



Adaptation and growth of black pine subspecies in a common garden at the southern limit of its range

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Abstract

The ability of forests to adapt to global changes has important socio-economic interests. Plantations of species or provenances suited to future climate conditions will require a good knowledge of genetic resources. Black pine (*Pinus nigra* Arn.) is a robust species with high intraspecific variability. This study investigated the potential for acclimation of 19 black pine provenances among four subspecies at the southern limit of their range. The experimental trial is located in a Kroumirie forest of Tunisia. The methodology used is based on dendrometric and dendrochronological approaches. Whatever the parameter studied, the analysis of variance revealed significant differences between black pine origins, indicating genetic control of these parameters. At the age of 51, the best performances were achieved by Brouzet-lès-Alès, Saint-Guilhem, Cazorla and Olette (*P. salzmanni* ssp.), Les Barres and Grancia (*P. laricio* ssp. of Calabria); at the opposite, poor performances were recorded in provenances Kustendil and Puget Theniers (*P. nigra* and *P. austriaca* ssp.) and Cosenza (*P. laricio* ssp. Calabria). In conclusion, the variability in morphological traits within *P. nigra* subspecies is related to the geographical origin of the provenances.

1. Introduction

The Mediterranean climate is characterized by an irregular distribution of rainfall over the year with a longer or shorter period of summer drought, which is the main constraint on vegetation [1]. The accentuation of this constraint, as expected by climate change projection, may become critical for Mediterranean vegetation [2]. Climate projections support the hypothesis of an average scenario characterized by a warmer and drier climate around 2030-2050. In this context, knowledge of genotypes reaction to environmental factors must be deepened in order to be able to select the best seeds for reforestation and to determine the ecological requirements suiting their optimum development.

The adaptive capacity of forest trees to climate change strongly depends on their genetic diversity and geographical origins [3, 4]. Genetic diversity is essential for the adaptive capacity of tree populations and it is at the centre of current concerns about the future of forest species facing expected climate change [5]. In contrast to most cultivated species, forest trees still remain in natural populations

with high genetic diversity. Adaptive genetic diversity is very high between forest species, between geographical origins of the same species and within each stand [6]. Compared with other groups, conifers have a very high genetic diversity, but the genetic diversity of pines is considered to be lower than in other genera [7]. Among pines, *Pinus nigra* is one of the most diverse species [9-11].

The collective species *Pinus nigra* Arn. occupies a vast and fragmented range in the circum-Mediterranean region, from North Africa to Crimea, and throughout southern Europe [12] covering more than 3.5 million hectares around the Mediterranean. The species gathers six subspecies: *Pinus nigra salzmanni*, *P. nigra nigricans*, *P. nigra laricio*, *P. nigra dalmatica*, *P. nigra pallasiana*, *P. nigra mauritanica* [13]. It has been the subject of several studies addressing the intraspecific variability of growth performance and responses to climate in order to select the best adapted sources to future climate conditions [14, 15, 16, 17]. This selection is carried out in comparative plantations which are experimental sites where species or several genetic units of the same species (geographical provenances, families, clones) develop under the same environmental conditions. The intra-species variability of black pine's adaptive capacities has been relatively little studied despite the species ecological and economic importance. In fact, this species, which is one of the most economically important indigenous conifers in southern Europe, is of great value due to its straight trunk, rich in resin and easy to work with [18]. Its juvenile growth is quite fast. It has been widely used in reforestation outside its natural range. In particular, Austrian black pine was used intensively in the 19th and early 20th centuries in large reforestation programs in the Southern French Alps [19], UK and the USA. Currently, *Pinus pinaster* is the most important reforestation species in some French regions and in southern England [12].

This study was carried out in a comparative plantation at the southern limit of the black pine's range (northwestern Tunisia), making it possible, in particular, to test possible differences between geographical origins. As environmental variations are controlled in a common garden, the differences observed in the expression of a given character (phenotype) are due to the phenotypic variability existing between the different phenotypes compared. In Tunisia, considerable efforts are being made in terms of management and reforestation with the aim to restore forest cover. Although reforestation policies are essentially based on the use of resinous species, black pine has not received the attention it deserves from managers and studies carried out to date on this species remain rare [20]. Indeed, reforestation programs are based on indigenous species such as *Pinus pinaster* Aiton and *Pinus halepensis* Mill. or on species introduced and acclimated in Tunisia (*Pinus pinea* L.), various species of the genus *Eucalyptus* and the genus *Acacia*.

