Drought effects on Buds Growth and Dynamic of Tunisian Cork Oak Populations

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Abstract

Forest species have adapted to their local climate by changing some of their phenological characteristics. Differential phenological responses may modify tree chance of survival by altering the competitive balance between them. The study of key phenological stages (budding, budburst, flowering, falling leaves ...) knew a renewed interest these last years for climate changes consequences researches. Characterizing the phenological variability response, of five Tunisian cork oak populations from contrasting climatic situations, in front to water deficit, has been the subject of this study. Large differences between populations from highest and coldest sites as well as those of lowest and warm sites were detected and adaptative responses specific to some populations were founded.

Keywords: water stress, phenology, Cork oak, climate changes.

Introduction

Mediterranean forests are subjected to the combined pressure of global climate changes and deforestation which could modify rapidly their local climatic conditions (Menzel et al. 2006). Climate scenarios predict a rise of temperature accompanied by precipitation decrease at the end of the XXIth century in the Mediterranean region (Giorgi 2006). If this change is faster than expected, moving of climatic zones could be faster than the migration itself of certain forest species (Higgins and Harte 2006).
Indeed, climatic disturbances manifested during the last decades deteriorated the Tunisian Cork oak forest which is located in a region with contrasting climatic conditions characterized by heavy rainfall most often of stormy character (Daoud 2004).
In Tunisia, the Cork oak forest (*Quercus suber* L.) in Kroumirie is the most important Mediterranean forest of this species. However, the regression of the Cork oak is estimated at 1.22% per annum (Ben M'Hamed et al. 2002). It covered 127.000 ha in 1950 (Boudy 1950; 1952) to became only 73.000 ha in 1995 (General Directorate of Tunisian Forests 1995) whom 45,000 ha simply of productive forest located on three quarters of Kroumirie (Abid and Selmi 1996). Various factors are responsible for the decline of these forests: aging populations, recently burned stands, important water deficit for facing south exposition trees or for stations having too low water reserves, insects or fungi attacks or human action by deforestation and cultivation practices as well as by bad stripping (Ben M'Hamed et al. 2002). In addition to these factors, climate changes recently observed exacerbate the alarming situation of these forests (Urbieta et al. 2008).
Predicted climate changes could have an impact on this forest ecosystem at a small- as at a big-scale (Ennajah 2010). At the plant scale, the study of growth rates is necessary to understand the ecology of the species (Salmon 2004; Ramírez-Valiente 2009). The plant development is made by a succession of phases characterized by morphological, anatomical, physiological and biochemical changes. These changes represent a response to environmental factors because of their implications in plant growth and

performances (Castro-Diez et al. 2006; Mahall et al. 2010; Sanz-Pérez et al. 2007). Nevertheless, the study of bud growth and development in the genus Quercus is little developed (Zhou et al. 2003).

The main purpose of this study was to explore the effects of increased water deficit on the phenological response of seedlings from five populations of *Quercus suber* L. originating from contrasting climatic situations. We sought to identify possible differential vulnerability of the latter, with respect to the imposed drought constraint. In other words, the population living in drier sites they are most sensitive to water deficit? and thus, the most vulnerable populations to climate changes would the most or the least constraints in the current climate conditions? This could eventually lead to improve predictions of the evolution of the distribution of this species in the context of climate changes.

Materials and Methods

In October 2008, over than 500 acorns were collected from the five biggest trees of each one of the five *Quercus suber* populations of Kroumirie in the northwest Tunisia.

Studied Cork oak populations were: Tabarka, Ain Drahem 2, Ain Drahem 4, Jendouba 3 and Jendouba 4, which are distributed along a gradient of aridity from the coast (Tabarka), belonging to the Mediterranean wet floor (El Afsa 1978), then through Ain Draham (AD2 and AD4) belonging to the Mediterranean wet floor with temperate winter variant (Emberger 1955) and finally to Jendouba (JE3 JE4 and) in the upper semi-arid bio-climate with temperate winters (El Afsa 1978) (Table 1).

Table 1. Geographic situation and bioclimatic data of the five provenances sampled.

