Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA)
Available online at www.inia.es/forestsystems
doi: http://dx.doi.org/10.5424/fs/2112211-11463

Forest Systems 2012 21(1): 128-140
ISSN: 2171-5068
eISSN: 2171-9845

Stand, tree and crown variables affecting cone crop and seed yield of Aleppo pine forests in different bioclimatic regions of Tunisia

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Abstract

In Tunisia, the Aleppo pine seed has a great importance, since in the last decades human consumption has risen considerable. Thus its regeneration and seed production capacities are important factors to take into account to reach the necessities of the country. To study the production of cones and seeds of Aleppo pine, Tunisia's native Aleppo pine forests were surveyed in summer 2006, using 79 plots (40 × 25 m: 1,000 m²) spread over four bioclimatic zones. Stand and tree characteristics, crown dimensions and cone/seed variables were measured from an average tree of each plot (i.e. a total of 79 trees). Recorded data were submitted to simple and multiple regression analyses for explaining the variability in crown volume and crown surface, cone number and seed yield per average tree. Results showed a negative correlation between the stand density, crown characteristics and number of cones and seeds harvested from the average tree. For crown volume and surface, age, stand density, tree height, diameter at breast height, crown diameter and crown height were important explanatory variables under multiple regression analyses. For cone number per tree, only the age, stand density and total height were the most determinant variables. Matures cone number per tree and cone mass per tree were the most informative parameters for the total seed yields per tree. Finally, forest managers should know that crown size affects cone and seed crop of the Aleppo pine individual tree grown in Tunisia, but has no effects on seed number per cone and seed mass per cone.

Key words: Aleppo pine; crown dimensions; cone number; seed yields; bioclimatic zones; Tunisia.

Resumen

Variables de parcela, árbol y copa que afectan la producción de piñas y piñones en bosques de pino carrasco de Túnez

En Túnez, la producción de piñones del pino carrasco tiene una gran importancia, ya que en las últimas décadas su consumo ha aumentado de forma considerable. Por ello, su regeneración y capacidad de producción de piñas/piñones en un factor a tener en cuenta en Túnez. En verano del 2006 se eligieron 79 parcelas de 1.000 m² (40 × 25 m) situadas en cuatro zonas bioclimáticas representativas de Túnez para el estudio de la capacidad de producción de piñas/piñones del pino carrasco. Teniendo en cuenta todos los árboles de las parcelas, se identificó el árbol promedio, del que posteriormente se medirían variables de árbol, dimensión de copa y producción de piñas/piñones. Los resultados demuestran una correlación negativa entre la densidad de la parcela, características de la copa y el número de piñas/piñones recolectados por cada árbol promedio. Para la descripción del volumen y superficie de copa, las variables más importantes fueron edad, densidad de parcela, altura y diámetro del árbol, y altura y diámetro de la copa. Las variables edad, densidad de parcela y altura del árbol fueron las más significativas para la determinación de número de piñas por árbol. Para el cálculo del total de piñones por árbol, las variables más informativas fueron el número de piñas por árbol y el peso total de piñas por árbol. Para los productores de piñones en Túnez es importante concluir que el tamaño de la copas es una de las características más influyentes en la producción final de piñas/piñones por árbol de pino carrasco.

Palabras clave: pino carrasco; dimensión de copa; producción de piñas y piñones; zonas bioclimáticas; Túnez.

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Received: 22-01-11. Accepted: 14-09-11.

Introduction

The Aleppo pine (*Pinus halepensis* Mill.) is the most important forest tree species in North Africa especially in Algeria and Tunisia (BenTouati and Bariteau, 2005; Nahal, 1986). In Tunisia, the Aleppo pine forests cover 361,221 ha, representing more than 53.19% of Tunisian woodlands (DGF, 2010). The native stands are mainly concentrated in the semiarid areas of northern and central Tunisia (Daly-Hassen and Ben Mansoura, 2005). The natural regeneration of Aleppo pine depends exclusively on seeds, since it has no resprouting capacity (Trabaud, 1987). Thus, the perpetuation of the species requires a sufficient and efficient storage of seeds to ensure the recruitment of new seedlings (Summers and Proctor, 2005). Additionally, rich pine seed banks are further required for the re-colonization of burned areas, especially where risk of fire recurrence is high (Tapias *et al.*, 2001). This is the case for most Mediterranean countries where the annually reported burned forest surface area has increased considerably during the last few decades (Grove and Rackham, 2001). Good crops of pine cones and seeds are also needed to provide food resources to wild fauna, such as insects, birds, mammals (Smith and Balda, 1979) and reptiles (Way, 2006), which presence in the forest ecosystem bears an utmost importance for maintaining a biotic equilibrium. Moreover, pine seeds are consumed by humans as cocktail preparations in a variety of food (Asset *et al.*, 1999). For instance, in Tunisia, they have historically constituted a basic food for local forest and, in the last few decades, among all the country's population. The rising demand for Aleppo pine seed is driven by the rampant popular enjoyment for relishing the black gravy prepared with the ground seeds. In Tunisia, the black gravy is increasingly made out of maritime pine seeds in years with insufficient Aleppo pine seed production to meet the market demand. Populations justify their preference for Aleppo pine seeds due to its better taste, an easier grinding and a thinner cuticle in comparison to maritime pine seeds. The latest increase of Aleppo pine seed consumption among the population has extended its area to the eastern parts of neighbouring Algeria. All these reasons call for greater cone and seed production (Nasri *et al.*, 2004).

Aleppo pine carries two types of cones, non-serotinous and serotinous cones (Goubitz *et al.*, 2002), allowing a strategy for a long time seed conservation and an important regeneration capability (Trabaud *et al.*, 1985). The production of cones and seeds is quite variable, with differences between years, stands and individual trees (Krannitz and Duralia, 2004). In the same line, Ordonez *et al.* (2005) found that large pine trees of *Pinus nigra* Arnold grown in Spain produced more cones than small trees and that the cone production varied with tree location. In a later study conducted by Turner *et al.* (2007) with *Pinus contorta*, a complementary result was found, showing a strong positive relationship between mean tree size (stem diameter) and the average number of cones per tree. In other studies the fructification of coniferous tree species has been explained by the complexity of the interaction between the temporal and the spatial variation of the individual tree size characteristics (Ayari *et al.*, 2010; Krannitz and Duralia, 2004; Menccucini *et al.*, 1995). It has also been found that there exists a correlation between pine seed cone production and the climatic factors expressed through the geographic coordinates such as longitude, altitude and latitude (Harfouch *et al.*, 2003; Nasri *et al.*, 2004; Turner *et al.*, 2007; Messaoud *et al.*, 2007; Ayari *et al.*, 2011a).

