion and prevent seed maturation in conifers.

Contrarily to stand density which had a negative effect on the average tree's cone crop and its seed yield, the basal area was positively correlated with both reproductive variables. This result agrees other studies in conifers which reported enhanced production of cones [33] as a result of greater basal area ratios. Under multiple regression analysis, both density and basal area were equally important as they remained significant regardless of their entry order but, the influence difference lies in the fact that the basal area

is including the number and size of the trunks present within a given surface area whereas the tree density only takes into account the number of pine trees. So, the Aleppo pine tree size is an overriding factor in determining its reproductive characteristics [20]. The tree size also effect on the cone crop and seed yield of Aleppo pine was provided by the positive correlations linking them. This parameter is related to the tree age but it showed the lowest correlation coefficient value, so size measurements are more important than age in affecting the tree's fructification ability, a statement previously made by [34]. Numerous authors showed proportionate cone and seed production to tree size measurements, such as total height [20] and trunk diameter [30, 34]. The tree crown size was another influencing factor, since a wider canopy covers have higher photosynthetic carbohydrate reserves to allocate to the production of cones and seeds [34]. In the present study, crown diameter and crown height outperformed all other tree size measurements, including DBH, for predicting respectively the average tree's cone crop but, under multiple regression analysis, only crown height was retained along with DBH. Nonetheless, a dual variable model using DBH and crown height may be justified only for the prediction of the seed yield due to the substantial improvement in the correlation coefficient value per comparison to single variable models.

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