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The impact of browsing intensity on argan trees in the Essaouira region of Morocco

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ABSTRACT

Pastoralism is a cornerstone of the argan forest ecosystem in Morocco, where the argan tree supports food production and livelihoods. However, overbrowsing threatens this ecosystem, underscoring the need for sustainable management strategies. This study assessed the impact of three browsing intensities on argan trees in the Essaouira region: no-browsing, moderate-browsing (managed browsing or the Agdal system), and heavy-browsing systems. Measurements of argan physiological and biochemical traits and soil parameters revealed significant differences among the three-browsing intensities. Heavily browsed argan trees exhibited reduced photosynthetic efficiency, stomatal conductance, photosynthetic pigments content, and leaf area index, while no-browsing system maintained optimal performances. The Agdal strategy significantly enhanced plant health compared to heavy browsing, improving physiological indicators and soil quality. Soil traits including electrical conductivity, moisture, and organic matter and total nitrogen content were notably better under managed browsing, promoting healthier argan ecosystems. Additionally, browsing intensity affected leaf biochemistry: overbrowsing induced a decline in protein content, while it enhanced total soluble sugars, malondialdehyde, and hydrogen peroxide content, and antioxidant enzymes activity (catalase, peroxidase, and polyphenoloxidase), reflecting heightened stress responses. Overall, even if the non-browsed trees performed best, the moderate-browsing system (Agdal) may be the most suitable of the three browsing systems, since it will be able to meet goats' feed needs while ensuring the sustainability of the argan forest ecosystem.

1. Introduction

Browsing domestic livestock in forested ecosystems is a globally widespread practice (Galleguillos et al., 2018), which is increasingly thought to affect vegetation in a number of ways, including on species structure and composition (Okick et al., 2025). Moreover, this practice is often associated with negative impacts on plant performances. Typically, herbivores reduce leaf area available for photosynthesis, withdraw biomass, and cause structural damage (Redondo-Gómez et al., 2010). These impacts collectively undermine plant growth and health, constituting a significant biotic stressor for numerous plant species (Shen et al., 2019). Moreover, the influence of livestock browsing on plant morphology is extensively documented revealing decreases in plant height, shoot internode length, and leaf area (Li et al., 2021).

Argania spinosa (L.) Skeels, a *Sapotaceae* tree, is indigenous to southwestern Morocco, with an area of around ~950,000 ha (El Abbassi et al., 2014; Kirchhoff et al., 2019). The tree plays an essential ecologic, botanic, and socio-economic purposes, particularly for the local rural population of southern Morocco (Chakhchar et al., 2022). More than 1.3 million people depend on the argan tree for their traditional sylvo-pastoral systems in rural areas (Chaussod et al., 2005). The argan tree is a well valuable species, primarily for the vegetable oil derived

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from its seeds, which has gained significant economic importance in international markets (Aabd et al., 2014; Charrouf and Guillaume, 2014; Lybbert et al., 2010). Over the past two decades, argan oil, famous for its nutritional and cosmetic benefits, has become increasingly popular, with its production largely managed by women cooperatives, showcasing its socio-economic and cultural significance (Diaz-Barradas et al., 2013).

Despite the fact that *A. spinosa* is well adapted to the arid conditions of southwestern Morocco, its population is threatened since it is the only source of forage during dry periods (De Waroux and Lambin, 2012; Kirchhoff et al., 2019). Goats consume both the leaves and the pulp of the argan fruit, either on the ground or through aerial browsing, and it is an important pastoral resource, accounting for about 75% of their diet in early autumn (El Aich et al., 2005). Research reported that the over-browsing and overexploitation of argan fruits are two interrelated factors that have led to reduced natural regeneration and tree density, which are major issues in maintaining the argan forest (Santoro et al., 2023). According to De Waroux and Lambin (2012), the density of argan trees decreased by 44.4 % in Awluz region (Morocco) between 1970 and 2007, where most of the small-sized argan trees were located in a deteriorated state (Kirchhoff et al., 2022). Additionally, by 2009, the rate of argan forest degradation was about 610 ha/year (Alaoui, 2009). However, recent studies are exploring innovative solutions for reforestation of the argan tree, using advanced biological and ecological technologies to improve reforestation success and densification of the argan grove (Chakhchar et al., 2022; Fassih et al., 2024).

Research indicates that browsing effects on plant photochemical efficiency are contingent upon the intensity and frequency of browsing. Depending on these variables, browsing may either enhance or diminish photosynthetic activity (Li et al., 2021). A previous study conducted in the Agadir region (Morocco) investigated the possible effects of browsing on physiological performance of the argan tree. The results showed that moderate browsing during the favourable season can stimulate photosynthesis, as trees compensate for herbivory-induced leaf loss by boosting photosynthetic activity and reducing water use and oxidative stress (Nait Douch et al., 2022). At present, we still do not completely understand argan tree physiological and biochemical behaviours that occur at different browsing intensities. Therefore, the objectives of the present study are: (i) to investigate the impact of three various intensities of browsing (a no-browsing control, a moderate (managed) browsing, and a heavy browsing) on *A. spinosa* physiological and biochemical traits, including chlorophyll fluorescence, stomatal conductance, pigment and compatible solute content, membrane lipid peroxidation, and antioxidant activities. (ii) to assess the impact of browsing intensities on soil physicochemical properties. We hypothesize that increasing the browsing intensity negatively impacts argan performances and soil health.

2. Materiel and methods

2.1. Study sites description

The study was carried out in the Boutazart argan forest (31°540 1800N, 8°020 0800W, 103 m altitude) in the Essaouira region, Morocco (Fig. 1). The climate of this area is semi-arid, with annual rainfall not exceeding 193.6 mm and 21.4 °C as average annual temperature.