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 and that are nowadays more important to the owners of these pine forests than any other forest product (Mutke *et al.* 2005). This fact has given impetus to several studies on the variables explaining cone and seed production for this species (Calama *et al.* 2008 and 2011; Mutke *et al.* 2005, 2007; Carrasquinho *et al.* 2010). Most of these studies show significant relationship between cone and/or seed production and the climate and soil variables, sometimes expressed as ecological units. Tree and stand characteristics have also been shown to be well related to cone production (Calama *et al.*, 2008 and 2011; Carrasquinho *et al.* 2010; Messaoud *et al.*, 2007, Arista and Talavera, 1996, Ayari *et al.*, 2010). Moreover, Mutke *et al.* (2007) have developed in Spain an interesting approach using the relationship between the cone weight of *Pinus pinea* and its nuts content.

In general, most authors agree that there is a relationship between the production of cones and seeds and various tree size measurements, such as total height (Moya *et al.*, 2008), trunk diameter (Stiell, 1988; Sutton *et al.*, 2002; Ordonez *et al.*, 2005; Messaoud *et al.*, 2007; Turner *et al.*, 2007), or both parameters (Oliva

and Colinas, 2007; Carrasquinho *et al.*, 2010), in addition to the tree crown size (Croker *et al.*, 1975; Sutton *et al.*, 2002). But there are no specific studies linking, on one hand, tree crown variables and cone number, and in the other hand, cone number per tree and seed mass per tree. Therefore, in the present study, we aimed:

(i) To study the relationship between crown variables of the average tree representing a forest stand, such as crown surface (*CrS*) and volume (*CrV*) and tree and stand characteristics (tree diameter (*DBH)* and height (*H)*; tree age (*age)*; and stand density (*shade)* and number of trees per ha (*N*));

(ii) To define the relationship between the number of mature cones of the average tree representing a forest stand (*C#/T*) and its crown dimensions such as crown diameter (*CrD*), crown height (*CrH*), crown projection area (*ProjS*), in addition to the diameter at breast height (*DBH*), total tree height (*H*), tree age and stand variables (*shade* and *N*);

(iii) To define the relationship between cone mass per tree (*CMT*) and other tree variables, including cone number per tree (*C#/T*);

(iv) To define the relationship between the total seed yield extracted per average tree (seed mass per tree, *SMT*) and the characteristics of the tree and stand used in the previous models as well as including also cone mass per tree (*CMT*).

(v) To analyse, in the previous relationships, the effect of the bioclimatic zone.

The final objective of the present study was to analyse how this new knowledge can help forest managers to reduce the cost or increase the efficiency of pine cone and seed production.

Material and methods

Study area

The study region covered Tunisian natural forests of Aleppo pine that are spread over four different bioclimatic zones, i.e. Sub-humid, Upper semiarid, Middle semiarid, Lower semiarid (Figure 1). The studied area included six administrative districts, Beja, Le Kef, Siliana, Zaghouan, Kairouan and Kasserine, where Aleppo pine forests are scattered over altitudes ranging between 250 and 1185 m above sea level (a.s.l.), latitudes between 35.17 and 36.53° N, whereas longitudes are comprised between 8.33 and 9.85° E. The study region has a typical Mediterranean climate with a rapidly increasing north to south aridity gradient, and two distinct wet and dry seasons, receiving a total average annual rainfall of 476 mm (Table 1). The different bioclimatic zones show a decreasing gradient in the annual rainfall, starting from 575 mm in the sub-humid areas and decreasing to 435 mm in the lower semiarid ones (Table 1). The maximum and minimum average annual temperature attains 32.9°C in July and 4.1°C in January, respectively (Table 1). The bioclimatic subdi-

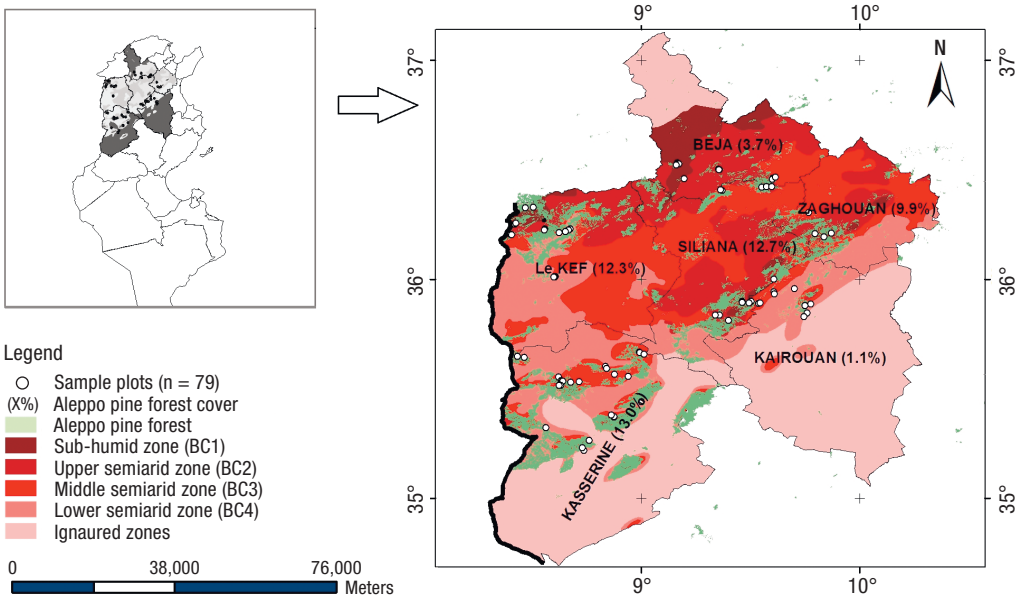

Figure 1. Map showing the plots surveyed in the four bioclimatic zones of the Tunisian Aleppo pine forests.

