Microclimate in Mediterranean pine forests: What is the influence of the shrub layer?

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Abstract

Forest cover creates a specific microclimate by buffering most environmental variables. If the influence of the overstory on microclimatic variables has been well studied, the role of the understory has received less attention. In this study we investigated how the shrub layer modifies solar radiation, air temperature (T), relative air humidity (RH), vapor pressure deficit (VPD) and soil moisture under different thinning treatments in an Aleppo pine forest (*Pinus halepensis* Mill.). Microclimatic variables were measured along a vegetation cover gradient made up of three pine densities (dense, medium, low) and open conditions, with or without the presence of shrubs. The results were analyzed with a focus on the summer period which represents a major bottleneck for plant development in the Mediterranean area.

Average T and VPD values increased with decreasing vegetation cover (+1.38°C and +0.21 kPa for the whole year) while RH decreased (-2.34%). Along the same gradient, daily amplitude of T, RH, VPD increased while the buffering capacity decreased. These patterns were more pronounced during the summer period compared to the whole year and were primarily driven by overstory transmittance. However, the shrub layer played a significant role in the low pine cover treatment where it was developed and in open conditions. Soil water content in the forest area was higher under low pine cover without shrubs than it was in the other treatments, though differences were less marked during summer drought episodes. In open conditions, soil moisture was always significantly lower beneath the shrub canopy than outside it. Despite a reduction in soil moisture, shrubs may represent safe sites for woody seedling development in sparse pine forests and in treeless areas by buffering the microclimate during the summer period.

Keywords: Temperature, vapor pressure deficit, light, soil water content, thinning, Aleppo pine.

Declaration of interest.

The authors have no competing interests to declare

Highlights

- A buffering effect on T, VPD, RH was noted for the overstory and the understory
- This effect was more pronounced in summer due to a stronger shading effect
- Shrub influence on T, RH, VPD was higher in low pine cover and in open conditions
- Soil moisture was reduced in the presence of a developed shrub layer

1. Introduction

Mediterranean forests are primarily threatened by climate change and its associated disturbances, in particular more severe and prolonged drought episodes as well as recurrent heat waves (e.g. Peñuelas et al., 2017). These disturbances result in an increase in tree mortality, shifts in species distribution and higher fire risk (Allen et al, 2010; Carnicer et al., 2011; Pausas and Fernández-Muñoz, 2012). In this context, management methods mitigating these risks and improving forest resistance and resilience are urgently needed. The reduction of stand density by thinning is certainly one of the most studied adaptive management practices (Vila-Cabrera et al., 2018). Thinning increases light availability and reduces competition between trees. It also has a large influence on the water budget of the ecosystem (e.g. Aussenac and Granier, 1988). The reduction of tree density decreases rainfall interception, limits stand transpiration and can therefore delay soil water depletion (Cabon et al., 2018) and reduce tree drought stress (Bréda et al., 1995). Recent studies have shown that this alleviation of water stress can improve drought resistance and recovery, but these effects vary greatly between site conditions, species and thinning intensities (Giuggiola et al., 2013, 2016; Sohn et al., 2016). However, the effects of thinning on tree water alimentation may be dampened by several factors. For example, the transpiration of the remaining trees can increase (Bréda et al., 1995) and the development of the understory and ground vegetation, boosted by the light increase, can drain above and below ground resources (Aranda et al., 2012; Simonin et al., 2007), possibly cancelling or even reversing the effects of thinning on stand water consumption (del Campo et al., 2019).

Thinning, by reducing the tree cover, leads to the modification of microclimatic conditions (*sensu* Geiger et al., 2003) in which we include air temperature, air humidity, air water vapor pressure deficit (VPD), light availability and soil moisture. A main effect of tree cover is to moderate most of the meteorological variables and several previous studies have highlighted this buffering ability by comparing the microclimate within forest stands and in nearby open areas (e.g. Renaud et al., 2011, von Arx et al., 2012, De Frenne et al., 2019). Below-canopy microclimates are generally characterized by lower annual and seasonal maximum temperatures, with higher minimum temperature and air humidity values (Gaudio et al., 2017; Renaud et al., 2011), although the magnitude of these effects varies with forest structure and site conditions. Buffering of daily microclimate variations has also been reported: air temperature increases less during the day and decreases less during the night, whereas the reverse trend was noted for relative air humidity (Aussenac, 2000; von Arx et al., 2012). Such fine-scale modifications of microclimate by forest cover have important implications for tree seedling and understory species establishment and diversity (e.g. De Frenne et al. 2015, Gavinet et al. 2016).

Several studies have explored the relationship between tree cover and microclimatic conditions in relation to overstory composition and structure (e.g. Heithecker and Halpern, 2007; Porté et al., 2004; von Arx et al., 2012). However, few have considered the influence of the understory vegetation on microclimatic conditions (Kovács et al., 2017; Giuggiola et al., 2018). In fact, the understory also influences light interception, water budget and variations in other microclimatic variables (Balandier et al., 2013; Giuggiola et al., 2018; Riegel et al., 1992). Moreover, understory composition and structure are affected by climate change and by the reduction of overstory cover (Bernhardt-Römermann et al., 2015, Coll et al., 2011; De Frenne et al., 2015). Lastly, the understory can be also impacted by certain management practices that involve reducing or removing the understory vegetation for economic purposes, such as biomass harvesting, or for fire risk limitation.

In this study, we explored the role of the understory vegetation on several microclimatic variables in a Mediterranean Aleppo pine (*Pinus halepensis* Mill.) forest and a nearby open area. We first thinned pine stands at different intensities to create a gradient of overstory cover conditions, and then conducted an understory removal experiment. The understory was composed of shrubs, which is very common in Mediterranean systems especially in open forests and in open habitats (e.g. garrigues, matorrals). Many of the microclimatic variables fluctuate with time and influence plant processes differently, depending on the season (Ogle et al., 2012) and should therefore be studied at different time-scales. We monitored the main microclimatic variables: soil water content (SWC), air temperature (T), relative humidity (RH), vapor pressure deficit (VPD) and light availability.

In Mediterranean areas, summer period represents a major constraint for many processes affecting plant development and is clearly identified as a bottleneck for vegetation dynamics (e.g. Castro et al., 2005; Gómez-Aparicio et al. 2004, 2005). Furthermore, climate models for the next few decades forecast even drier and warmer climate during summer, that puts most ecosystem functions at risk (Cramer et al., 2018). We therefore specifically studied the fluctuations of microclimatic conditions during summer and compared them with those recorded during the whole year. More specifically, our questions were the following:

i) To what extent are variations in microclimatic variables affected by overstory and understory cover?

ii) How do interactions between the overstory and the understory influence microclimate?

iii) Are there any seasonal patterns in the effect sizes of below-canopy microclimate? In particular, we have investigated how the microclimate was modified during the summer period compared to the whole year.