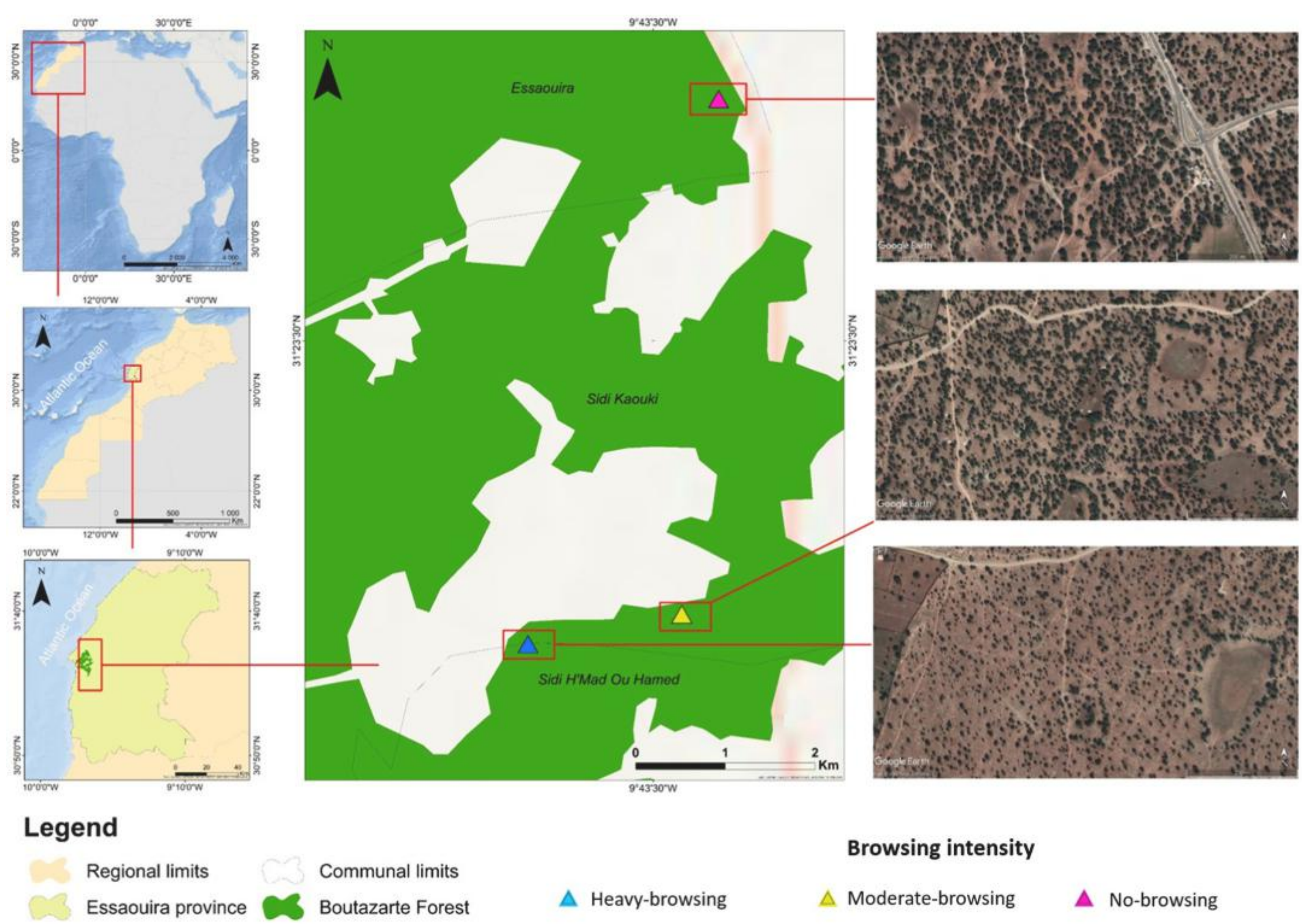

Fig. 1. Study site locations in the Boutazart forest, Essaouira region, Morocco.

January sees the lowest absolute temperature of 5.07 °C, while August sees the highest absolute temperature of 47.7 °C. In the study area, the most browsed and dominant species is *A. spinosa*, accompanied by some grass. The grass contribution to the goats' diet is very low (less than 5 %) and limited to the period after the rains which means that the main source of the goat's feed is the argan tree. Over the last few years, the number of goats has been considerably reduced due to periods of drought and very expensive feed. The Boutazart area has between 400 and 500 goats browsing every day, corresponding to around 1000 to 1200 ha. In December 2022, three 1-ha sites of different intensity of browsing were defined to evaluate the effects of pastoralism on the argan ecosystem (Fig. 1). A no-browsing system (31°24′57.3″N, 9°43′06.4″W) without pastoral activity and a density of argan trees of around 59 trees per hectare. A moderate-browsing system (Agdal system) (31°21′51.3″N, 9°43′19.7″W) with a daily pastoral activity from mid-August to mid-May and a density of about 69 trees per hectare. The browsing is suspended from mid-May to mid-August to allow argan fruit ripening and harvest. A heavy-browsing system (31°21′40.6″N, 9°44′15.2″W) subjected to daily pastoral activity throughout the year, where the density of argan trees is around 48 trees per hectare.

At each browsing system, ten similar-size trees were randomly and permanently labelled for the study experiment, aiming to monitor the same argan trees during the period of the study. Measurements were performed, in the field, each month during the annual cycle (from December 2022 to November 2023). Physiological measurements were conducted on sunny and cloud free different days each month taking in consideration that the three days of measurement are as close together as possible. The leaf and soil sample collection were made on sunny days across four seasons winter (February), spring (May), summer (August), and autumn (November) of the same study period. The soil sampling was performed in the rhizospheric area at 20–30 cm depth.

2.2. Measurements of physiological attributes

Stomatal conductance (gs) was recorded under field conditions on the abaxial surface of randomly chosen, fully expanded argan leaves that were exposed to full sunshine on sunny days between 9:00 and 11:00 a.m. using a portable porometer (Leaf Porometer LP1989, Decagon Device, Inc., Washington, DC, USA). Two gs measurements were performed to provide one average value per tree.

Measurements of chlorophyll fluorescence (Fv/Fm) were performed on randomly selected, fully developed argan leaves using a portable fluorometer (Opti-sciences OSI 30p, Hudson, NY, USA). Two measurements were made to provide one average value per tree. The selected leaves were clipped and allowed to acclimate in the dark for 30 min before taking measurement. Following the application of a saturating actinic light pulse, the maximal fluorescence (F_m) was measured after the first minimal fluorescence (F_0) was recorded (Baker, 2008). The fluorimeter automatically determined the ratio of variable to maximal fluorescence (F_v/F_m) as follows:

$$\frac{Fv}{Fm} = \frac{(Fm - F0)}{Fm}$$

Leaf area index (LAI) and photosynthetically active radiation (PAR) measurements were performed using a SunScan sensor type SS1 (Delta-T Devices, Cambridge, ENGLAND) as described by Oguntunde et al. (2012). Five measurements were taken horizontally at different heights for each tree and the average of these measurements was considered as one replicate with ten replicates per browsing system. The time frame for the measurements was 10:00 a.m. to 2:00 p.m. (clear weather).

The quantification of photosynthetic pigments, including chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), total chlorophyll (Chl T), and carotenoids was carried out spectrophotometrically at 663, 645, and 480 nm according to Arnon (1949). The aforementioned pigments were extracted using acetone (80 %) from fresh frozen argan leaves samples, which were subsequently centrifuged for 10 min at 10,000×*g*. The pigment concentrations were calculated as follows:

$$Chlorophyll\ a\left(\frac{mg}{g}\right) = [(12.7 \times A663) - (2.69 \times A645)] \times \frac{V \times FW}{1000 \times DW}$$

$$Chlorophyll\ b\left(\frac{mg}{g}\right) = [(22.9 \times A645) - (4.68 \times A663)] \times \frac{V \times FW}{1000 \times DW}$$

$$Total\ Chlorophyll\left(\frac{mg}{g}\right) = [(20.2 \times A645) - (8.02 \times A663)] \times \frac{V \times FW}{1000 \times DW}$$

$$Carotenoids\left(\frac{mg}{g}\right) = [A480 + (0.114 \times A663) - (0.638 \times A645)] \times \frac{V\ x\ FW}{1000 \times DW}$$

where, V = final volume of the extract, FW = fresh weight, DW = dry weight, and A = absorbance.

2.3. Biochemical leaf attributes

Argan leaves were evaluated for their total soluble sugars (TSS) content using Dubois et al. (1956) method. Briefly, fresh frozen leaves sample (0.1 g) was homogenized in 8 mL of ethanol (80%). After centrifugation for 10 min at 5,000×*g*, 200 μL of phenol (5 %) and 1000 μL of sulfuric acid were added to 200 μL of the supernatant. Thereafter, the absorbance (A) was recorded using a spectrophotometer (spectrophotometer UV-3100PC) at a wavelength of 485 nm.

For the determination of total soluble protein content and antioxidant enzyme activities, 0.1 g of fresh frozen argan leaves were homogenized in 1 M phosphate buffer (pH 7) with 5 % polyvinylpolypyrrolidone. The obtained mixture was centrifuged at 18,000×*g* for 15 min at 4 °C. The resulting supernatant was used for soluble protein content and antioxidant enzyme activity determination. The first parameter was assessed using the Bradford method (Bradford, 1976) and the absorbance was measured at 595 nm with bovine serum albumin (BSA) as a standard. Catalase (CAT) enzymatic activity was measured according to Aebi (1984) method and following the degradation of hydrogen peroxide (H_2O_2). A volume of 100 μL of the extract was combined with 1 M potassium phosphate buffer (pH 7.0), 0.1 mM ethylenediaminetetra-acetic acid (EDTA), and 20 mM H_2O_2. The absorbance was recorded at 240 nm for 60 s. The results are expressed as μmol H_2O_2 mg^{-1} protein min^{-1}. The activity of peroxidase (POX) was determined following the methodology described by Polle et al. (1994). The mixture contained 100 mM potassium phosphate buffer (pH 7.0), 100 μL extract sample, 10 mM H_2O_2, and 20 mM guaiacol in a 3 mL volume. The absorbance was measured at 470 nm for 3 min. The activity of polyphenoloxidase (PPO) was measured by following the catechol oxidation at 410 nm as described by Gauillard et al. (1993). The solution used consisted of a 100 mM K_2HPO_4/KH_2PO_4 buffer (pH 6), 50 mM catechol, and 0.1 mL of enzyme extract. The activity of PPO was given in μmol of catechol min^{-1} mg^{-1} of protein.

