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Physiological and Morphological Response of *Argania spinosa* (L.) Skeels to a Competing Liana: Case Study under Arid Climate

Laila Boukhalef [1], Aicha Nait Douch [1], Laila Bouqbis [1], Abdelhafed El Asbahani [2], Mourad Touaf [1] and Fatima Ain-Lhout [1,*]

1   Equipe d'Ecologie et Sciences de l'Environnement, Faculté des Sciences Appliquées, Université Ibn Zohr, Azrou 86153, Morocco
2   Laboratoire de Chimie Appliquée et Environnement, Faculté des Sciences, Université Ibn Zohr, Agadir 80000, Morocco
*   Correspondence: f.ainlhout@uiz.ac.ma; Tel.: +212-6660-21070

Abstract: Lianas are woody climbing plants and are thought to impact the hosting trees negatively. *Ephedra altissima* is a liana rising on the Moroccan endemic tree *Argania spinosa* (L.) Skeels. In this study, our objective was to investigate the impact of the liana on the Argan tree's physiology and leaf morphology. For that purpose, we compared gas exchange, relative water content, photosynthetic pigment content, and leaf dry mass per unit area of Argan trees associated and not associated with the liana. Our study on individual leaves does not give evidence of the existence or absence of aboveground competition between the liana and the hosting tree. Indeed, photosynthetic rates may suggest that no aboveground competition is occurring. In contrast, pigment content suggests a shading effect of the liana on the hosting tree during the winter season. Otherwise, Argan associated with the liana exhibited a high Chl a/b ratio at the beginning of the dry season, suggesting a belowground competition for nutrient resources. On the other hand, WUEi results indicate that the impact of the liana on the Argan tree may go through seasons with belowground competition for water during spring. The increased LMA values registered in trees associated with the lianasuggest the existence of belowground competition for nutrient resources that persist throughout the year.

Keywords: *Argania spinosa*; *Ephedra altissima*; photosynthesis; water use efficiency; pigment content; leaf dry mass per unit area (LMA)

1. Introduction

Plant-plant interactions are known as the main biotic factors in vegetation dynamics. Hence, understanding these processes is beneficial for the management of phyto-resources. The interaction mechanisms are very numerous and specific. They depend on the characteristics of the species involved and the nature of the physical environment in which they live [1]. Competition has been widely studied and regarded as the predominant interaction in plants. Competition for resources profoundly influences communities' composition, biodiversity, and dynamics. Consequently, it is considered an essential process in community organizations [2,3].

Lianas are woody climbing plants from a polyphyletic guild. They add significantly to forest dynamics, structure, diversity, and complexity [4]. For millions of years, trees and lianas coexist and the capacity of terrestrial plants to climb is an early innovation [5]. Currently, lianas are expanding in abundance and size relative to co-occurring trees [6–9]. This reported increase in lianas might result from the interaction of several global change mechanisms, such as elevated CO_2, increasing temperature, drought, and changing soil nutrient cycles [10,11].

Trees and lianas compete mainly for resources (nutrients and light), this type of interaction has been described by Stewart and Schnitzer [12] as an antagonistic interaction.

Indeed, lianas are effective aboveground and belowground resource competitors such as light, water, and nutrients [13]. They have pronounced negative effects on the hosting trees, especially on growth and survival [14–19], reproduction [20,21] and recruitment [22,23], and impact tree demography [24]. For example, in a study in the tropical forest of Panama, Visser et al. [24] found that the liana decreased tree survival, growth, and reproduction, with a pronounced effect on the survival of fast-growing and light-demanding tree species. In several cases, they can increase the mortality of the trees that support them [25].

Other studies have led to the conclusion that lianas may have positive effects on co-occurring plants and animals [26]. For instance, lianas can reduce the solar radiation reaching the hosting trees' canopy. Hence, trees' leaves are protected from rising temperatures and increased evaporative demand under the tropics [27]. In addition, by diminishing the soil temperature, lianas can maintain favorable soil conditions (water content and temperature) and protect critical soil biota and carbon reservoirs [28]. In a more recent large-scale study in a dry forest in Panama, including 41 tree species, Estrada Villegas et al. [29] found that liana removal did not affect tree biomass accumulation. More, a decrease in growth rate was registered in only three out of the 41 studied species. According to the authors, these results may have several causes:—they can be due to the allocation of the resources to the roots;—the lack of competition at the root level between trees and lianas, after the liana removal;—the solar radiation involves soil drying;—the water limitation in the dry forests, compensating the negative effects of the liana presence.