Table 1. Bioclimatic characterisation of Tunisian forests of P. halepensis Mill. used to estimate the cone and seed production

	Bioclimatic zones				Overall (79*)
	Bc1 (8*) Sub-humid	*Bc2* (35*) Upper semiarid	*Bc3* (22*) Middle semiarid	*Bc4* (14*) Lower semiarid	
[1] P (mm)	575	502	437	435	476
[2] T_{max} (°C)	33.9	33.1	32.3	32.2	32.9
[3] T_{min} (°C)	4.8	4.4	3.5	3.5	4.1

* Number of sampled plots. [1] P: annual rainfall, [2] Tmax: maximum mean temperature, [3] Tmin: Minimum mean temperature.

vision also shows decreasing trends in temperatures from 33.9 to 32.2°C for their maximum, and from 4.8 to 3.5°C for their minimum, with the lowest values occurring in the lower semiarid zones, and the highest values in the sub-humid zone. The soil of the study area is typically Mediterranean and varies among and within the different bioclimatic zones (Rejeb *et al.*, 1996). The vegetation is usually dominated by *P. halepensis* Mill.*, Juniperus phoenicea* L.*, Ceratonia siliqua* L., and *Erica scoparia* L.

Sampling procedure

Between June and September of 2006, 79 rectangular plots of 1,000 m² (40 m x 25 m) were sampled in the study region. Stand selection and delimitation were based on the requirement of the total absence of anthropogenic disturbance. The diameter at breast height (DBH) and height (H) of all Aleppo pine trees within the plots were measured (a total of 7,868 trees). Thereafter, to define the average tree of the study, the average of all measured *DBH* and *H* was calculated (Ayari *et al.*, 2011b). Thus, a tree with *DBH* and *H* close to the calculated average DBH and H was selected in each plot for further measurements (named average tree). All closed mature cones were collected from the 79 average trees (one tree per plot). Harvested mature cones typically have a reddish brown or grey colour, whereas immature cones, which were ignored, generally are green or yellowish. Cones showing either partially or fully opened scales were ignored. Several measurements of the average tree such as crown height, using an expandable pole, and age, using an increment borer by extracting a core of wood, were also measured. Four crown radii (r_i) were also measured to determine the horizontal projection surface of the crown (*ProjS*) and the respective crown diameter (*CrD*) for each average tree per stand as follows (Rondeux, 1993):

$$ProjS = \frac{\pi}{4}\sum_{i=1}^{4} r_i^2 \quad [1]$$

$$CrD = \sqrt{\frac{4}{\pi}\ ProjS} \quad [2]$$

where r_i is the crown radius at each of the 4 measurements.

Crown volume (*CrV*) (eq.3) and surface (*CrS*) (eq.4) were calculated according to the expressions defined by Rondeux (1993), Garchi and Ben Mansoura (1999) and Lim (2007);

$$CrV = \frac{\pi}{3}\left(\frac{CrD}{2}\right)^2 CrH \quad [3]$$

$$CrS = \frac{\pi}{4}\ CrD\ \sqrt{4CrH^2 + CrD^2} \quad [4]$$

where *CrH* refers to crown height. Stand characteristics such as stand density (*N*) and *shade* (canopy coverage) were also determined following Rondeux (1993) and Kim *et al.* (1996). The canopy coverage (*shade)* in each stand was calculated using the *ProjS* that was multiplied by the total number of the trees in this plot and then divided by the area of the experimental unit (1,000 m²) and multiplied by 100 as it was expressed in percent (%).

In the laboratory, all harvested cones (8,890 cones) were counted and their length and width were measured to determine the average cone volume per tree (*ACV*) (eq.5).

$$ACV = \frac{\pi}{3}\left(\frac{CW}{2}\right)^2 CL \quad [5]$$

ACV was later used to calculate the total cone volume (*TCV*) produced per average tree by multiplying *ACV* per the total harvested cone number. All cones were left for 21 days at a well aerated room and the air-dry weight

was recorded. Afterwards, they were introduced in an oven set at 55°C where they stayed for 5 days in order to induce the opening of their scales (Tapias *et al.*, 2001). 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 weighed for each cone separately.

For clarification, the variables used in this study and the respective symbols are summarized below:

Stand variables:	Stand density (*N*) and percent crown cover or shade (*shade*).
Average tree size variables:	Tree age (*age*), diameter at breast height (*DBH*) and total tree height (*H*).
Average tree crown variables:	Crown diameter (*CrD*), surface of the crown (ProjS), crown height (*CrH*), crown surface (*CrS*) and crown volume (*CrV*).
Cone size:	Cone diameter (*CW*), cone length (*CL*) and average cone volume (*ACV*).
Cone production per average tree:	Cone number per tree (*C#/T*), cone mass per tree (*CMT*) and total cone volume per tree (TCV).
Seed production per average tree:	Seed number per tree (*SNT*) and seed mass per tree (*SMT*).

Statistical analysis

As a first step, data were analysed in order to compare the measured tree, stand, cone and seed variables among bioclimatic regions. Significant differences were detected (at the 0.05 significance level) using LSD tests.

Simple regression analyses was used to study the relationships between stand variables, average tree size, average tree crown variables, cone size and average tree cone and seed production.

Multiple regression analyses was then performed to investigate the relationships between:

— Average tree crown characteristics (*CrS*, *CrV*) and tree and stand characteristics;

— Cone yield variables for the average tree (*C#/T* and *CMT*) and average tree/stand characteristics, including crown variables;

— Seed yield variables for the average tree (*SMT*) and cone yield variables (*C#/T*, *ACV*, and *CMT*) as well as tree and stand variables;

— Cone mass per tree (*CMT*) and cone number per tree (*C#/T*).

The variables to be included in the multiple regression models were selected using a stepwise procedure controlled by entry and out significance levels of p = 0.15, followed by the fitting of all possible regressions obtained by combination of the variables selected in the stepwise procedure.. The final model was selected among the alternative according to the biological meaning and interpretation of the signs of the coefficients. In case of alternative models with similar performance and different number of variables, the simpler models were preferred. Multicolinearity among the selected variables for the final model was evaluated using the variance inflation factors (VIF) and models with VIF > 10 were ignored.

