

Research Article

Short Shoot Growth and Reproduction Response to Light Conditions Vary with Order Branching in the Proximal Part of *C. atlantica* Crown

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This study compared the effects of shading in individual branch orders 2 and 3 on the needle survival, growth, and reproduction of five categories of short shoots of the proximal part of wild Atlas cedar (*Cedrus atlantica* (Endl.) G. Manetti ex Carrière). The sun exposure did not affect the number of short shoots in the two branch orders, whereas light compared to shade only stimulates the unbranched short shoot elongation of the branch order 3. The impact of shade exposure compared to sun on the loss of needles depends on the order of branching; it is weak to order 2 and increases to higher order. This effect in the branch order 3 is achieved by a significant decrease of the fallen leaf number in the unbranched short shoot SSnr and the short shoot SS/T worn by Twigs while in the branch order 2 only short shoot SS (nr + r) loses significantly few needles. In terms of short shoot extension and needle loss, the SS/T of the branch order 3 behaves in the same way as the SS (nr + r) of the branch order 2. The shadow compared to sunlit only decreases significantly the production of pollen strobili of the branch order 2. Close relationships between short shoot extension, leaf life span, and pollen strobili production of axillary products in the proximal part of *C. atlantica* crown were found.

1. Introduction

Beyond a broad range of species, the relationship between location and the fate of axillary buds controls the branching process which is known to be a more complex event [1]. This process has been extensively addressed in many species of deciduous and conifers and a decrease in the length of the laterals has been observed from the top of the bearing shoot [1–6]. In part of these species, some shoots depend on their location and age, and the numbers of laterals and branching characteristics were found to decrease with plant development and ageing in many woody species, including *C. atlantica* [7–10]. Similarly, on six apple cultivars, Costes and Guédon [1] reported that branching is organized along the annual shoot according to particular lateral type locations. Moreover, Millet [11] and Vennetier et al. [12] have found that, for young to adult conifers, the annual shoot length also

decreased from the hierarchical order 1 to the following orders 2 and 3. Colombo and Templeton [13] have revealed that the annual shoot length was strongly correlated with branch position in the crown, thus with branch age in pines and spruce. In the same way to the latter authors, Buisson et al. [14] demonstrated that the annual shoot length and the total number of branches and whorled branches were highly variable and decreased with age and with increasing branching order for *Picea mariana*, *Pinus banksiana*, and *Pinus strobus*. In contrast, Remphrey and Davidson [15] announced that generally, older branches tend to grow slowly whereas lengths of current shoots of major order 1 branches were found to decrease with increasing depth in the crown [16].

Several studies have been done on the effect of light on growth [17–19]. Aussenac [17] has shown that the decrease in light produces a reduction in the palissadic tissue of the

needles of four conifers. In a study of Suzuki [18], it was found that *Cleyera japonica* annual shoot length and light environment were positively correlated within the same order branches. Recently, on *Picea glehnii*, Chen and Sumida [19] showed that the production of current-year shoots on a primary branch increased with increasing light whereas secondary branches at the distal part of a primary branch produced more current-year shoots and exhibited a lower death than proximal branches. While they note that, for the primary and secondary branches, the mean shoot lengths in the lower crown were not significantly different between sunlit and shaded trees and they conclude that local light intensity alone cannot fully explain the growth and survival of primary branch in contrast to secondary branch. On the other hand, it has been shown that the age of the oldest leaves (longevity) on a branch of conifer leaves varies with species and habitat conditions (elevation, latitude, fertilization, and irrigation) and such intravariation is largely interpreted as environmentally determined phenotypic acclimation [20]. Furthermore, it was reported that different-aged needles of conifers affect the net photosynthesis and significant differences in mobile sugar concentrations in these needles [21] and the correlation between an increase in tree height or age and a decrease in CO₂ assimilation rates were found [22].