Administrative region	Station code	Altitude (m)	Temperature Annual mean(°C)	Precipitations Annual mean (mm)	Drought mean mm/year	Bioclimatic floor	Soil type	Coordinates	
								Latitude	Longitude
Tabarka	TA	50	14	1020	600	Humid	Sandy	38°58,21 °N	8° 53,41 °E
Ain Drahem	AD4	640	12	1200	350	Humid	Flynch	36°43,77 °N	8° 39,35 °E
Ain Drahem	AD2	800	10.5	1550	400	Humid	Flynch	36°46,98 °N	8° 43,79 °E
Jendouba	JE3	340	16	370	800	Semiarid	Grey	36°38,84 °N	8° 39,56 °E
Jendouba	JE4	320	16	370	750	Semiarid	Grey	36°39,02 °N	8° 39,20 °E

Due to the sensitive differences in elevation, these environments have for low horizontal distances, weather patterns of comparable diversity to regions located at very different latitudes. The acorns were germinated in a greenhouse inside bags of polyethylene (1L) each filled with 1kg of a mixture of dry nursery substrate composed of 1/3 clay and 2/3 sand. From the 500 acorns collected, more than 300 have sprouted in optimal weather conditions (without stress).

In March 2009, the seedlings were transplanted and grown thereafter in pots (27cm diameter to 30cm deep) under non-limiting water conditions. They were placed in a nursery and irrigated regularly until July 2009. Watering was carried out with deionized water to avoid the risk of leaching and loss of nutrients in pots. From July 2009, 100 plants of uniform size were selected and divided into 5 blocks of 20 plants each (still in pots). Each block has two sets of 10 plants each, one maintained continuously on the field capacity (ψb=-0.3±0.2 Mpa) and the other at a stress level equivalent to ψb=-1.8±0.2 Mpa reached gradually after three weeks of application. Both treatments were randomized within each block. The basic leaf water potentials were determined using a pressure chamber (Boyer 1967; Albouchi et al. 1997). To determine the level of stress over time and to determine the amount of water required for the process maintain, first, we kept saturation irrigation on all plants (Albouchi et al. 2003). After 48 hours soak, the weight of potted plants corresponds to 100% of field capacity. Water supplies corresponding to the treatment of water stress on the eighth match of the field capacity. In this experiment, we tried to apply a level of water deficit approximating to natural drought summer conditions in which are our natural cork oaks populations. Throughout the year of study (from July 2009 to June 2010), the amount of water returned to each pot and the manual irrigation frequency of stressed plants were readjusted every 15 days by measures of Ψb and simultaneously by monitoring the weight of seed per batch. It should be noted that the temperature was recorded daily throughout the experimentation (Table 2).

On the measurements, we followed the growth dynamics of the whole plant and its apical bud since their first potting (March 2009) until the end of the study period in June 2010. Each week, we measured the total height of seedlings along a main axis (cm), fixed for each seedling. Meanwhile we followed weekly phenological phases of the apical bud. The bud is considered ridden when at least one sheet is visible for the seedling. Volume (mm^3), the burst rate (%), and apical buds mortality rate (%) were also measured.

Finally, we monitored the growth (mm) of new growth units 'g.u' and counted the number of primordial leaves through the apical bud burst.

Table 2. Monthly mean temperatures recorded in the nursery (ºC).

Year	January	February	Mars	April	May	Jun	July	August	September	October	November	December
2009	8,9	8,6	10,7	14,9	19,5	24,1	26,1	27,2	24	20,4	14,4	11,3
2010	10,8	11,4	12,7	13,5	20,7	24	27,3	28,9	26	19,5	15,5	11,5

For statistics, we tested the effect treatment × population on our measurements by the analysis of variance (ANOVA) with two factors in risk threshold of 5% using the software Stastistica. This analysis was complemented by a multiple comparison of means by the Newman-Keuls test.

Results and Discussion

The analysis of variance showed a significant difference regarding the factor provenance (Table 3). Figure 1 shows the growth in length of the five cork oak populations under the two applied water regimes. Throughout the observation period, the population JE3 remarkably distinguished from the other four populations by significantly lower height growth, both in control and under stress conditions. The maximum height of the primordial axis reached 50 cm for TA, and 30 cm for JE3 at the end of the experiment. At the end, growth records showed that the growth of the main axis during the first year (2009) was significantly higher than that of the following year (2010) even for plants control.