2. Material and methods

2.1 Study site and experimental design

The study site is located in Southeastern France (43°4'N; 5°0'E) at about 30 km Northwest of the city of Marseille, on a flat area at an altitude of 130 m. Mean annual temperature is 14.5°C and mean annual rainfall is 550 mm based on historical records (1961-2010) of the nearby weather station of Istres (Météo France). However, as it is often observed in the Mediterranean climate, rainfall fluctuations are pronounced: 2014 and 2015 were ‘wet’ years (705 and 619 mm) whereas 2016 and 2017 were ‘dry years’ (382 and 318 mm). Differences in total rainfall during the summer period were even more pronounced between 2014-2015 (138 mm and 157 mm) and 2016-2017 (17 mm and 35 mm). The soils developed on a calcarenite bedrock composed of sandy limestone material and fossil shells. Alteration of this bedrock has led to calcareous soils (mean depth 60 cm) with mostly sandy textures (52% ± 0.7), followed by silt (34% ± 0.5) and clay (14% ± 0.6).

The site was covered by a 60-year-old *Pinus halepensis* forest that had naturally established on former agricultural fields. The tree layer was composed of Aleppo pine solely, with the evergreen holm oak (*Quercus ilex* L.) present in some places in the sub-canopy layer, the shrub layer was dominated by *Quercus coccifera* L., *Quercus ilex*, *Rosmarinus officinalis* L., *Phyllirea angustifolia* L. and the herb layer was scant.

In 2007, we established twelve 25 m × 25 m plots (Fig. 1) in the pine forest and thinned eight randomly selected plots according to two intensities (4 plots per thinning intensity): heavy thinning removing 2/3 of the basal area and moderate thinning removing 1/3 of the basal area. Four plots were not thinned and left as control. This led to three levels of ‘pine cover treatments’: low cover (L) after heavy thinning, medium cover (M) after medium thinning and dense cover (D) in the unthinned control. In February 2016, half of the surface of the shrub layer that had developed was removed from each plot of the L and M treatments, while the other half was left untouched. Shrub removal was not performed in plots of the D treatment as the shrub cover was already very low. Shrub regrowth was then suppressed each year during the winter period in the shrub removal treatments. Stand characteristics of the overstory and the understory are summarized in Table 1 and pictures of the treatments are provided in the supplementary material.

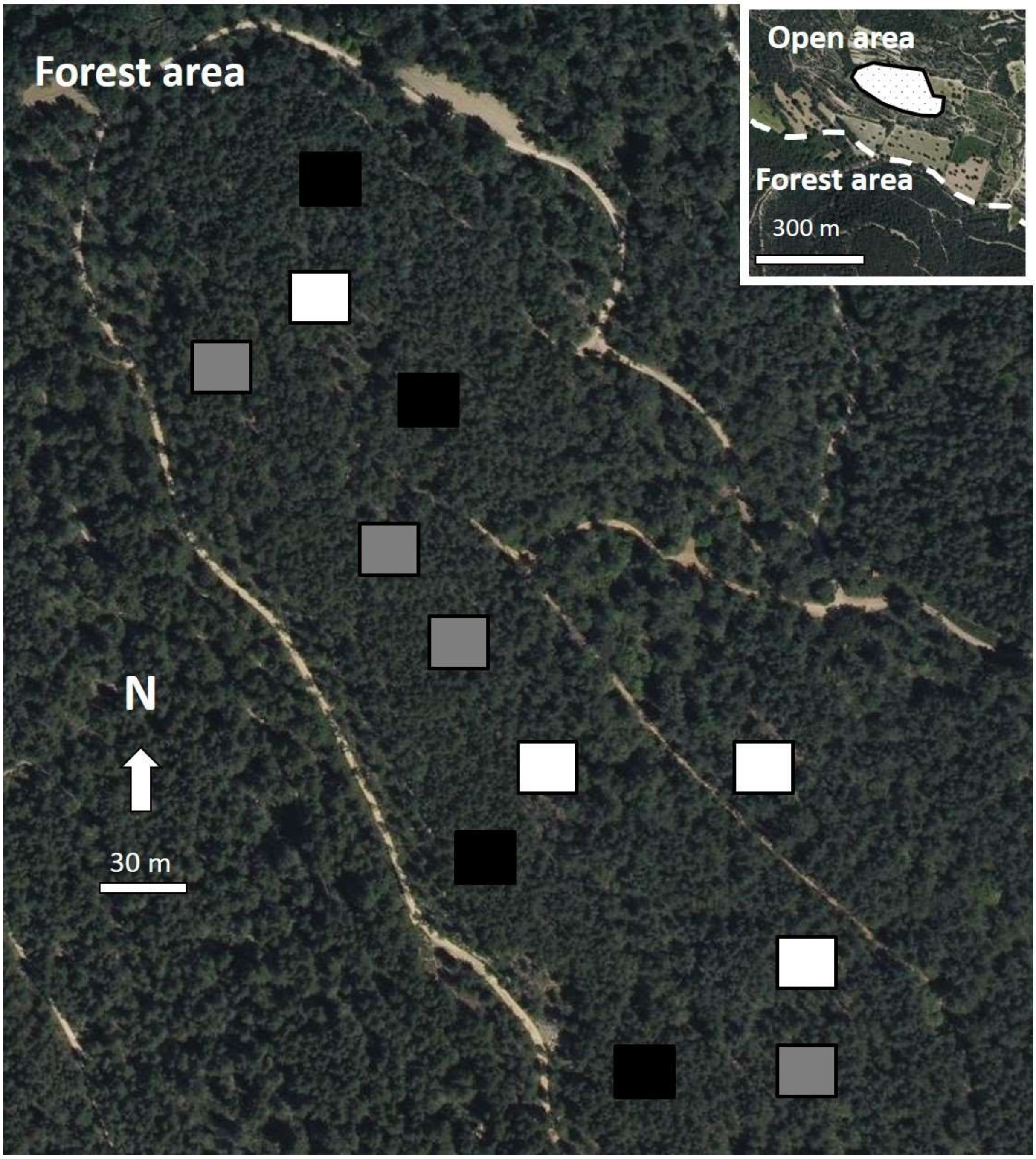


Figure 1. Location of the 12 plots (squares) in the forest area and the open treeless area (in the insert). Treatments are as follows: low pine cover (L, after heavy thinning, white squares), medium pine cover (M, after medium thinning, grey squares) and dense cover (D, no thinning = control, black squares).

Table 1. Mean characteristics (mean ± se) of the plots in 2016

Treatment	Pine density (/ha)	Basal area (m^2/ha)	Pine circumference (cm)	Cover of the shrub layer (%)	Height of the shrub layer (cm)
Dense cover	1192 (±111)	37 (±0.9)	58.2 (±1.3)	12.5 (±2.9)	47.6 (±7.6)
Medium cover	632 (±47)	28 (±1.5)	70.8 (±1.8)	33.1 (±2.9)	92.7 (±5.4)
Low cover	236 (±30)	17 (±0.3)	91.4 (±2.9)	46.8 (±2.8)	107.0 (±6.1)

In addition to the forest plots, we also selected a nearby open area (O, see Fig. 1) that was covered by a discontinuous shrub layer with the same species as in the forest area.