Cedar growth has been found to be relatively long when compared to other resinous such as fir [23]. The branching process in adult and young *Cedrus atlantica* (Endl.) G.Manetti ex Carrière tree has been studied by counting the number, length, and position of short and long shoots [24, 25]. Other studies have been made on growth dynamics and morphology of annual shoots according to their architectural position in young *C. atlantica* [8] and have found that annual final shoot length, duration of extension, and maximum extension rate decreased with increasing branching order. The inter- and intraspecific variation of the polycyclism was found in *Cedrus*, to genetically discriminate between *Cedrus* species, and is considered a way of adaptation to adverse climatic conditions [26]. Like for *Eurya japonica* [27], Sabatier and Barthélémy [8] have found that annual shoot length decreased with increasing branching order for *C. atlantica* (Endl.) and have reported that the types and numbers of sylleptic axillary shoots produced are linked with both final length and extension rate of the parent shoot in young *C. atlantica*. Similarly, Courbet et al. [28] have constructed a model to predict branch vertical position which can be used as inputs for branch diameter and mortality models for Atlas cedar. This model shows that the vertical location of branches in the crown partly governs their further growth and mortality from which depend (i) the stem growth and form and (ii) the quality of lumber and veneer, including wood knots.

Many other studies have been made on the cedar response to environment and have furthermore shown that (1) the better light and water availability induce higher growth rates, wider tree rings, and lower leaf area index in Lebanon Cedar [29], (2) the low precipitation during summer limits tree growth on Lebanon Cedar [30], (3) the adverse climatic conditions and soil fertility affect the polycyclism and annual shoot length in *Cedrus* [26], (4) the low nutrient availability

reduces the growth unit size, life duration of branch, and shoot number and modifies the axillary product category and their distribution in *C. atlantica* [24], (5) the high water status and low global radiation increase the duration of the daily growth period in *C. atlantica* [23], (6) the dry set decreases height growth for *C. atlantica* more than *C. brevifolia* and vice versa in the well-watered set [31] proving that *C. atlantica* is the last drought-tolerant compared to *C. brevifolia* and *C. libani*. Recently, Bell et al. [32] found that variability of pollen grain size and production within individual samples of Atlas cedar may result from the irregular development of pollen without any evidence for climatic and nutrient influences and concluded that it is influenced by a number of complex factors. Consequently, they underscore the need for further investigation of the complex controls on pollen and strobili development because it would not be possible to use this for the moment as a proxy for environmental reconstitution and cedar conservation.

All these studies show that branching processes and needle death of the genus *Cedrus* like other species depend on plant development, age, location, and environment but furthermore, might be conditioned by the neighboring branch order in the proximal part of the tree. Moreover, as said above, the effects of conditions on growth and survival appear to be studied extensively [33–35]. Besides this, more evaluations of the individual tree and stand leaf formation have been built for several resinous species, but until now no studies have been conducted on the link of branch growth with the fallen leaves and the sexuality of the short shoots in Cedar forest under light and shade exposures. Likewise, no one has attempted to estimate the lifespan of the leaves in the proximal part of the crown of adult trees of *C. atlantica* and its relationship to the extension of short shoots, the order of branches, and the number of strobili (male cone) per branch although the knowledge of these relationships is fundamental for the study of basic exchange processes in the canopy and the conservation of cedar forests in Morocco. The aim of this study is to understand how light availability affects needle survival, short shoot growth, and their sexuality within an adult tree crown of *Cedrus*.

2. Materials and Methods

2.1. Site of Sampling. Materials for the study were collected from the Ifrane regions of the Moroccan Middle Atlas in 2017 of a mixed forest of Atlas cedar and *Quercus ilex*. The soils of cedar trees have a sandy texture with a proportion of silt and clay. Climatic variations in recent decades give minimums and maximums ranging from 342.1 to 812.4 mm/year of precipitation and between 12.56 and 14.86°C/month of temperature [36]. This study was conducted on an isolated adult tree of *Atlas cedar* (diameter at breast height (DBH) = 1.75 m, tree height = 15.08 m) at the edge of the forest but gradually exposed to the sun from morning to evening on these three sides while its fourth side remains in the shade all day from spring to autumn (Table 1). At noon, the light intensity which is measured at the luxmeter at each branch is reported in Table 1. On this tree, twenty-four branches have been sampled at the rate of six per condition of illumination

TABLE 1: Light conditions of sampled cedar branches.