The models selected from the analyses explained above were further worked in order to find out the effect of the bioclimatic zone in each one of the relationships. Four dummy variables — *Bc1*, *Bc2*, *Bc3* and *Bc4* — were defined to represent each one of the 4 bioclimatic zones (with value = 1 if the stand belongs to the bioclimatic zone and value = 0 otherwise) and the significance of adding these dummy variables to the model as well as their interactions with the variables already in the model were tested using a procedure similar to the one proposed by Milliken and Johnson (2002), testing the hypothesis that the slopes are equal (common slopes for all bioclimatic zones):

1. If fail to reject, compare the effect of the regions by comparing the intercept (parallel models).

a. If fail to reject, keep the model without the influence of the bioclimatic regions

b. If reject find the model on the basis of a procedure similar to the one used in the selection of the model without the influence of the regions, but applied to all the variables present in the model previously selected plus the dummy variables for the bioclimatic.

2. If reject find the model on the basis of a procedure similar to the one used in the selection of the model without the influence of the regions, but applied to all the variables present in the model previously selected plus the dummy variables for the bioclimatic regions and their interactions with the independent variables previously selected.

The statistical software package SAS version 9.0 (SAS Institute, Cary, North Carolina, USA) was used to perform all the aforementioned procedures.

Results

Average tree and crown dimensions

The comparison of stand, tree and crown characteristics, as well as cone and seed production, showed no significant differences between the four biocli-

matic zones ($p < 0.05$), except for tree height and tree crown height (Table 2). These variables showed significant differences between *Bc1*, the sub-humid bioclimatic zone, and the semiarid zones (*Bc2*, *Bc3* and *Bc4*). In all other stand, average tree and crown dimension variables (*shade*, *N*, *age*, *DBH*, *ProjS*, *CrS*, *CrV*) no significant differences ($p > 0.05$) were found between the four bioclimatic zones.

In what concerns the correlations between stand, tree and crown characteristics, stand density (*N*) showed a significant negative correlation ($p < 0.01$) with all other tree and stand variables except with stand shade (Table 3). On the contrary, stand shade was only significantly correlated with the variables that are related to crown size (*CrD*, *ProjS*, *CrS* and *CrV*), being these correlations positive. All tree variables (*age*, *DBH*, *H*) correlated positively among them ($p < 0.01$), and they showed a strong positive correlation with all crown characteristics ($p < 0.01$), being the strongest correlation between *DBH* and *CrS* ($r = 0.819$) and the lowest between height and *CrD* ($r = 0.446$).

The evaluation of the combined effects of stand and tree characteristics on crown surface (*CrS*) and crown volume (*CrV*) was analysed with multiple regression analysis. The stepwise regression procedure used lead to the following models for *CrS* ($R^2 = 0.85$) and *CrV* ($R^2 = 0.83$) (see details on Table 4):

$$CrS = -9.028 + 2.302\ DBH + 0.152\ shade - 8.762\ N/1000 \quad [6]$$

$$CrV = -27.205 + 2.291\ DBH + 0.151\ shade + 0.156\ age - 6.835\ N/1000 \quad [7]$$

Table 2. Mean ± standard error) for stand and tree characteristics (shade, density, age, *DBH*, height), crown characteristics (*CrH*, *CrD*, *ProjS*, *CrS*, *CrV*), cone/seed variables at cone level (*ACV*, *ASM*, *S#/C*, *SMC*) and cone/seed variables at tree level (*C#/T*, *CMT*, *TCV*, *S#/T*, *SMT*) for the four bioclimatic zones (*Bc1-Bc4*) and overall. Different letters for differences among bioclimatic zones

	Bioclimatic zones				**Overall**
	Bc1 **Sub-humid**	***Bc2*** **Upper semiarid**	***Bc3*** **Middle semiarid**	***Bc4*** **Lower semiarid**	
Stand variables					
Shade (%)	92.77 ± 12.42**a**	114.22 ± 9.52**a**	107.51 ± 10.02**a**	82.76 ± 17.07**a**	104.60 ± 6.07
N (tree/ha)	869 ± 95**a**	1054 ± 82**a**	990 ± 89**a**	804 ± 116**a**	973 ± 50
Tree variables					
Age (yr)	45 ± 5**a**	44 ± 3**a**	44 ± 4**a**	47 ± 5**a**	44 ± 2
H (m)	8.78 ± 0.77**a**	6.47 ± 0.31**b**	6.10 ± 0.37**b**	5.82 ± 0.32**b**	6.49 ± 0.21
DBH (cm)	16.36 ± 1.51**a**	13.01 ± 0.78**a**	13.06 ± 1.18**a**	12.87 ± 1.76**a**	13.34 ± 0.59
Crown variables					
CrH (m)	5.39 ± 0.73**a**	3.83 ± 0.22**b**	3.90 ± 0.25**b**	3.91 ± 0.36**b**	4.02 ± 0.16
CrD (m)	3.73 ± 0.27**a**	3.86 ± 0.22**a**	3.92 ± 0.31**a**	3.76 ± 0.34**a**	3.85 ± 0.14
ProjS (m^2)	11.34 ± 1.64**a**	13.09 ± 1.64**a**	13.64 ± 2.22**a**	12.29 ± 2.21**a**	12.92 ± 1.03
CrS (m^2)	34.82 ± 6.29**a**	27.98 ± 3.17**a**	29.16 ± 4.04**a**	27.96 ± 4.96**a**	29.00 ± 2.08
CrV (m^3)	21.93 ± 5.66**a**	18.86 ± 3.71**a**	20.06 ± 4.41**a**	18.59 ± 5.14**a**	19.46 ± 2.28
Cone/seed variables at cone level					
ACV (cm^3)	47.66 ± 4.06**a**	46.33 ± 1.97**a**	53.84 ± 2.04**a**	48.64 ± 1.87**a**	48.96 ± 1.20
ASM (mg)	17.93 ± 1.02**a**	14.48 ± 0.64**b**	15.67 ± 0.74 **b**	17.28 ± 0.76 **a**	15.65 ± 0.41
S#/C	97 ± 5**a**	77 ± 3**b**	82 ± 4 **b**	88 ± 5 **ab**	82 ± 2
SMC (g)	1.72 ± 0.11**a**	1.12 ± 0.06**c**	1.27 ± 0.08**bc**	1.53 ± 0.13**ab**	1.29 ± 0.05
Cone/seed variables at tree level					
C#/T	160 ± 34**a**	115 ± 13**ab**	119 ± 22**ab**	70 ± 6**b**	113 ± 9
CMT (kg)	3.96 ± 0.67**a**	2.04 ± 0.23**b**	2.37 ± 0.42**b**	1.63 ± 0.18**b**	2.25 ± 0.18
TCV (dm^3)	8.46 ± 2.40**a**	5.10 ± 0.54**b**	6.19 ± 1.09**ab**	3.41 ± 0.31**b**	5.45 ± 0.47
S#/T (×1000)	15.59 ± 3.18 **a**	8.57 ± 0.92**b**	9.31 ± 1.70 **b**	6.05 ± 0.59 **b**	9.04 ± 0.75
SMT (g)	261.54 ± 46.43**a**	118.41 ± 12.13**b**	144.09 ± 25.71**b**	106.16 ± 12.03**b**	137.89 ± 11.23