Hereafter we refer to the seven different treatments resulting from the canopy cover and the shrub treatments as follows: dense pine cover without shrubs (D), medium pine cover with (M+S) and without (M) shrubs, low pine cover with (L+S) and without (L) shrubs, open area with shrubs (O+S) and without shrubs (O).

2.2 Measurements of the microclimatic variables

2.2.1 Light transmittance of the pine cover

Light availability in the photosynthetically active radiation (PAR) domain was measured in the forest plots using 65 measurement points distributed along transects in the different plots and treatments, below pine canopy (D, M, L) and below pine + shrub canopy (M+S, L+S). At each measurement point, light availability (µmol m^{-2} s^{-1}) was recorded every minute for 24 hours by a solarimeter tube of 30 cm length (DPAR/LEC1C, Solems S.A., France) installed at 40 cm height. Data were recorded during two successive clear days of April 2017. Light was also measured simultaneously in the open area as a proxy of above tree canopy light availability (full light conditions) using two solarimeters. Light transmittance was computed as the ratio of below canopy light availability at each forest point to light availability in the open.

2.2.2 Light transmittance of the shrub cover

To accurately investigate the interception of light by the shrub layer in the forest area, we measured the light under shrubs using two different methods. Light availability above and below the shrub canopy was measured at 314 points distributed in the different plots with shrub manipulation (M+S, L+S, O+S) with a PAR ceptometer (AccuPAR LP 80, METER Group, Inc. USA). Because shrub transmittance may strongly vary within the day, we additionally measured shrub transmittance using continuous measurements over 24 hours on 17 additional points, using light sensors (SKP 215, Skye Instrument, UK, Supp. Fig. S1C) installed above and below the shrub canopy. At each measurement point, shrub cover was visually estimated in 5% classes using a 1 m^2 square grid. Light transmittance (below/above) of the shrub layer was established by computing the mean values for each 5% shrub cover class.

Finally, in the open area, light availability below shrub canopy was measured using a PAR ceptometer during a clear day in July. A total of 24 shrubs of the same species as those recorded in the forest area were selected and light was measured above and below the canopy at different time intervals during the day. The light transmittance was then computed for each shrub.

2.2.3 Air temperature and relative air humidity

We used 26 loggers (DS1923, iButton®, Maxim int., USA) in the forest plots to measure air temperature (T, ± 0.06°C) and relative air humidity (RH, ± 0.04%), distributed among the different treatments and 6 additional loggers distributed in the O and O+S treatments. The loggers were placed in a small meteorological shelter 30 cm above the ground, below the shrub canopy (M+S, L+S, O+S) and outside shrub influence (D, M, L, O). Data were collected from June 2016 to November 2018 at a one-hour time interval.

2.2.4 Soil water content

Soil volumetric water content (%, SWC) was monitored from June 2016 to November 2018 with a total of 42 soil moisture probes measuring the dielectric constant of the soil based on capacitance technology (EC-5, Decagon Device, UK) and distributed among the different treatments of the forest area. Only 8 of the 12 plots presenting the most similar soil conditions were sampled (2 plots in the control treatment D, and 3 plots in each of the two thinning treatments, L and M). Probes were initially calibrated in the laboratory before being installed at 30 cm depth in the field. Data were collected every 4 hours with CR 800 data loggers (Campbell Scientific Ltd, France). For the open area, soil moisture was measured in 2014 and 2015 using 6 EC-5 probes installed at 30 cm depth below the shrub canopy and 6 probes outside of the shrub canopy.

2.3 Data analysis

By analogy with the Beer-Lambert's law, light transmittance as a function of shrub cover was described by fitting an exponential negative regression model as follows : $T = e^{-k \times \text{Shrub cover}}$, where T, the light transmittance (%) and k, the extinction coefficient, which depends on the shrub cover properties (Sonohat et al., 2014).

T, RH, SWC data series were quality-checked before analysis by checking maximum and minimum range limits, and variability over time, in order to detect any unusual behavior of the probes and data outliers which were discarded from later analyses. The T and RH data were used to produce the hourly VPD using the following formula:

$VPD\ (Pa) = (1\text{-}RH/100) \times 610.7 \times 10^{\ 7.5T/(237.3+T)}$ where T, the temperature in °C.

The hourly data were used to compute daily maximum and minimum values for the summer period (from the summer of 2016, 2017 and 2018, respectively) and for the whole observational period (from October 2016 to October 2018) for each treatment. SWC mean daily values were also calculated for each treatment.

The buffering capacity was defined as the difference between the open area and the below canopy in daily maximum temperature (ΔTmax), relative air humidity (ΔRHmax) and vapor pressure deficit (ΔVPDmax).

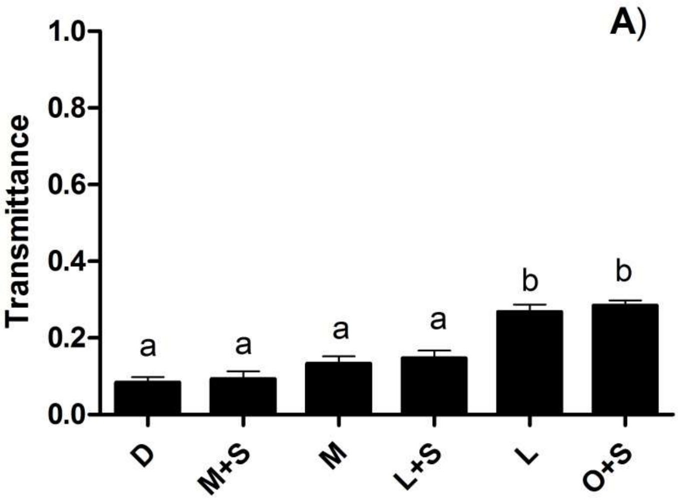
Treatment effects on the different environmental variables were tested by one-way ANOVA followed by post-hoc Tukey's test. We used logarithm or power transformation to satisfy the assumptions of normality (Kolmogorov-Smirnov test) and homogeneity of variance (Levene's test). When these conditions were not met, we performed non-parametric Kruskal-Wallis test that was followed by multiple comparison test according to Siegel and Castellan (1988). In both cases, statistical differences were assumed at $P<0.05$. All statistical analyses were performed using R (R core Team, 2017), for multiple comparisons related to the Kruskal-Wallis test, the 'pgirmess' package was used.

3. Results

3.1 Light transmittance

There was a gradient of increasing light availability in the pine plots from dense cover to light cover without shrub (Fig. 2A). However, due to the high variability of light transmittance below forest vegetation cover, we did not detect significant differences among the treatments D, M, M+S and L+S, although values ranged from 0.08 for D up to 0.15 for L+S. In contrast, there was a clear difference between these later treatments and the L and O+S treatments, both of which showed higher light transmittance values (0.27 and 0.28 respectively).

In the forest area, despite high variability, we found a significant negative exponential relationship between light transmittance and shrub cover with an extinction coefficient k of 0.019 (Fig. 2B).