Branch	L2	D2	L3	D3
Luminosity (klx)	97.5	4.08	94.24	6.24
Light exposition				
Morning	Indirect light	Shade	Indirect light	Shade
Afternoon	Direct sunlit	Shade	Direct sunlit	Shade

L2: sunlit order 2 branches; D2: shaded order 2 branches; L3: sunlit order 3 branches; D3: shaded order 3 branches.

and types of branches: sunlit order 2 branches (L2), shaded order 2 branches (D2), sunlit order 3 branches (L3), and shaded order 3 branches (D3) (Table 1).

2.2. Analysis. Cedar growth was determined by measuring the length at double decimetre (± 1 mm) and counting (i) the number of each type of short shoots carried by the parent branch of orders 2 and 3: unbranched short shoot SSnr carried by parent branch, branched short shoot SSr carried by parent branch, sum of branched and unbranched short shoot SS ($nr + r$) carried by parent branch, short shoot SS/T carried by twigs of parent branch, short shoot SS/T/LS carried by the twigs of the long shoots of the parent branch, and short shoot SS/LS carried by the long shoots of the parent branch, (ii) the number of existing needles and fallen leaves of the branches L2, D2, L3, and D3 counted under the magnifying glass. The origin of the different types of short shoots mentioned above has been determined as described in Table 2 according to Sabatier and Barthelemy [37] and Sabatier and Barthelemy [26], and (iii) the number of sexual short shoots carrying male strobili and the number of vegetative ones of five types of short shoots of the four experimental branches were counted. The frequency of sexual short shoots was determined by the following formula:

$$\text{frequency} = \frac{\text{no. of short shoots carrying pollen strobili}}{\text{no. of total short shoots}} \times 100. \quad (1)$$

2.3. Statistical Analysis. All the parameters discussed above have been subjected to the analysis of variance (ANOVA), and the means were compared by Fisher's least significant difference (LSD) post hoc test at $P < 0.05$. All data were analysed statistically using IBM SPSS Statistics software (version 20.0, 2011).

3. Results

The total and mean number of short shoots carried by the order 2 and order 3 branches showed no significant differences between the branches of orders 2 and 3 neither in light (L2 and L3) nor in shadow (D2 and D3) and between the sunlit branches (L2 and L3) and the shaded branches (D2 and D3) of the same order (Figures 1(a) and 1(b)). On the other hand, the mean length of short shoot SSnr and SS ($nr + r$) on the order 3 branches is significantly less important on the shaded branches than on the sunlit ones. But

no significant difference has been showed on the order 2 branches (Figure 1(c)).

The total number of needles and fallen leaves shows no significant difference between shaded and sunlit branches, neither on order 2 nor on order 3 branches (Figure 2(a)). But, when we compare between the effect of light and darkness on the fallen leaf mean number of each short shoot type, we find that short shoot of the order 3 branches lost significantly more needles than the order 2 branches. In the order 3 branches, the needle loss concerns the short shoot SSnr, SS ($nr + r$), and SS/T, whereas in the order 2 branches the needle loss concerns only the short shoot SS ($nr + r$) which lost significantly more needles (Figure 2(b)).