The diversity and abundance of liana species vary across ecosystems, climates, and regions but are much higher in tropical forests than in temperate ones [30]. It is noteworthy that during the last 30 years, liana-tree interactions have been studied extensively in tropical ecosystems [13,15,17,18,20,21,24,25,29,31–37]. However, this aspect of ecology has yet to be studied in arid ecosystems.

The occurrence of lianas in arid and semi-arid climate forests is lower than in other environments [38]. However, *Ephedra altissima* is a commune in Argania ecosystems and often behaves similar toa liana (more than 3 m long) with climbing stems rising on the Moroccan endemic *Argania spinosa* (L.) Skeels tree. The liana's leaves are reduced in size. The total assimilation rate of the leaves is neglected because it is significantly smaller than the total assimilation rate of the green shoots of the liana [39].

The Argan is the most prominent tree in the vegetation of Morocco. Argan forests cover 900,000 hectares in the west central arid and semi-arid areas of Morocco [40], where they play an essential role for the local population [41] and constitute an ecological barrier against desertification [42]. *A. spinosa* is a slow-growing tree well adapted to arid environments. These species adjust the leaves' traits and physiological responses to grow under arid, harsh conditions where no other tree can live. Physiological mechanisms of *A. spinosa* adaptations to drought under different environmental conditions have been identified [43–53]. In addition, it has been shown by Alados and El Aich [54] that this tree can adjust its aerial structure in response to browsing and drought conditions. Despite being declared in 1998 UNESCO Biosphere Reserve, the Argan forest is suffering a pronounced fragmentation of its habitat. Indeed, around half of the forest disappeared in the last century, and the forest density decreased to fewer than 30 trees per hectare [41].

Given the ecological and socio-economic importance of the Argan tree and the local threats to the species, it is of interest to investigate the impact of the liana on the Argan tree's physiology and leaf morphology. For this purpose, we seasonally measured net photosynthetic rate, stomatal conductance, instantaneous water use efficiency, relative water content, chlorophyll, and carotenoids pigments content, and leaf dry mass per unit area in Argan trees associated and not associated with the liana *E. altissima*.

2. Material and Methods

2.1. Study Site and Plant Material

The study was conducted in the Souss valley, in the Admin forest(30°40′86.3″ N, 9°12′74.6″ W). According to the Köppen Climate Classification System, the climate is

Arid-Steppe-hot arid [55]. During the studied period (February 2016–January 2017), the highest average temperature was recorded in July (28 °C), while the lowest average temperature was registered in December and January (9 °C). Precipitation is irregular in space and time, with an average annual of 230 mm. The Admine forest is located in an area described by several authors as the ecological optimum for the *A. spinosa* species [50,56]. The daily climatic data of the study site were obtained from the NASA Power Data Access Viewer [57] (https://power.larc.nasa.gov/data-access-viewer, accessed on 15 August 2022). The natural vegetation in the study site is very scarce. Moreover, the *A. spinosa* and *E. altissima*, these vegetations are limited to some spiny shrubs such as *Ziziphus lotus*.

Four periods were selected to study the liana's impact on the *A. spinosa* tree's physiological response and leaf morphology throughout the climatic seasonality: February, characterized by water availability and low temperatures combined with high solar radiation; early June, which coincides with the end of the growing period of spring season; September, end of summer, maximal water deficit, high temperature, and solar radiation; early December, end of autumn which coincides with the recovery period after autumn precipitations.

Ten well-developed trees were selected according to the presence or absence of association with one individual of the liana *E. altissima* (Table 1). The Lianas were with approximately similar biomass. Hereafter, Argan trees associated with the liana are called Arg-Eph., and Arg. are the trees not associated with the liana.

Table 1. Tree morphological traits (trunk perimeter, tree height, canopy size, leaf area), and liana canopy cover.