Table 3. Analysis of variance on measured growth parameters and apical buds dynamic of the five cork oak populations.

Year	Source of variation	d.f	Mean square	F - signification
Total height (cm)	Provenance	4	1162,3	12,283***
	Drought	1	28,6	0,302 NS
	Provenance x Drought	4	32,2	0,340 NS
Apical bud volume (mm3) on 16/04/2010	Provenance	4	349,92	1,01829 NS
	Drought	1	5843,31	17,00425***
	Provenance x Drought	4	268,72	0,78199 NS
Apex length growth (cm)	Provenance	4	29,3455	0,77700 NS
	Drought	1	597,1181	15,81027***
	Provenance x Drought	4	29,3455	0,77700 NS
Primordial leaves number	Provenance	4	13,615	1,2076***
	Drought	1	246,490	21,8627
	Provenance x Drought	4	36,715	3,2565 **

NS, ** and ***: Not significant, significant at the 5% and 1% levels of probability, respectively.
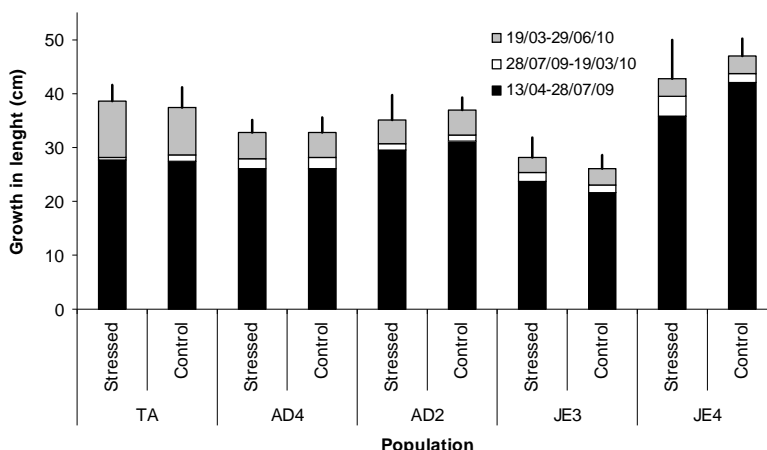
Figure 1. Growth in length of five cork oak populations under two water stress levels.
TA, Tabarka ; AD4 and AD2, Ain Drahem4 and Ain Drahem2 ; JE3 and JE4 ; Jendouba3 and Jendouba4.

Growth on volume of the apical bud was significantly different between the two treatments, the buds of control seedlings was always larger than that in stressed-seedlings (15-50%), with no significant difference between populations (Table 3). Figure 2 shows the apical bud volume under the two water regimes regarding the five Cork oak provenances just before bud break.
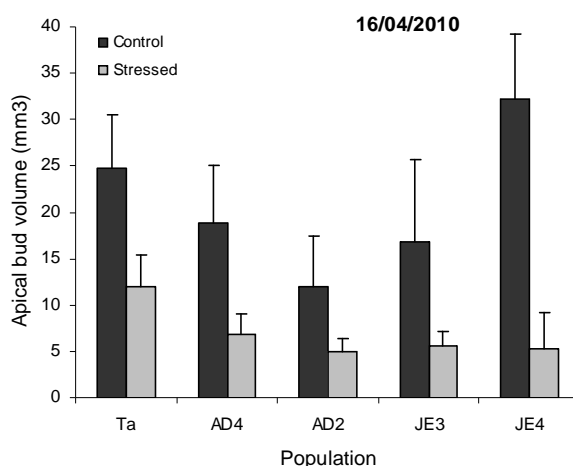
Figure 2. The apical bud volume (mm^3) under the two water regimes regarding the five Cork oak provenances; just before bud break (16/04/2010).
TA, Tabarka; AD4 and AD2, Ain Drahem4 and Ain Drahem2; JE3 and JE4; Jendouba3 and Jendouba4.