The analysis of the mean frequency of the sexual short shoot over four experimental branches has revealed that the production of pollen strobili per branch was about five times more in the sunlit order 2 branches (L2) as compared to shaded order 2 branches (D2) (Figure 3). Similarly, two times more production was observed in the sunlit order 3 branches (L3) than shaded order 3 branches (D3). Elevated mean frequency of the sexual short shoot was observed in L2 and L3 branches, with an average number of 5.588% and 1.62% of the total number of short shoots per branch, respectively (Figure 3). The ANOVA of the mean values of the sexual short shoot frequency per branch has revealed a significant effect of shade ($P = 0.032$) in the order 2 branches whereas we found no significant effect in the order 3 branches ($P = 0.458$). There is no significant difference between the two orders of branches neither in the shade ($P = 0.919$) nor in the light ($P = 0.093$) (Figure 3). However, interactions of order \times light availability were only significant when comparing branches L2 and D3 ($P = 0.027$) but not branches (L3) and (D2) ($P = 0.518$).

The sunlit order 2 and 3 branches carry five types of sexual short shoot with male strobili at the frequency of 2.15 to 11.39% (Table 3). Both shaded order 2 branches (D2) and particularly shaded order 3 branches (D3) reduced drastically the mean frequency of male short shoots of each type of axillary product as compared to the sunlit order 2 and 3 branches (L2 and L3) (Table 3). Of all the short shoots carried by the shaded branches of order 3, only those not branched could form a single male strobili, while in the shaded branches of order 2, only two types of short shoots had not formed male strobili: the branched short shoots SSr and the short shoot SS/T/LS carried by the twigs of the long shoots of the parent branch (Table 3). There was no significant treatment effect ($P < 0.05$) with respect to the mean frequency of sexual short shoot production per type of short shoot (Table 4).

TABLE 2: Morphological features of the axillary products of the branch studied in *Cedrus atlantica* as described by Sabatier and Barthelemy [37].

Long shoot	Twig	Short shoot
Carries pseudowhorls of 1 to 2 twigs and shorts shoots	Wear only short branches	Can carry a short shoot
Can be born on the branch or on the trunk	Can be carried by the long shoot, branch, or trunk	Worn by all axis categories

