Autecology and growth of Aleppo pine (*Pinus halepensis* Mill.): a comprehensive study in France

Michel Vennetier ^{*(1+2)}, Christian Ripert ⁽¹⁾, Cyrille Rathgeber ⁽³⁾

* Corresponding author: michel.vennetier@irstea.fr, tel. +33 4 42 66 99 22 FAX:+33 4 42 66 99 23 / 99 65

(1) Irstea, UR RECOVER / EMR, 3275 route de Cézanne, CS 40061, Aix-en-Provence cedex 5, France

(2) ECCOREV, Fédération de recherche, Europôle Méditerranéen de l'Arbois, BP 80, 13545 Aix-en-Provence cedex 4, France

(3) UMR LERFoB, AgroParisTech, INRA, 54000, Nancy, France

Highlights

- Aleppo pine growth depends on both climate, soil, parent-rock and topography
- Local water balance weight more than climate for Aleppo pine growth to date
- Two models were computed to assess a tree height site index in all environments
- A practical tool was developed to be used by forest managers
- This tools can easily be adapted to most of Aleppo pine distribution area

Abstract

Aleppo pine (*Pinus halepensis* Mill.) is one of the dominant conifer species in the Mediterranean area. Many studies have investigated the role of climate variables (precipitations, temperature) in its occurrence and growth, but few have taken the effect of local site conditions into account, nor their interaction with climate.

This study aimed at thoroughly assessing forest sites potential for Aleppo pine in France, and designing a practical tool to help forest managers implementing these results. The study is based on a network of 512 plots laid out in the French Mediterranean area, where 2158 trees were measured. A site index was computed using a height growth model calibrated on these plots. Using neural networks and partial least square

regression models (PLS), we disentangled the effects of climatic factors and local site conditions in Aleppo pine presence and growth.

Local water balance (assessed through topography, soil, geology and legacies of past human activities) was the main factor driving Aleppo pine productivity in the study area. Climate played a significant role as a whole but more important at the species distribution margins, frost and snow limiting Aleppo pine range northwards and in elevation. Based on these results, a practical tool was designed for two different types of mother rocks to help assessing forest site potential for Aleppo pine.

As the span of climate conditions in south-eastern France includes most of those found in Aleppo pine distribution area, except the driest and hottest ones found in its southernmost locations, this study could easily be used or adapted in most other concerned countries. Because of the ongoing climate change and increasing drought in the Mediterranean area, the balance between local and climate factors may change in time and space. Our results show that without an accurate knowledge of local conditions, the impact of climate change cannot be predicted.

Keywords

Pinus halepensis; Mediterranean forest; Tree growth; Site index; Climatic change

1 INTRODUCTION

Aleppo pine (*Pinus halepensis* Mill.) is one of the most common tree species in the western half of the Mediterranean basin, where it dominates vegetation cover on 3.5 millions hectares (Le Houérou, 2005a). In France, it is abundant on 250,000 ha along the Mediterranean coast, from sea level up to 800 m of altitude (figure 1). The area dominated by Aleppo pine in France was multiplied by 7 in the last 150 years. Most of this expansion was gained by natural regeneration, encroaching in abandoned fields and grassland, or densifying existing stands after wild fires.

Aleppo pine plays a key role in Mediterranean landscape dynamics. Therefore, its biogeography is well documented (Barbéro et al., 1998; Le Houérou, 2005; Ne'eman et al., 2000).

Fig. 1 Limit of Aleppo pine distribution in France. A map of the 523 sampled points of this study is given in appendix 3.

It can grow in hot and dry environments, on low fertility soils as well as on rocky calcareous soils (Ne'eman et al., 2000; Quézel et al., 2003). Thanks to its high resistance to heat and drought stresses and to its serotinous cones tolerant to heat (Daskalakou et al., 1996; Verkaik et al., 2006), it is, as a pioneer and undemanding species, one of the main contributors to forest recovery after wildfires (Dubravac et al., 2006; Pausas et al., 2004) as well as on abandoned agricultural land (Achenar et al., 1984; Taton et al., 1994a). It even proved to be potentially an invasive species when introduced in new environments (Ganatsas et al., 2010; Zalba et al., 2008). It is also much used for soil protection and rehabilitation in degraded and semi-arid areas (Maestre et al., 2004; Rincon et al., 2006). Relationships between its diameter growth and climate parameters are known through dendroecological studies (De Luis, 2013; Novak et al., 2016; Olivar et al., 2012; Pasho et al., 2012; Sarris et al., 2011; Serre, 1976). Because of its sensitivity to climate, Aleppo pine is an interesting model species for ecophysiologicals (Borghetti et al., 1998; David-Schwartz et al., 2016; Prieto et al., 2009) and for plant functioning modellers (Gaucherel et al., 2008; Misson et al., 2004; Rathgeber et al., 2003; Simioni et al., 2016) studying the processes of resistance and adaptation to drought and climate change.

Finally, hundreds of papers give each a part of knowledge on Aleppo pine ecology and adaptation to its environment. But surprisingly, may be because of its plasticity and because it is confined to areas with low wood production potential (Trasobares et al., 2004), comprehensive studies on Aleppo pine site-growth relationships and autecology are rare in scientific literature (Bueis et al. 2017, Olarieta 2000). However, such studies are necessary to assess the future of Aleppo pine and to design management strategies in the context of climate change.

An autecological model for a given species aims to predict the effect of all environmental variables and their interactions in the probability of occurrence, the health status and growth of this species (Pianka et al., 2008). A general autecological approach is sometimes used to assess the limits and optimum range for forest trees (Diaz-Maroto et al., 2006). However in forestry, tree development is often associated with biomass or wood production, and autecology to site-yield relationships. "Site" refers to a location, whatever its size, which physical environment is homogeneous. In this context, site index (SI) equate with the overall potential of site environmental parameters to sustain tree growth. Forest productivity is supposed to correlate well with tree height growth (Hägglund, 1981) for a wide range of stand density (Eichhorn, 1904). Thus SI is generally derived from the height of individual trees in unevenaged stands, or from the mean or dominant height of evenaged stands, at a given reference age; it is then defined as "age-height SI" (Skovsgaard et al., 2004). With climate change

leading to increasing and more frequent drought stresses, stand density may become a concern: competition for limited water resources between trees, or between dominant trees and the undergrowth, may reduce tree growth and increase mortality risk (Allen et al., 2010), thus question the basis of age-height SI reliability in time. Adaptive management, particularly through more intense or frequent thinnings and clearings, is often recommended to release competition for a sustained height and diameter growth (Gavinet et al. 2015; Giuggiola et al. 2018; Olivar et al., 2014; Sohn et al., 2016).

The goals of this study were: (i) to develop an autecological model, based on a comprehensive study of the relationships between Aleppo pine height growth and occurrence and environmental factors including geography, climate, soil, geology, topography and legacies of past human activities; (ii) to derive from this model a practical tool for forest managers.

2 Materials and Methods

2.1 Study area

The study area is the French distribution range of Aleppo pine (*figure 1*), between 42 and 44° of latitude (N), between 2 and 8° of longitude (E), and below 1,000 m of altitude.