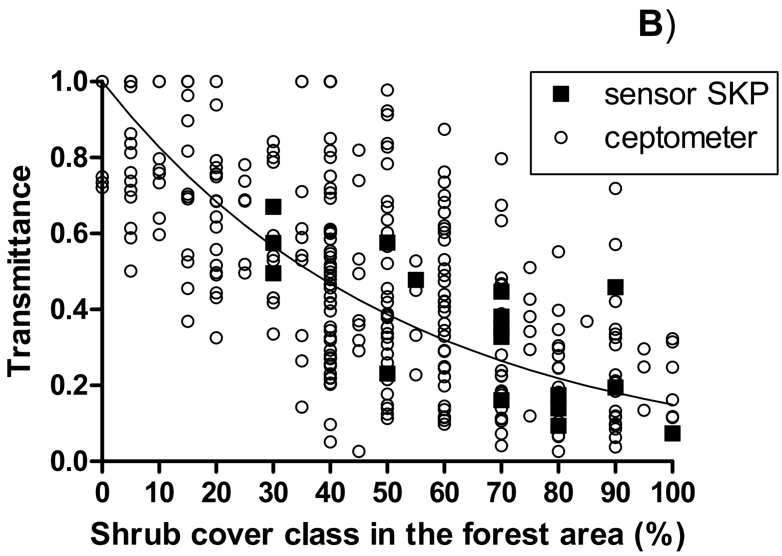
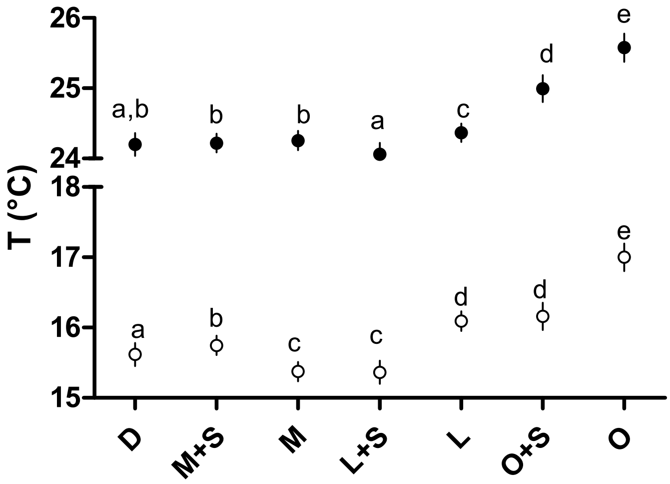
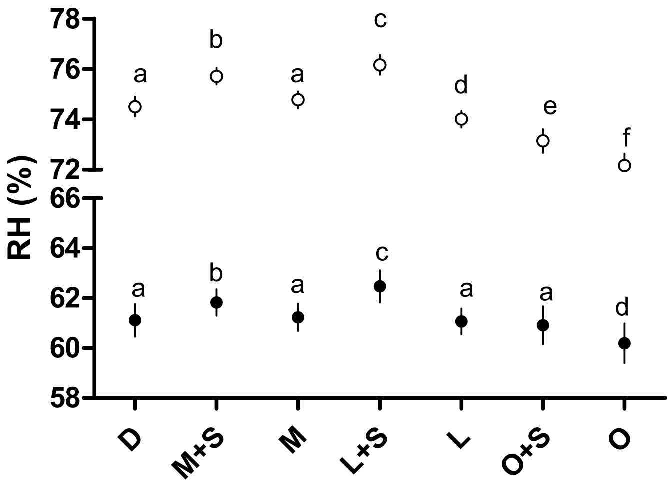


Figure 2. A) Light transmittance (mean ±SE) according to the treatments, computed as the ratio of light availability below canopy compared to open conditions (O). D=dense cover, M=medium cover, L=low cover, O=open, S=presence of the shrub layer. Letters indicate statistically significant differences according to Tukey's post-hoc test (F= 30.2, P<0.001). B) Light transmittance according to shrub cover class in the forest area. The corresponding regression curve is shown (y = exp(-0.019× cover class), R^2=0.35, P<0.001). The black squares indicate the daily measurements based on SKP sensors, whereas the white circles indicate the instantaneous ceptometer measurements.

3.2 Air temperature, relative humidity and VPD

Mean daily values of T and VPD followed similar trends among the different treatments (Fig. 3, Table S1): although the lowest values were recorded in the L+S treatment, they remained comparable among the treatments D, M, M+S and L+S. In contrast, a significant increase was noted for the low cover treatment without shrub layer (L), for both the summer season and the whole year. The influence of the shrub layer on the forest area was only noticeable in the L treatment. The increase of T and VPD was marked in the O+S and O treatments, particularly for the summer season. In contrast to these two factors, RH exhibited a regular decrease from the L+S treatment to the O treatment. However, this decrease was less pronounced in the summer season than during the year. Overall, L+S had the highest mean RH.





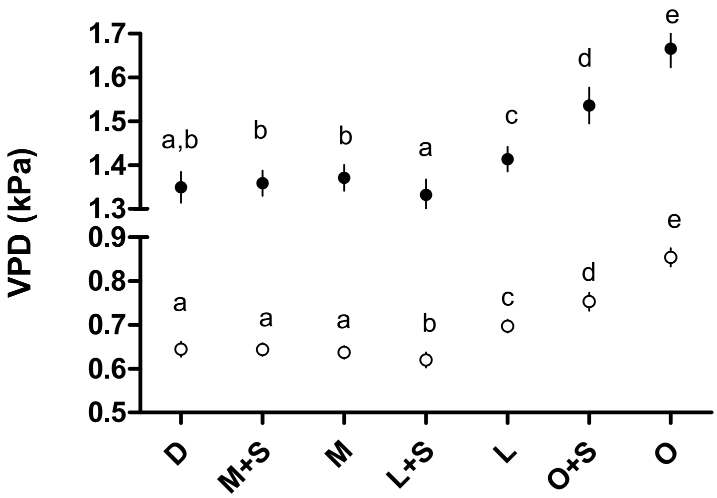
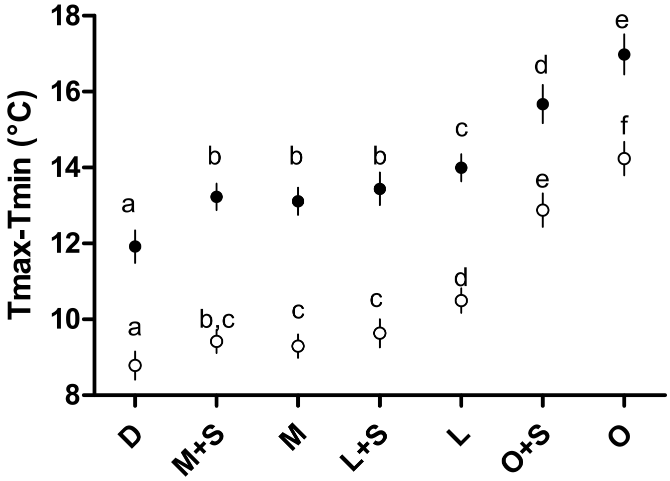
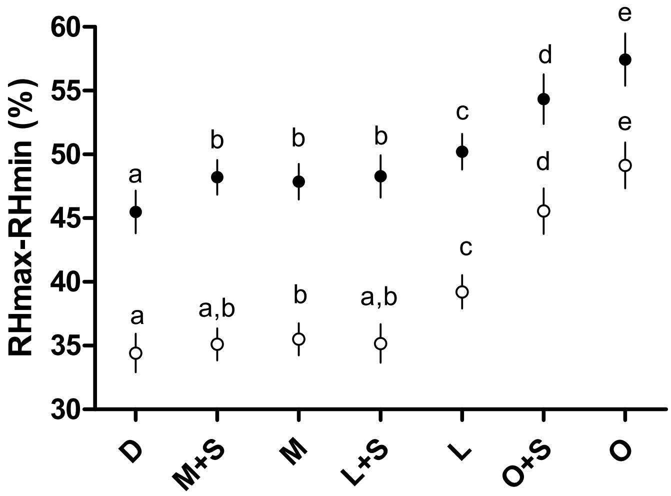