	Trunk Perimeter (m)	Tree Height (m)	Canopy Size (m^3)	Leaf Area (cm^2)	Liana Canopy Cover (%)
Arg.	1.44 ± 0.04	4.26 ± 0.33	112.95 ± 6.53	1.94 ± 0.29	-
Arg-Eph.	1.51 ± 0.08	4.21 ± 0.37	119.93 ± 15.96	1.85 ± 0.35	10–20%

At the level of each tree and during the four periods, leaf samples were collected and then kept in the freezer at −24 °C, until analysis.

2.2. Gas Exchange

Measurements were carried out during sunny days, in the morning between 8:00 a.m. and 11:00 a.m. Four measurements per tree were carried out by an infrared gas exchange analyzer (LCi-SD, ADC, Hertfordshire, UK) equipped with a measurement chamber. CO_2 assimilation rate (A_{Net}, μmol CO_2 m^{-2} s^{-1}) and stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}) were measured in both trees, infested and not infested by the liana. We noted that throughout the study period, the host trees produced practically no leaves in the crown parts where the liana developed (Figure 1). So, we selected sun-exposed leaves to avoid shading by the tree leaves (self-shading).An estimation of instantaneous water use efficiency (WUE_i, μmol mmol^{-1}) was made by calculating the ratio between the net photosynthesis rate and the transpiration rate. As the results of the photosynthetic activity are expressed based on leaf area, all the recorded leaves were scanned, and their leaf area was calculated by the software Midebmp [58].

2.3. Water Status

The relative water content (RWC) was calculated according to [59]:

$$\text{RWC (\%)} = \frac{\text{FW} - \text{DW}}{\text{TW} - \text{DW}} \times 100$$

where FW, TW, and DW are respectively the fresh, turgid (after allowing the leaves to hydrate to saturation in distilled water), and dry mass (after drying them at 80 °C until a constant weight was obtained).
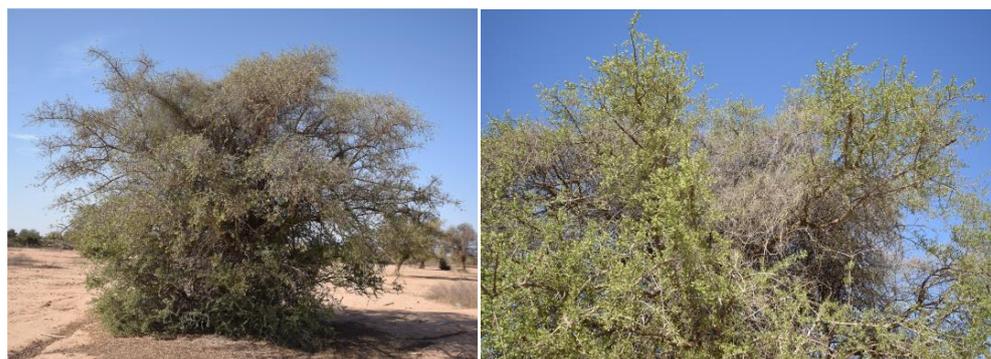
Figure 1. *Argania spinosa* associated with the liana *Ephedra altissima*.

2.4. Photosynthetic Pigment Content

In order to determine the Chlorophyll content ($\mu g\ cm^{-2}$) and carotenoid content ($\mu g\ cm^{-2}$), pigments were extracted under low irradiance with 100% acetone from leaf samples ($n = 20$). The homogenate was filtered, and the absorbance was measured by a spectrophotometer at the wavelengths of 661.6 nm, 644.8 nm, and 470 nm for Chlorophyll a (Chl a), Chlorophyll b (Chl b), and carotenoids (Car), respectively. The concentration was calculated according to [60].

2.5. Leaf Dry Mass per Unit Area

The leaf dry mass per unit area (LMA, $g\ m^{-2}$) was estimated by the ratio between the dry weight of a leaf and the surface area of the same leaf. At the level of each tree, well-developed sun-exposed leaves were measured ($n = 20$). At the level of each leaf, the surface area was calculated by Midebmp digitization software [58], then the dry weight was measured after drying in an oven at 80 °C until a constant weight was obtained.

2.6. Statistical Analysis

The statistical analyses were conducted by SPSS statistical software (IBM SPSS Statistics 20, Inc., Chicago, IL, USA). A Two-way ANOVA test was performed to assess the effect of independent variables (tree and season) on the dependent variables (Ecophysiological parameters). When normality was not assumed, the Kruskal-Wallis test was performed. Post-hoc Tukey or Tamhane tests were used to compare pairwise differences within the season. We considered that the statistical tests were significant at $p < 0.05$.