The climate is typically Mediterranean. It is characterized by a summer drought lasting two to four months on average combined with very high temperatures, by mild and wet winters, and by rainfall peaks in autumn and spring with a high interannual variability. The annual rainfall and mean temperature range from 450 mm / 16°C, along the western coast and on small islands, to 1100 mm / 9.3°C in mountain ranges, respectively, with averages around 700 mm / 13.8°C. The study area can be split into 3 Mediterranean bioclimates (Rivas-Martínez et al., 2004): the thermomediterranean bioclimate in a narrow strip along the coast, the mesomediterranean bioclimate for plains and low plateaus, and the supramediterranean bioclimate above 500 to 600 m asl for northern and southern aspects respectively. Aleppo pine cannot be found in France in the oromediterranean bioclimate.

In the study area, Aleppo pine often forms irregular stands issued from natural encroachment on abandoned grasslands and agricultural land. It is sometimes pure, mainly when planted or when issued from natural regeneration of recent forests after wildfire; but it is more frequently mixed with holm oak (*Quercus ilex* L.) at low elevation and downy oak (*Quercus pubescens* Willdenow) in the supramediterranean bioclimate.

2.2 Sampling design

Plots were chosen to be representative of the main ecological gradients, as determined by previous studies in the same area (Vennetier et al. 2008, 2010): at least five and a maximum of eight plots were chosen in each of the 96 units of a sampling plan crossing all classes of the following variables:

- Two bioclimate levels (e.g. thermo + meso vs supra-Mediterranean);
- Four altitude classes: three classes from 0 to 600 m asl with a span of 200 m and one class over 600m asl;
- Four soil types associated with corresponding parent-rock types: (1) alteritic soil on limestone and assimilated carbonated hard rocks; (2) soil on colluvium or alluvium without superficial hard bedrock ; (3) soil on soft carbonated rocks (marl and carbonated clay-stone); (4) non-carbonated soils on other types of parent-rocks, mainly metamorphic as shales, exceptionally sandstones or sand);
- Three classes of solar energy budget, based on Becker index (Becker, 1984) combining orientation and slope (hot, neutral, cool). See *appendix 2.c* and *figure 9* for details.

Within solar energy classes, we also balanced the hot vs very hot and cool vs very cool sites (*figure 9*). Within each unit of the sampling plan, we tried to balance as far as possible the classes of two other important local factors:

- topography in three classes: (1) concave (i.e. favourable conditions); (2) plane (neutral) (3) convex (i.e. unfavourable);.
- soil total depth in three classes (0-30; 30-60; >60 cm)

Replicates within each sampling design unit were chosen scattered throughout the study area to avoid geographic biases. The sampling plan includes 523 sites, the density of plots being proportional to the surface of Aleppo pine in each county of the study area. The standard plot is a 400 m² circle. But rectangular plots were used in linear environments as thalwegs and ridges to guaranty homogeneity on site scale.

In order to limit the impact of various disturbances, we chose sites with low levels of recent human activities *i.e.* no logging, grazing, clearing, trampling or prescribed fires in the last 30 years. No wildfire impacted these plots since the establishment of dominant trees (inferred from the absence of any fire scar on their bole and from the age of broadleaved species found in the plot or in the surroundings). Evidences of ancient human activities (terraces, stone piles or walls, ditches) were noted, as they concern a large proportion of current forests in the study area. But agricultural practices and extensive grazing stopped at least 50 years ago and generally far more, according to forest structure and land registry.

Only healthy dominant trees among the highest in evenaged stands, and the highest of their generation

in unevenaged stands, were considered. Five trees per dominant species were chosen in each plot (or all tall trees if less than 5 were present), but up to seven were sampled in unevenaged stands in order to target the different age classes. Tree age was estimated either on cores (three per tree including one as low as possible), or on the stump at soil level after logging in case of stem analysis. 2158 pines (age / height couples) were finally retained. Comparing different sampling methods, Ayari et al., (2011) confirmed that the choice of dominant trees was best suited to examine site fertility for Aleppo pine.

2.3 Used variables

The description of variables finally kept in the models is given in *table 1*. The patterns of variable transformation described in table 1 are detailed and justified in the first part of the result section: indeed, the shape of site index response to each variable couldn't be decided before the analyses, as it was tested and validated in the modelling process, with several feedback steps. This shape is important to understand the ecology of Aleppo pine, thus it is part of the results.

The study used two types of variables:

- (1) *Climatic and geographic variables* were generally measured on maps or computed using a GIS: this group includes rainfall and temperature, altitude, the local solar energy budget (Becker, 1984) and topography on landscape scale. For climatic variables, we used 113 meteorological stations of the French National Meteorological Network with complete series of monthly data over 36 years (1961-96) and 29 additional stations with incomplete series (4 - 30 years) but filling gaps in the National Network (high elevation, slope gradients, shaded slopes). These stations cover the whole study area, and no plot was farer than 25 km from a meteorological station, 85% of them being closer than 10 km. Climatic variables were interpolated by simple kriging for rainfall and co-kriging with elevation for temperature, on a grid of 50 x 50 m for the whole study area.

- (2) *Local variables* were directly measured or calculated in the field. They describe topography on local scale, geology, soil and past human impact. A soil profile was studied in each plot, as deeply as possible, up to the unweathered mother rock for relevant geological conditions. It was completed by at least five soil cores, one extracted close to the middle and four close to plot limit at cardinal points. Root density and soil texture were measured in each soil layer. The textural WHC was computed taking the depth of each layer, its proportion of coarse elements, and the WHC of these coarse elements for porous rocks into account. After the first steps of modelling, several variables were split in classes in such a way that the final model can easily be rendered as a practical tool for forest managers.

Table 1: Description, classes, limits and transformation (when relevant) of significant variables used in the PLS models. The first four variables are considered as "Climate variables", topography on landscape scale as geographical variable, and all other ones are part of "local variables".

The patterns and reasons of variable transformation are detailed in the first part of the result section.