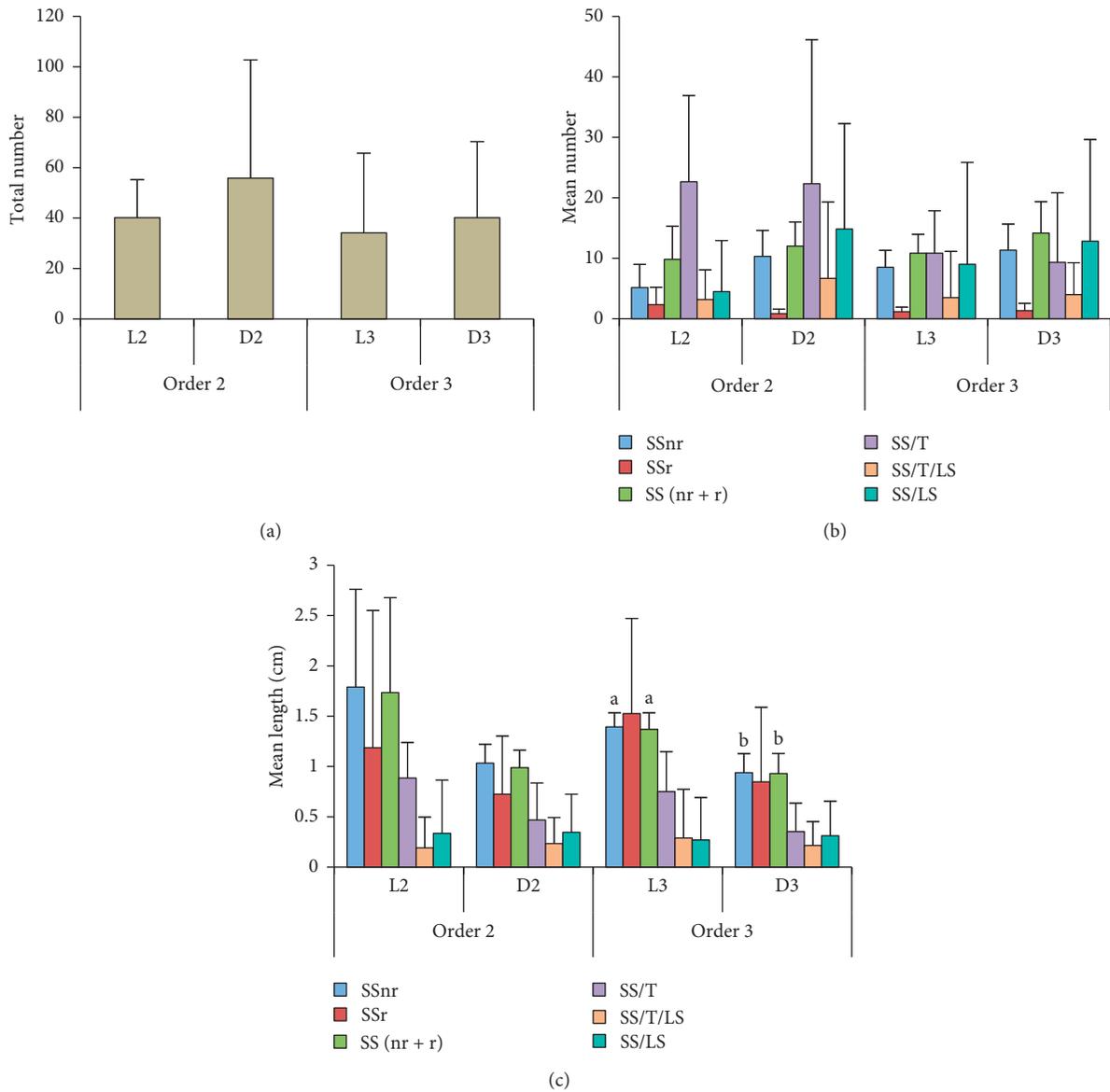


FIGURE 1: Variation of the total number of short shoots: (a) the mean number of short shoot (b) and the mean length of short shoot (c) among L2, D2, L3, and D3 branches exposed to different light intensities as described in Table 1. Different letters indicate only significant differences among branches ($P < 0.05$, $n = 6$).

4. Discussion

This study shows that neither the order nor the light affects the production of short shoots and that the young branches of order 3 behave in the same way as those of lower order vis-à-vis of the light availability. Buissart et al. [14] for many conifers established that the total number of branches and whorled branches decreased with increasing branching

order. However, Sabatier and Barthélémy [8] have showed that sylleptic axillary shoot occurred only on annual shoots of the branch orders 1 and 2 when the extension rate was at its highest but did not occur in branch order 3. Such results are in congruence with this study and suggest that, in the same light condition, the two studied order branches have reached their full extension rate and thus produced similarly the same number of short shoots in both light and shade