In the present paper, present results obtained in the provenance trial of black pines experimented in the Souiniet site in north-west Tunisia. The objective is to select the black pine provenances that are best adapted to the future local pedoclimatic conditions.

2. Materials and methods

2.1. Experimental site

The black pine provenance trial is part of the Souiniet arboretum and was installed by planting in 1964. The experimental site is located in North-West Tunisia, about ten kilometres from Aïn Draham (8°48' E 35°54' N, 492 m) (Figure 1). The Souiniet station refers to the humid Mediterranean bioclimate with a temperate variant. The arido-humidity index of Giacobbe is 14.7, which makes it possible to assign the station in the semi-arid summer season (Table 1). The annual rainfall is 1534 mm/year. The average annual temperature is 15.6°C. The hottest month is July with an average of 31.0°C, and the coldest month is January with an average of 4.4°C. The soil is sandy-clay loam (Table 1).

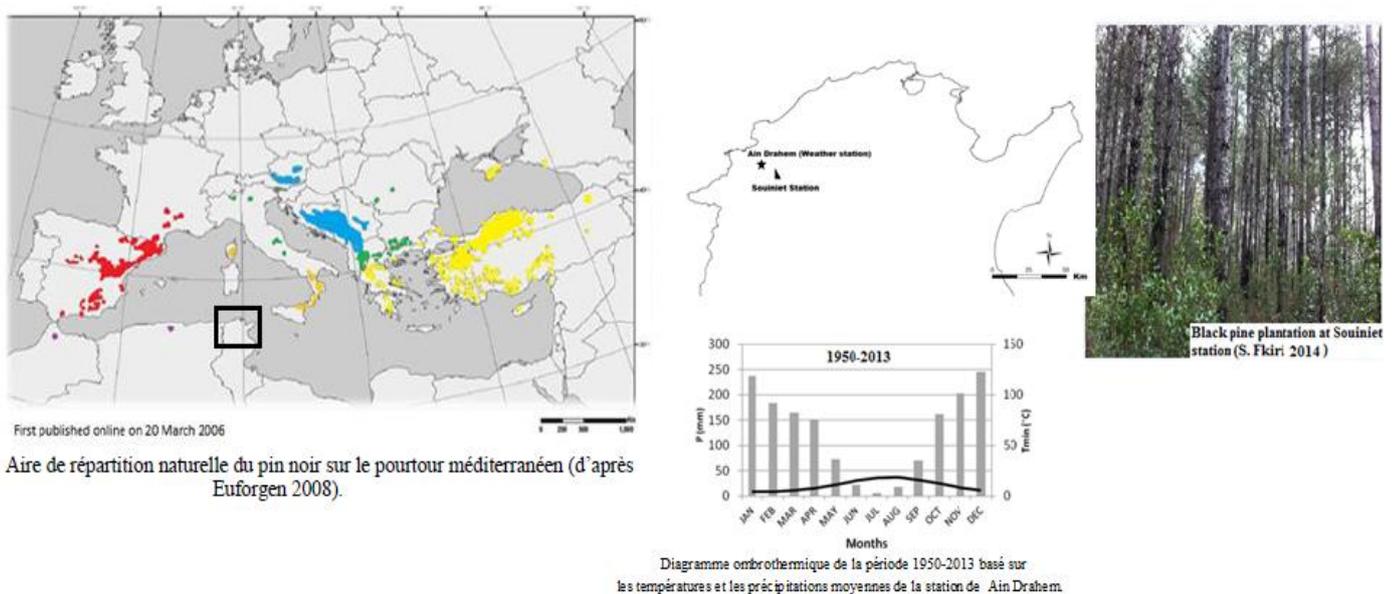


Figure 1: Study site.