Variable	Limits or classes	Description and transformation when required
Altitude	30 – 820m	Variable transformation: symmetrization ^(a) on both sides of the optimum (200m).
Mean annual temperature	10.8 – 16.2 °C	Variable transformation: a symmetrization on both sides of the optimum (14.5°C).
Annual rainfall without summer	400 - 1150 mm	Annual rainfall excluding summer rainfall. Variable transformation: symmetrization on both sides of the optimum (850 mm), and constant value (500) under 500.
Summer rainfall	58 – 180 mm	Cumulated rainfall of June, July and August. Variable transformation symmetrization on both sides of the optimum (145 mm).
Topography landscape scale	5 classes, values from 1 to 5	Bottom of valleys and thalwegs (5),concave lower slope (4), plain, plateau (3), regular slope (2), summit, convex ridge or higher slope (1)
Total soil depth	0 – 400 cm	Depth up to unweathered mother rock if relevant. Transformation = constant value (=120) over 120 cm.
Colluvium depth	0 – >200 cm	Transformation = constant values respectively under 25 cm and over 100 cm, log transformation between 25 and 100 cm.
Coarse fragments percentage	0 -95 %	No transformation. On soft carbonated rocks, the percentage of non-weathered parent rock is considered as coarse fragments percentage.
Water holding capacity index	70-200 mm/m	Assessed from soil texture in classes following the classical texture triangle for texture classes and table 4 in <i>Appendix 2b</i> . Exponential transformation. Referred thereafter as Textural WHC.
local topography parallel to form lines	3 classes from 1 to 3	Along form lines: concave (1), flat (0), convex (-1).
Dip angle ^(b)	5 classes from -2 to +2	Sum of two variables = dip angle respectively parallel and perpendicularly to form lines with 3 classes each: unfavourable (-1), intermediate (0); favourable (1). See <i>appendix 2.a</i> for details
Slope angle	0-45°	Variable (y) transformation: y = 0 below 20°, and y-20 over 20°
Rock outcrop %	4 classes = 0-3 0%; 1-10%; 10-30%; >30%	No transformation
Coarse fragments cover at soil surface	0-100%	Free rock fragments (pebbles, stones, blocks, excluding alterite outcrops) at soil surface under or over the litter. No transformation
Bedrock vertical fissuration	5 classes: number of large cracks/m: NA, 0; 1-2; 3-4; ≥5	Only relevant on hard rocks. Soft carbonated rocks are noted without cracks (class 1). Set to NA for statistical analyses (non applicable) when unknown due to a deep soil.
Active lime	4 classes: 0-3	Field test of fine earth reaction to HCl (diluted at 10%) after sifting at grain size ≤ 0.5mm 0 = no reaction to HCl, 1 = week reaction, few bubbles; 2 = significant and audible reaction but moderate or partial, 3 = strong audible reaction on all the sample
Past land uses *	4 classes: 0-3	0 = no remainder or signs of past agriculture; 1 = light: signs of stone removal (stone piles, walls); 2 = strong: sign of cultures (ridges, ditches); 3 = topographic transformation (terrasses)

(a) Symmetrization: for an optimum of x, variable y transformed in $y_{sym} = |x-y|$.

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* quantifies the level of anthropization of the environment, i.e. the intensity and percentage of topographic and pedological transformations (Tatoni et al., 1994a, b). Classes are sorted according to the impact of these transformations on local water budget (see discussion for details).

2.4 Height growth model and site index

Developing a model based on an age-height SI supposes that a height growth model pre-exists. Vennetier et al. (2010) made a synthesis of all previous works conducted in France (e.g. Rathgeber et al., 2004), and calibrated a new model adapted to any type of stand for Aleppo pine in France, which was used in this study. There was no significant discrepancy between this last model and the older ones, nor with sub-regional models which were tested, proving that Aleppo pine height growth patterns were rather homogeneous in France despite strong climate variability.

Our height growth model (*appendix 1*) uses Chapman-Richards equations (Richards, 1959). After calibration with our dataset, this model gave the growth curves of *figure 2*. All details about the height growth modelling are given in *appendix 1*.

Fig. 2 Aleppo pine height growth model and limits of fertility classes in France. Within the span 40 - 110 years, average prediction error on tree SI compared to the real value from stem analysis is always less than 10 %

2.5 Site index modelling, statistical analyses and practical tool for forest managers

2.5.1 Modelling and statistical steps

We used PLS regression for site index modelling. This method was designed to handle many correlated variables with relatively few observations (Cramer et al., 1988) and it is optimal for linear relationships. After a first round of raw variables selection (initially 50 environmental variables were available), we used neural networks as proposed by Guiot (1991) to obtain the response pattern of site index to each remaining variable (*figure 3*) and transformed these variables when necessary to linearize the response (*table 1*). An ascending and descending stepwise PLS regression was used for the final selection of variables. Considering previous studies using most of the same plots, and the first results of this one, we used this process to compute the

model with all plots or for four groups of plots (two types of parent rocks and, on one of these types, two types of soils (see *table 2* and *figures 4* and *5*). Selected models were transformed in a tool easy to use in forest management (*figure 6*): variables were first split in classes which can be discriminated in the field and, when relevant, classes limits were chosen according to SI response pattern; then each class was given a sign related to the response of SI to this variable and a value related to the relative weight of the variable in the model.

2.5.2 Detailed statistical processes

In a first step, we chose the number of significant components for a PLS regression with a 10,000-replications permutation test on observations. Components whose percentage of explained variance was not passed by more than 5 % of the permutations were kept.

In a second step, variables were assessed through a 1,000-resampling cross-validation test. We rejected variables when the confidence interval (95 %) of their partial correlation coefficient included zero.

Neural network were optimized with a 200-replication bootstrap, each replication including 3000 calibration steps. After the optimization of a neural network, the response of each variable (*figure 3*) was plotted on its whole variation interval, the other variables being maintained at their mean value if they were not correlated with the tested one, or maintained successively at their first, second and third thirds for those which were correlated. In the last case, the three responses were combined in a sliding weighted mean to obtain the global response. We only transformed a variable according to a non-linear relationship proposed by neural networks when this relation was stable throughout these many tests, while it enhanced whether the total explained variance of the model, or variable partial correlation coefficient in the model.

We used R software (R Development Core Team, 2010) for PLS regression and PPPhalos software (Guio, 1991) for neural networks.

The distribution of plots is not homogeneous in the fertility classes. It follows a Gaussian curve with few plots in the highest and lowest classes which are rare. Without weighting, the intermediate classes are over-represented and the models hardly predict the better and worse SI with residuals often over 4 m. We corrected this unbalanced distribution weighting each plot by the square of the distance between its site index and the mean site index of the whole sample (*equation 1*). With such a correction, the mean residual of both extreme fertility classes were reduced by 20%, while they remained nearly unchanged for intermediate classes (+5%). The mean standard deviation of for all errors was also reduced by more than 10%.

Equation 1 Plot weight related to its site index relative value:

$$P_i = 1 + (H_{70} - H_i)^2 / 10.5$$

P_i = weight for plot i , H_{70} = mean site index for all plots, H_i = site index of plot i ,

10.5 = half of the total span of site index variation

3 RESULTS

3.1 Age classes of sampled trees

The age of sampled trees ranged from 35 to 180 years, with a mean of 70. Over 600 m asl, we never found healthy Aleppo pines over 100 years old nor standing individuals over 120 years. At such elevation, most of old sampled trees were suffering from severe fungus attacks on the bole and heartwood rotting, preventing us to reach the pith with the cores, and playing a prominent and visible role in their early death through windthrows. At the northern limit of Aleppo pine distribution, and over 800m in elevation, nearly all Aleppo pines were shaped by the after-effects of repeated breaks by snow or freezing fog on the bole and in the crown, making it difficult to accurately assess past height growth without a thorough stem analysis. No tree older than 100 years was found in these conditions. This demonstrated a strong physical limitation of Aleppo pine distribution by cold climates.

3.2 Thresholds, optima and limits of site conditions

The relationships between SI and the main environmental variables are complex (Figure 3). SI was higher below an elevation of 300 m with a slight fall under 100 m and between 13.8 and 15.3°C, with optima around 200 m and 14.5°C. The ideal rainfall ranged, for summer rainfall and annual mean minus summer rainfall, from 120 to 150 mm and from 750 to 950 mm, respectively. These limits corresponded, for sampled plots, to an annual rainfall between 850 and 1100 mm.

Two thresholds were observed for colluvium depth: up to 25 cm, few differences were found with a pure alterite. Over 25 cm, SI increased sharply up to 70 cm and remained stable over 100 cm. These two limits cohered with the 110 cm threshold observed for soil total depth, over which SI stagnated. Site index responded linearly to the percentage of coarse fragments, with only a slight inflexion below 20%. The water holding capacity index (WHC) responded on both ends of its distribution, but finally, an exponential transformation better improved its contribution to the model. Slope had no impact on SI up to 20 degrees and a linear negative effect over this limit.