3. Results

Precipitations through the study period were typical of the region, with rains during winter, spring, and autumn and drought during four months from May to September (Figure 2b). The annual precipitations and mean temperature registered during the study period were 290 mm and 22.15 °C, respectively.

Net photosynthesis rate (A_{Net}), stomatal conductance (g_s), and instantaneous water use efficiency (WUE_i) exhibited no significant differences between Arg. and Arg-Eph. (ANOVA, $p > 0.05$). On the contrary, significant differences were registered in A_{Net} and WUE_i throughout seasons (ANOVA, $p < 0.001$). A consistent decrease in A_{Net} and WUE_i was recorded during summer in both groups of trees (Figure 3). Maximum values of A_{Net} and WUE_i were recorded during autumn, 10.71 ± 2.56 and $10.51 \pm 5.43\ \mu mol\ CO_2\ m^{-2}\ s^{-1}$ for A_{Net}, and 5.85 ± 1.79 and $6.37 \pm 2.15\ \mu mol\ mmol^{-1}$ for WUE_i, respectively in Arg. and Arg-Eph. Moreover, the Students' *t*-test results showed a significant difference in WUE_i between both groups during spring ($p < 0.05$).It is noteworthy that high values in standard deviation are due to the pronounced intraspecific phenotypic variation. This results from a high level of heterozygosity in *A. spinosa* [61].