Stand variables - *N*: stand density, Shade; Tree variables - *DBH*: diameter at breast height; *H*: total height; Crown variables-*CrH*: crown height; *CrD*: crown diameter; *ProjS*: projection surface; *CrS*: crown surface; *CrV*: crown volume: Seed/Cone variables at cone level - *ACV*: average cone volume; *ASM*: average individual seed mass; *S#/C*: seed number per cone; *SMC*: total seed mass per cone; Seed/Cone variables at tree level - *C#/T*: cone number per tree; *CMT*: cone mass per tree; *TCV*: total cone volume; *S#/T*: total seed number per tree; *SMT*: seed mass per tree.

Table 3. Pearson correlation coefficients linking stand and tree characteristics (shade, density, age, *DBH*, height,), crown characteristics (*CrH*, *CrD*, *ProjS*, *CrS*, *CrV*), cone/seed variables at cone level (*ACV*, *ASM*, *S#/C*, *SMT*) and cone/seed variables at tree level (*C#/T*, *CMT*, *TCV*, *S#/T*, *SMT*). (For variables description see table 2)

	N	*Shade*	*Age*	*DBH*	*H*	*CrH*	*CrD*	*ProjS*	*CrS*	*CrV*	*ACV*	*ASM*	*S#/C*	*SMC*	*C#/T*	*CMT*	*TCV*	*S#/T*
Shade	0.201	1																
Age	–0.420*	0.129	1															
DBH	–0.664*	0.057	0.694*	1														
H	–0.426*	0.053	0.579*	0.809*	1													
CrH	–0.446*	0.106	0.457*	0.689*	0.687*	1												
CrD	–0.540*	0.622*	0.589*	0.684*	0.446*	0.494*	1											
ProjS	–0.524*	0.576*	0.617*	0.719*	0.463*	0.501*	0.981*	1										
CrS	–0.556*	0.438*	0.653*	0.819*	0.625*	0.793*	0.901*	0.918*	1									
CrV	–0.522*	0.425*	0.669*	0.814*	0.576*	0.713*	0.891*	0.937*	0.982*	1								
ACV	0.110	–0.114	0.026	0.010	0.121	0.165	–0.122	–0.090	0.035	0.041	1							
ASM	–0.094	–0.201	0.262	0.161	0.238	0.200	–0.061	–0.053	0.069	0.054	0.469*	1						
S#/C	0.143	0.046	–0.262	–0.177	–0.041	–0.064	–0.132	–0.113	–0.111	–0.102	0.291	0.067	1					
SMC	0.051	–0.134	–0.028	–0.044	0.110	0.050	–0.168	–0.150	–0.073	–0.075	0.488*	0.717*	0.728*	1				
C#/T	–0.441*	0.184	0.313*	0.585*	0.550*	0.504*	0.563*	0.572*	0.618*	0.596*	–0.074	–0.143	–0.145	–0.211	1			
CMT	–0.437*	0.155	0.419*	0.660*	0.644*	0.640*	0.562*	0.589*	0.698*	0.677*	0.176	0.178	0.008	0.099	0.882*	1		
TCV	–0.406*	0.161	0.352*	0.608*	0.606*	0.607*	0.534*	0.550*	0.660*	0.634*	0.237	0.018	–0.061	–0.066	0.916*	0.940*	1	
S#/T	–0.401*	0.194	0.230	0.540*	0.539*	0.504*	0.523*	0.546*	0.598*	0.583*	0.010	–0.153	0.173	–0.003	0.921*	0.878*	0.889*	1
SMT	–0.422*	0.121	0.326*	0.604*	0.628*	0.605*	0.492*	0.518*	0.630*	0.605*	0.157	0.162	0.181	0.208	0.860*	0.960*	0.906*	0.927*
	Stand variables		Tree variables			Crown variables					Cone/seed variables at cone level				Cone/seed variables at tree level			

* P < 0.01.

Table 4. Parameter estimates and respective standard errors (s.e) of the models for crown variables of the average tree (*CrS* and *CrV*), the number and mass of mature cones of the average tree (*C#/T* and *CMT*), the total seed yield extracted per average tree (*SNT* and *SMT*)

Model	Variable	Parameter estimate	s.e.	Pr > |t|
Tree crown surface (*CrS*)	*Intercept*	–9.028	4.896	0.0691
	DBH	2.302	0.221	<.0001
	shade	0.151	0.016	<.0001
	N/1000	–8.762	2.651	0.0015
Tree crown volume (*CrV*)	*Intercept*	–27.205	5.764	<.0001
	DBH	2.291	0.319	<.0001
	shade	0.151	0.019	<.0001
	age	0.156	0.074	0.0381
	N/1000	–6.835	3.114	0.0313
Cone number per tree (*C#/T*)	*Intercept*	–82.990	27.592	0.0036
	H	18.985	4.573	<.0001
	age	–1.454	0.531	0.0077
	shade	–0.366	0.179	0.0444
	crD	45.557	9.292	<.0001
Cone mass per tree (*CMT*)	*Intercept*	0.287	0.136	0.0377
	Bc1	1.028	0.271	0.0003
	CNT/1000	16.557	0.990	<.0001
Seed mass per tree *(SMT)* Model 1	*Intercept*	–36.683	29.710	0.2208
	Bc1	101.640	29.847	0.0011
	ProjS	4.197	1.017	<.0001
	H	16.967	5.351	0.0022
Seed mass per tree *(SMT)* Model 2	*Intercept*	6.652	5.224	0.2067
	Bc1	29.948	10.746	0.0067
	CMT	**56.866**	**2.002**	**<.0001**