3.3 Choice and optimization of several PLS models

Variables were first transformed according to the shape of SI response in neural networks analysis. When all plots were included in the model, the mean absolute prediction error was high (1.7 m). Twelve residuals were over four meters and 38 between 4 and 3.3 m, over the span of one fertility class. In fact, most of these outliers laid on soft carbonated rocks (SCR) as marls and carbonated clay-rock, often in degraded sites referred to as “badlands”. Their SI was generally overestimated by the model, with a few exceptions showing an underestimation. These substrates induce specific chemical and physical constraints (Antoine et al., 1995; Esteves et al., 2005) discussed in the next section. Thus, two models were computed, separating the 40 plots on SCR and other plots (figure 4), with a better explained variance and lower residuals (table 2). In the model with all plots together, soils on alterite had a significantly lower mean SI than soils on colluvium in the same classes of soil

depth. Distinguishing these two types of soils was part of the sampling design. According to the response of SI to colluvium depth, showing a threshold of 25 cm for the colluvial superficial layer, we computed a PLS model for each group of plots: with (colluvium) and without (alterite) more than 25 cm of colluvium (figure 5). None of these two models was better than the model with all plots excluding SCR for SI prediction (table 2), and although a little bit worse in terms of mean absolute prediction error, they had similar standard deviations for prediction errors and residuals. Thus we considered these two models as an alternative to the model with all plots without SRC. Their differences helped disentangling the respective roles of some variables (soil depth, colluvium depth, past land uses, water holding capacity, rock fissuration, coarse fragment) in Aleppo pine growth, through site water balance and Aleppo pine root system adaptation to different constraints. They highlight important aspects of Aleppo pine ecology, which are further discussed

Fig.3 Response of Site Index to the main environmental variables requiring a transformation, according to neural networks analysis. Vertical bars give the confidence interval (5th-95th percentiles). Other variables showed a linear response

Table 2 Comparison of the five PLS models, including (1) all the plots (2) two groups of plots: with and without soft carbonated rocks (SCR) and (3) two groups of plots: with (colluvium) and without (alterite) a significant colluvium (>25 cm depth). NS means non-significant. This table gives the mean for absolute values of the prediction error.

		Nb of PLS components	% explained variance	Comp 1 %	Comp 2 %	Mean abs. prediction error	SD. prediction error	SD of residuals
1	All plots	2	51	45	6	1.7	1.7	3.0
2	Without SCR	2	55	49	6	1.3	1.1	1.9
	SCR	1	56	56	NS	1.4	1.1	1.9
3	Colluvium	2	48	41	7	1.6	1.1	1.9
	Alterite	1	44	44	NS	1.5	1.0	1.8

Fig.4 Partial correlation coefficients of the PLS models for (i) all parent-rocks excluding soft carbonated rocks (SCR) and (ii) for SCR only. All displayed variables are significant ($p < 0.05$) in the PLS regression. Variables are sorted by decreasing weight in the model without SRCs.

Fig.5 Partial correlation coefficients of the PLS models without SCR for (i) alterites and (ii) soils with more than 25 cm of colluvium. All displayed variables are significant ($p < 0.05$) in the PLS regression for at least one of the groups. Variables are sorted by decreasing weight in the model for alterite.

3.4 Comparison between models & additional results

Aleppo pine productivity was significantly responsive to many factors: topography on local and landscape scale, several soil parameters (structure, depth, rockiness and coarse fragment content, active lime, water holding capacity), characteristics of superficial bedrocks (dip and fissuring, outcrops), climate (temperature and rainfall) and past land uses.

Local factors dominated in all models compared to climate and altitude. When summed together, they represented ~75% of SI explained variance on non-SCR rocks, and 90% on SCR.

On SCR, annual rainfall and altitude were not significant, and climate as a whole had a very light weight in the model (represented by mean annual temperature and summer rainfall with very small coefficients). Topography and past land uses had a smaller weight on SCR than on other substrates. Active lime was significant for all groups of plots except, logically, SCR where its percentage is always very high. Except dip, bedrock characteristics used in this study were irrelevant on SCR.

Geological factors as well as soil total depth and surface stone cover were more important on alterite than on colluvium. Conversely, local topography, soil water holding capacity, past land uses and the percentage of coarse elements were more important on colluvium.

Mean SI was higher in the eastern part of the study area than in its western part. Soil texture, driving water holding capacity, also had a significant influence on rooting density; a balanced texture mixing a significant proportion of the three main components (sand, silt and clay) increased by 60% root density in the soil profile compared to unbalanced textures limited to one or two of these components (11.5 vs 7 roots/dm², $P < 0.01$).

3.5 Practical tools for site index assessment

The practical tool derived from the PLS models is shown in *figure 6*. As splitting soil in alterite and colluvium did not improve the accuracy of predictions nor reduced the standard deviation of errors, a single practical tool was developed for all rocks excluding SCR. Models for alterite and colluvium may be useful for research purpose, for in depth field surveys and for further investigations in sites badly predicted by the proposed practical tool.

4 DISCUSSION

4.1 Reliability of site index (SI)

The tenets of height/age SI concept can be questioned:

- (1) On one hand, thinnings may interfere with site quality in stand growth (Olivar et al, 2014; Skovsgaard et

al., 2008). But none of our plots were thinned in the last 30 years, and most of them remained unmanaged since at least the 50's. As 80% of studied stands can be considered as unevenaged and irregular, with rather low densities and low to moderate competition between dominant trees, computing individual tree SI was compulsory. Young Aleppo pines in these plots occupy former gaps resulting from natural hazards as storms, snow, deep frosts and insect outbreaks. But we did not choose plots with recent accidents, nor young trees strongly competing with older ones. Finally, tree density at individual level can be considered as rather stable in our plots and probably have little influence on observed growth patterns.

- (2) On the other hand, assessing forest growth from age-height SI supposes that, for a given site, height growth pattern is stable in time. A static definition of "site" ignores environmental dynamics that may improve or hamper tree growth, such as global and climate change (Cannel, 1998), land-use change and derived soil evolution (Glatzel, 1998). Indeed, convergent results in France (Becker et al., 1994; Rolland et al., 1998), in Europe (Spiecker et al., 1996) and throughout the world (Backer et al., 2004; Cook et al., 1991; D'Arrigo et al., 1996; Szeicz, 1997) show that tree height growth varied in the 20th century, and particularly since the 60's. Most of the time a significant acceleration was reported, and Aleppo pine clearly followed this general trend (Vennetier et al., 1998). We got around this problem with the correction of site index according to tree age (equation 3), so that our model should not be biased by the global change-related height growth evolution.