Table 1: Geographic and pedoclimatic characterization of experimental site

Localisation	North-West of Tunisia
Latitude	35°54'
Longitude	8°48'
Altitude (m)	491
Bioclimat	Humid to temperate variant
Mean precipitation (mm)	1140
Mean temperature	15,6°C
Maximal Temperature	31,0 °C
Minimal Temperature	4,4°C
Emberger Coefficient	187
Index of aridity-humidity of Giacobbe	14,7
Type of Soil	Clay-limestone-sand

2.2. Plant material and experimental device

The study covered four subspecies of *Pinus nigra*: *salzmanni*, *laricio*, *pallasiana* and *nigra*, all represented by 19 provenances (Table 2). These provenances were implemented in a comparative trial in the Souiniet arboretum. The trial was set up according to an experimental device (3x7) with 21 complete blocks (A to U) of single-tree plot with 21 trees per provenance adopting a spacing of 3 meters between trees, i.e. a total of 399 individuals. The plantation was carried out on 26 December 1964.

2.3. Survival

The survival rate is given by the ratio of the number of living trees to the number of trees initially installed expressed in percentage (%). This ratio was obtained in 1968, 1991, 1997, 2013 and 2016.

2.4. Growth monitoring

The total height of all standing trees (in cm) was measured individually using a telescopic ruler graduated in centimeters in 1968 and 2016. The measurement of the diameter at 1.30 cm from the ground was carried out for all living trees using a "forest compass" graduated in centimeters in 1997, 2013 and 2016.

Table 2: List of black pine origins (origin and geographical coordinates)

Sous-espèce	Variété	N° de prov	Provenance	Pays d'origine	Altitude (m)	Latitude (degré)	Longitude (degré)
<i>Salzmanni</i>	-	P1	Brouzet-lès-Alès	France	-	44°07 N	4°05 E
		P12	St Guilhem	France	350-400	43°41 N	3°35E
		P16	Cazorla	Espagne	1500	37°50N	3°00O
		P18	Olette (Pyr-Orient)	France	-	42° 36 N	2°14E
<i>Laricio</i>	<i>Calabrica</i>	P2	Trenta	Italie	1050	39°25N	16°35E
		P3	Les Barres	France	150	47°50N	2°45E
		P4	Cosenza	Italie	1300	39°15N	16°17E
		P10	Cantanzaro	Italie	-	38°54N	16°34E
		P14	Grancia	Italie	850	39°41N	16°58E
		P15	Aspromonto	Italie	1300	38°05N	16°00E
		P17	Tavola	Italie	950	39°25N	16°35E
		P19	les Barres	France	150	47°50N	2°45E
	<i>Corsicana</i>	P5	Bois Frerot (Ardennes)	France	100	-	-
		P11	les Barres (leint)	France	150	47°50N	2°45E
		P20	Marghese (Corse du sud)	France	1100	41°39N	9°12E
<i>Nigra</i>	<i>Austriaca</i>	P6	Puget Théniers	France	1600	33°52N	4°04E
	<i>Nigricana</i>	P8	Kustendil	Bulgarie	-	43°57N	6°53 ^E
<i>pallasiana</i>	-	P9	Alaçam	Turquie	800-1000	39°35N	28°35 ^E
		P13	Crimée	Russie	500	44°33N	34°17 ^E

2.5. Cumulative growth curves

Cores were collected at 1.3 m height by using a Swedish increment corer. Ring widths of each provenance (11 cores per provenance) for the period 1969-2014 were measured to an accuracy of 0.01 mm on eleven individuals for each provenance using a LINTAB6 measuring table and WinTSAP software (Rinntech®) [21]. Ring widths were used to build up mean chronologies and cumulative growth curves.

2.6. Statistical analysis

Differences between the provenances of the studied parameters were assessed by means of an analysis of variance. This analysis of variance was followed by a comparison of the means by the Student-Newman-Keuls (SNK) test at $p < 0.05$ using SAS software, version 9.0 (ANOVA procedure).