Figure 3 shows the dynamics of the apical budburst (%) in oaks seedlings under the two treatments. All individuals reached maturity in the control treatment except JE4 (80%) and AD4 (90%) seedlings, and this for a period of time equivalent to about two weeks. The final rate of stressed-bud burst was significantly lower against that in control conditions for all populations. The burst rate was approximately about 70%, with a lower assigned rate for Jen4 Jen3 wich stilled above 90%. AD4 population was the most affected by the drought, both in terms of final rate of bud and speed bud.
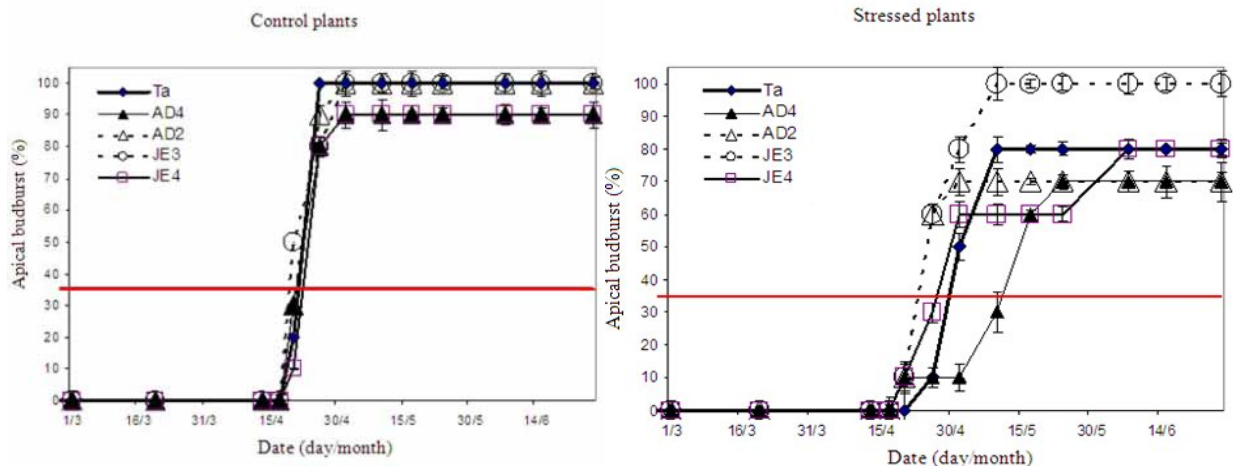
Figure 3. the dynamics of the apical budburst (%) in oaks seedlings under the two treatments in spring 2010. TA, Tabarka; AD4 and AD2, Ain Drahem4 and Ain Drahem2; JE3 and JE4; Jendouba3 and Jendouba4.

It is also to be noted that a bud shift of a week was observed between control and stressed seedlings (Figure 4). This offset varied between subsequent populations and even reached up to 21 days in the population AD4 to 50% bud break.
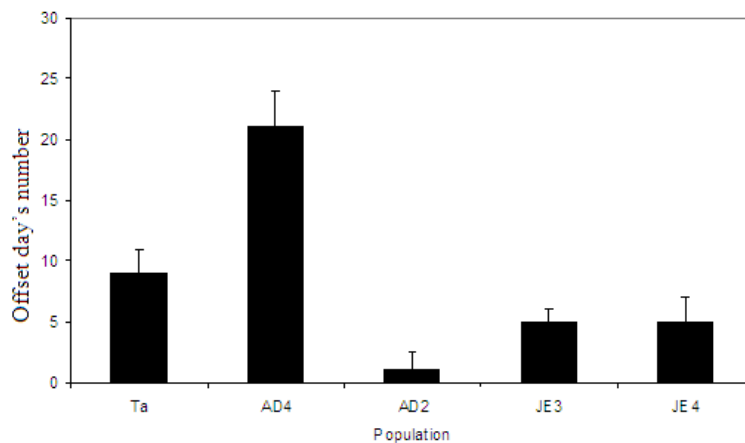

Figure 4. The offset day's number observed between the two treatments (control and stress) to 50% bud break.
TA, Tabarka ; AD4 et AD2, Ain Drahem4 et Ain Drahem2 ; JE3 et JE4 ; Jendouba3 et Jendouba4.