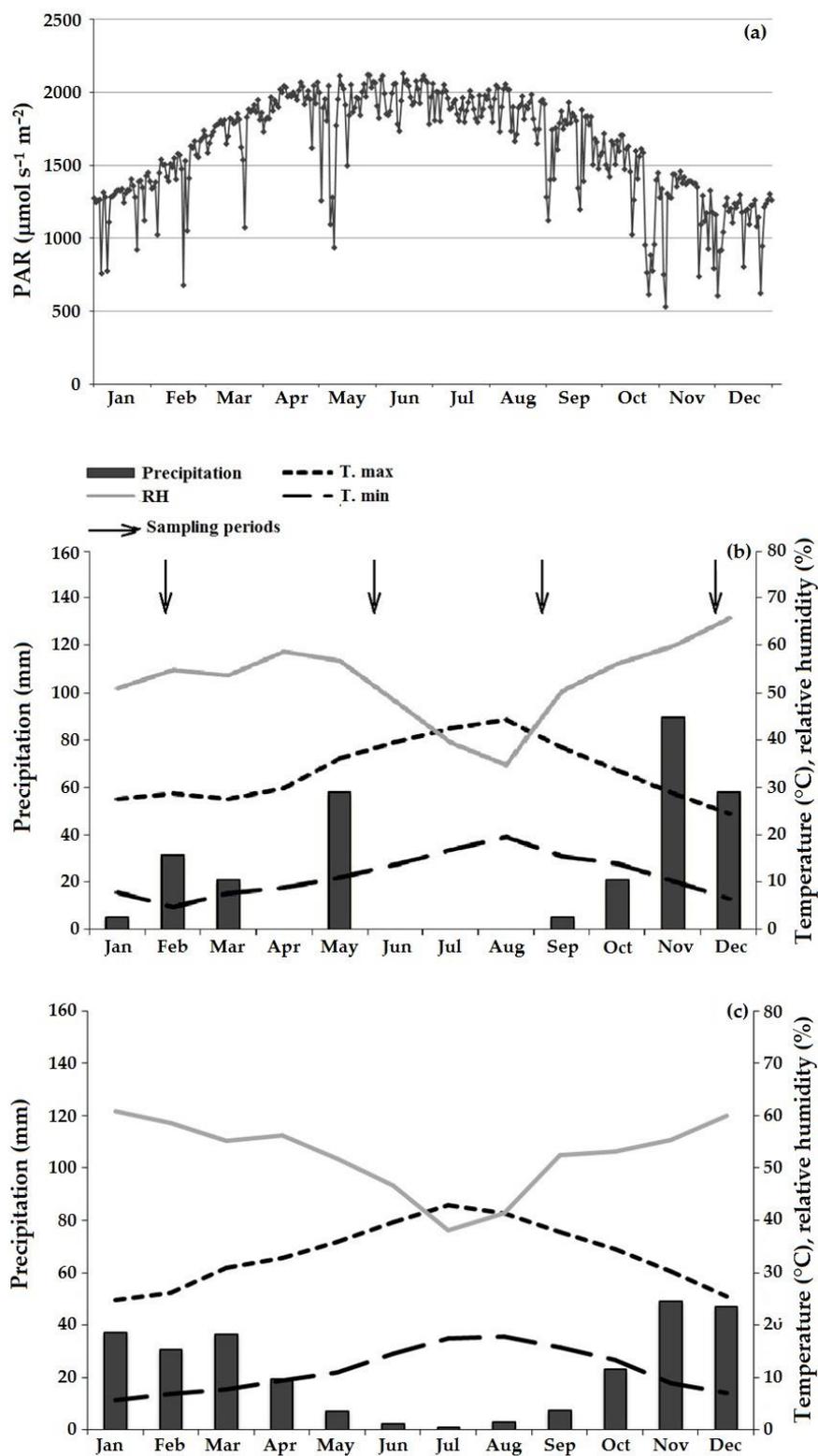
Figure 2. (**a**) Daily maximum photosynthetically active radiation (PAR, µmol s^{-1} m^{-2}), and (**b**) Annual precipitations (mm), monthly relative humidity (RH, %), monthly maximum and minimum temperature (°C) during the study period (from January to December 2016) in the Admine forest.(**c**) Average (1996–2015) annual precipitations (mm), monthly relative humidity (RH, %), monthly maximum and minimum temperature (°C) in the Admine forest.
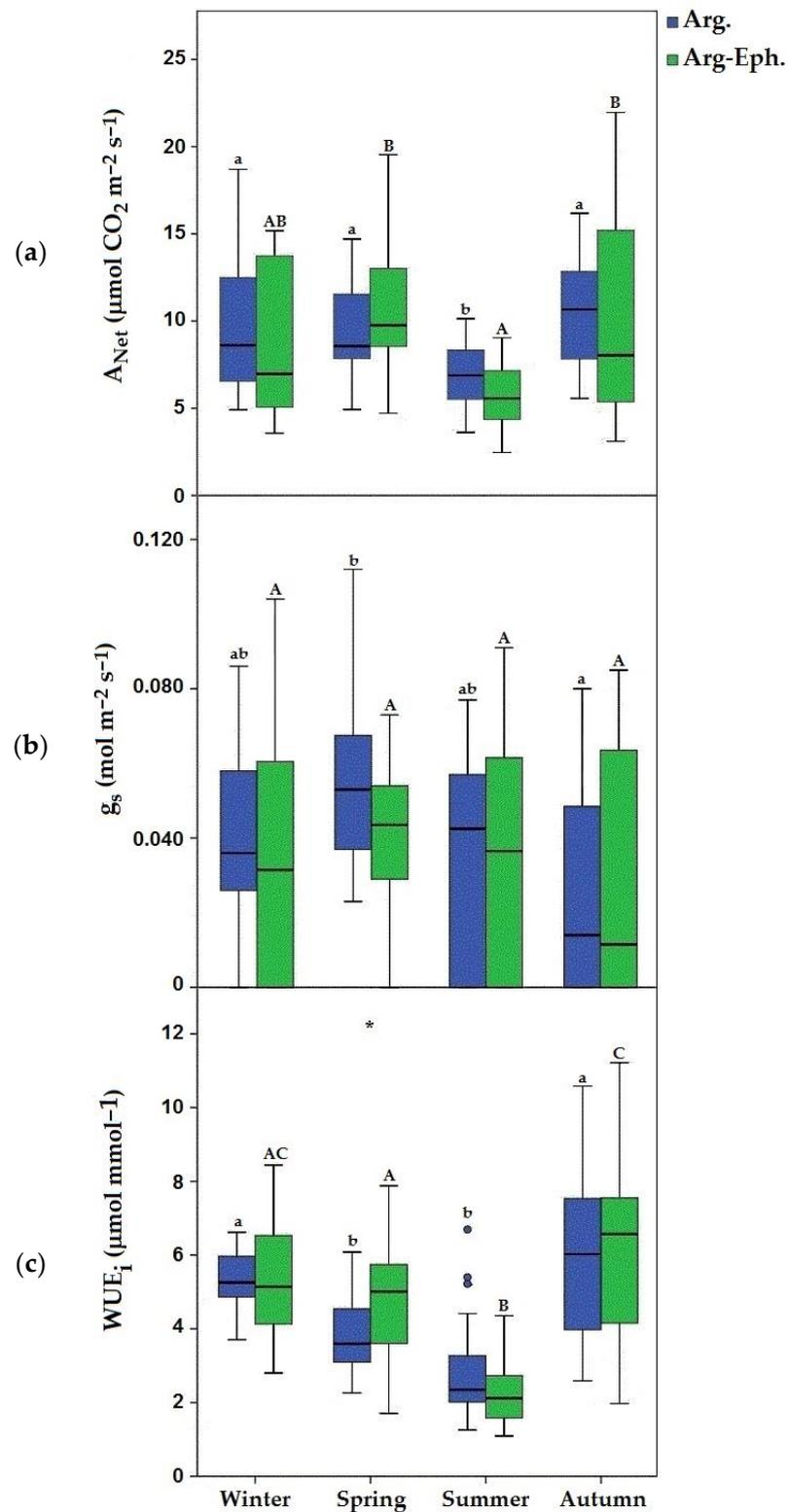
**Figure 3.** Box plots of the Net photosynthetic rate, A_{Net} (**a**), stomatal conductance, g_s (**b**) and instantaneous water use efficiency, WUE_i (**c**), of the Argan trees with (Arg-Eph.) and without the liana (Arg.) throughout the study period. The asterisks show significance levels when comparing the two sites within each season by students' *t*-tests (* $p < 0.05$). Lower-case and upper-case indicate Post-hoc test results.