3. Results

3.1. Survival rate

The analysis of variance revealed significant differences ($p < 0.001$) between subspecies for the survival rate. Indeed, the subspecies *salzmanni* has shown the highest survival rate (>70%) since 1991. At the opposite, subspecies *nigra* has shown the lowest survival rate (<50%). The survival rate of the

provenances decreased significantly but differently between 1986 and 2016 by an average of 28% with the exception of three provenances: Les Barres (P3) and Grancia (P14) (*P. laricio* ssp. from Calabria), and Saint-Guilhem (P12) (*P. salzmanni* ssp.). However, a significant mortality of 75% was recorded in the provenance Puget-Théniers (P6) (*P. nigra nigra* ssp.). The survival rate of the provenances Cosenza (P4), Bois Frerot (P5), Kustendil (P8) and Crimée (P13)) has decreased by half since 1968. The provenances Brouzet-lès-Alès (P1), Cazorla (P16), Tavola (P17), Les Barres (P19) and Marghese P (20) have shown a survival rate of over 70% at 50 years. A rather weak survival rate (ca. 30%) was recorded in the provenances Alaçam (P9), Catanzaro (P10), Aspromonto (P15) and Olette (P18). Another *P. laricio* ssp., Les Barres (leint) (P11), recorded the lowest survival rate at 4 years (Table 3).

Table 3: Survival rates patterns (over a period of 51 years) of *Pinus nigra* Arn. in the Souiniet experimental site

N°	Subspecies	Provenances	1968	1991	1997	2013	2016
P1	<i>Pinus nigra salzmanni</i>	Brouzet-lès-Alès	85.71	85.71	80.95	71.43	71.43
P2	<i>Pinus nigra calabrica</i>	Trenta Coste	90.48	85.71	80.95	61.90	52.38
P3	<i>Pinus nigra calabrica</i>	Les Barres	85.71	85.71	80.95	80.95	80.95
P4	<i>Pinus nigra calabrica</i>	Cosenza	85.71	85.71	71.42	61.904	42.86
P5	<i>Pinus nigra Corsicana</i>	Bois Frerot	80.71	80.95	71.42	57.14	47.62
P6	<i>Pinus nigra austriaca</i>	Puget-Théniers	76.19	71.43	52.38	38.09	19.05
P8	<i>Pinus nigra nigricana</i>	Kustendil	76.19	80.95	76.19	47.62	42.86
P9	<i>Pinus nigra pallasiana</i>	Alaçam	85.71	85.71	85.71	80.95	61.90
P10	<i>pinus nigra calabrica</i>	Catanzaro	90.48	85.71	76.19	71.43	61.90
P11	<i>Pinus nigra Corsicana</i>	les Barres (leint)	71.43	71.43	71.43	61.90	61.90
P12	<i>Pinus nigra salzmanni</i>	Saint-Guilhem	90.48	90.48	90.48	90.48	90.48
P13	<i>Pinus nigra pallasiana</i>	Crimée	95.24	85.71	76.19	66.66	52.38
P14	<i>Pinus nigra calabrica</i>	Grancia	90.48	90.48	90.48	90.48	90.48
P15	<i>Pinus nigra calabrica</i>	Aspromonto	90.48	80.95	66.66	61.90	57.71
P16	<i>Pinus nigra salzmanni</i>	Cazorla	95.24	95.24	85.71	80.95	76.19
P17	<i>Pinus nigra calabrica</i>	Tavola	95.24	95.24	80.95	76.19	71.43
P18	<i>Pinus nigra salzmanni</i>	Olette	80.95	76.19	76.19	71.43	57.71
P19	<i>Pinus nigra calabrica</i>	les Barres	95.24	95.24	90.48	85.71	71.43
P20	<i>Pinus nigra Corsicana</i>	Marghese	95.24	95.24	90.48	85.71	76.19

The means of the same column with different letters are significantly different ($p < 0.05$)

3.2. DBH and height

Table 4 summarizes the main results of the analysis of variance carried out on the diameters and heights of the nineteen black pine provenances at different ages. The analysis of variance revealed significant differences ($p < 0.0001$) between provenances and subspecies for the diameter and height growths and the absence of a significant effect of the provenance * age interaction ($P > 0.01$) (Table 4). The subspecies *salzmanni* showed a high growth in diameter and height; subspecies *nigra* recorded the lowest growth. In 2016, the both diameter and height growth of black pine varied between 11.72 cm and 25.26 cm and 9.94 m and 15.74 m, respectively (Tables 5 and 6). The provenance Les Barres (P3) (*P. calabrica* ssp.) showed the highest growth in diameter and height (25.26 cm and 15.74 m) (Table 5). All provenances showed a growth peak in 2013.