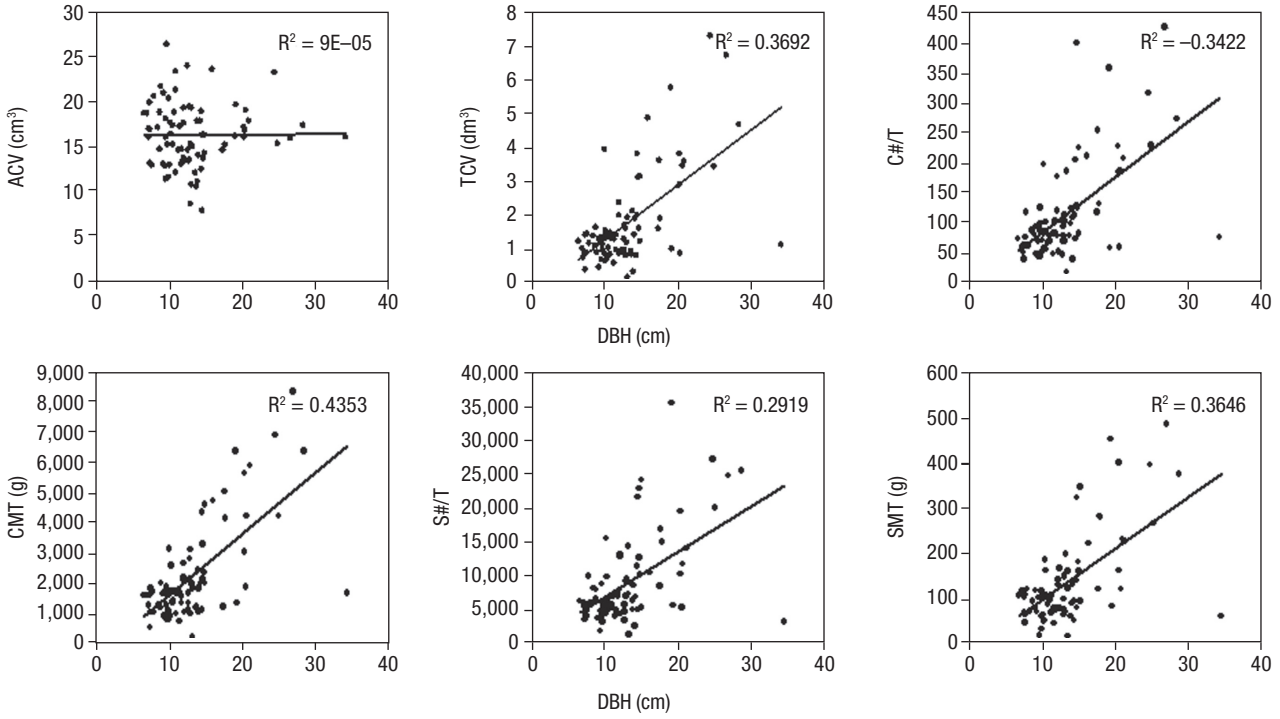

Figure 2. Influence of tree diameter on cone size and cone and seed yield of average tree in Tunisian forests of *P.halepensis* Mill. (Variables; – *DBH*: diameter at breast height; – *ACV*: average cone volume; – *TCV*: total cone volume; – *C#/T*: cone number per tree; *CMT*: cone mass per tree; *S#/T*: total seed number per tree; *SMT*: seed mass per tree).

The bioclimatic regions were not significant indicating that models 6 and 7 can be used in all these four Tunisian bioclimatic regions.

Cone production

The results obtained for cone number per tree (*C#/T*), total cone mass per tree (*CMT*), and total cone volume per tree (*TCV*) showed significant decreasing tendencies ($p < 0.05$) from the sub-humid (*Bc1*) to the lower semi-arid areas (*Bc4*) (Table 2). On the contrary average cone volume (*ACV*) was not significantly different among the four studied zones. Overall, stand shading had no significant ($p > 0.05$) correlation, whatsoever on average cone volume (*ACV*), cone number per tree (*C#/T*), cone mass per tree (*CMT*) and total cone volume (*TCV*) (Table 3). Similar to stand shade effect, no significant relationship was found between stand density and *ACV*. By contrast, density showed a high negative significant ($p < 0.001$) relationship with *C#/T* ($r = –0.441$), *CMT* ($r = –0.437$) and the respective *TCV* ($r = –0.406$). Among all cone variables, *ACV* showed no significant correlations with any other studied stand, tree, and crown variables. On the contrary, the remaining tree crop variables correlated strongly and positively ($p < 0.01$) with all crown variables, being the strongest correlation between *CMT* and *CrS* ($r = 0.698$) and the lowest between *SMT* and *CrD* ($r = 0.590$) (Table 3). No significant correlation was found between *ACV* and *C#/T* or *CMT* (Table 3). Among the various tree size measurements, age had the lowest correlation coefficient value for predicting either *C#/T*, *CMT* and *TCV*. Generally, cone and seed yield correlated better with tree diameter and crown size and, at stand level, with stand density. Figure 2 shows the relationship of cone and seed yield with tree diameter (relationships with crown size are similar) and Figure 3 the relationship between the same variables and stand density.