At the end of the experiment, we observed damages at the apical buds in the five cork oak populations with high mortality rates especially among stressed-seedlings (Figure 5). They reached 50% for the TA population, 40% for AD2 and AD4, 20% for Jen3 and only 10% for JE4. Buds controls have finished their phenological cycles without damages, except for AD4 population with 10% of mortality and JE3 with 20%.
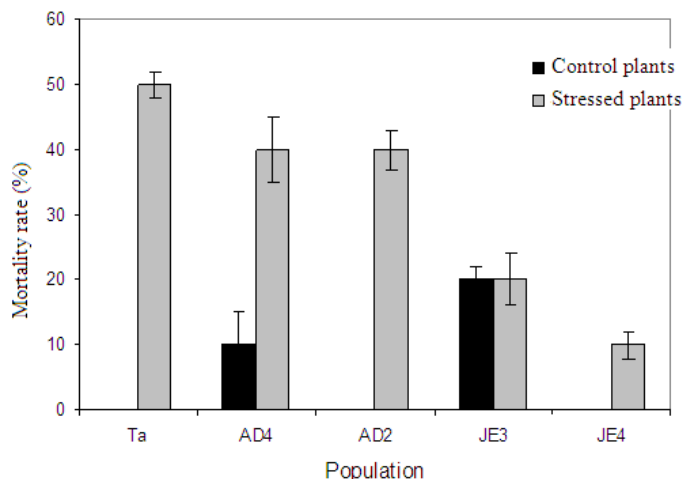
Figure 5. Mortality rate of apical buds created in 2010.
TA, Tabarka ; AD4 et AD2, Ain Drahem4 et Ain Drahem2 ; JE3 et JE4 ; Jendouba3 et Jendouba4.

For the increase of the new growth unit's length (Figure 6), a significant difference was identified for this parameter between the two treatments (Table 3). TA population had the largest growth in the control treatment. Under stress treatment, we noted a significant decrease in all populations. However, the difference in growth was very important for TA compared to JE3 population. AD4 and TA populations were those most affected by water deficit.
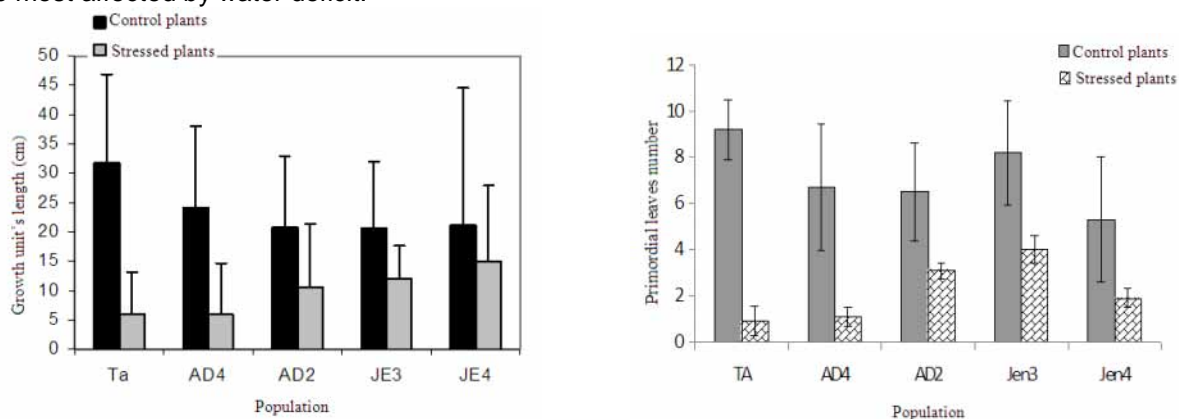

Figure 6. The growth in length of the new units and the number of primordial leaves between the two treatments and the five populations.
TA, Tabarka ; AD4 et AD2, Ain Drahem4 et Ain Drahem2 ; JE3 et JE4 ; Jendouba3 et Jendouba4.