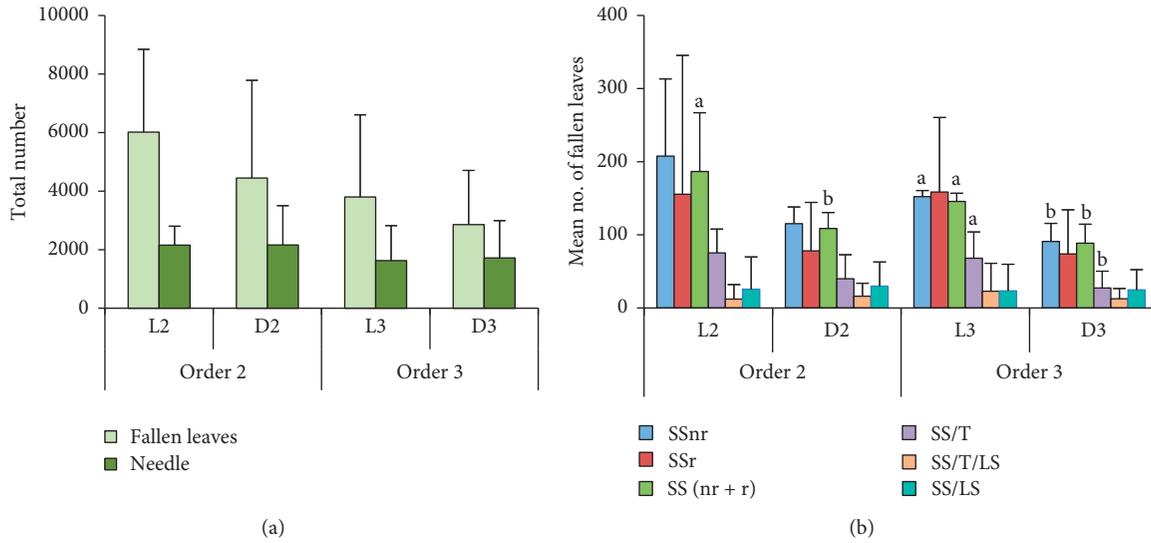


FIGURE 2: Variation of the total number of production and death of short shoot needles: (a) the mean number of fallen leaves of different short shoot needles (b) among L2, D2, L3, and D3 branches exposed to different light intensities as described in Table 1. Different letters indicate only significant differences among branches ($P < 0.05$, $n = 6$).

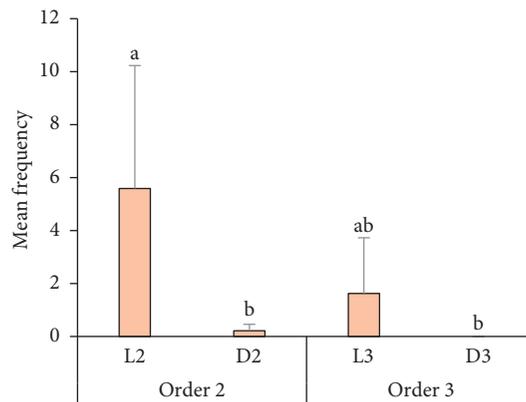


FIGURE 3: Variation of the mean frequency per branch of short shoots carrying pollen strobili in different light intensities as described in Table 1. Different letters indicate significant differences among branches ($P < 0.05$, $n = 6$).

TABLE 3: The mean frequency of sexual short shoot per type of short shoot of the four experimental branches exposed to different light intensities as described in Table 1 ($n = 6$, \pm standard deviation).

	SSnr	SSr	SS (nr + r)	SS/T	SS/T/LS	SS/LS
L2	11.39 ± 11.53	8.33 ± 14.43	11.30 ± 11.61	7.48 ± 10.83	2.15 ± 3.72	3.87 ± 4.95
D2	0.61 ± 1.06	0	0.60 ± 1.04	0.22 ± 0.38	0	0.13 ± 0.23
L3	3.43 ± 4.35	0	3.18 ± 4.01	0.81 ± 1.40	0.83 ± 1.44	2.62 ± 4.54
D3	0.70 ± 1.22	0	0	0	0	0

exposures. Moreover, Henriksson [38] has found null and strong effect of shade on the production of long shoot in *Betula pubescens* depending on the year, suggesting that Atlas cedar is less sensitive to shading because the short shoot production of neither the branch order 2 nor the branch order 3 was affected by shading.

Suzuki and Maki Suzuki [27] reported that, in *Eurya japonica*, the annual shoot length decreased with increasing branching order as has been found for many young and adult conifers [11, 12, 14] like pines and spruce [13].

However, Sabatier and Barthélémy [8] also found that annual final shoot length, duration of extension, and maximum extension rate decreased with increasing branching order. This study showed that below the annual shoot, the length of all types of axillary short shoots did not significantly vary between branching orders 2 and 3 in the same light condition (Figure 1(c)). On the other hand, the order 3 branches behave differently than the lower order one with regard to the effect of sun exposure on the short shoots SSnr and SS (nr + r) (Figure 1(c)). The increase of the length of the short

TABLE 4: ANOVA ($P < 0.05$) of the effect of order and light availability on the mean frequency of sexual short shoot produced per type of short shoot in experimental branches exposed to different light intensities as described in Table 1.