In the multiple regression analyses, the evaluation of the combined effects of the forest stand and average tree characteristics on the cone number per tree (C#/T) led to the following multivariate model (with $R^2 = 0.49$) (see details on Table 4):

$$C\#/T = –82.990 + 18.985\ H –1.454\ age – – 0.366\ shade + 45.557\ CrD \quad [8]$$

Adding the bioclimatic regions did not significantly improve the model for *C#/T.* On the contrary, the bio-

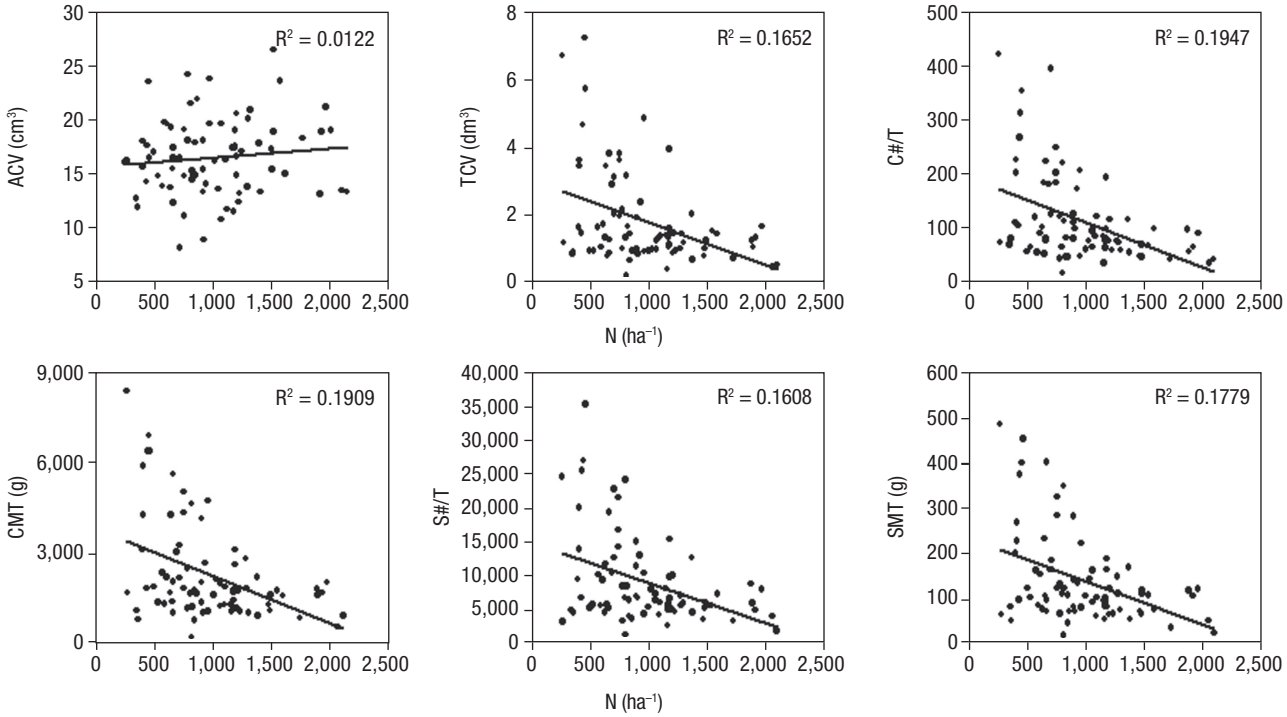

Figure 3. Influence of stand density on cone size and cone and seed yield of average tree in Tunisian forests of *P.halepensis* Mill. (Variables; – *N*: Stand density; – *ACV*: average cone volume; – *TCV*: total cone volume; – *C#/T*: cone number per tree; *CMT*: cone mass per tree; *S#/T*: total seed number per tree; *SMT*: seed mass per tree).

climatic regions were significant in the model that expresses *CMT* as a function of *C#/T* (with $R^2 = 0.81$). The model selected has a different intercept for the sub-humid region (details on Table 4):

$$CMT = 0.287 + 1.028\ Bc1 + 0.166\ C\#/T \quad [9]$$

Where *Bc1* is the dummy variable for the sub-humid region (= 1 for stands in this region; = 0 otherwise).

Seed yield

Decreasing tendencies were observed from the sub-humid to the semiarid zones in all seed yield variables such as seed number per cone (*S#/C*), seed mass per cone (*SMC*), average individual seed mass (*ASM*), total seed number per tree (*S#/T*) and total seed mass per tree (*SMT*). Moreover, significant differences ($p < 0.05$) were found between the sub-humid (*Bc1*) and the upper semiarid bioclimatic zones (*Bc2*) in all aforementioned variables (Table 2).

Overall, *shade* had no significant ($p > 0.05$) correlation with *SMT* (Table 3), *S#/C*, *SMC*, *ASM* and *S#/T* under simple regression analyses. Similarly, density had no significant effects on *S#/C*, *SMC* and *ASM*, but had a negative and significant relationship ($p < 0.001$) with *SMT* ($r = –0.422$) and *S#/T* ($r = –0.401$). A positive significant relationship was found between average tree *age* and the *SMT* with a correlation coefficient of $r = 0.326$. In fact, all tree and crown dimension variables had positive relationships ($p < 0.001$) with *SMT*, e.g. a high correlation coefficient was recorded between the *C#/T* and *SMT*($r = 0.860$, $p < 0.0001$). In addition, positive significant relationships were found between *ACV* and *SMC* and *ASM* (Table 3).

In the multiple regression analyses, two multivariate models explaining the variability of seed yield (*SMT*) were selected. The first one took into account the combined effects of forest stand and average tree characteristics, reaching a multi-variable model (eq. 10) with only *Bc1*, *ProjS* and *H* as explanatory variables, whereas age, density, shade, all crown measurements, and cone characteristics were non-significant ($p > 0.05$). The multivariable model obtained for explaining the variability in the *SMT* depended also on the bioclimatic region, showing a different intercept for the sub-humid region:

$$SMT = –36.683 + 101.640\ Bc1 + \\ + 4.197\ ProjS + 16.967\ H, \quad [10]$$
$$(R^2 = 0.53)$$