Flora composition, as an integrated indicator of site conditions, was sometimes used independently or combined with abiotic variables to assess site index (Berges et al., 2006). In the Mediterranean region, flora composition is generally constrained by millenniums of severe disturbances (Blondel and Aronson, 1999) and, even dozens of years after the release of anthropic pressure, may still be in fast evolution (Tatoni et al., 1994b) and not representative of site environment. Moreover, trees like Aleppo pine can reach deep water and nutrients resources inside bedrocks (Sarris et al., 2013), out of reach of most other plants. This is demonstrated by the importance of geological variables for Aleppo pine growth, and particularly parent rock fissuration and dip. Such variables did not appear in the bioclimatic model calibrated on the whole flora in the same study area, and for a large proportion on the same plots (Vennetier et al., 2008). Thus we used only abiotic variables to model the site index, to allow the model to be used accurately in any circumstance and place whatever the degradation level or the evolution stage of present or future vegetation.

Fig. 6: Tables and graphs to assess Aleppo pine Site Index with simplified field data. The value "Total all variables" from each table must be used in the corresponding graph of fig 6.3 to get the predicted site index (SI).

Fig. 6.1 Tool for all parent rocks except soft carbonated rocks (for SRC, see fig 6.2).

Climate

Climate																						
Variable	Summer rainfall (mm) ⁽¹⁾						Mean annual rainfall (mm) ⁽¹⁾						Mean annual temperture (°C) ⁽¹⁾									
Classes	<70	70-85	85-95	95-115	115-160	>160	<600	600 - 700	700 - 780	780 - 850	850 - 1050	>1050	<10.9	10.9 - 11.6	11.6 - 12.1	12.1 - 12.6	12.6 - 13.2	13.2 - 14.4	14.4 - 15	15 - 15.5	>15.5	
Value	-0.5	-0.3	0	0.3	0.5	0	-1.8	-0.6	0	0.9	1.8	0	-0.93	-0.65	-0.33	0	0.5	0.9	0.465	0	-0.3	
Note																						
																						Total climate

Landform

Landform										
Variable	General topography					Transversal Topo			Terrasses	
Classes	Valley thalweg	Concave lower slope	plain plateau	regular slope	Convex ridge or higher slope	concave	plane	con- vex	yes	no
Value	2.2	0.7	0	-0.3	-1.5	2.0	0	-2.0	4.0	0
Note										

Soil surface

Variable	Coarse fragments			Rock outcrops				Colluvium depth (cm)			
Classes	<10%	10-30%	>30%	0	1-10%	10-30%	>30%	<25	25-40	40-70	>70
Value	0.5	0	-0.5	1.0	0.4	-0.4	-1.0	0.0	0.2	0.4	0.7
Note											

Bedrock

Variable	Rock layers dip ⁽²⁾					Rock fracturation			Plates ⁽³⁾	
Classes	-2	-1	0	1	2	low	mean	high	yes	no
Value	-0.6	-0.3	0	0.3	0.6	-0.6	0	0.6	-1.8	0
Note										

All rocks except SCR

Total rock

Soil

Variable	Water holding capacity (mm/m) ⁽⁴⁾					Soil total depth (cm)							% coarse elements							
Classes	<100	100 - 140	140 - 180	180 - 196	>196	<35	35 - 60	60 - 75	75 - 90	90 - 110	110 - 180	>180	0	1 - 20	20- 40	40 - 60	60 - 80	80 - 95	>95	
Value	-1.3	-0.6	0	0.8	1.3	-2.6	-0.9	-0.3	0	0.6	1.2	1.7	0	1.4	0.5	0	-0.5	-1.0	-1.4	
Note																				

Total soil

(1) to be adapted to local climate gradients and constraints in other regions

(2) see in annex 2.a how to assess dip classes

(3) alterite in imbricated parallel plates

(4) see in annex 2.b WHC classes according to soil texture

All rocks except SCR

Total all variables

Fig 6.2 Tool for soft carbonated rocks (SRC): marls, carbonated clay-rock and similar rocks

Climate															
Variable	Mean annual rainfall (mm) ⁽¹⁾						Summer rainfall (mm) ⁽¹⁾						Mean annual temp ⁽¹⁾		
Classes	<600	600 - 700	700 - 780	780 - 850	850 - 1050	>1050	<70	70 - 85	85 - 95	95 - 115	115 - 160	>160	<11.6	11.6 - 15	>15
Value	-1.3	-0.5	0	0.7	1.3	0	-0.5	-0.3	0.0	0.3	0.6	0	-0.9	0	-0.6
Note															

Total climate

Landform																		
Variable	General topography					Transversal topogr			Terrasses		Slope angle (°)			Altitude (m) ⁽¹⁾				
Classes	Valley thalweg	Concave lower slope	plain plateau	regular slope	Convex ridge or higher slope	con-cave	plane	convex	yes	no	<20	20-30	>30	<100	200 - 300	300 - 450	450 - 600	>600
Value	1.8	0.6	0	-0.2	-1.2	2.2	0	-2.2	2	0	0	-0.5	-1.5	0	1.2	0	-0.4	-1.2
Note																		

Total landform

Rock									
Variable	Parent rock outcrop				Local rock layer dip (*2)				
Classes	0	1-10%	10-30%	>30%	-2	-1	0	1	2
Value	0.5	0.2	-0.2	-0.5	-1.9	-9.5	0.0	1.0	1.9
Note									

Soft carbonated rocks (SCR)

Total bedrock

Sol																		
Variable	Colluvium depth					Water holding capacity (mm/m)					Soil total depth							
Classes	0	5 - 30	30 - 50	50 - 80	>80 ^(*3)	<100	100 - 140	140 - 180	180 - 196	>196	<35	35 - 60	60 - 75	75 - 90	90 - 110	110 - 180	>180	
Value	-1.7	-0.8	0	1.3		-0.6	-0.3	0	0.4	0.6	-3.2	-1.1	-0.4	0	0.8	1.5	2.2	
Note																		

Total soil

Total all variables

(1) to be adapted to local climate gradients and constraints in other regions

(2) Local bedrock dip must be taken into account only in case of alternance between SCR and different other rocks, with layers from a few meters to a few tenth of meters thick, allowing roots to penetrate deeply in the soil and the rocks between unfavorable SCR layers. See in annex 2.a how to assess dip classes.

(3) With more than 80 cm of colluvium over SCR, particularly when the colluvium originates from an other type of rock, the general key should be used.

Fig 6.3 Graphs for respectively all rocks but soft carbonated rocks and for SCR:

The Site Index is obtained by the projection in the graph of the total note obtained from the corresponding tool.

4.2 Response to environmental variables

4.2.1 Climate variables

Site index response to altitude follows (with logically a symmetric pattern) its response to temperature. But although temperature and altitude correlate well for our sample ($r^2=0.65$, $p<0.01$), it was impossible to eliminate one of these two variables from the model without losing a lot of explained variance: geographic gradients (east-west, continentality, distance to the sea) change their relationship particularly through (1) differences in the daily and annual span of temperature as well as its relative extremes, (2) cloudiness and air humidity patterns and, (3) the number of windy days, average wind speed and main direction. These gradients also modify the frequency of heavy snow episodes which severely damage Aleppo pine crown, thus its growth and related SI.

The optimum temperature range (13.8-15.3°C) is associated with a rather long summer drought but also with a long growth season. Aleppo pine growth is favoured by high temperatures in the end of winter, i.e. January-February (Vila et al., 2008). On shallow soils with few water reserves and in Mediterranean areas, an early growth season is necessary to benefit from the water stored during previous winter months, as drought may occur since May (Thabeet et al., 2009). With a growing season split in two parts, polycyclic species as Aleppo pine can also take advantage of long and hot fall to develop new shoots (Girard et al., 2011) and produce a second flush in cambium activity, leading to a bimodal ring growth significantly increasing ring width (Pacheco et al. 2017). Budburst and shoot elongation can even occur in winter in the absence of frost (Vennetier et al, 2011).