		SSnr	SSr	SS (nr + r)	SS/T	SS/ T/LS	SS/ LS
Effect of light	L2 * D2	0.066	0.195	0.066	0.142	0.224	0.21
	L3 * D3	0.606	1	0.545	0.86	0.621	0.962
Effect of order	L2 * L3	0.155	0.195	0.145	0.173	0.444	0.661
	D2 * D3	0.986	1	0.907	0.961	1	0.962
Order \times light	D2 * L3	0.594	1	0.622	0.898	0.621	0.391
	L2 * D3	0.068	0.195	0.054	0.132	0.224	0.196

shoot SSnr and SS (nr + r) of the order 3 branches in sun exposure shows that when the cedar is more exposed to the sun rays, it reacts by extension of the short shoot of the youngest branches. This response of the order 3 to light availability is supported by the fact that *C. libani* is found to be a light-demanding species [39] and when growing under better light and water availability showed higher growth rates and wider tree rings [29]. In contrast to our result (Figure 1(c)), Remphrey and Powell [16] and Remphrey and Davidson [15] reported that the length of current shoots of major order 1 branches decreases with decreasing light and the older branches grow slowly, while Suzuki [18] found that *Cleyera japonica* annual shoot length and light environment were positively correlated within the same order branches and particularly the order 2. They also reported that the lower-order 2 branches *Cleyera japonica* lengthened to a certain extent even if light availability was relatively low as in this study for branch order 2, whereas they observed that higher-order 3 and 4 branches did not grow vigorously even when light availability was relatively high. Our observations with those of Suzuki [18] are not corroborated with the observations of Remphrey and Powell [16] and Remphrey and Davidson [15] and Chen and Sumida [40] who found that for the primary and secondary branches, the mean shoot lengths in the lower crown were not significantly different between sunlit and shaded trees of *Sakhalin Spruce*. The low shoot length growth of a shaded order 3 branch compared to sunlit one obtained here is due to correlative inhibition and sink/source competition between sunlit and shaded branch for the partially shaded tree resources as explained by Milton's law of resource availability and allocation [35, 41–44]. Moreover, the observation that sunlit branches, as in the case of order 2 branch, cannot usually grow longer than shaded branches shows that competition between shaded and sunlit branch for the partially shaded tree resources is branch age-dependent and can be tested by branch anatomy analysis as suggested by Umeki and Seino [10].

The impact of light on needle retention depends on the order and the type of short shoot so that the shade increases needle retention with increased order only in SSnr and SS/T short shoots (Figure 2(b)). This action is due to the higher water status of the branch order 3 than the branch order 2 and is in agreement with the data of Suzuki [18] and Grönlund et al. [45] who reported that specific leaf area conductivity of new shoots declined with parent branch age

and increased with simulated transpiration rate of the shoot. Furthermore, Jalkanen et al. [46] found a lower decrease of the mean annual summer needle retention in northern than in southern Finland and suggested that a tree's carbon balance may better explain the variation in needle retention. This explanation is in agreement with the idea of shade preserves branch water level by stimulation of stomata closure and reduction of water use in photosynthesis and growth as observed by Robakowski et al. [47].

In the order 2 branches, we found that only short shoot SS (nr + r) that does not lengthen significantly more under the effect of sun exposure loses significantly more needles compared to shade. Contrarily in the order 3 branches, only short shoot SSnr that elongates significantly more under the effect of sun exposure loses more needles whereas SS/T that does not extend more under sun exposure also loses their needles more significantly compared to shade. These results show that in the proximal area of the adult cedar crown, the short shoot SS/T of the young branches behaves in the same way as the short shoot SS (nr + r) of the older branches in terms of extension and needle loss. They also show close relationships between short shoot extension and needle life span of axillary products in the proximal part of *C. atlantica* tree crown.