Table 4: Analysis of variance performed on 19 black pine provenances (4 subspecies) in Souiniet arboretum.

Parameters	Years	Factor	Degree of freedom	Mean square	F and signification
DBH (cm)	1997	Provenance	18	118.95	4.39***
		Subspecies	4	365.87	12.55***
	2013	Provenance	18	136.86	3.67***
		Subspecies	4	352.50	8.74***
	2016	Provenance	18	117.48	3.06***
		Subspecies	4	242.67	5.83***
Height (m)	1968	Provenance	18	0.060	2.33***
		Subspecies	4	0.125	4.71***
	2016	Provenance	18	21.36	2.52***
		Subspecies	4	35.96	3.95***

***: Highly significant difference

Table 5: Growth patterns of DBH (at 1.30 m) of black pine provenances corresponding to 3 years of measurement (1997, 2013 and 2016) in the experimental system of Souiniet arboretum (North-West Tunisia) (For each column, the values with the same letter are not statistically different ($p < 0.5$)).

Code	Subspecies	Provenance	DBH 1997 (cm)	DBH 2013 (cm)	DBH 2016 (cm)
P1	<i>Pinus nigra salzmanni</i>	Brouzetlès-Alès	17.15ab	21.03ab	21.95abc
P2	<i>Pinus nigra laricio calabrica</i>	Trenta Coste	14.21bc	16.58 bcd	18.25abcd
P3	<i>Pinus nigra laricio calabrica</i>	Les Barres	20.41a	24.29a	25.26a
P4	<i>Pinus nigra laricio calabrica</i>	Cosenza	11.23bcd	13.62dc	14.78bcd
P5	<i>Pinus nigra laricio Corsicana</i>	Bois Frerot	13.20bcd	16.83bcd	18.85 abcd
P6	<i>Pinus nigra nigra austriaca</i>	Puget-Thénières	8.27d	10.14d	13.50dc
P8	<i>Pinus nigra nigra nigricana</i>	Kustendil	9.78dc	11.00cd	11.72d
P9	<i>Pinus nigra pallasiana</i>	Alaçam	16.53ab	19.91ab	23ab
P10	<i>Pinus nigra laricio calabrica</i>	Catanzaro	14.06bc	16.20bcd	17.94 abcd
P11	<i>Pinus nigra laricio Corsicana</i>	les Barres (leint)	13.97bc	16.35bcd	16.90 abcd
P12	<i>Pinus nigra salzmanni</i>	Saint-Guilhem	17.50ab	19.55ab	20.18 abcd
P13	<i>Pinus nigra pallasiana</i>	Crimée	13.00bcd	16.58bcd	17.79 abcd
P14	<i>Pinus nigra lario calabrica</i>	Grancia	15.95ab	18.76ab	19.72 abcd
P15	<i>Pinus nigra laricio calabrica</i>	Aspromonto	14.39bc	16.00bcd	16.59 abcd
P16	<i>Pinus nigra salzmanni</i>	Cazorla	15.92ab	18.22abc	18.94 abcd
P17	<i>Pinus nigra laricio calabrica</i>	Tavola	13.97bc	15.63bcd	16.60 abcd
P18	<i>Pinus nigra salzmonni</i>	Olette	15.97ab	18.87ab	18.71 abcd
P19	<i>Pinus nigra laricio calabrica</i>	les Barres	16.39ab	19.31ab	19.57 abcd
P20	<i>Pinus nigra laricio Corsicana</i>	Marghese	14.08bc	15.94bcd	16.97 abcd

The means of the same column with different letters are significantly different ($p < 0.05$)

Kustendil (P8) and Puget-Théniers (P6) (*P. nigra* ssp.) showed the lowest diameter growth at different ages. The lowest heights were recorded in the provenance Kustendil (P8) and Cosenza (P4) (*P. laricio* ssp.) (Table 6).