Relative water content (RWC) showed a seasonal pattern in both studied trees (Table 2). ANOVA test results showed significant differences between seasons ($p < 0.001$), but no significant differences were recorded between both groups of trees ($p = 0.791$). Minimal values were recorded at the end of the summer season (68.51 $\pm$ 4.00 and 65.41 $\pm$ 8.51% for Arg. and Arg-Eph., respectively), and maximum values in autumn (82.35 $\pm$ 3.58 and 83.07 $\pm$ 4.91% for Arg. and Arg-Eph., respectively).

Table 2. Leaves attributes mean values ($\pm$SD) of the Argan trees with (Arg-Eph.) and without the liana (Arg.) throughout the study period. The asterisks show significance levels when comparing the two sites within each season by students' *t*-tests (* $p < 0.05$). Lower-case and upper-case indicate Post-hoc test results.

	Winter		Spring		Summer		Autumn	
	Arg.	Arg-Eph.	Arg.	Arg-Eph.	Arg.	Arg-Eph.	Arg.	Arg-Eph.
RWC	68.7 $\pm$ 2.41 a	70.63 $\pm$ 5.56 AB	71.85 $\pm$ 5.58 a	72.60 $\pm$ 4.90 B	68.51 $\pm$ 4.00 a	65.41 $\pm$ 8.51 A	82.35 $\pm$ 3.58 b	83.07 $\pm$ 4.72 C
Chl a	40.58 $\pm$ 14.74 a*	54.16 $\pm$ 13.55 A*	48.55 $\pm$ 9.01 a	56.39 $\pm$ 12.64 A	39.03 $\pm$ 11.72 a	35.80 $\pm$ 10.54 B	50.12 $\pm$ 8.66 a	48.90 $\pm$ 8.96 A
Chl b	17.70 $\pm$ 7.34 a*	24.96 $\pm$ 6.89 A*	28.99 $\pm$ 7.24 b	24.24 $\pm$ 7.29 A	17.27 $\pm$ 6.42 a	20.69 $\pm$ 8.90 A	21.97 $\pm$ 5.50 ab	25.70 $\pm$ 7.10 A
Chl a/b	2.44 $\pm$ 0.42 a	2.25 $\pm$ 0.27 AB	1.77 $\pm$ 0.24 b*	2.72 $\pm$ 0.76 B*	2.41 $\pm$ 0.45 a*	1.94 $\pm$ 0.33 A*	2.37 $\pm$ 0.31 a	2.08 $\pm$ 0.63 AB
Car	14.08 $\pm$ 5.15 a*	18.97 $\pm$ 6.02 A*	17.15 $\pm$ 2.93 a	18.61 $\pm$ 5.13 A	13.04 $\pm$ 3.96 a*	16.46 $\pm$ 5.20 A*	15.24 $\pm$ 3.11 a	15.92 $\pm$ 2.66 A
LMA	117.81 $\pm$ 13.37 a	131.12 $\pm$ 35.10 AB	133.87 $\pm$ 20.83 b*	149.1 $\pm$ 34.63 B*	138.96 $\pm$ 21.35 b	144.25 $\pm$ 25.70 B	110.15 $\pm$ 19.78 a	113.8 $\pm$ 20.31 A