The H_2O_2 content in fresh argan leaves was assessed in accordance with the method of Velikova et al. (2000). Briefly, leaf sample (0.25 g) was mixed with 5 mL of 10% (w/v) trichloroacetic acid (TCA) and then centrifuged at 15,000×*g* for 10 min. A volume of 0.5 mL of the obtained supernatant was then homogenized in 1 mL of potassium iodide (1 M) and 0.5 mL of potassium phosphate buffer (10 mM, pH 7). The mixture was then incubated in the dark for 1 h and the absorbance was recorded at 390 nm.

The malondialdehyde (MDA) content in fresh frozen argan leaf samples was determined spectrophotometrically according to Savicka and Škute (2010). The extract was obtained by homogenizing 0.25 g of the sample in 10 mL of 0.1% (w/v) TCA. The mixture was then centrifuged at 18,000×*g* for 10 min. The reaction solution for MDA content assessment contained 1 mL of the supernatant mixture and 2.5 mL of thiobarbituric acid (TBA), resulting in the formation of a chromogen. After incubation of the mixture at 95 °C for 30 min, the tubes were placed in an ice bath to stop the reaction. The absorbance was recorded at 450, 532, and 600 nm. The concentrations of MDA were obtained following the equation below:

$$[\mathrm{MDA}] = 6.45 \times (\mathrm{A532} - \mathrm{A600}) - 0.56 \times \mathrm{A450}$$

2.4. Soil physicochemical characteristics

Soil physico-chemical traits including soil texture, pH, electrical conductivity (EC), soil moisture, and total nitrogen (NTK), total organic matter (TOM), and assimilable phosphorus (AP) content were assessed from air-dried and sieved (2 mm) samples taken every three months in the argan rhizospheric zone. Soil texture determination was performed using the hydrometer method whereas pH and EC were determined using a pH meter and a conductivity meter on a 1/5 (w/v) diluted soil suspension. NTK content assessment was carried out by the Kjeldahl method (Bremner, 1960) using an automated Kjeldahl distiller (KJA-9840 Model, Shandong, China). TOM content was measured according to the procedures described by Aubert (1978). AP was measured in accordance with the method described by Olsen and Sommers (1982). Finally, soil moisture was measured under canopy by the SWM 5000, which uses Frequent Domain Reflectometry (FDR) technology to quickly and accurately measure soil moisture. The stainless-steel measuring probe is manually inserted into the ground at 20 cm depth.

2.5. Data analysis

Data are given as averages of ten replicates (n = 10) per browsing system for gs, Fv/Fm, PAR, and LAI and five replicates (n = 5) per browsing system for photosynthetic pigment content, biochemical analyses, and soil physico-chemical characteristics. Data pre-processing was performed using R Studio software (version 4.4.0). Prior to statistical analysis, the data were subjected to a normality test (Shapiro-Wilk test) and a test of homogeneity of variances (Levene's test) to verify the prerequisites for applying repeated measures analysis of variance (repeated measures ANOVA) using the package rstatix (Alboukadel, 2023). These tests ensured that the distributions of the variables met the required assumptions of normality and homogeneity of variance. Multivariate analyses, including principal component analysis (PCA) and linear discriminant analysis (LDA), were performed using the package stats (R Core Team, 2024) for the PCA and the package MASS (Venables and Ripley, 2002) for the LDA analysis. PCA was used to explore the overall structure of the data without any prior assumptions, while LDA was used to statistically test the separation between the defined groups (browsing intensity and seasons). These two approaches are therefore complementary: PCA describes the major trends and LDA confirms the validity of the discrimination between groups, The data were aggregated as averages for each combination of browsing regime and season. The values were then standardized to obtain a mean of zero and a standard deviation of one in order to have the same variation and ensure reliable interpretation of the components. This approach provided a synthetic and integrated representation of physiological, biochemical, and edaphic variations according to the different experimental treatments.

3. Results

3.1. Physiological attributes

3.1.1. Stomatal conductance and chlorophyll fluorescence

The gs and Fv/Fm of *A. spinosa* significantly ($P < 0.001$) differed among the three-study browsing systems and seasons (Table 1). The values of both parameters were low during the winter season and then increased starting from spring (Fig. 2a and b). Trees under no-browsing system exhibited the highest gs and Fv/Fm values where they exhibited

Table 1
Repeated measures ANOVA results showing the effects of browsing intensity, time (month or season), and their interaction on the physiological, biochemical, and soil variables tested.

	Browsing intensity			Month			Browsing intensity x Month		
Variables	df	F	*p*	df	F	*p*	df	F	*p*
Fv/Fm	2	557.874	0.001[a]	11	2231.630	0.001[a]	22	83.609	0.001[a]
gs	2	37.521	0.001[a]	10	206.229	0.001[a]	20	14.450	0.001[a]
PAR	2	6454.155	0.001[a]	11	1058.402	0.001[a]	22	99.696	0.001[a]
LAI	2	3181.044	0.001[a]	11	225.221	0.001[a]	22	62.925	0.001[a]

	Browsing intensity			Season			Browsing intensity x Season		
Variables	df	F	*p*	df	F	*p*	df	F	*p*
Chl a	2	52.022	0.001[a]	3	96.994	0.001[a]	6	0.771	0.598
Chl b	2	240.248	0.001[a]	3	2227.668	0.001[a]	6	0.553	0.764
TChl	2	608.748	0.001[a]	3	3229.826	0.001[a]	6	0.978	0.454
Carot	2	20.691	0.001[a]	3	103.265	0.001[a]	6	13.398	0.001[a]
Prot	2	213.479	0.001[a]	3	1729.533	0.001[a]	6	99.916	0.001[a]
TSS	2	5895.208	0.001[a]	3	866.453	0.001[a]	6	31.446	0.050[a]
MDA	2	63.499	0.001[a]	3	714.467	0.001[a]	6	19.984	0.001[a]
H_2O_2	2	86.442	0.001[a]	3	90.752	0.001[a]	6	41.275	0.001[a]
CAT	2	455.104	0.001[a]	3	899.579	0.001[a]	6	11.892	0.334
PPO	2	982.348	0.001[a]	3	403.856	0.001[a]	6	43.989	0.010[a]
POX	2	332.199	0.001[a]	3	859.040	0.001[a]	6	15.004	0.206
pH	2	3477.800	0.001[a]	3	6.54E+04	0.010[a]	6	4.93E+04	0.001[a]
EC	2	106.410	0.001[a]	3	94.092	0.001[a]	6	7.375	0.001[a]
AP	2	453.355	0.001[a]	3	0.879	0.461	6	23.532	0.051
TOM	2	1145.135	0.001[a]	3	62.344	0.010[a]	6	43.828	0.010[a]
S moist	2	662.305	0.001[a]	3	309.022	0.001[a]	6	23.984	0.047[a]

[a] indicates significant results; df: degrees of freedom; F: fisher index; p: P value; AP: available phosphorus content; Carot: carotenoids content; CAT: catalase activity; Chl a: chlorophyll *a* content; Chl b; chlorophyll *b* content; EC: electrical conductivity; Fv/Fm: chlorophyll fluorescence; gs: stomatal conductance; H_2O_2: hydrogen peroxide content; LAI: leaf area index; MDA: malondialdehyde content; NTK: total nitrogen Kjeldahl content; PAR: photosynthetically active radiation; POX: peroxidase activity; PPO: polyphenol oxidase activity; Prot: Protein content; S moist: soil moisture; TChl: total chlorophyll content; TOM: total organic matter content; TSS: total soluble sugars content.