Figure 3. Mean temperature (T), relative humidity (RH) and vapor pressure deficit (VPD) hourly values (mean ± 5SE) by treatments. Letters indicate statistically significant differences for the summer period (black points) and the whole year (white points).

The daily range for the three variables followed the same trend (Fig. 4, Table S1): they increased along the decreasing vegetation cover gradient from dense pine cover (D) to open conditions (O) and always showed higher values in summer than for the whole year. The influence of the shrub layer was not significant in the medium cover treatment but was clearly marked for the light cover and open treatments. Similar results were found for the maximal daily temperatures, which ranged from 31.10°C in D to 34.96°C in O when averaged over the summer season and from 20.64°C to 25.02°C for the whole year. Similarly, maximum daily VPD values were the lowest in D (summer: 2.89 kPa, whole year: 1.43 kPa) and the highest in O (summer: 3.95 kPa, whole year: 2.22 kPa).


Tmax-Tmin (°C)
18
16
14
12
10
8
a
b
b
b
c
d
e
a
b,c
c
c
d
e
f
D
M+S
M
L+S
L
O+S
O


RHmax-RHmin (%)
60
55
50
45
40
35
30
a
b
b
b
c
d
e
a
a,b
b
a,b
c
d
e
D
M+S
M
L+S
L
O+S
O

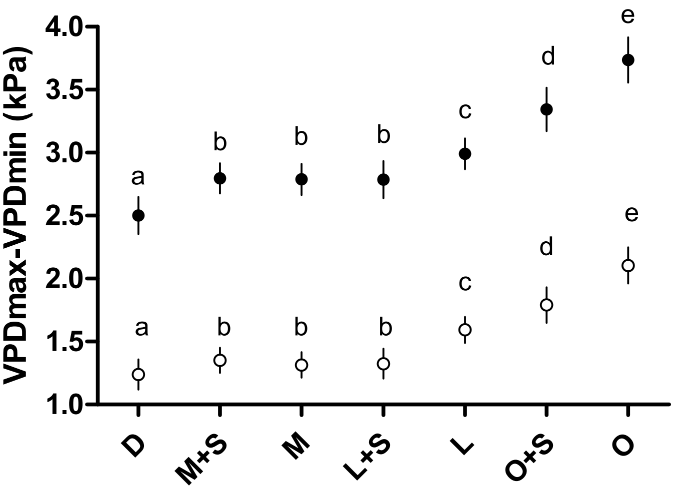
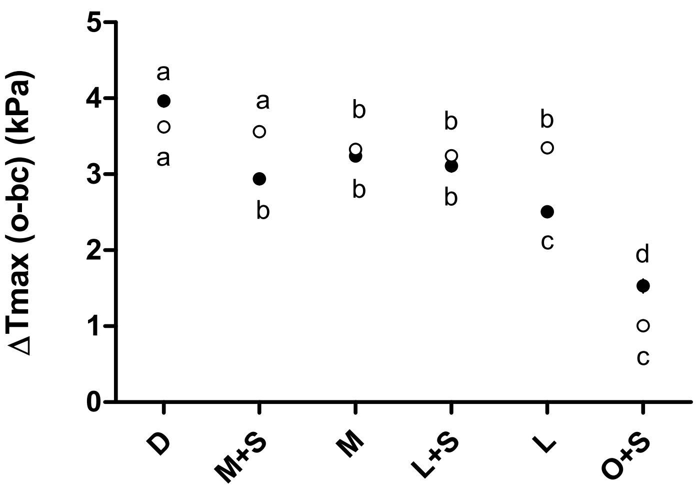
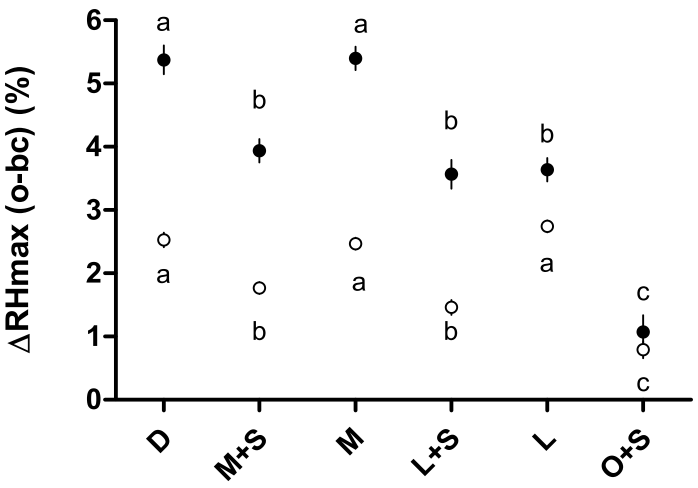

VPDmax-VPDmin (kPa)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
a
b
b
b
c
d
e
a
b
b
b
c
d
e
D
M+S
M
L+S
L
O+S
O

Figure 4. Temperature (T), relative humidity (RH) and vapour pressure deficit (VPD) mean daily range values (mean ± 5SE). Letters indicate statistically significant differences for the summer period (black points) and the whole year (white points)

The buffering capacity, represented as the difference between open area and below canopy in daily maximum temperature (ΔTmax), relative air humidity (ΔRHmax) and vapor pressure deficit (ΔVPDmax), globally decreased along the vegetation gradient (from D to O) as shown in Fig. 5 (see also Table S1). It must be noted that all values were positive even for RHmax due to more frequent water condensation in the open favored by stronger daily temperature differences. The buffering capacity was higher in summer compared to the whole year for RH and VPD but not for T in the intermediate cover treatments. The buffering capacity was consistently the highest in the dense cover treatment (respective values in summer for T, RH and VPD: 3.96°C, 5.37%, 1.19 kPa) and the lowest in the O+S treatment (1.53°C, 1.07%, 0.46 kPa). During the summer season, the effect of the shrub layer on the forest area was pronounced in the light cover treatment for T and VPD but not for RH. In contrast, its effect was not significant in the medium cover treatment although ΔRHmax was higher in M than in M+S.