Table 6: Growth patterns of height (m) of nineteen provenances of black pine in the Souiniet arboretum

Code	Subspecies	Provenance	Height 1968 (m)	Height 2016 (m)
P1	<i>Pinus nigra salzmanni</i>	Brouzet-lès-Alès	0.59a	13.90abc
P2	<i>Pinus nigra laricio calabrica</i>	Trenta Coste	0.42abc	12.91abc
P3	<i>Pinus nigra laricio calabrica</i>	Les Barres	0.55abc	15.74a
P4	<i>Pinus nigra laricio calabrica</i>	Cosenza	0.37c	10.78bc
P5	<i>Pinus nigra laricio Corsicana</i>	Bois Frerot	0.46abc	13.30abc
P6	<i>Pinus nigra nigra austriaca</i>	Puget-Théniers	0.39bc	15.50b
P8	<i>Pinus nigra nigra nigricana</i>	Kustendil	0.41abc	9.94c
P9	<i>Pinus nigra pallasiana</i>	Alaçam	0.48abc	13.88abc
P10	<i>pinus nigra laricio calabrica</i>	Catanzaro	0.46abc	14.96ab
P11	<i>Pinus nigra laricio Corsicana</i>	les Barres (leint)	0.53abc	14.54ab
P12	<i>Pinus nigra salzmanni</i>	Saint-Guilhem	0.48abc	13.95abc
P13	<i>Pinus nigra pallasiana</i>	Crimée	0.44abc	13.64abc
P14	<i>Pinus nigra lario calabrica</i>	Grancia	0.46abc	14.13abc
P15	<i>Pinus nigra laricio calabrica</i>	Aspromonto	0.50abc	13.54abc
P16	<i>Pinus nigra salzmanni</i>	Cazorla	0.48abc	12.50abc
P17	<i>Pinus nigra laricio calabrica</i>	Tavola	0.43abc	12.87abc
P18	<i>Pinus nigra salzmanni</i>	Olette	0.57ab	15.21b
P19	<i>Pinus nigra laricio calabrica</i>	les Barres	0.50abc	14.13abc
P20	<i>Pinus nigra laricio Corsicana</i>	Marghese	0.49abc	14.06abc

The means of the same column with different letters are significantly different ($p < 0.05$)

3.3. Cumulative radial growth

The cumulative radial growth curves (mm) follow a logarithmic function with two growth phases (Figure 2). In the juvenile phase, all sources grew rapidly until the age of 16, while in the second decade (since 1981) the growth rate was significantly lower. The provenance Les Barres (P3) had the highest growth rate (Figure 3). In 1988, growth increased suddenly for all provenances. The growth of Kustendil (P8) has risen since 1990 with the increase in temperature and the decrease in precipitation in the study area (Figure 3).