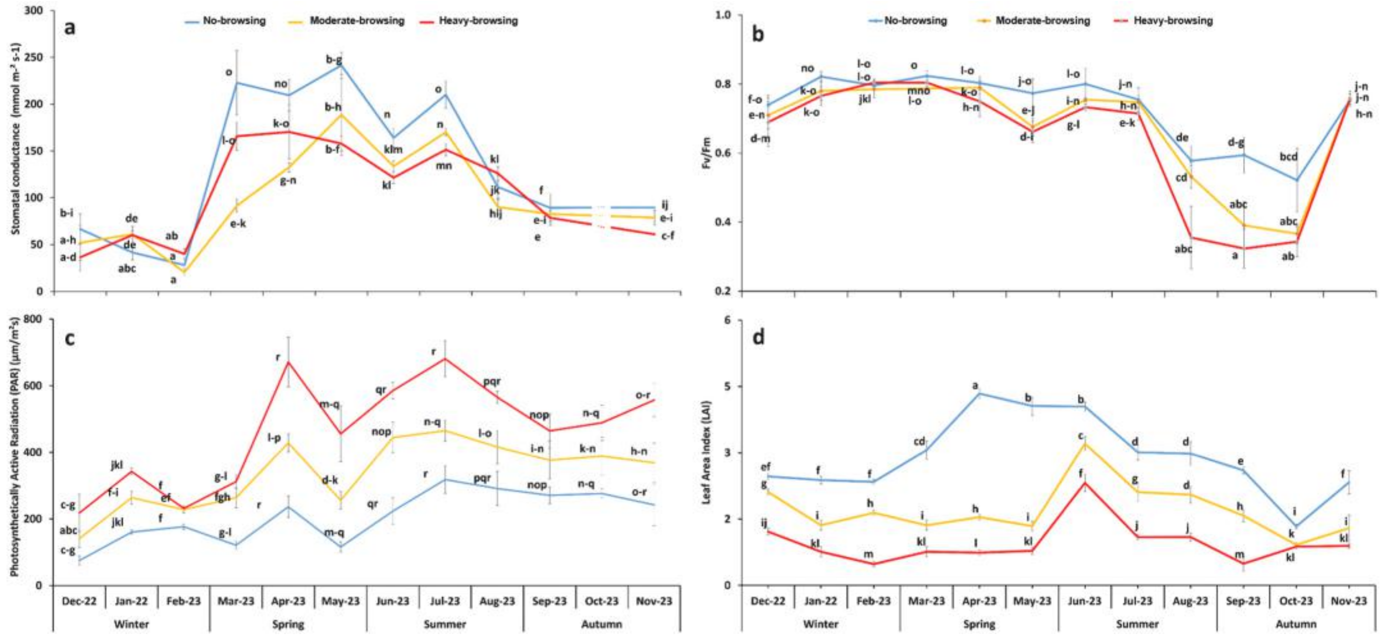

Fig. 2. Monthly variation of stomatal conductance (gs, a), chlorophyll fluorescence (Fv/Fm, b), photosynthetic active radiation (PAR, c) and leaf area index (LAI, d) of *A. spinosa* in the three-browsing intensities during the study period. Different letters indicate significant differences among sites and seasons/months following Tukey's test at $p < 0.05$.

the highest values in May and January respectively. The increases of gs in this browsing regime were 28 and 53 % compared to the moderate- and heavy-browsing systems, respectively, while they were 5 and 6 % for Fv/Fm in comparison to the same regimes. A seasonal decline in both parameters was evident starting from mid-summer to continue during autumn (especially for gs), with the lowest values mainly recorded in the heavy-browsing system. The interaction Browsing intensity x Month was significant ($P < 0.001$) for both parameters.

3.1.2. Photosynthetically active radiation and leaf area index

The PAR and LAI measurements revealed significant ($P < 0.001$) differences among the three-browsing systems and seasons (Table 1). The values of both parameters were low during winter and then started their increase in spring (Fig. 2c and d). The heavy-browsing regime exhibited the highest PAR values in July, showing an increase of 114 %, followed by the moderate-browsing system with 46 % increase, both compared to the no-browsing system. In April, the argan population in the latter exhibited significantly higher LAI values with 182 % of increase compared to that of the moderate-browsing system and 486 % higher than that of the heavy-browsing system. The no-browsing regime consistently recorded the lowest PAR whilst the lowest LAI levels were noticed in the heavy-browsing one throughout the study period. The interaction Browsing intensity x Month was significant ($P < 0.001$) for both variables.

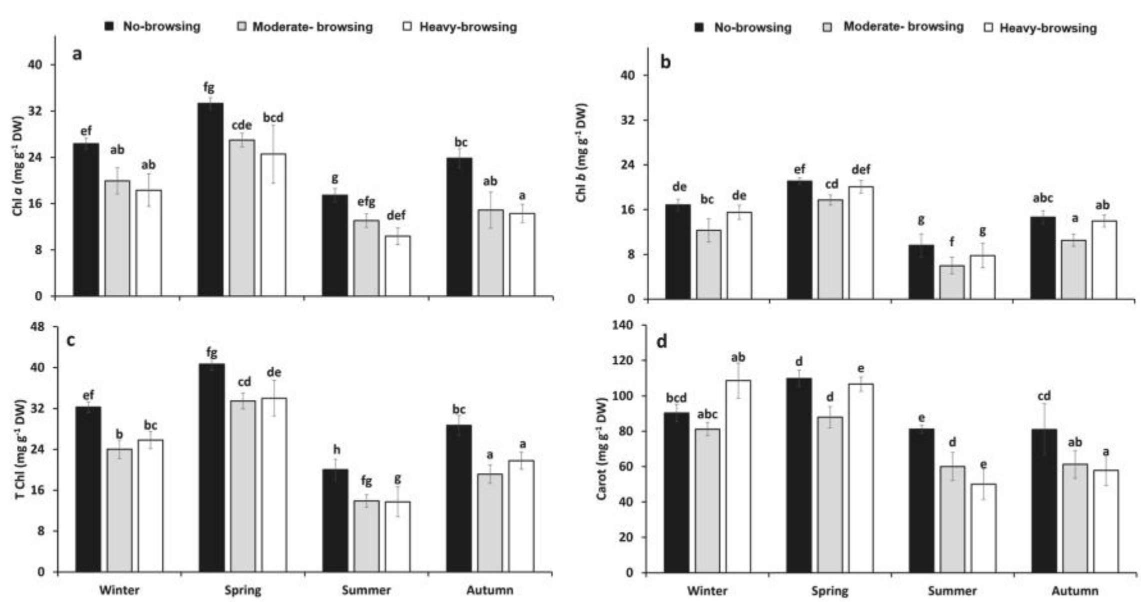

Fig. 3. Seasonal variation of photosynthetic pigments content in the three-browsing intensities during the study period. Chl a, chlorophyll *a*; Chl b, chlorophyll *b*; T Chl, total chlorophyll; Carot, carotenoid. Different letters indicate significant differences among sites and seasons/months following Tukey's test at $p < 0.05$.

3.1.3. Photosynthetic pigments content

The photosynthetic pigments content exhibited significant ($P < 0.001$) differences between the three argan populations and seasons (Table 1). Throughout the study, the no-browsing system mainly recorded the highest levels of Chl *a*, Chl *b*, total chlorophyll, and carotenoids, followed by the moderate- and heavy-browsing systems (Fig. 3). In addition, these parameters were most significant during spring, followed by winter and autumn, whereas the lowest levels were observed in summer. The concentration of Chl *a* showed the greatest disparity between the three-browsing systems in autumn with the no-browsing regime recording 60 and 67 % increase than that of the moderate- and heavy-browsing ones, respectively. In contrast, the levels of total chlorophyll and carotenoids recorded the highest disparity between the three-browsing regimes in summer where the no-browsing one showed 44–45 and 35–62 % enhancement in comparison to the moderate- and heavy-browsing systems, respectively. The interaction Browsing intensity x Season was only significant ($P < 0.001$) for carotenoids content.

3.2. Biochemical leaf attributes

3.2.1. Stress markers, osmoregulation and antioxidant enzyme activity

Our results revealed a consistent seasonal pattern for all biochemical traits with significant ($P < 0.001$) differences observed across the study browsing systems and seasons (Table 1). Argan trees subjected to heavy browsing consistently displayed the highest levels of MDA and H_2O_2 throughout all seasons, particularly during summer (Table 2). During this season, MDA and H_2O_2 levels peaked in the heavy-browsing system exceeding those in the moderate- and no-browsing ones (by 75 and 80 % for MDA content and by 39 and 87 % for H_2O_2 content), respectively. The lowest values of this stress marker were recorded in spring in the no-browsing system. The TSS content also exhibited the same trend as MDA and H_2O_2 contents with the highest values recorded in spring in the heavy-browsing system (62 % higher than that in the moderate-browsing system and 99 % higher than that in the no-browsing one). In contrast, the protein content showed the greatest values in the no-browsing regime particularly in winter and spring. During this season, protein content in the no-browsing system was 39 % higher than that in the moderate-browsing one and 45 % higher than that in the heavy-browsing one.