Temperature and rainfall are inversely correlated in the study area ($r^2=0.31$, $p<0.01$), but SI response is quite the same to both of them. It shows that neural networks and PLS regression correctly disentangled their respective weight and interactions in various parts of the study area. Annual and summer rainfall are optimum for values far over their average for the study area, 950-1000 mm and 130-140 mm, respectively. These optimum are also far over the rainfall associated with Aleppo pine preferred altitude and temperature. So that the ideal site for both geography and climate cannot be found in the study area. The highest mean index in the eastern part of this area is explained by higher rainfall than in the western part for equivalent temperatures. SI decreases for the highest values of rainfall. In fact, these extremely rainy situations are all situated at high elevation, over 750 m for the study area, where Aleppo pine growth is hold back by frost and snow (Falusi et al., 1984; Girard et al., 2012; Serre, 1976, Vennetier and Hervé, 1998), in addition to the observed shortening of its life span over 600 m of elevation. , The absolute limit in elevation is of

course varying with local climate conditions in other regions.

Aspect and potential solar energy were never significant in Aleppo pine SI models, although they are important in water balance and flora composition in the same area (Vennetier et al., 2008). Close to the coast and at low elevation, southern orientation increases water stress and limits Aleppo pine growth, while at high elevation and in the colder hinterland, southern aspects limiting frost constraints are the only favourable sites. Reciprocally, northern slopes are all the more favourable to Aleppo pine than the local climate is hot and dry, and they are unfavourable in cold areas. Thus, orientation and Becker index can be considered as important (positively or negatively) only at both ends of its distribution area, and their effect added manually to improve model predictions. Relations and interactions between geographic and climatic factors are of course related to their specific combination in the study area. However, optimum values and some thresholds are probably relevant in most of Aleppo pine distribution area, as French Mediterranean region include a large proportion of the span of these factors for this distribution, except the driest and hottest parts. Some variations may occur due to the genetic adaptation of Aleppo pine to other local combination of climate and landform (Calamassi et al., 2001; Michelozzi et al., 2011).

4.2.2 Local variables

The weight of soil, mother rock and topography

The favorable effect of colluvial material on Aleppo pine growth appears in all analyses. A significant colluvium generally hangs together with favorable topographic positions and limited erosion. However, our sampling plan successfully limited such correlations.. Moreover, colluvial layers have a more favorable physical structure than alterites. Thanks to the movements along the slope, coarse elements overlapping in alterites, which constrains root development, are randomly distributed in colluvium. Colluvial layers are also generally less compact than their mother alterites. Finally colluvial material, especially if it is native from other parent-rocks, mask partially the specific unfavorable factors of SCR as discussed in the next sub-section.

Whatever soil structure, SI increases rapidly between 20 and 80 cm of depth because, on shallow soils, every extra centimeter is critical for soil available water content. If the limit of 100 to 120 cm may be considered as sufficient for Aleppo pine good development in the study area, it corresponds also with the limit over which uncertainties on the observations are increasing. Site index also slightly increased with total soil depth between 160 and 200 cm. As alterites rarely exceed 100 cm in the study area, most favorable soils for Aleppo pine seem to be structured with a 50-100 cm

colluvium over the same depth or more of alterite. In such conditions, roots can rely on both good rooting conditions in superficial layers, and on long lasting water reserves in the cracks of the alterite and parent rock. This hypothesis holds with the significant role of parent-rock fissuration in the model. Indeed, this last variable is more important on pure alterite, as parent bedrocks are closer to the surface than on colluvial soils. Lapiés, which presented high SIs for Aleppo pine in the study area, exemplify the important role of deep cracks and alterite pockets, compensating their high percentage of coarse fragment and rock outcrops close to the surface. Rock outcrops are rare enough on colluvial soil to have no significant role in the model. On alterites, they are good indicators of shallow and eroded soil, and thus are among strong variables.

The percentage of coarse fragments (CF%) in the soil directly and proportionally reduces global soil water holding capacity. As a result, its negative impact on Aleppo pine SI is strong and linear from 20 to 95%. CF% weight is high mainly in colluvial soils in which it is highly variable, with a balanced distribution in our sample. Conversely, it is most of the time high for alteritic soils, so that its weight in the corresponding model is low due to this limited variability. However, a few high SIs could be found for very rocky soils on porous rocks: coarse fragments from these rocks may contribute to long lasting water reserves, from 1 to 20 % of their volume, according to their level of alteration (Hanson et al., 1979; Witty et al., 2003).

The cover percentage of coarse fragments at soil surface (SCF) is negatively correlated with Aleppo pine SI. Yet, a dense cover by such fragments may have a positive role, limiting present erosion and evaporation. Thus, this variable is an indirect indicator of several soil conditions. On alterites, independently from erosion, it is more or less proportional to soil depth and to the percentage of these elements in the soil. When it is higher than the percentage of these elements in soil upper layers, it allows assessing past erosion rates (Biro, 1981) and related losses of fertility and soil depth... The link between erosion and SCF is confirmed by the absence of weight of SCF in the model for colluvial soils, where erosion is supposed to be absent or low.

Aleppo pine SI responds significantly to textural water holding capacity (WHC), mainly for the low (< 110mm/m) and high values (>160 mm/m). These high values correspond to textures where sand is absent or minority, except for the highest class (200 mm/m). This maximum value is tied to balanced textures with nearly equivalent proportions of sand, clay and silt. Such fully balanced forest soils, rich in nutrients and rarely compact, harbour a rich biological activity with a minimum of physical constraints and are consequently densely structured in micro and macro-aggregates. Their real WHC and porosity is higher than the one determined in

laboratory after soil homogenization and standard preparation, most of the time for arable soils (Teepe et al., 2003). Aleppo pine was particularly responsive to these qualities, as highlighted by higher rooting density and significantly better SI. The small improvement of SI with WHC in the lowest values of this variable (figure 3) corresponds to the transition between pure sands (rare in the study area) and soils with a small proportion of silt or clay. As for soil depth in its lowest class, any additional millimetre of WHC is critical for vegetation. Moreover, even a small proportion of silt or clay increases significantly soil nutrient content compared to pure sand.

Although unanimously considered in literature as adapted to carbonate soils, Aleppo pine thrives better and grows faster when decarbonation partially or totally alleviates active lime constraints in superficial horizons, and on non-carbonate rocks. In France, Aleppo pine is rare on acidic soils where maritime pine (*Pinus pinaster* Aiton) was historically preferred for its faster growth, straighter bole and more abundant resin. On such soils, SI index is generally high and slightly underestimated by the model: however, computing a specific model for this special case was impossible, as the number of plots was less than 15, and useless as concerned surfaces are very limited. More resistant to drought, Aleppo pine should be considered as a possible alternative in the future at the southern and lower edges of maritime pine distribution, where this last species is at risk (El Korchani et al., 2007). As very acidic or poor leached-out soils are not found in French Mediterranean area, our model is not relevant in such situations.