The number of primordial leaves (Figure 6) was also significantly different between populations (Table 3). In the control treatment, the TA population produced more leaves after bud break, compared to the population JE4, at the end of the experiment. Other populations were at an intermediate level. Similarly, for this setting, there was a strong effect of water deficit that differed significantly from population to the other (Table 3). For populations TA and AD4, it spent from 9.6 sheets to 2.7 after the application of water deficit, and from 7.0 to 2.4 respectively. This difference between the stressed and control treatments was not significant for populations JE4 and weakly significant for JE3 and AD2, indicating that these populations were less or not at all affected, in terms of number of primordial leaves, by water deficit. Populations Jen4 and Jen3 at the end of the experiment under stressed conditions, even more leaves than other populations.

The present results show that the effect of water deficit was highly significant in almost all physiological traits. Monitoring of growth variables and dynamics of apical buds showed that they were strongly influenced by the applied drought. These poor conditions of water, limit intake sap, root growth, photosynthesis, absorption of nutrients (Sanz-Pérez and CastroDiez 2010), which explains the general decrease of these parameters.

We observed a significant decrease in the volume of the apical bud in the five stressed oak populations. The water factor appeared leading towards buds development (Pinto et al. 2011). Size decrease of the buds after water deficit and the date late of their buds break could also be related to the decrease in abscisic acid

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amount during stress period (Arora et al. 2003) which stops plant growth and induces the early formation of buds (Horvath et al. 2003). Indeed, the period of activity of apical bud varies depending on the regional medium, local medium and even according to the conditions in the immediate organ vicinity. This phenoplaste seems to be spread or restricted depending on the factors conducive to the growth and elongation of the bud, such as lack of water (Aubert 1976).

Environmental conditions that favour the emergence of the quiescence and bud break seem to be related to light, high temperatures and also to the amount of water available to the plant (Penuelas al. 2004; Pinto et al. 2011). The study shows that the apical stressed bud break shifts a week comparing to controls. We noted a delay of a week of bud break with high mortality rates at the end of the experiment. Burst rate of apical buds reached 100% in controls and declines to 40% in stressed conditions.

We also note that after bud break, the water factor binding has already reduced the amount of sap and energy in the apical buds in stressed oak plants, seems to give rise to new less vigorous growth units than those under continuous irrigation. As young leaves have higher photosynthetic potential than older leaves (Ninemets et al. 2005), water deficit retards the date of bud burst and thus reduces this potential. The evolution of the morphology of growth units is also accompanied by a change in the amount of different tissues of stems. They are clearly defined entities within the plant (Quero et al. 2006). The stressed growth units contain a smaller amount of xylem, phloem and cortical parenchyma. Meristems functioning modalities responsible for their constructions are closely related to those of apical buds.

Better water management, is also a character often attributed to the difference between phenological forest populations (David et al. 2007), and a guarantee of survival in the face of prolonged drought (Montserrat et al. 2009).

In general, forest trees such as oak cork show a phenological variability as well as morphology, as shown by several provenance tests (Nardini et al. 1999; Gandour et al. 2007). Phenological character variability observed between populations can depend on two factors: the intra-populational variability and the inter-populational variability related both to the effect of the environment and to the genetic structure of the population (Vitasse 2005).

Indeed, our study shows that there were significant differences in growth parameters between the different studied cork oaks populations, facing to water deficit. Some populations reduce the height of their seedlings, increase the life of their leaves, reduce their leaves total number, reduce their radial growth and biomass and increase the length of their roots (Reich et al. 1995, Givnish 2002; Bezzala 2005, Wright et al. 2004, 2005). This is what has been observed in populations Jendouba especially JE3 population who presented some of these adaptation characteristics such low growth in length (Figure 1), the highest number of leaves at the end of the experiment (Figure 6), the lowest mortality rate of apical buds than other populations (Figure 5) and the highest number of primordial leaves at bud (Fig. 6). Acorns from this provenance had a lower size and volume during the harvest and so thereafter shorter growth and less robust over time (Aizen and Woodcock 1992; Diaz-Fernandez et al. 2004). To survive and cope with the great competition with the other species, they have acquired over the years a great capacity to mobilize soil water reserves stored during the winter and to regulate their evapotranspiration (El Aouni 1980; Chuine and Court 1999). The growth unit's of these provenances, wearing a fairly high number of leaves after bud reflecting a certain tissue organization and storage and some structural maturity (Heath et al. 1947), unlike other provenances. These oaks have acquired over time features of morpho-physiological adaptations against drought (Zhang et al. 2010). Indeed, the use of reserves in the glands and the extending of the survival period of the new offspring are closely linked to the first year of growth (Cantos et al. 2003). This new generation is a direct descendant of cork oak trees located on the south side of the Kroumirie at low altitude and subjected to continental influences with very hot and very dry summers. These trees are small and have low circumference 1.30 m; regarding the oaks of altitude (Ennajah 2005).