The antioxidant activity analysis mainly revealed higher activity in argan plants subjected to heavy browsing across all seasons especially for the PPO activity (Table 2). The enzyme activities of these highly browsed plants mainly reached their peak during summer and autumn seasons, while the lowest values were recorded in spring. Indeed, CAT activity showed significantly higher values in the heavy-browsing system during summer with 35 and 62 % of increase compared to those of the moderate- and no-browsing systems, respectively. Similarly, POX activity in the heavy-browsing regime exceeded that of the moderate- and no-browsing systems by 12–40 % during summer and 22–45 % during autumn, respectively. PPO activity followed the same trend, with the heavy-browsing regime exhibiting higher levels in summer with 91 and 275 % of increase compared to those of the moderate- and no-browsing systems, respectively. The interaction Browsing intensity x Season was significant ($P < 0.001$) for all the biochemical traits except for CAT and POX activities.

Table 2
Seasonal variation in biochemical traits of argan leaves across the three studied browsing intensities.

Parameters	Browsing intensity	Winter (February)	Spring (May)	Summer (August)	Autumn (November)
Proteins content (mg g^{-1} DW)	**No-browsing**	26.18 ± 1.71 $^{b-e}$	32.87 ± 2.49 ^{f}	17.12 ± 1.64 ^{g}	14.86 ± 1.55 $^{b-e}$
	Moderate-browsing	17.88 ± 2.77 ^{a}	23.66 ± 1.29 ^{cd}	13.26 ± 0.65 ^{ef}	12.30 ± 1.45 ^{ab}
	Heavy-browsing	15.55 ± 3.13 ^{abc}	22.62 ± 3.28 ^{abc}	14.07 ± 3.09 ^{def}	12.19 ± 1.18 ^{abc}
Total soluble sugar content (mg g^{-1} DW)	**No-browsing**	85.51 ± 9.20 ^{ab}	101.95 ± 11.63 ^{bcd}	65.10 ± 5.43 $^{c-f}$	76.57 ± 6.98 ^{a}
	Moderate-browsing	117.11 ± 4.47 ^{de}	125.57 ± 4.86 ^{ef}	81.92 ± 8.36 ^{f}	101.72 ± 9.51 ^{abc}
	Heavy-browsing	182.28 ± 3.32 ^{g}	203.73 ± 11.45 ^{h}	158.00 ± 8.09 ^{i}	157.51 ± 7.70 ^{g}
MDA content (nmol g^{-1} DW)	**No-browsing**	14.15 ± 1.11 ^{ab}	12.18 ± 2.93 ^{a}	72.71 ± 6.05 ^{f}	27.46 ± 2.32 ^{cd}
	Moderate-browsing	16.13 ± 4.30 ^{abc}	16.61 ± 3.19 ^{abc}	70.90 ± 7.60 ^{f}	28.86 ± 2.87 ^{d}
	Heavy-browsing	52.45 ± 5.24 ^{e}	24.51 ± 3.62 ^{bcd}	127.63 ± 5.24 ^{g}	62.10 ± 8.92 ^{ef}
H_2O_2 content (nmol g^{-1} DW)	**No-browsing**	102.46 ± 8.79 ^{ab}	75.66 ± 14.48 ^{a}	133.21 ± 16.29 ^{bc}	170.61 ± 14.8 ^{c}
	Moderate-browsing	168.11 ± 8.97 ^{c}	112.98 ± 14.33 ^{b}	191.53 ± 9.04 ^{cd}	229.08 ± 3.83 ^{c}
	Heavy-browsing	265.47 ± 12.06 ^{d}	199.41 ± 20.35 ^{c}	403.40 ± 25.47 ^{e}	319.13 ± 7.39 ^{c}
CAT activity (μmol mg^{-1} protein min^{-1})	**No-browsing**	52.35 ± 5.38 $^{c-f}$	37.98 ± 2.97 ^{ab}	79.55 ± 7.86 ^{a}	89.20 ± 6.50 $^{c-f}$
	Moderate-browsing	68.89 ± 13.50 ^{dfg}	53.5 ± 3.71 ^{bcd}	95.39 ± 7.53 ^{ab}	99.95 ± 12.34 ^{efg}
	Heavy-browsing	89.40 ± 14.97 ^{gh}	73.56 ± 15.53 $^{c-g}$	128.96 ± 14.09 ^{bce}	117.98 ± 9.61 ^{h}
POX activity (μmol mg^{-1} protein min^{-1})	**No-browsing**	0.28 ± 0.04 $^{d-g}$	0.24 ± 0.01 ^{abc}	0.47 ± 0.06 ^{a}	0.53 ± 0.05 ^{def}
	Moderate-browsing	0.45 ± 0.06 $^{e-h}$	0.32 ± 0.01 ^{cde}	0.59 ± 0.02 ^{ab}	0.63 ± 0.07 ^{fgh}
	Heavy-browsing	0.59 ± 0.10 ^{h}	0.43 ± 0.07 $^{e-h}$	0.66 ± 0.06 ^{bcd}	0.76 ± 0.10 ^{gh}
PPO activity (μmol mg^{-1} protein min^{-1})	**No-browsing**	0.09 ± 0.00 ^{bcd}	0.08 ± 0.00 ^{ab}	0.28 ± 0.04 ^{a}	0.25 ± 0.03 ^{cde}
	Moderate-browsing	0.27 ± 0.04 ^{def}	0.19 ± 0.01 ^{abc}	0.55 ± 0.02 $^{a-d}$	0.42 ± 0.05 ^{ef}
	Heavy-browsing	0.92 ± 0.22 ^{g}	0.57 ± 0.10 ^{g}	1.05 ± 0.25 ^{f}	0.87 ± 0.11 ^{g}

MDA, malondialdehyde; H_2O_2, hydrogen peroxide; CAT, catalase; POX, peroxidase; PPO; polyphenoloxidase. Different letters indicate significant differences among browsing intensity and seasons/months following Tukey's test at $p < 0.05$.

3.2.2. Soil physico-chemical properties

Soil physico-chemical traits revealed significant ($P < 0.001$) differences among the three browsing systems and seasons except for AP content which did not significantly differ across seasons (Table 1). The results of the soil textural analysis revealed significant variations among the three browsing regimes where the no-browsing system exhibited a sandy loam texture, while both the moderate- and heavy-browsing systems had a sandy clay loam texture (Table 3). The soil analysis also revealed that the soils across the three-study browsing regimes exhibited a slightly alkaline pH, ranging from 7.5 to 7.7, with the highest pH recorded in the heavy-browsing system during the study period. Electrical conductivity and soil moisture exhibited the highest values in the moderate- and heavy-browsing systems, while the no-browsing regime showed the lowest ones for both traits. In terms of nutrients, the moderate-browsing system showed the highest NTK levels with significant increase during winter and autumn (58 and 230 % increases in comparison to the heavy- and no-browsing systems, respectively). The same trend was recorded for TOM which showed higher values in the moderate-browsing system in winter and autumn with significant increase in comparison to the no-browsing regime (106 and 127 %,

Table 3
Seasonal variation of soil physicochemical traits in the three studied browsing intensities.