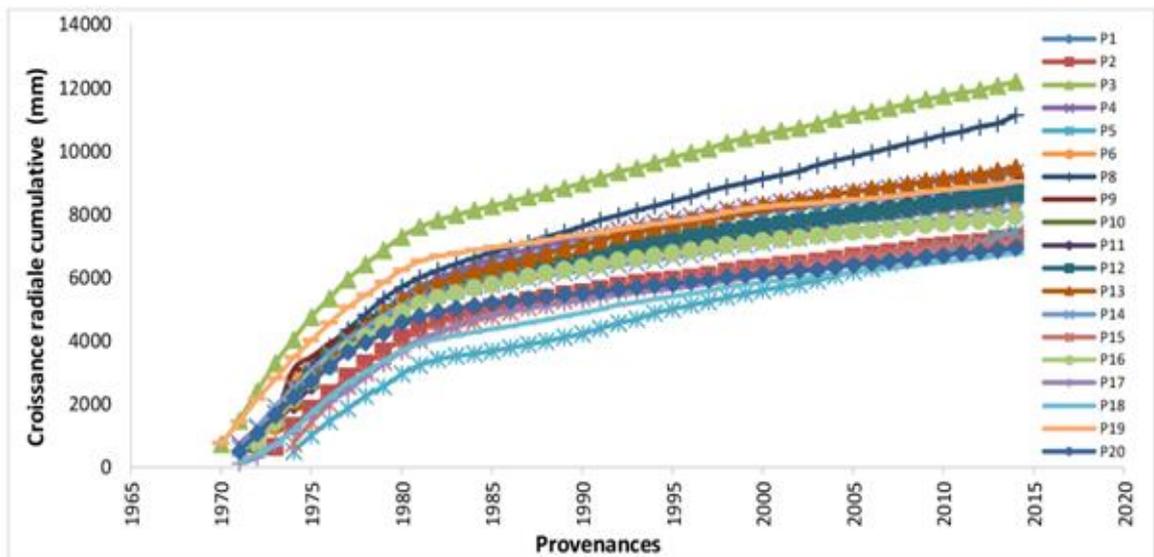


Figure 2: Average cumulative radial growth curves of 19 black pine provenances at 1.3 m for the period 1969-2013 at Souiniet

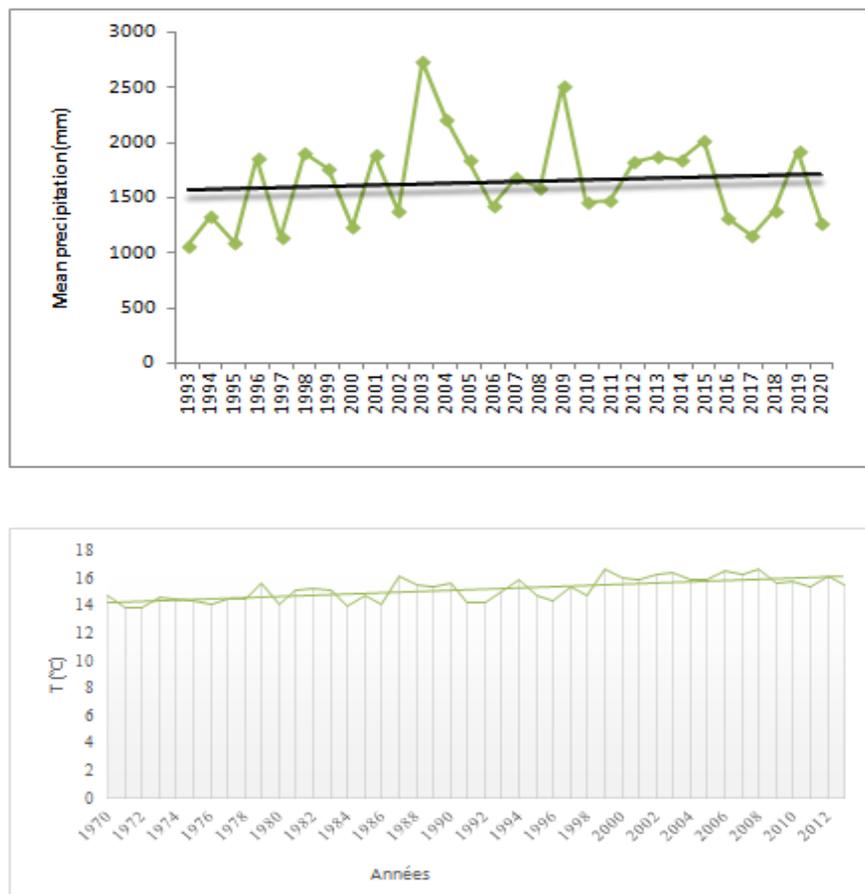


Figure 3: Graph showing the evolution of annual average precipitation (1993-2020) and temperature (1970-2013)

4. Discussion

The main objective of setting up comparative provenance plantations at the Souiniet arboretum is to guide the forestry service towards a more appropriate choice of the most suitable provenances for colonizing the forests of the mid-mountain region of Kroumirie. That extends the work of [22, 20] and