The specificities of soft carbonated rocks

Aleppo pine is one of the rare tree species surviving on shallow soils developed on soft carbonated rocks (SCR) in a purely Mediterranean climate. Marls and carbonated clay-rocks present constraints to plant germination and growth which vary according to the level of alteration and may be hard to assess precisely: toxic levels of active lime, high impermeability and compacity along with a trend to be saturated and lead to root-asphyxiation when wet (Esteves et al., 2005), volume variations with water content leading to cracks and root rupture after drying, strong water retention limiting water availability for roots. Root development in unaltered SCR is almost impossible. SCR weathering alleviates these constraints (Vallauri et al., 1999), but the high erodibility of the soils developed on SCR when they are not densely vegetated generally rejuvenate them rapidly. When predicted with the general model, Aleppo pine SI on SCR shallow soils is grossly overestimated. Conversely, soils derived from SCR can be very fertile when the parent-rock have been deeply weathered for a long time, and partially decarbonated. This is demonstrated by the higher weight of 'rock outcrops in the SCR model

compared to the non-SCR model, as an indicator of partial upper bedrock alteration. (figure 4). The model computed for SCR, although statistically significant, must be considered and handled with care, because of the rather low number of plots and an unbalanced distribution in the study area. The low weight of climate variables in this model is probably mainly due to the overwhelming physical and chemical constraints, but also partially to the incomplete distribution of plots in climate gradients of the study area. Slope angle is significant, unlike the three other models, because of the high sensibility of SCR to erosion (Oostwoud Wijdenes and Ergenzinger, 1998). Coarse fragments are irrelevant for this type of rocks. Colluvium depth is dominant because any type of colluvium, but particularly those coming from other parent-rocks, hide the constraints of SCR. With more than 80 cm of colluvium, a site on SCR can be assessed with the general model. The importance of dip in the model for SCR shows that any hard bedrock intercalated within SCR improves their suitability for Aleppo pine. Particularly when dip angle is high, water can take advantage of these other rocks to penetrate soil in depth. Roots following these beds benefit from the high water holding capacity of SCR at the interface.

Legacies of past land uses

A long lasting impact of land use and particularly agriculture on the environment (Dupouey et al., 2002) is demonstrated by Aleppo pine growth. Former cultivated terraces, even when they have nearly disappeared, increase SI index by about two meters. Traces of old fields (ploughing lines, stone heaps and walls) are also associated with a positive impact. Erosion control, soil retention and higher infiltration rates thanks to terraces and walls, remnant phosphorus and nitrogen higher rates, a lower compacity of superficial layers due to ploughing, lower evaporation under stone piles and slower wind at soil surface near the walls, may explain together the global improvement of the environment. The weight of past land use is mainly visible on colluvial soils: terraces and cultures were in priority laid out on good soils and avoided when possible superficial and stony alterites. On initially shallow soils, terraces artificially fixed a colluvium with time, or soil was brought from the neighbourhoods. On the other hand, cultivated areas are opposed with former grazing land which represents the large majority of the study area, most of the time degraded by millennia of overgrazing, fire and erosion (Blondel and Aronson, 1999). The scattered stone heaps and loose wall networks of these extensive pastures are not sufficient to improve significantly their fertility level. So that the positive impacts of past cultivation, and of related land transformation practices, may be highlighted and statistically magnified by the contrast with the negative impacts of other traditional landuses.

The key role of water balance

The relative weight of local variables for Aleppo pine may be relevant anywhere: as in the bioclimatic model calibrated on the flora of many of these plots (Vennetier et al., 2008), it highlights their contribution to water balance. Water availability is the main limiting factor for tree growth in Mediterranean regions, as confirmed for Aleppo pine by Olivar et al. (2014). This explains the importance of topography at both local and landscape scales, which is always among dominant variables whatever the model. Topography directly contributes to water balance through water flows control and indirectly drives many important soil variables (depth, colluvium, texture, past land uses). Consistently, topography appears as a key factor in forest dynamics with increasing drought in Spain (José Vidal-Macua et al., 2017).

One missing factor in this study is soil richness for the main nutrients, which was never significant, as the study area does not include very poor or very acidic soils.

4.2.3 Towards a new balance between local and climate variables with climate change?

As a foretaste of the climate forecasted by RCP4.5 scenario of IPCC 2013 for the middle of the 21st century (Christensen et al., 2013; Kirtman et al., 2013), the eastern part of the study area experienced during the 1998-2008 decade, an exceptionally hot and dry spell. As a result, Aleppo pine current mortality doubled (French-Forest-Health-Department, 2003-2008) while its productivity dropped, and its crown development was seriously altered (Girard et al., 2012), showing that critical thresholds of water stress were passed. As a sign of what may happen in the future in southern France and in regions with a similar climate in southern Europe, Aleppo pine has already been suffering for decades from significant growth reduction and die-back in Tunisia (El Khorchani et al., 2007). This doesn't challenge our models in the short term: within local variables, the relative weight may not significantly change, except for geological variables allowing root systems to reach deep water reserves (cracks in bedrocks, dip angle) which increasing role with aridification was recently underlined (Sarris et al., 2013).

However, the spatial distribution of fertility classes in the landscapes will be submitted to northward and elevation shifts with higher temperatures and a drier growing season. Such local changes are forecasted in other types of biomes with a local reduction of the age-height site index (Sharma et al. 2015Dip angle classes).

To some extent, the relative weight of climate variables would probably have to be increased in our practical tool when drought stress becomes extremely limiting, which may happen in the study area before the end of the 21st century. For the same

reasons, the balance between climate and local variables should be reassessed if our models and tool are used in regions which climate is out of the range of the one of the study area.

Aside tree growth, reproduction is an important function contributing to the presence and persistence of a species in a specific area. Our study didn't tackle reproduction, but several authors specifically addressed this problem. Ayari et al (2011a) found variations of cone and seed production along geographical and elevation gradients, with a better production in more humid areas. Girard et al. (2012) showed that cone production could be severely reduced after 4 to 5 years of exceptional drought, but recovered rapidly.

One of the challenges in terms of forest management will be to maintain tree growth and limit mortality in a more arid climate. Olivar et al. (2014) showed that soil water availability during the growing season was the main driver of Aleppo pine growth, and that thinnings can contribute to release the effects of water limitations (Giuggiola et al., 2016). Many species are positively affected by thinnings in a drought context (Sohn et al., 2016). However, this impact depends on other components of forest structure: thinnings may favour the development of dense undergrowth which water demand offsets the water savings of a reduced canopy (Gavinet et al., 2015).

Aleppo pine is still not at risk in France, neither for survival for growth nor for reproduction, as it is far from its bioclimatic limits, particularly from those observed in Northern Africa and Israel. In south-eastern Spain, José Vidal-Macua et al. (2017) showed that it has gained ground against broadleaved evergreen species in the last decades. Even with a reduced growth, it remains highly competitive (Vila et al. 2008).

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5 Conclusion and prospects

This paper offers a new and deep insight in the ecology of Aleppo pine. Assessing precisely Aleppo pine adaptation and potential productivity requires a thorough investigation of site conditions, including climate, soil characteristics down to deep layers and parent-rock, and topography on several scales.