RWC relative water content (%), *Chl a* Chlorophyll a (μg cm^{-2}), *Chl b* Chlorophyll b (μg cm^{-2}), *Chl a/b* ratio of chlorophyll a to chlorophyll b, *Car* Carotenoids (μg cm^{-2}), *LMA* leaf surface area (g m^{-2}).

Chl a content showed minimal values during the summer season (Table 2), around 39.03 $\pm$ 11.72 μg cmg^{-2} and 35.80 $\pm$ 10.54 μg cmg^{-2} respectively in Arg. and Arg-Eph. Maximal values occurred in autumn for Arg. (50.12 $\pm$ 8.66 μg cmg^{-2}), and in spring for Arg-Eph. (56.39 $\pm$ 12.64 μg cmg^{-2}). Significant differences were recorded between Argania trees associated and not associated with the liana for Chl a and Chl b during winter (students' *t*-test, $p < 0.05$). Concerning the Chl a/b ratio, students' *t*-test results showed no significant differences between both groups of trees during winter and autumn (Table 2). In contrast, significant differences were recorded during spring and summer ($p < 0.05$). The Argan trees associated with the liana showed a peak in the Chl a/b ratio (2.72 $\pm$ 0.75) during spring. Car content showed significant differences between both groups of trees during winter and summer (students' *t*-test, $p < 0.05$).

For LMA, analysis of variance detected significant differences between trees and seasons, respectively, $p < 0.05$ and $p < 0.001$. The Argan trees associated with the liana exhibited the highest values of LMA during all of the studied periods (Table 2). Argan trees with and without liana exhibited the lowest values of LMA during the autumn season, 113.80 $\pm$ 20.31 g m^{-2}, in the Arg-Eph., and 110.15 $\pm$ 19.78 g m^{-2} in the Arg. trees. The highest values were recorded during the summer season, with values of about 149.1 $\pm$ 34.63 g m^{-2}, in the Arg-Eph. and 138.96 $\pm$ 21.35 g m^{-2} in the Arg. trees.

4. Discussion

In our study trees associated and not associated with the liana exhibited a similar trend in carbon assimilation and stomatal conductance throughout the year with a seasonal variation. A decrease in the A$_{Net}$ and stomatal conductance were registered at the end of the summer season. This strategy is common in plants to conserve water under drought conditions. Consequently, CO_2 fixation is limited, and assimilation rates are reduced [50,52]. In addition, other factors may decrease CO_2 assimilation rates, such as mesophyll limitation and Rubisco kinetic [62]. Furthermore, when water was available in autumn, we registered a decrease in stomatal conductance in both groups of trees. This suggests the existence of other mechanisms of control, such as leaf phenology or photoinhibition [63]. The same results have been described in previous work on the same species [50].

Concerning liana-tree interactions, lianas compete aboveground with the hosting tree by displaying their leaves on the tree crown, diminishing the light the plant below intercepts [16]. We noted that the host trees produced practically no leaves in the crown parts where the liana grows. In addition, the leaves of the liana *E. altissima* are small in size. Given these two considerations, it is expected that the *E. altissima* shading effect may be reduced compared to lianas growing under tropical ecosystems.

Our results show that the Argan trees associated and not associated with the liana exhibit similar photosynthetic rates. This finding may suggest that no aboveground competition is occurring between the liana and the host tree based on this parameter. Still, our experimental design does not allow us to confirm it—the present study assessed photosynthetic rates on Argania's sun-exposed leaves.