The second selected multivariate model took into account, the total mass per tree (*CMT*). The following model was selected (with $R^2 = 0.93$):

$$SMT = 6.652 + 29.948\ Bc1 + 56.866\ CMT, \quad [11]$$

Discussion

One of the aims of the present investigation was to compare the cone/seed production of the Aleppo pine in Tunisian four different bioclimatic zones. According to our results, the forest location in different bioclimatic zones is an important factor affecting some cone and seed production variables by the average Aleppo pine tree in Tunisia. This result agrees with previous research works showing that climatic variables influence the production of, for instance, cones in white pine (*Pinus monticola*) (Eis, 1976), seeds in loblolly pine (*Pinus taeda*) (Cain and Shelton, 2004) growing in North America and the cone and nuts production of stone pine (*Pinus pinea*) in Spain (Calama *et al.*, 2007 and 2011). Other authors demonstrated the effect of meteorological variables, such as temperature, in determining the production of cones and seeds (Caron and Powell, 1989, Mutke *et al.*, 2007), as well as acorns (Sork *et al.*, 1993). In our study, the sub-humid areas produced substantially heavier cones with better seed fills in comparison to the lower semiarid zones. Other previous studies showed that stand density also affects the cone production per tree, reducing the production due to the higher tree densities within the stand (Ayari *et al.*, 2010; 2011a), that is associated with an increased tree competition (Arista and Talavera, 1996; Karlsson and Orlander, 2002). In the present study, stand density affected negatively the crown dimension of the average tree, especially *CrS* and *CrV*. Similar negative effect of the stand density was observed on cone and seed characteristics except in *ACV*, *S#/C* and *SMC*.

Under simple regression analysis no significant correlations were found between cone/seed characteristics at cone level (*ACV*, *S#/C*, *SMC* and *ASM*) and crown dimensions, meaning that crown size has no effect on the number or characteristics of the seed per cone. On the contrary, crown size characteristic showed good relationships with number of cones per tree and cone mass per tree, affecting at the same time the total seed number per tree and seed mass per tree. It was hypothesised that individual trees with larger crowns would have higher photosynthetic reserves to allocate high fructification in terms of cone and seed production. High positive relationships linking *ACV* with *SMC* and *ASM* were found, i.e., larger cones contained more seeds than small ones. Similarly, high positive relationships were found between cone crop (*C#/T* and *CMT*) and seed yield (*S#/T* and *SMT*) at tree level. This study showed that all crown traits including *CrS* and *CrV* were largely linked to cone abundance. Compared to small individual trees with smaller crown dimensions, big individual trees with larger crown characteristics contain more cones and seeds. This may suggest that due to light competition, neighbouring trees can reduce the rate of light received by dominated and suppressed trees of the stand. Similarly, Sutton *et al.* (2002) also found that red pine (*Pinus resinosa* Aiton) trees with larger *CrS* growing in Canada produced higher cone crop.

Tree age, stand density and tree height were significant variables for explaining the variability of both *C#/T* and *SMT*. But, according to equation (11) the seed yields produced by the average tree may also be linked to cone characteristics such as *C#/T* and *CMT* since they were good explanatory variables of seed production. These results corroborate that tree size is the overriding factor in determining its reproduction and fructification ability, as previously demonstrated by others researchers (Greene *et al.*, 1999; Ordonez *et al.*, 2005; Turner *et al.* 2007, Carrasquinho *et al.,* 2010). Thus, it is obvious that any factor affecting tree/crown dimension will at the same time affect the cone/seed production. For instance tree age was positively correlated with both tree dimension and crop production. Previous research work showed this positive and significant linkage between tree dimensions and age (Ryan and Yoder, 1997). Moreover, other authors such as Krugman and Jenkinson (1974) and Richardson (1998), concluded that pine cone crop is largely determined by environmental factors, tree size as well as tree age. In the same line, our results showed that among the tree variables, tree size measurements were more important than tree age when affecting fructification ability, while age offered the lowest correlation coefficient values with cone/seed production. In this study, all proposed models to explain single tree cone and seed production were similar with those proposed by previous works for other pines species in Spain (Calama *et al.*, 2007 and 2011; Mutke *et al.*, 2007). The most important management rule extracted from this study is to reduce the stand density thus increasing individual tree cone and seed production, in addition to reducing collection

costs (Ayari et al, 2010). In fact, tree age and height, bioclimatic zone and shade were also required as predictors in the models for cone predictions. However, neither age, density nor shade was selected for Aleppo pine seed prediction that depends on tree height and *DBH*, bioclimatic zone and *ACV*. Tapias *et al.* (2001) showed that the number of cones tended to increase with age, as was observed in our results (Figure 2). Numerous authors showed proportional correlations between cone and seed production of pine with its DBH and height (Moya *et al.*, 2008; Messaoud *et al.*, 2007; Turner *et al.*, 2007; Oliva and Colinas, 2007). Croker *et al.* (1975) demonstrated that a tree with large crowns growing in open stands was the best cone producer. Sutton *et al.* (2002) explained this situation showing that larger crowns had higher photosynthetic carbohydrate reserves to allocate into the fructification phenomena. In the present study, crown traits dominate all other tree dimensions, including *DBH* and total height, for predicting the cone number and seed mass per tree. Then, the individual Aleppo pine trees growing in dense stands may be affected by light competition, having less photosynthetic surface and limited resources for cone development.

Conclusions

The influence of environmental factors, including ecological variables, on the reproductive ecology of Aleppo pine has been assessed for trees growing in Tunisia. Our study confirms previous research with other pine species, that several factors influenced the reproduction of Aleppo pine. The number of cones per tree was found to be negatively correlated with density and positively correlated with tree size, tree age and all crown dimensions. However, both tree and crown dimensions did not affect *ACV*, *S#/C*, *SMC* and *ASM*. Thus, what it should be clear for the forest managers is that crown size affects cone and seed crop of the Aleppo pine individual tree grown in Tunisia, but has no effect on the seed number per cone and seed mass per cone. In this sense, managers should be aware of the forest management practices to increase the crown size of the trees, reducing tree/crown competition. Thus, in future investigation, it would be important to find the optimum stand density, which reduces the tree competition, increasing the cone/seed production per tree, but at the same time, it does not sacrifice the total cone/seed production per stand.

Acknowledgments

The authors would like to thank the support and funds provided by the Spanish I + D + I National Programme CYCIT-AGL 2008-03602/FOR and CONSOLIDER-INGENIO 2010: MONTES (CSD 2008-00040). The second support was provided by the Fundación Española para la Ciencia y la Tecnología (FECYT), the Spanish Ministry of Education and the FCT (SFRH/BPD/63979/2009). AGORA European project as well as the Instituto Superior de Agronomia (ISA) are also gratefully acknowledged.

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