Parameters	Browsing intensity	Winter (February)	Spring (May)	Summer (August)	Autumn (November)
Texture	**No-browsing**	Loamy sand			
	Moderate-browsing	Sandy clay loam			
	Heavy-browsing	Sandy clay loam			
EC (mS cm^{-1})	**No-browsing**	0.27 ± 0.01^{a}	0.28 ± 0.06^{ab}	0.36 ± 0.02^{cd}	0.26 ± 0.01^{a}
	Moderate-browsing	0.37 ± 0.01^{d}	0.34 ± 0.05^{bcd}	0.42 ± 0.01^{e}	0.35 ± 0.01^{c}
	Heavy-browsing	0.31 ± 0.01^{b}	0.30 ± 0.01^{abc}	0.44 ± 0.01^{e}	0.31 ± 0.01^{b}
NTK (g Kg^{-1})	**No-browsing**	93.99 ± 14.19^{ab}	89.88 ± 6.40^{b}	93.91 ± 3.74^{ab}	90.97 ± 1.53^{a}
	Moderate-browsing	88.53 ± 2.42^{f}	80.39 ± 8.52^{e}	83.91 ± 3.88^{e}	84.92 ± 9.91^{f}
	Heavy-browsing	57.55 ± 14.44^{cd}	69.13 ± 12.74^{de}	69.13 ± 12.74^{cde}	60.82 ± 7.13^{c}
AP (mg Kg $^{-1}$)	**No-browsing**	0.26 ± 0.04^{d}	0.26 ± 0.05^{d}	0.20 ± 0.04^{d}	0.20 ± 0.08^{d}
	Moderate-browsing	0.50 ± 0.06^{bcd}	0.41 ± 0.04^{bcd}	0.41 ± 0.04^{bcd}	0.46 ± 0.02^{cd}
	Heavy-browsing	0.37 ± 0.04^{a}	0.31 ± 0.09^{abc}	0.34 ± 0.02^{ab}	0.34 ± 0.02^{a}
TOM (%)	**No-browsing**	0.99 ± 0.14^{ab}	1.25 ± 0.21^{ab}	1.18 ± 0.15^{a}	0.93 ± 0.12^{a}
	Moderate-browsing	3.27 ± 0.25^{d}	2.58 ± 0.20^{cd}	2.63 ± 0.10^{bc}	3.19 ± 0.24^{d}
	Heavy-browsing	2.07 ± 0.06^{bcd}	2.31 ± 0.06^{bc}	2.37 ± 0.45^{bc}	2.09 ± 0.09^{bc}
Soil moisture (%)	**No-browsing**	9.47 ± 0.63^{ab}	8.52 ± 0.64^{ab}	7.19 ± 0.49^{a}	7.19 ± 0.97^{a}
	Moderate-browsing	12.87 ± 1.53^{cd}	13.62 ± 1.90^{cd}	9.74 ± 0.62^{ab}	8.88 ± 0.64^{ab}
	Heavy-browsing	13.96 ± 1.28^{d}	13.49 ± 0.57^{cd}	10.82 ± 1.63^{bc}	11.43 ± 1.59^{bcd}

AP, available phosphorus; EC, electrical conductivity; NTK, total nitrogen content; TOM, total organic matter. Different letters indicate significant differences among browsing intensity and seasons/months following Tukey's test at $p < 0.05$.

respectively). Even if the no-browsing system had the highest levels of AP, no significant differences were recorded with the other browsing regimes except in winter and autumn where the values of this system recorded significant increase in comparison to those of the heavy-browsing one. The interaction Browsing intensity x Season was significant ($P < 0.001$) for all soil physico-chemical parameters except for AP content.

3.3. Principal component analysis and linear discriminant analyses

Principal component analysis (PCA), as illustrated by the biplot (Fig. 4a), reveals that the first two components (PCA1 and PCA2) explain a considerable portion of the total variability in the data (71.5 %), with PCA1 alone accounting for 47.8 % of this variance. This principal component (PCA1) is strongly positively associated with pigment content, such as chlorophyll (Chl_a, Chl_b, T_Chl), proteins (Prot), leaf area index (LAI), and available phosphorus (AP), with these variables pointing to the right side of the graph. Conversely, PCA1 is negatively correlated with stress markers such as hydrogen peroxide (H_2O_2) and malondialdehyde (MDA), as well as various enzymes (PPO, POX, CAT), pH, and total soluble sugar (TSS) content, with these variables projecting toward the left side. Observation of the sample clusters on the biplot highlights a clear and predominant separation by browsing system. Samples from the heavy-browsing regime are clearly grouped on the left (red ellipse), reflecting stress conditions and reduced metabolic activity. Conversely, the samples from the no-browsing system are clustered on the right (green ellipse), characterizing a state of high physiological activity. As for samples from the moderate-browsing system, they are clustered in the center (light blue ellipse). These represent transitional phases, with their clusters positioned between the winter and summer

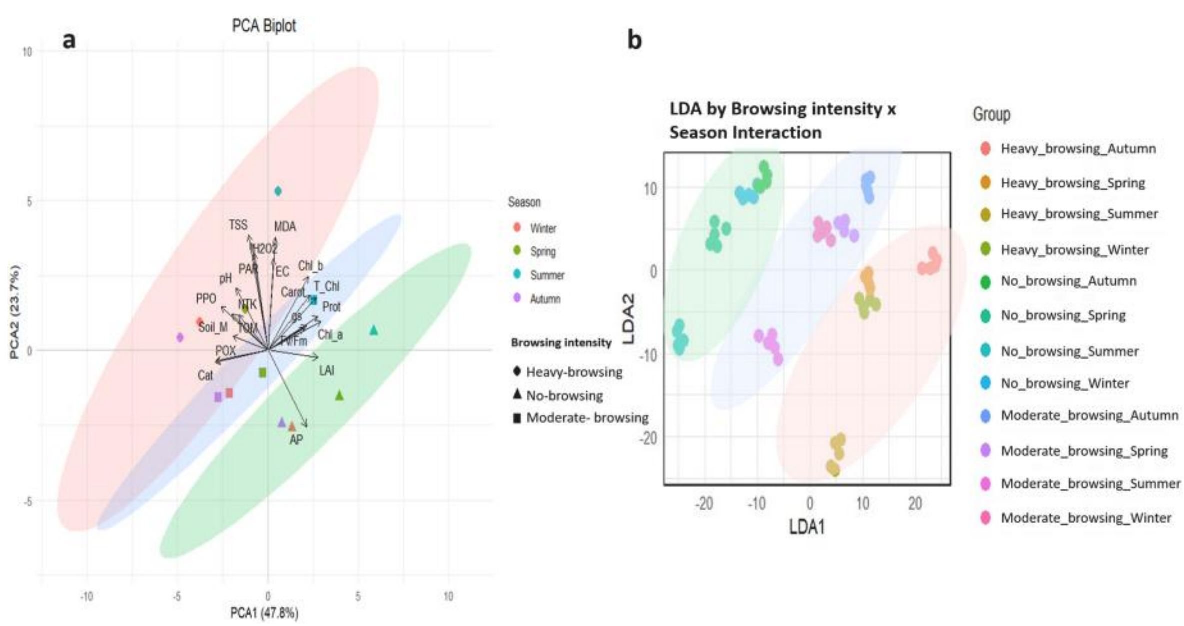

Fig. 4. Principal component analysis Biplot (PCA, a) and Linear discriminant analyses (LDA, b) between browsing intensity, seasons and measured parameters. AP: available phosphorus content; Carot: carotenoids content; CAT: catalase activity; Chl a: chlorophyll *a* content; Chl b; chlorophyll *b* content; EC: electrical conductivity; Fv/Fm: chlorophyll fluorescence; gs: stomatal conductance; H2O2: hydrogen peroxide content; LAI: leaf area index; MDA: malondialdehyde; NTK: total nitrogen Kjeldahl; PAR: photosynthetically active radiation; POX: peroxidase activity; PPO: polyphenol oxidase activity; Prot: Protein content; Soil_M: soil moisture; T_Chl: total chlorophyll content; TOM: total organic matter content; TSS: total soluble sugars content.

poles, indicating a gradual or regressive evolution of conditions and metabolic responses. Although the samples come from different types of browsing intensity (no-, moderate-, and heaving-browsing, distinguished by different shapes), their distribution within the seasonal ellipses shows that browsing regime type is the most influential factor in determining biochemical and physiological profiles, masking a clear distinction based solely on browsing intensity in these first two dimensions of PCA. Overall, this analysis underscores the significant influence of browsing intensity levels and seasonal changes on plant performances and soil conditions.

Linear discriminant analysis (LDA), illustrated in Fig. 4b, demonstrates a remarkable ability to discriminate between groups defined by the Browsing intensity × Season interaction, with each colored cluster representing a unique combination of these factors. The high degree of separation between most groups confirms that the measured variables, when combined by the discriminant functions (LDA1 and LDA2), are highly effective in differentiating these specific ecological conditions. This analysis reveals that not only is season a key modulator of ecological profiles (with seasonal groups being distinct within each browsing intensity), but more importantly, that the interaction between browsing intensity (no-, moderate-, and heaving-browsing) and season creates unique and highly distinct ecological signatures. The pronounced isolation of certain groups, such as "Heavy-browsing_Summer," highlights specific responses to stress or adaptations specific to disturbed environments during critical periods. The absence of major overlaps between clusters attests to the robustness of the discrimination and validates the hypothesis that the combined effects of browsing intensity and seasonal variations are major determinants of the observed variability.