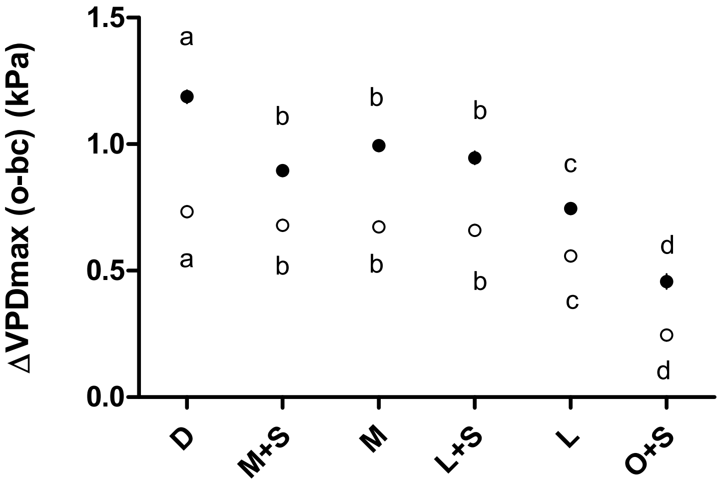
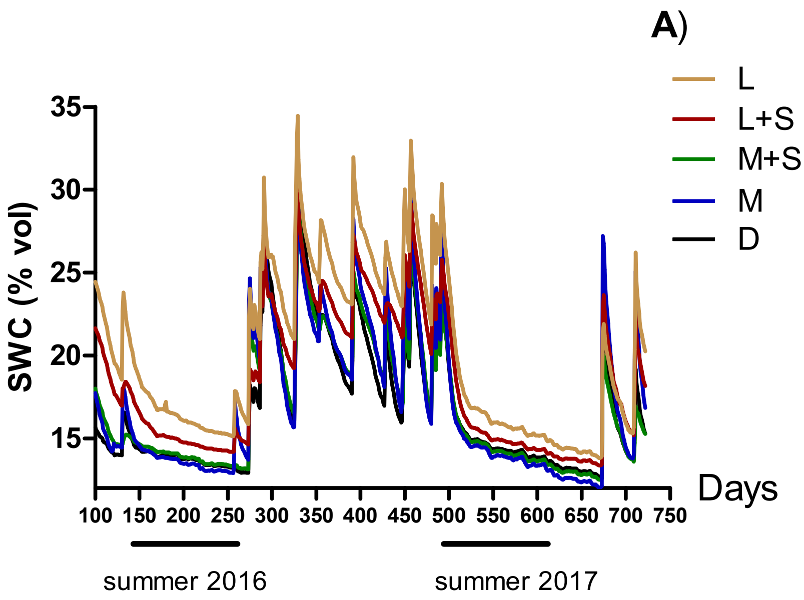
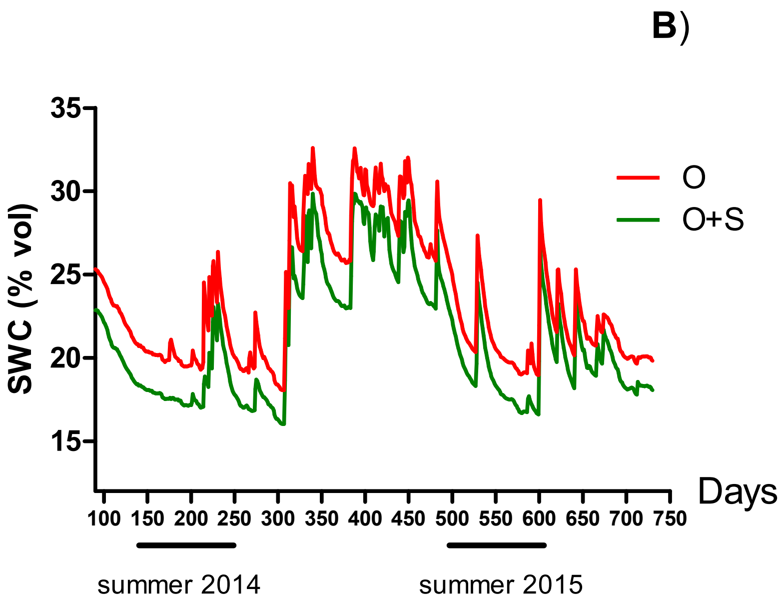


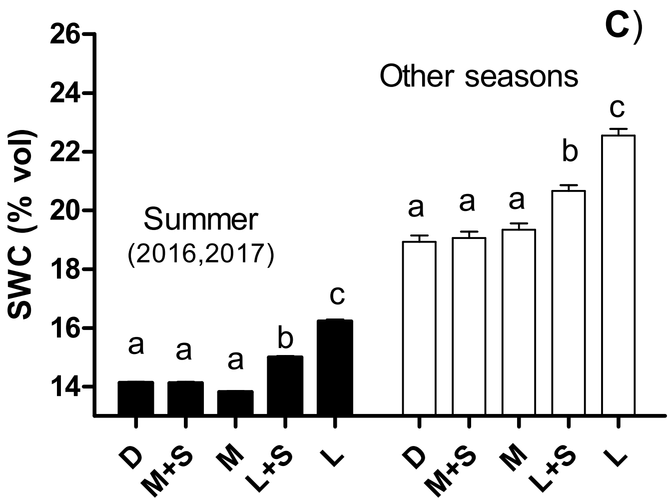
Figure 5. Buffering capacity (mean ± SE) calculated as the difference in maximum daily temperature (ΔTmax), relative humidity (ΔRHmax) and vapor pressure deficit (ΔVPDmax) between treatment O (o, open area) and below-canopy treatments (bc). Letters indicate statistically significant differences for the summer period (black points) and the whole year (white points).

3.3 Soil water content

Variations in soil volumetric water content in both forest and open areas were characterized by several peaks corresponding to rainfall events and a marked decrease during the summer season (Fig. 6A and 6B). In the forest area (Fig. 6A), the L treatment consistently exhibited the highest soil moisture throughout the year. However, the differences among the treatments were less pronounced in summer, particularly during the dry year 2017 (values ranging from 13.8% to 16.2%), compared to the other seasons (18.9% to 22.6%, Fig. 6C). The shrub cover had a negative effect on soil moisture in the L treatment, both during the summer and the whole year. Similarly, in the open area, soil moisture values were always higher outside the shrub canopy than beneath the shrub canopy for the two years of measurement (Fig. 6B). As summers were wetter in 2014 and 2015 (years of SWC measurement in the open area), variations in soil moisture values were similar between the summer period (18.7% to 21.2%) and the other seasons (22.3% to 24.8%) (Fig. 6D).