Our results show that the light conditions affect the needle life span of the length of the short shoot particularly for order 3 branches. The main response to the shadow here is the length of unbranched short shoot suggesting that the nature of short shoot may vary between vegetative state and extremely specialized state with a role of "mega leaf" carrying the sexual organ (male or female strobili). This observation suggests that the shadow may be suspected to also affect cedar male and female sexual functions carried by the unbranched short shoot as reported by Nuñez et al. [48] for *Austrocedrus chilensis* (D. Don) who found that male trees were more abundant on high-radiation slopes, while low-radiation slopes had higher abundances of females. On the other hand, the effect of shade on the needle life span of the length of unbranched short shoot was higher in young than in old branches (Figures 1(c) and 2(b)), while the effect of shade on the production of male strobili was higher in old than in young branches (Figure 3 and Table 3). We suggest that this is an index of the plant actively extending its canopy towards a preferred light environment, temporarily giving up of functions less vital than vegetative growth.

As regards reproduction, the pollen strobili production per branch was about five times more in the sunlit order 2 branches (L2) as compared to shaded order 2 branches (D2). This result is in agreement with data of Henriksson [38] who has found that the nonshaded branches of the partially shaded trees of Scots pine grew well and produce more male catkins than the shaded branches of the same tree because sunlit branches are believed to be strong sinks for water and carbon on partially shaded tree [44]. For example, if within the sunlit order 2 branches which are nonshaded branches, the net photosynthesis and the stomata conductance are increased after shading the lower branches, in this case shaded order 2 branches (D2), this will, in long term, inevitably lead to increases of the production of sexual short

shoot at the costs of the shaded branches. This competition for resources favours sunlit L2 branch reproduction while that between L3 and D3 branches favours sunlit L3 branch growth and is in accordance with the sink/source competition. Henriksson [38] believed it to play a role in determining where the growth and reproduction occurred in the canopy.

On the other hand, in this study, both sunlit branches of orders 2 and 3 were found to be relatively similar in their growth and reproduction whereas both shaded branches of orders 2 and 3 are similar in reproduction but differed in their growth in comparison with sunlit branch of the same order (Figures 1–3). The shaded branches D2 are similar to sunlit L2 one in growth while the shaded branches D3 grew less than sunlit L3 one. This indicates that both sunlit branches which are strong sink branches drained more resources to the unbranched short shoot, at the cost of the growth and reproduction of shaded branch. This observation is supported by the fact that growth of short shoot of the old sunlit branches is not affected by shade while their sexual short shoots are more decreased and vice versa for the young branch (Figure 3 and Table 3). This means that the old branches have a much larger pool of carbohydrates to allocate throughout their short shoots because they become able to compensate for the growth expenses it has in shade but in sunlight fix enough carbon to repay pollen strobili construction costs. Many studies have showed that differential reproductive effort between sexes that is not compensated for may translate into different vegetative growth rates [49–57] also support this conclusion. As evidenced by ring widths, Nuñez et al. [48] have found that female trees of *Austrocedrus chilensis* were able to compensate for the reproductive expenses they have only in low-radiation exposures whereas in this study Cedar partially shaded tree is not able to compensate for the production of male strobili costs it has in shaded branch.

It has been reported that the productivity, the interval of production, and the release of pollen strobili depend on year, population, and species [58, 59] while for Atlas cedar Smith [60] noted “irregularity” with the development of pollen and Bell et al. [32] found no significant relationships between climate, soil nutrient availability, and pollen size. Besides buffering against these unpredictable factors, we argue that the age affects the branch sexuality sensitivity of *Cedrus* to shade and must be considered at the individual tree level. This is of immense value particularly for tree breeders because pollen strobili availability is a major constraint of tree reproductive success. Furthermore, other studies must be done on female strobili of different crown parts to better understand the effect of environmental change on the reproduction of Atlas cedar which is fundamental to the conservation of Cedar forests in Morocco.

Data Availability

The data used to support the findings of this study are included within the article.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

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