[23] who recommend the use of other fast-growing exotic resinous species in reforestation in addition to the usual species utilized until now in this region. According to the first author, two Mediterranean species, *P. nigra* in particular the *laricio* ssp. and two American species, *P. insignis* and *P. taeda* are recommended. [24] have shown that the species adapted to the average climatic conditions of Kroumirie are divided into species with high wood texture like *P. laricio* and *P. radiata* and species with lighter wood texture like *P. pinaster* and *P. taeda*. In our study, the comparative trial of black pine provenances showed significant differences related to the geographical origin of the seeds. Indeed, after 51 years of establishment, in the context of the climatic change observed in recent decades in Tunisia [25], only the most adapted provenances to the pedoclimatic conditions specific to Kroumirie have been able to survive and develop [21, 26]. A fair adaptation was observed in the provenances Les Barres (P3), Grancia (P14), Tavola (P17), Les Barres (P19) and Marghese P (20) (*P. laricio* ssp.) and Saint-Guilhem (P12), Brouzet-lès-Alès (P1), Cazorla (P16) (*P. salzmanni* ssp.). At the opposite, the provenances Puget-Théniers (P6) and Kustendil (P8) (*P. nigra* ssp.), Cosenza (P4) and Bois Frerot (P5) (*P. laricio* ssp.) were identified as the least suitable in the study area. Poupon [24] concluded that, under the conditions of the Souiniet site, the performance obtained by *P. laricio* pine (Calabria and Corsica) and maritime pine resulted in a long growth period and a high average growth rate .

It must be stressed that until 1997, the system showed no signs of decline caused by biotic factors [23]. However, in 2016, the symptoms of decline and mortality that were identified were mostly of sanitary origin with a significant difference between species and provenances. Some provenances were attacked by bark beetles, including Puget-Théniers ssp. *nigra* with the highest decline index [27], reflecting a low survival rate for this provenance.

.Thus, the soil characteristics of the site may have an influence on the growth of black pine [28]. Indeed, the chemical fertility of the Souiniet site is edaphically homogenous, but not necessarily adapted to the requirements of each subspecies and provenance. The soil is degraded, poor in humus, and deficient in phosphorus to ensure optimal growth of certain provenances [24]. The nitrogen requirements of *P. nigra nigra* var *nigricans* are very limited and its growth is therefore not dependent on soil nitrogen availability. Only phosphorus nutrition seems to be of real importance [29]. Several other factors have been reported to limit the growth of black pine, such as competition [30]. The results of the study conducted by [31] showed that there is a high level of competition between trees for light, nutrients and water. Indeed, it has been reported that light is generally the environmental resource limiting the growth of plantations. When competition for light between trees is high, diameter growth is significantly more affected by competition than height growth [32, 33]. However, it has been found that competition in black pine trials is very low on the basis of functional trait comparisons [21]. Climate variables may also be involved. By means of studies addressing the growth-climate relationships on this plantation, we found that temperatures are significantly related to radial growth in January/February and May/June respectively for some subspecies and provenances and to rainfall in April [21]. Therefore, the balance between the positive and negative effects of water availability and winter-spring temperatures on radial growth could determine the future performance of black pine provenances planted at Souiniet These findings are in good agreement to those obtained recently [34-36].

5. Conclusion

The results of this study revealed highly significant differences between the provenances in terms of adaptation to soil and climate conditions of Kroumirie. The provenances "Brouzet-lès-Alès", "Saint-Guilhem" and "Cazorla" (*P. salzmanni* ssp.) "Les Barres", "Grancia", "Tavola", and "Marghese" (*P. laricio* ssp.) are those that seem the best adapted to these conditions and can be recommended for

reforestation in Kroumirie (from 400 m to 1200 m of altitude). On the opposite, the provenances "Puget-Theniers" and "Kustendil" (*P. nigra* ssp.), "Cosenza" and "Bois Frerot" (*P. laricio* ssp.), which all were identified as being the least adapted ones as regards the high mortality rates, could not be recommended for reforestation in Kroumirie. As a perspective, an extension of this study to other comparative plantations that are already available (El Ghorra in a hyper-humid bioclimate and Jebel Birino in a semi-arid bioclimate) or that are to be established can be advisable in order to further assess *P. nigra* provenances within a broader spectrum of pedoclimatic conditions.

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