B)
SWC (% vol)
35
30
25
20
15
O
O+S
Days
100 150 200 250 300 350 400 450 500 550 600 650 700 750
summer 2014
summer 2015


C)
Other seasons
SWC (% vol)
26
24
22
20
18
16
14
Summer
(2016,2017)
a a a b c
a a a b c
D M+S M L+S L
D M+S M L+S L

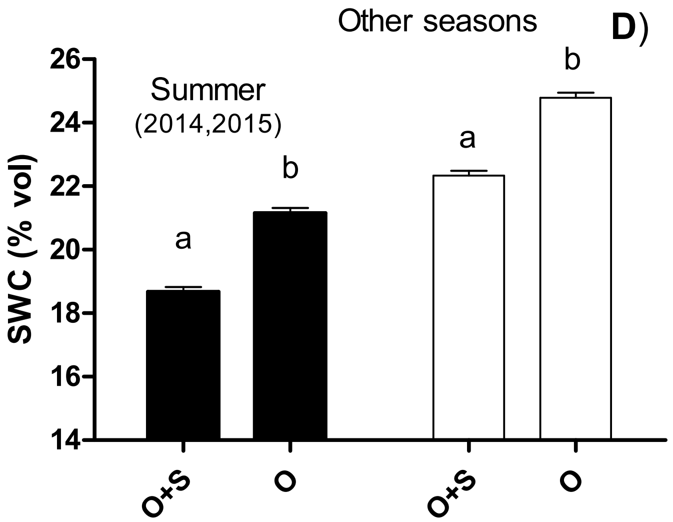

Other seasons
D)
SWC (% vol)
26
24
22
20
18
16
14
Summer
(2014,2015)
a b
a b
O+S O
O+S O

Figure 6. Variations in soil volumetric water content (SWC, at 30 cm depth) according to the treatments A) in the forest area (18 April 2016 to 18 April 2018), B) in the open area (18 April 2014 to 18 April 2016). Mean SWC according to the treatments during summer and other seasons C) in the forest area and D) in the open area. Letters indicate significant differences among the treatments for a given period (summer/other seasons).

4. Discussion

4.1 Variation in microclimatic variables

Values of pine transmittance in the PAR domain are in the same range as those recorded in previous studies on Aleppo pine forests. Cooper et al. (2014) recorded in Israel a transmittance of 14-23% for a basal area between 14-16 m^2 ha^{-1}, while in Spain, it ranged from 14.7% in dense closed pine stands (32 m^2 ha^{-1}) to 36% in more open stands (12.4 m^2 ha^{-1}) (Gavinet et al., 2015). The shrub transmittance was strongly correlated with its cover percentage following the formalism of the Beer-Lambert's law (Fig. 2B). The extinction coefficient (k) of 0.019 found in this study indicates moderate light interception compared to other species. For instance, in temperate forests, the transmittance of *Calluna vulgaris* (L.) Hull was found to be very high (k between 0.004 and 0.012) but it was considerably reduced by *Rubus fruticosus* L. (k=0.074) (Gaudio et al., 2011; Balandier et al., 2013). The influence of the understory vegetation on transmittance was only clearly marked in the light pine cover treatment and in the open treatment, whereas in the medium pine cover treatment the moderately developed understory only had a weak effect on light interception.

The increase in transmittance with decreasing pine cover mainly explains the gradient of increased T and VPD and decreased RH from closed canopies (D) to open conditions (O). The effect of the shrub layer on the microclimate was also consistently significant and more pronounced in the light pine cover and open treatments. This is probably linked to a shading effect and the reduction of air movement, leading to higher humidity and a reduced temperature gradient (Kovács et al., 2017; Unterseher and Tal, 2006). In mixed oak stands, Clinton (2003) also found that the sclerophyllous evergreen shrub *Rhododendron maximum* L. significantly lowered air temperature; while Williams and Ward (2010) found that relative air humidity was positively related to the development of a thorny invasive shrub (*Berberis thunbergiide* DC.) in eastern USA. These gradients are more pronounced during the summer season than the whole year due to stronger solar radiation, which varies on average from 269 W/m^2 in summer to 168 W/m^2 for the whole year in our study area.

4.2 The effect of the vegetation cover on daily range and the buffering capacity

The daily ranges for T, RH and VPD (Fig. 4) increased along a decreasing vegetation gradient (from D to O). Shading provided by the overstory and understory vegetation cover, prevents the solar shortwave radiation from reaching the forest floor and warms up the near-surface air, resulting in lower Tmax and VPDmax values, and higher RHmin values. Furthermore, fluctuations are dampened in the presence of vegetation cover due to the reduction of the longwave radiative losses during the night (Rambo and North, 2009). Amplitudes are also higher during the summer season. This is mainly driven by the increase in solar radiation during the summer period which results in a stronger buffering effect of the vegetation layers, as has been reported in previous studies (Renaud and Rebetez, 2009; Renaud et al., 2011; von Arx et al., 2012).

The buffering capacity (Fig. 5) was more significant under dense cover than under sparse cover (Renaud and Rebetez, 2009; De Frenne et al., 2013; von Arx et al., 2013). This buffering capacity was also more intense during the dry summer period for VPDmax compared to the whole year. In contrast, in sparse evergreen temperate forests in Switzerland, von Arx et al. (2013) noted an absent or very low buffering capacity during the summer dry season on Tmax and VPDmax. They attributed this finding to more intense solar radiation during this period and less cooling by soil evaporation. The ΔTmax, contrary to ΔVPDmax and ΔRHmax, showed similar values in summer and in the whole year, a result also reported in a previous study (von Arx et al., 2012). Certain factors could have played a role, such as lower soil moisture in summer resulting in an attenuation of the evaporative cooling effect (von Arx et al., 2012).

The effect of the shrub layer on buffering capacity was particularly marked where there was a well-developed shrub layer i.e. in the open and light pine cover treatments. This strong buffering capacity is mainly linked with the light interception of these two treatments. In fact, light dropped down from 100% to 28% under the shrub canopy in open conditions and from 27% under light pine cover without shrub cover to 15% in the presence of shrubs. Taken together, we can conclude that the daily range of microclimatic variables and buffering capacity were primarily driven by overstory cover, as was also reported by Ehbrecht et al. (2019). However, under low overstory cover (L+S), microclimatic variables and buffering were mostly driven by the shrub layer where it was more developed. It must be noted that the buffering capacity of tree cover has not always been observed in the case of pine species. For instance, during the very hot summer of 2003, Renaud and Rebetez (2009) observed in Switzerland that the maximum daily air temperature was higher below the pine canopy, composed of Scots pine and Mugo pine, than in open conditions. They explained this finding by the higher transparency in the crowns at their site that was caused by high pine mortality rates. The role of thermal inertia of the air mass should be also considered in the process of buffering. Indeed, the air temperature in forest stands has been reported to decline more slowly in the afternoon on summer days than would be otherwise expected based on the decline in solar radiation (Gaudio et al., 2017). In contrast, our Aleppo pine stands were healthy, with dense crowns that intercepted about 70% of incoming light.