We concluded that the result of this study is that the third population JE3 which has the most chance of survival under drought conditions; similar water conditions to those applied on stressed seedlings in the nursery. Under controlled water conditions, under stress, it is the most productive population at the apical buds and in which it has been less mortality. The cork oaks were promoted by human activities (Barbero et al. 1992) is its ability to withstand thermal conditions, soil and water variables which allows it a wide distribution from the semi-arid floor to the per-humid floor. A significant difference was generally observed between populations from contrasting environments from the geographic and climatic point of view (Jermstad et al. 2001; Hower et al. 2003). Ecophysiological behaviour of the population JE3 represents a population model of type 'resistance model' or type 'stabilisation model' (Ramírez-Valiente et al. 2009). Thus we can say that the oak has a large variability in its phenological response at an interpopulational level along an altitudinal gradient, with considerable differences between provenances from the highest and lowest altitudes (Hatta et al. 1999; Vitasse 2005).

Given its botanical, physiological and ecological characteristics from a hand, and its economic interest in the other hand, the cork oak is undoubtedly a species of great importance in the western Tunisian forest.

This is the first study, to our knowledge, to characterize the phenology of cork oak populations along a marked altitudinal and climatic gradient. Also, it leaves presage a significant impact of climate changes on the distribution of this forest species and their interaction. Thus it has been shown that the stress led to a decrease of almost all parameters (seedling growth and buds dynamics) and demonstrated adaptive responses specific to certain populations. This high coefficient of variability could be explained by very different populations at the genetic level or by a high phenological plasticity of this species (Vitasse 2005).

This study, conducted exclusively under controlled conditions, provides more knowledge on the behaviour of different oaks populations under water deficit, equivalent to a summer drought in natural conditions, and therefore provides the potential changes of the repartition of this species facing the hardening climates. It is therefore essential that more experimentation in pots, make a monitoring in situ along the altitudinal gradient with respect to the exposure. Thus, our results can be confirmed and completed and study limits at small scale will be identified in case of different results. Therefore, phenological plasticity can be quantified by comparing the magnitude of populations' responses in situ and these same populations under a common environment (nursery).

Finally, our study provides the knowledge necessary to understand the potential changes of the repartition range concerning this species. Numerous studies show the possibility of significant changes in the species composition of populations and their distributions, due to changes in environmental conditions and the emergence of multiple stresses (Aber 2001). Our results suggest that the growth and the development of the cork oak populations are sensitive to local climatic conditions. The early stages of oak population's seedlings development are affected differently by changes in soil water reserves and temperatures. Over the next century, we can expect that this strong selection, induced by gradual climate changes (Vitasse 2005), at the early stages, promotes the selection of suitable individuals if the adaptive genetic variability intra-populational is sufficiently high. However, the intensity of global warming is so large (Harvey 2000) that some authors predict that this selection will not fast enough, causing local extinctions (Hampe and Petit 2005).

One also wonders whether the rapid rate of future climate changes will challenge the reproduction and dispersal abilities of some populations. These changes also depend on the degree of groups adaptability (Shafer et al. 2001), the magnitude of climate changes and especially their speed (Solomon and Bartlein 1992). Factors such as topography (Hansen et al. 2001), soil type (Bugmann and Solomon 1995), species composition and initial development of the canopy affect the magnitude of groups response. Finally, this work will contribute to the development of growth models and future distribution of different populations by adding a phenology module.

Acknowledgments

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