4. Discussion

Livestock browsing has long been known to dramatically affect the photosynthetic capacity of plants by reducing total photosynthetic area and altering ecosystem structure and functioning in drylands worldwide (Briske and Richards, 1994; Liu et al., 2019a,b). Herbivores induce structural damage and withdraw plant biomass, further reducing the leaf area available for photosynthesis (Redondo-Gómez et al., 2010). In the present study, the physiological performance of *A. spinosa* trees exposed to browsing in both moderate- and heavy-browsing systems were significantly lower than those in the no-browsing one. Indeed, the argan population under the no-browsing regime exhibited the highest values of gs and the maximum photochemical efficiency of photosystem II (PSII), refer to as Fv/Fm, during spring season. These findings are in accordance with pigments content results, with highest values recorded in the no-browsing system during the study period. Similar to our finding in physiological traits, Ren et al. (2017) found that no-browsing significantly increased photosynthetic parameters of *Livistona chinensis* individuals under field conditions. Furthermore, gs values in the heavy-browsing system were higher than those of the moderate-browsing system during the same season. This increase in stomatal conductance may enhance CO_2 availability for assimilation and thus stimulate photosynthesis; however, it generally results in lower intrinsic water use efficiency, as more water is lost per unit of carbon gained (Shen et al., 2019). A previous study carried out on the argan reported that the tree is an herbivore-tolerant species and that at some level, browsing has a positive effect on photosynthesis during the favourable season. This is because in order to make up for the loss of leaf surface following herbivore attacks, trees increase photosynthetic activity in their leaves (maybe as a result of increased stomatal conductance) and consume less water, indicating less oxidative stress (Nait Douch et al., 2022). However, in the present study, the browsed argan populations didn't show higher photosynthetic activity (Fv/Fm) compared to the unbrowsed one. A previous study showed that the decreases in photosynthesis were caused by overbrowsing, which were co-regulated by the stomatal dimensions and chlorophyll content under field conditions (Ren et al., 2017). Furthermore, the decline in Fv/Fm values below the optimum (0.7–0.8) during the summer season in all the three browsing intensity systems could be explained by the photoinhibition effect caused by drought and a prolonged dryness during this season. These results are in accordance with multiple studies (Björkman and Demmig, 1987; Nait Douch et al., 2022). Previous research reported that plants adapt to browsing by changing how they absorb and use sun energy. After browsing, plants leaves face more light availability because of the decreased shade; nevertheless, the reduced leaf area may make it more difficult for them to get enough (Stagnari et al., 2018). If the amount of photons input exceeds the photosynthetic capacity of the plant, increased light may also result in photoinhibition and lower photosynthetic efficiency (Hanelt et al., 1992; Ma et al., 2016). Furthermore, reactive oxygen species (ROS) are built up as a result of surplus energy that cannot be properly released. According to Liu et al. (2019b), ROS harm the photosynthetic machinery, enhance lipid peroxidation, and inhibit the synthesis of PSII proteins in the chloroplasts.

It is well known that browsing has a pronounced and direct impact on leaves, with alterations in leaf morphology closely linked to corresponding physiological changes (Song et al., 2020). Thus, the LAI is one critical factor influenced by browsing since it defines the plant-atmosphere interface. It also plays a pivotal role in mediating energy and mass exchanges between plants and their surrounding environment (Weiss et al., 2004). In this study, browsing resulted in a reduction of LAI in both moderate- and heavy-browsing systems due to the removal of leaf biomass, consequently diminishing plant cover and productivity. It has been documented that LAI significantly decreased with the drop of above-ground biomass which explains part of the decline in the browsing sites' photosynthetic capacity (Liu et al., 2019b). For instance, heavy browsing in desert phreatophyte communities has been shown to significantly reduce LAI, underscoring the detrimental effects livestock can have on plant cover (Bresloff et al., 2013). It has also been documented that higher LAI of the non-browsed canopy intercepted more rainfall and facilitated higher evaporative losses from leaf surfaces, thereby reducing soil water infiltration compared to the browsed canopy. This may result in reduced precipitation interception, higher soil water availability, and reduced transpiration (Harrison et al., 2010). Virgona et al. (2006) have also reported that the reduction in LAI, caused by browsing, can manifest itself as a transient accumulation of water in the soil following browsing. Furthermore, decreasing the canopy density through a drop in the LAI promotes light penetration by letting previously shaded leaves to receive more PAR leading to an enhancement in photosynthesis in browsed plants. However, in this study, even with high light availability, overbrowsing caused a decrease in photosynthetic activity. This suggests that factors beyond light limitation such as stomatal closure (Flexas and Medrano, 2002), oxidative stress (Chaves et al., 2009), or damage to the photosynthetic apparatus (Guidi and DeglInnocenti, 2011) may be responsible for the observed reduction in photosynthetic performance under intense browsing pressure.

Chlorophyll plays a crucial role in photosynthesis, assisting in light harvesting, energy transfer, and light energy conversion. It is the primary photosynthetic pigment found in chloroplasts and is an essential biochemical component (Ashraf and Harris, 2013; Muñoz-Ortuño et al., 2017). Chl *a* and Chl *b* are the two main types of chlorophyll and their concentrations are important markers of plant health and photosynthetic capacity (Muñoz-Ortuño et al., 2017; Zhang et al., 2014). This study findings showed a decrease in Chl *a*, Chl *b*, and total chlorophyll content in both moderate- and heavy-browsing systems where the two argan populations are exposed to browsing. There is considerable evidence that plants exposed to harsh environments have lower concentrations of vital photosynthetic pigments such as chlorophyll (Du et al., 2017; Li et al., 2021). One of the two possible causes of stress-induced changes in leaf chlorophyll concentration is either an acceleration of pigment degradation or an impairment of the processes involved in pigment production (Ling et al., 2019). Carotenoids act as precursors in signal pathways during plant development under biotic and abiotic stresses, thus playing an important role in photosynthetic photoprotection (Ashraf and Harris, 2013). The reduction in carotenoids content in the leaves of the argan trees under the heavy-browsing regime during summer and autumn was a response to the browsing stress and prolonged drought, similar trends were found in both *Stipa purpurea* and *Achnatherum inebrians* under browsing stress in previous study by Li et al. (2021) suggesting that this reduction may lead to impairment of either photosynthetic activity or photosynthetic protection.

At the biochemical level, we noted that protein concentrations followed the same trend observed for photosynthetic pigments content with argan populations under browsing in both moderate- and heavy-browsing systems showing significantly reduced protein contents compared to those in the no-browsing system. Our results align with previous research indicating that leaf soluble protein content declines with increasing browsing intensity (Liu et al., 2019a). Furthermore, browsing-induced protein degradation releases amino acids like glutamic acid, aiding plants in defending against herbivores, especially in nitrogen-limited environments (Caldana et al., 2011; Zhou et al., 2015). It has been also documented that heavy browsing reduces nitrogen content and affects enzyme activity necessary for nitrogen assimilation and protein production (Zhu et al., 2021). However, light browsing can stimulate plant growth by maintaining efficient photosynthesis, water use efficiency, and protein synthesis (Liu et al., 2019b). On the other hand, the findings revealed high levels of soluble sugars in the argan leaves in the heavy-browsing system, particularly during the dry season. This aligns with a research by Liu et al. (2019a), who found that overbrowsing increases soluble sugar concentrations in plants as a response to mechanical stress. They found that intensively browsed plants tend to accumulate sugars to sustain metabolic processes during herbivory and drought, serving as an adaptive strategy for regrowth and energy storage. Similarly, research on desert steppe vegetation reported higher sugar content in heavily browsed plants, likely due to increased metabolic demands (Zhu et al., 2021). In contrast, browsing exclusion has been associated with lower sugar levels, as observed in a study on the Chinese desert steppe, where protected plants had lower sugar concentrations compared to the grazed ones (Li et al., 2022; Wang et al., 2021).