4.3 Variations of soil moisture

Reducing pine densities (L) increased soil water availability in summer and for the whole year, as reported in other studies (e.g. Bréda et al., 1995; Aussenac, 2000; Giuggiola et al., 2016). In this study, we observed a clear effect of the shrub layer in the light pine cover and open conditions. In both cases, reduced soil moisture beneath shrub canopy was noted. For the forest area, this finding is in line with previous studies. In an understory removal experiment in a Scots pine forest at a dry site in Switzerland, Giuggiola et al. (2018) observed an increase in soil water content at 5 and 30 cm depth. A similar result was found by Zahner (1958) in a mixed *Pinus taeda* - *Pinus echinata* stand in a dry site in USA. However, such an effect is debated in Mediterranean conditions. Under heavy radiation, soil evaporation represents a significant part of the water losses of the ecosystem. In a semi-arid, low density (300 stems ha^{-1}, LAI=1.5) Aleppo pine forest in Israel, Raz-Yaseef et al. (2010) found that soil evaporation could represent 36% of the annual precipitation. In a Mediterranean cork oak (*Q. suber*) stand invaded by *Cistus ladanifer*, Caldeira et al. (2015) found that shrub presence increased soil moisture in the upper 40 cm but decreased it below this point, resulting in an overall reduction in water availability for the oak trees.

In fact, the influence of the shrub layer on the soil moisture depends on several factors. On the one hand, water loss by soil evaporation is reduced due to the shading provided by the shrubby vegetation. In some cases, higher water availability below the shrub layer can also be linked to hydraulic lift (Prieto et al., 2011) or modified soil properties such as porosity, organic matter or texture (Pugnaire et al., 2004). On the other hand, the shrub layer has a detrimental effect on the water budget by transpiration (Simonin et al., 2007; Rascher et al. 2011; Caldeira et al. 2015) and by intercepting a substantial amount of the rainfall. For instance, Llorens and Domingo (2007) in a literature review, reported a mean relative throughfall of about 49% for shrubs and bushes with large variation depending on species and environmental conditions. In our study, the balance between these different processes results in a negative effect on soil moisture which is particularly prominent in open conditions but is not noticeable under moderate and dense pine covers. However, some studies have reported an absence of soil moisture variation between shrubs and nearby open areas (e.g. Gómez-Aparicio et al., 2004) while others have noted higher soil water content beneath the shrub canopy (e.g. Allegrezza et al., 2016). The impact of the shrub canopy on soil moisture may also differ depending on total soil depth (Caldeira et al., 2015) and therefore the water reservoir size. This suggests that the effect of shrubs on the water budget depends on multiple factors such as the species considered, and the climatic and edaphic conditions (Butterfield et al., 2016). It must also be emphasized that during the drought episode of 2017 (46 mm for the period June-October), the soil water content was very low and varied little among treatments in the forest area, suggesting that the influence of the shrubby understory cover is downplayed during such extreme episodes.

5. Conclusions

Very few studies have manipulated the vegetation layer to investigate the role of the understory in regulating forest microclimate. Our experiment reveals the buffering effect of both the overstory and understory on temperature, air humidity and VPD in Mediterranean pine woodlands. This effect is more clearly expressed during the summer period in link with the dominant role of light interception (reduction of the radiative forcing). The influence exerted by the pine overstory on microclimatic variables and their fluctuations is of primary importance. It is only when the tree cover is strongly reduced that the role of the shrub layer is more pronounced and could substitute the overstory which is the primary regulator of microclimatic conditions. These results have management implications for the development of adult trees and woody seedlings. In highly thinned stands (below 20 m^2 ha^{-1}), a well-developed shrub layer can lead to a reduction in soil moisture during the growing season, increasing water stress and thus limiting tree growth. As a consequence, a reduction of the shrub layer can be an option to limit these negative effects on growth. In contrast, the positive effect of shrubs on seedling development has been emphasized by many previous studies, particularly in opened Mediterranean environments (e.g. Gómez-Aparicio et al., 2004, 2005; Heydari et al., 2017). Our results have shown that this positive effect is due to the amelioration of the aerial microclimate, in particular a strong reduction of T, VPD and radiation, although the soil moisture is reduced under the shrub cover. However, this effect also depends on seedling stress-tolerance and ecophysiological strategy (Gavinet et al., 2016) such as sensitivity to air (VPD) and soil droughts (Saccone et al., 2009).

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Supplementary Material

Photos of the treatments: A) treatment M and M+S, the shrub layer was removed on the left part, only young planted seedlings with their protectors were retained B) treatment L (right) and L+S (left). C) Measurement of light beneath the shrub layer with sensor SKP 215. D) Meteorological shelter for iButton logger.

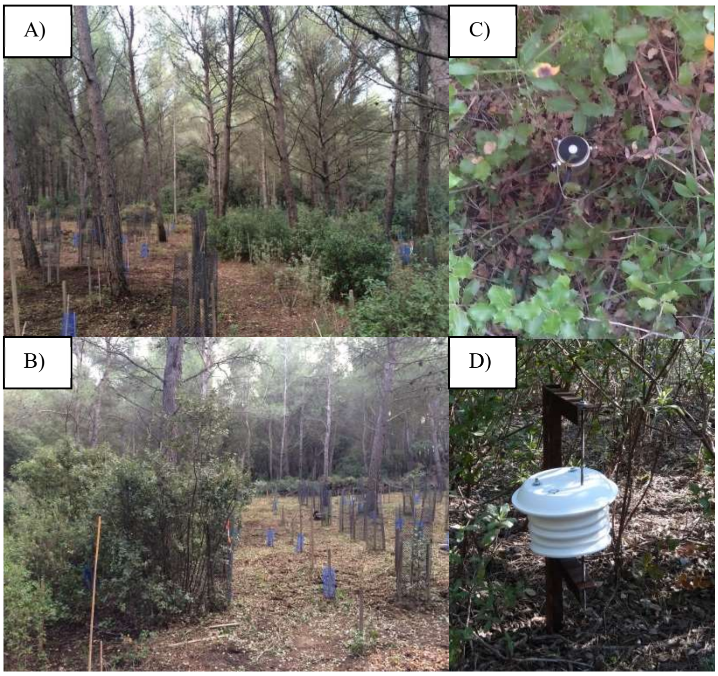

Table S1. Statistics for the different microclimatic variables for the summer period and the whole year.

	Summer		**Whole year**	
	F-value	P-value	F-value	P-value
Mean T	146.01	<0.001	262.92	<0.001
Mean RH	18.46	<0.001	261.23	<0.001
Mean VPD	163.30	<0.001	476.50	<0.001
Tmax-Tmin	319.64	<0.001	666.54	<0.001
RHmax-RHmin	125.19	<0.001	341.11	<0.001
VPDmax-VPDmin	157.87	<0.001	157.87	<0.001
ΔTmax (o-bc)	94.19	<0.001	297.92	<0.001
ΔRHmax (o-bc)	48.33	<0.001	42.50	<0.001
ΔVPDmax (o-bc)	80.69	<0.001	201.92	<0.001