Otherwise, no significant differences in stomatal conductance were recorded between trees associated and not associated with the liana. The same result was found by Dillenburg et al. [33] in a study on *L. styraciflua* where the stomatal conductance of the tree was not affected by competition with liana vines growing above it.

However, during winter, infested trees exhibited higher Chl a and Chl b content than no infested trees. This increase in chlorophyll content may be due to the shading effect of the liana. Indeed, an increment in chlorophyll content under shade conditions has been described in several studies [64–66]. Otherwise, during the spring season, Chl a increased while Chl b was maintained at a similar level in infested trees, resulting in a higher Chl a/b ratio. Hikosaka and Terashima [67] suggested that this ratio increases under high solar radiation combined with low nitrogen availability. Under high light, when N supply becomes limiting, N allocation to the PSII is increased, whereas N allocation to the LHCII is maintained at a similar level. Moreover, Kitajima and Hogan [68] suggested that the Chl a/b ratio can be used in plant response to nitrogen limitation studies since it indicates nitrogen partitioning among the different photosynthetic components. Many studies showed that the Chl a/b ratio might increase in response to a decrease in the leaf's nitrogen content [67–71]. Maximal annual solar radiations are registered at the end of spring (Figure 1a). In addition, the host tree may be competing for soil nutrient resources with the liana [12], which decreases the N availability for the infested trees in comparison with no infested trees. Both tree groups showed a drop in chlorophyll content in the summer season. This behavior is a typical symptom of oxidative stress induced by drought and excess radiation [67,72–74] and has been described in several Mediterranean communities [13].

One of the major traits of the water economy, functioning, and survival capacity of plants is the WUE [75,76]. Trees from both groups show a similar pattern for WUE_i, with progressively decreasing values from winter to summer season. Students' *t*-test showed a significant difference between both groups during spring ($p < 0.05$). Indeed, the Argan trees with liana exhibited increased values of WUE_i than the Argan trees without liana during that period. This result indicates that the Argan infested by the liana uses water more economically during the growing period of spring [77]. This finding suggests that the impact of the liana may go through seasons of reduced and increased competition from lianas, as described by Toledo-Aceves [16] and Alvarrez-Cansinoet et al. [37]. During the growing season of spring, competition for water may induce infested trees to use water more economically, maintaining a water status similar to those not infested by the liana. Indeed, RWC results showed no significant differences between both groups of trees in spring. Similar results were found by Barker and Pérez-Salicrup [34] in an experiment on *Swietenia macrophylla* trees with and without lianas. Trees exhibited similar water relation status even during the dry season. In our study, RWC results showed a seasonal pattern with maximal values during the favorable season and minimal values during the dry season. This indicates that after the summer stress, all the trees recovered after the autumn precipitations, which is common in arid and semi-arid lands [78]. Among the leaf morphological characteristics, the LMA (biomass quantity invested in the construction of a unit area) is closely related to the plants' ecological performances [79]. Our results

show that the liana has a significant impact on the LMA of the hosting tree. The Argan trees associated with the liana exhibited the highest values of LMA in all seasons. It is well known that an increase in LMA can be induced by several environmental stresses [80], drought stress [81], low winter temperatures [82], elevated radiations [83], or nutrient limitation [84]. WUE_i and Chl a/b ratio results suggest a belowground competition for water and nutrients during the growing season, spring. These outcomes follow the LMA results, which suggest that competition for nutrient resources may persist throughout the year.

5. Conclusions

Our study on individual leaves does not give evidence of the existence or absence of aboveground competition between the liana and the hosting tree. Indeed, photosynthetic rates may suggest that no aboveground competition is occurring. In contrast, pigment content suggests a shading effect of the liana on the hosting tree during the winter season. WUE_i results showed that the impact of the liana on the Argan tree might go through seasons with belowground competition for water during the growing season. LMA results suggested the existence of belowground competition for nutrient resources that persist throughout the year.

Further investigations should consider the whole plant level to give more insights into *A. spinosa* and *E. altissima* interactions. It must include a liana-cutting experiment monitoring over an extended period. In addition, under the actual context of climate change and the imposed stress by the environment, especially drought, a further study, including interactions between the liana and *A. Spinosa*, under a controlled experimental survey (with contrasting water and soil nutrient availability), might provide broader insights into this competition process.

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