Mechanical stress and excessive light during browsing can cause ROS (including H_2O_2) to be produced, which will directly harm the cell and chloroplast membranes (Kurepin et al., 2015; Liu et al., 2019a,b). Under these circumstances, MDA is produced, which is a marker of oxidative stress (Ma et al., 2016). In the present study, MDA and H_2O_2 content of argan leaves exposed to browsing in the heavy-browsing system was significantly higher than that in the no-browsing regime, especially in summer, suggesting that the browsing stress induced ROS accumulation and then peroxidation of cell membrane lipids. Furthermore, leaves, as the main organ impacted by herbivores present greater MDA levels, enhancing free fatty acid and free sterol contents, and reducing cell membrane fluidity (Mansour et al., 2005). In addition, it is known that H_2O_2 has a crucial function in plant behaviour under environmental stresses. Numerous studies have reported increased H_2O_2 concentrations following exposure to various stress conditions (Ait-El-Mokhtar et al., 2023; Boutasknit et al., 2024; Ikan et al., 2024; Kacperska, 2004; Neill et al., 2002). The extent of MDA and H_2O_2 production is impacted by the stress duration and intensity (Ślesak et al., 2007). Thus, the high levels of both variables in the heavy-browsing system indicate that browsed argan plants exhibited high oxidative stress levels characterizing herbivory stress. To cope with this situation, plants have developed multiple strategies of defense that utilize antioxidant enzymes, such as superoxide dismutase (SOD), CAT, POX, and PPO, to protect cells from damage caused by excessive ROS. These antioxidant enzymes are essential in scavenging these compounds (Chen et al., 2019; Ouhaddou et al., 2024; Liu et al., 2019a,b). In the present study, POX, CAT, and PPO activities were significantly higher in the leaves of the argan plants in the heavy-browsing system. This increase in antioxidant enzyme activity may be an adaptive response to elevated oxidative stress in browsed environments, revealed in this study through high MDA and H_2O_2 accumulation. According to Liu et al. (2019a), such enzyme activity helps plants cope with ROS accumulation induced by browsing stress. According to Rajput et al. (2021), under stress conditions, the scavenging process starts with the SOD which plays a critical role by catalyzing the removal of superoxide radicals ($\bullet O_2^-$) through their dismutation into O_2 and H_2O_2. Subsequently, CAT and POX convert the accumulated H_2O_2 into water and O_2, thereby mitigating oxidative damage. Additionally, PPO activity has been shown to be essential in plant defense against herbivory, as it produces toxic phenolic compounds. PPO also plays a role in reducing leaf digestibility and altering tissue quality, which has been observed across multiple plant species (Constabel et al., 2000; Constabel and Barbehenn, 2008).

Browsing intensity is not only affecting plant performance but it also a key factor influencing soil properties (Candel-Pérez et al., 2024; Sun et al., 2014). It affects soil both directly and indirectly through livestock trampling, plant consumption, and nutrient deposition *via* excretion (Chai et al., 2019). Our study indicated that soil pH did not vary much in response to the investigated pasture systems even with a slight enhancement in winter and summer in the highly browsed site. In a study conducted by Wang et al. (2024), authors stated an enhancement in pH under high browsing which was potentially linked to the effect of urine return. It has also been documented that urine from browsing animals increases soil EC due to the salts present in the urine (Orwin et al., 2010) which could justify the rise in EC in the heavy-browsing system especially during summer. In the same vein, soil moisture recorded the high levels of water content in high browsing site which could be explained by the difference in soil texture among the three-browsing intensities. Generally, sandy loam soils (no-browsing system) have lower water retention capacity compared to clay loam soils (moderate- and heavy-browsing systems). This is due to the larger particle size and higher porosity, which allows water to drain more quickly (Lut et al., 2019). In addition, soil moisture can also be increased by browsing since Pereyra et al. (2017) revealed that overbrowsing enhanced water storage in the soil compared to areas with low browsing intensity. This is may be due to browsing reducing plant biomass, water uptake, and transpiration, which are the main evaporative losses in soil below 5 cm of depth (Golluscio et al., 2022). Furthermore, our results revealed that soil NTK and TOM values in the moderate-browsing system were significantly higher than those of the no-browsing regime. According to Manley et al. (1995), browsing activity may enhance soil organic carbon and nitrogen in the top 30 cm of soil and improve overall soil quality. Consistent with our findings, Dai et al. (2022) also found that light browsing promotes soil organic carbon and total nitrogen, which are essential for nutrient availability. On the other hand, Zhang et al. (2022) showed that high browsed areas can reduce soil quality compared to low browsed ones because long-term high browsed areas can cause loss of soil nutrients. Regarding AP, results showed that its content was mainly reduced under overbrowsed site compared to the non-browsing site. Our findings are in line with previous studies (Bastani et al., 2023; Hashemi et al., 2019; Jaafari et al., 2014). According to Bastani et al. (2023), AP content is sensitive to soil compaction due to browsing pressure. This decline in soil AP concentration might likely be attributed to the reduced accumulation of litter in plots under high browsing intensity, as suggested by El-Dewiny et al. (2006). In addition, browsing has also been reported to be associated with reduced extractable phosphorus in some grasslands, indicating negative effects on phosphorus availability (Lavado et al., 1996).

Principal component analysis (PCA) and linear discriminant analysis (LDA) reveal and quantify the complex interconnections between environmental and biological parameters, thereby structuring ecosystem responses. The PCA axes highlight a gradient where, in the unprotected site, particularly during unfavorable seasons, co-occurrences of high EC and low TOM in the soil are logically associated with a marked decrease in photosynthetic associated traits (Fv/Fm, Chl a, Chl b, T_Chl, and gs). This constellation of factors is strongly correlated with increased oxidative stress (H_2O_2 and MDA), where the increase in antioxidant enzymes such as CAT, POX and PPO, although present, is often insufficient to prevent cellular damage reflected by the accumulation of MDA. In contrast, the no-browsing system, particularly during optimal growing season, is characterized along the PCA vectors by reduced stress markers and antioxidant activity combined with optimal PAR. These conditions promote robust plant growth, canopy development (LAI) and highly efficient photosynthesis (great values of Fv/Fm, Chl a, Chl b, T_Chl, and gs), resulting in high Prot accumulation (reflecting efficient assimilation of NTK) and high levels of TSS, signs of vigorous energy production. The LDA refines this distinction by demonstrating how specific "Browsing intensity x Season" interactions produce distinct groups of responses, confirming that seasonal variations are not uniform but amplify or attenuate the distinct ecological profiles observed by the PCA for each browsing intensity.

5. Conclusion

The findings of this study revealed that the argan trees from the no- and moderate-browsing systems showed better physiological performance compared to areas with high browsing pressure, with the greatest values observed in the unbrowsed argan. Furthermore, the heavily browsed argan trees were more stressed since they displayed high accumulation of MDA, H_2O_2, and TSS as well as promoted antioxidant activity (CAT, POX, and PPO), while the unbrowsed trees recorded the lowest values of these parameters. The *agdal*-ized argan trees (Agdal system) showed intermediate values between both aforementioned systems. Additionally, the study showed that managed browsing improved soil quality by enhancing nutrient content, such as NTK and TOM; factors critical to the growth and health of argan trees. Although the no-browsing system is the most appropriate system for the argan performances, the Agdal strategy (moderate-browsing) is the most sustainable browsing management tool since it can meet the need of the goat browsing activity and help maintaining the resilience and productivity of the argan forest.

CRediT authorship contribution statement

Boujemaa Fassih: Writing – original draft, Methodology, Formal analysis, Data curation. **Mohamed Ait-El-Mokhtar:** Writing – review & editing, Supervision, Resources, Methodology, Formal analysis, Data curation, Conceptualization. **Aicha Nait Douch:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Abderrahim Boutasknit:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Raja Ben-Laouane:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Badia Aganchich:** Writing – review & editing, Supervision, Methodology, Formal analysis. **Said Wahbi:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Use of AI statement

The authors declare that they have not used any type of generative artificial intelligence in the preparation of this manuscript.

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Declaration of competing interest

The authors declare no conflicts of interest in relation to this study, including commercial, financial, and political. The funder had no role in the design of the study.

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Data availability

Data will be made available on request.

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