When summed together, local factors are more important than climatic factors for Aleppo pine growth in the study area. The French Mediterranean climate is not very limiting for Aleppo pine growth. Even at the driest and hottest places, deep and good soils and a favourable local topography allow its growth to reach at least the mean fertility class. However, frost and snow hold it back at high elevation and northward, while the increase in humidity shortens its lifetime. Moreover, with climate change acceleration, the influence of rainfall and temperature factors may increase, as worsening water stress will no longer be sufficiently compensated by local conditions.

As the span of climate conditions in south-eastern France includes most of those found in Aleppo pine distribution area, except the driest and hottest ones found in Northern Africa and in some Mediterranean islands, this study could be easily used or adapted in all concerned countries. In countries where Aleppo pine climate/growth relations were already established, this study can help improving forest site assessment.

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Appendices

Appendix 1: Height growth modelling

As most sampled stands were irregular and unevenaged, site index was computed tree by tree (tree SI) with the height growth model for the base age of 70 years, and plot SI was calculated as the average of concerned individual tree SI. Sampled trees were 70 years-old in average, which is also the recommended logging age for Aleppo pine on medium to high fertility sites in French managed forests (Couhert and Duplat, 1993). As tree height growth is irregular before 30 years, and the number of studied trees limited over 120 years, the use of the growth curves is only perfectly accurate between these two limits (figure 2, Vennetier et al., 2010).

Equation 2: height growth model inversed to calculate tree SI.

$$SI_i = h_i \cdot \left[\frac{1 - \exp(-0.021 \times age_{ref})}{1 - \exp(-0.021 \cdot age_i)} \right]^{1.5385}$$

were

- * **SI_i** : SI for tree *i* = estimated tree height at 70 years,
- * **h_i** and **age_i** : present measured height and age of tree *i*,
- * Age_{ref.} = reference age, 70 years for this study
- * **-0.021 et 1.5385**: general parameters fitted to the whole sample.

As demonstrated by a previous study in Provence (Vennetier et al., 1998), a significant increase of Aleppo pine height growth occurred in Southern France during the 20th century. This is highlighted by the significant difference in height -age SI for trees of different age classes within unevenaged plots. Following the same protocol, and thanks to the homogeneity of site conditions within each plot, we computed this acceleration as the slope of the regression between differences of SI and differences in age of concerned individual trees (equation 3 and figure 7).

Equation 3: height growth acceleration (*a*)

$$(SI_{ij} - SI_j) = a * (age_{ij} - age_j) \text{ were}$$

- * **SI_{ij}** and **age_{ij}** = SI and age of each tree *i* in plot *j*, respectively,
- * **SI_j** and **age_j** = mean height and mean age of all measured trees of plot *j*, respectively.
- * **a** = height growth acceleration in the concerned period

The acceleration computed for the 20th century was 0.041 m* year⁻¹ (r² = 0.26, P<0.01, figure 7).

Fig.7 Intra-plot SI variation according to tree age, showing Aleppo pine height growth acceleration in the 20th century

Tree SI were thus age-dependent, underestimated by older trees and overestimated by younger ones. They were corrected according to the difference between tree age and the reference age (70) with equation 4.

Equation 4: correction of tree SI according to tree age (same meaning of the symbols as equation 2):

$$SI_{ij_{cor}} = SI_{ij} + (Age_{ij} - 70) * 0.041$$

The final plot SI (**SI_{jcor}**) was calculated as the average of **SI_{ijcor}**. We chose to split site index in five fertility classes with an equal span of 3.35 m (figure 2).

Appendix 2: Classes of some used variables

A2.a: Dip angle classes

For dip angle parallel to form lines and on flat ground, limits between the 3 classes (1 = favourable, 0 = neutral and -1 = unfavourable) are 15° and 35° from horizontal.

When the slope is significant, *table 3* gives the equations to calculate these limits upslope and downhill for dip perpendicular to form lines, and limits of classes with a 5° span. *Figure 8* illustrates the dip variable with the example of a 30° slope.

The final note is obtained by the sum of dip classes, parallel and perpendicular to form lines, and varies from -2 to +2

Table 3: Limits of dip angle classes. Equations of the limits for favourable, neutral and unfavourable situations upslope and downhill according to slope angle. y = dip angle with horizontal, x = slope angle with horizontal (x and y in degree). -1 = unfavourable; 0 = neutral; 1 = favourable. These equations are valid for dip angle parallel and perpendicular to form lines and on flat ground.

Limit between dip classes

Upslope			Downslope		
limit -1 / 0	$y = 0.8333x - 15$		limit -1 / 0	$y = 0.75x + 15$	
limit 0 / 1	$y = 0.6667x - 45$		limit 0 / 1	$y = 0.5x + 35$	
Ground slope (°)	Upslope		Ground slope (°)	Downslope	
	-1 / 0	0 / 1		-1 / 0	0 / 1
0	-15.0	-35.0	0	15	35
5	-10.8	-31.7	5	18.75	37.5
10	-6.7	-28.3	10	22.5	40
15	-2.5	-25.0	15	26.25	42.5
20	1.7	-21.7	20	30	45
25	5.8	-18.3	25	33.75	47.5
30	10.0	-15.0	30	37.5	50
35	14.2	-11.7	35	41.25	52.5
40	18.3	-8.3	40	45	55
45	22.5	-5.0	45	48.75	57.5

Figure 8: Examples of dip limits separating unfavourable, neutral and favourable situations for (i) flat ground (slope 0°) and dip parallel to form lines, and (ii) a 30° slope.

A2.b. Textural Water Holding Capacity (WHC)

Table 4: Water holding capacity (mm/m) of fine soil material for each texture class

sa = sand; si = silt; c = clay. Capital letters indicate a dominant proportion, lower case a minority presence. In the last class (Sa.Si.C) the texture is balanced between the three materials. The CC class corresponds to heavy compact clays.

Sa	Sa.si	Sa.si.c	Sa.Si	Sa.c	sa.Si	Sa.C	Sa.si.C	Sa.Si.c	CC
70	100	117	122	135	145	152	157	160	165
sa.C	sa.Si.C	C	Si	sa.Si.C	C.si	s.Si.C	Si.C	Si.c	Sa.Si.C
170	170	175	175	176	180	181	187	195	200

Data adapted from GEPPA-SESCPF (1981)

A2.c. Classes of solar energy budget.

The energy budget is based on Becker index (Becker 1984). The Becker index corresponds to the ratio between the solar energy received on a plane area with a given orientation and slope and the same horizontal area. It is computed by equation 5:

Equation 5 Becker index

$$IKR = (\sin(H - \arctan(P \cdot \cos(E)))) / \sin(H) \quad \text{with:}$$

H = mean annual angle of the sun with the vertical at the studied site.

P = Slope of the site with the horizontal, in radians.

E = angle between the orientation of the site and the north, in radians.

The five classes used in this study (very hot, hot, neutral, cool and very cool) are shown in Figure 9.

IKR impact on Aleppo pine Site Index is climate dependent and inverse between cold-humid and hot-dry environments (see discussion end of section 4.1.2).

Fig. 9: Classes of Becker index (solar energy budget) according to slope angle (concentric circles) and orientation of the site.

Appendix C: Map of the study area with all 523 sample points (circles with a central dot). Many points are superposed at this scale, particularly in the middle of the study area where Aleppo pine stands are dominant but the overall density of point by sub-region is respected. © IGN Scan1000.

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