PHOTOSYNTHETICA 48 (3): 348-354, 2010

Differential photosynthetic performance of three Mediterranean shrubs under grazing by domestic goats

S. REDONDO-GÓMEZ[+], J.M. MANCILLA-LEYTÓN, E. MATEOS-NARANJO, J. CAMBROLLÉ,
and A. MARTÍN-VICENTE

*Departamento de Biología Vegetal y Ecología, Facultad de Biología, Universidad de Sevilla,
Avda. Reina Mercedes, 41012 Sevilla, Spain*

Abstract

The impact of grazing by domestic goats, *Capra hircus*, on the photochemical apparatus of three co-ocurring Mediterranean shrubs, *Erica scoparia*, *Halimium halimifolium*, and *Myrtus communis* was evaluated. Seasonal course of gas exchange, chlorophyll fluorescence and photosynthetic pigment concentrations were measured in the field in grazed and ungrazed plants. Net photosynthetic rate was higher in grazed plants of *E. scoparia* and *H. halimifolium* in May, while there were not significant differences in *M. communis*. Photosynthetic enhancement in grazed plants of *E. scoparia* could be explained largely by higher stomatal conductance. On the other hand, the lack of differences in stomatal conductance between grazed and ungrazed plants of *H. halimifolium* could indicate that carboxylation efficiency, and ribulose-1,5-bisphosphate (RuBP) regeneration may have been enhanced by grazing. Overall grazing has little effect on the photochemical (PSII) apparatus, however grazed plants of *M. communis* showed chronic photoinhibition in the short term. Finally, seasonal variations recorded on photosynthesis, photochemical efficiency and pigment concentrations may be a physiological consequence of environmental factors, such as summer drought and competition for light, rather than an adaptation to grazing.

Additional key words: chlorophyll fluorescence; gas exchange; photosynthetic pigments; stomatal conductance.

Introduction

Grazing has been generally considered to have negative effects on plant fitness. Herbivores cause structural damages, remove plant biomass, decreasing the leaf area available for photosynthesis (Kotanen and Rosenthal 2001, Castro *et al.* 2003). However, the effects of herbivores on plants can be positive as well. Compensatory photosynthesis, defined as an increase in the photosynthetic rates of foliage on damaged plants relative to foliage of the same age on undamaged plants (Belski 1986), has been observed to be one underlying factor affecting plant response to herbivory (Larson 1998). Furthermore, the degree of compensation depends on the plant species, mode of herbivore damage, environmental conditions, the time and the intensity of herbivore attack (Maschinski and Whitham 1989, Thomson *et al.* 2003).

Appart from its influence on leaf physiological characteristics, the impact of herbivores can indirectly increase photosynthesis. The removal of leaves may improve light penetration into partially defoliated canopies (Anten and Ackerly 2001, Hayashi *et al.* 2007). Van Staalduinen and Anten (2005) showed that defoliated *Leymus chinensis* had greater average photosynthesis per unit leaf area, resulting in reduction in self-shading. Effects of herbivores on the photosynthetic capacity of plants have also been attributed to changes in carbon source-sink relationships (Thomson *et al.* 2003, Retuerto *et al.* 2006), and, in turn, these changes have been attributed to alterations in both mesophyll and stomatal conductances to CO_2 (g_m and g_s, respectively; Layne and Flore 1995).

Received 11 February 2010, *accepted* 11 June 2010.

[+] Corresponding author; tel.: +34-95-4557165, fax: +34-95-4615780, e-mail: susana@us.es

Abbreviations: C_i − intercellular CO_2 concentration; Chl *a* − chlorophyll *a*; Chl *b* − chlorophyll *b*; $Cx+c$ − carotenoids; F_0 − minimal fluorescence level in the dark-adapted state; F_m − maximal fluorescence level in the dark-adapted state; F_v/F_m − maximum quantum efficiency of PSII photochemistry; g_m − mesophyll conductance; g_s − stomatal conductance; NPQ − non-photochemical quenching; P_N − net photosynthetic rate; PSII − photosystem II; RuBP − ribulose-1,5-bisphosphate; WUE − water-use efficiency; Φ_{PSII} − quantum efficiency of PSII.

Acknowledgements: We thank Dr. Fernandez-Ales for the manuscript revision. We also thank the Ministry of the Environment of the Junta of Andalusia for its support (project nº 2007/665). Special thanks to Staff of Doñana National park and Dehesa Gato S.L. for their help and assistance.

Numerous studies have been conducted to characterize the effects of herbivory on growth and reproduction of Mediterranean shrubs (Vila and Lloret 1996, Riba 1998, Alonso and Herrera 2000, Midoko-Iponga *et al.* 2005, Ronel *et al.* 2007). However, few studies have been carried out on its effect on gas exchange. Thus, we performed a field experiment in order to investigate the effects of grazing by domestic goats, *C. hircus*, on the photochemical apparatus (PSII photochemistry) and gas-exchange characteristics of three co-ocurring Mediterranean shrubs, *E. scoparia*, *H. halimifolium* and *M. communis*.

Materials and methods

Plant material and experimental conditions: The experiment was conducted in a pine forest of 100 ha situated in Doñana Natural Park (37º14'46''N, 2º37'7''W; SW Spain) that had not been grazed for five years. The climate in this area is typically Mediterranean, with wet and mild winters and long dry summers. Rainfall during the experiment period reached 556 mm and mean annual temperature is 17ºC. The dominant tree is *Pinus pinea*, accompanied in some areas by cork oaks (*Quercus suber*) and holm oaks (*Quercus ilex*). The understory is covered with a Mediterranean shrubs, including common species such as *Cistus salvifolius*, *E. scoparia*, *H. halimifolium*, *H. calycinum*, *M. communis*, *Phillyrea angustifolia*, *Pistacia lentiscus*, *Rosmarinus officinalis* and *Thymus mastichina* ssp. *donyanae*.

To evaluate the effect of goat grazing on Mediterranean shrubs we selected three species: *E. scoparia* L., *H. halimifolium* (L.) Willk. and *M. communis* L. We selected these species because Mancilla-Leytón and Martín Vicente (2009) detected that goats showed preferences for them. Accordingly, ten adult plants of similar size of each of the three species were randomly selected, and five of them were fenced. Then, a herd of 350 goats (3.5 goats ha^{-1}) was introduced in the pine forest during the afternoon (4–5 hours of grazing) from May 2007.

Ecophysiological measurements (gas exchange, chlorophyll fluorescence and photosynthetic pigments) were made on the 7th of November 2007, the 5th of January, the 6th of May and the 22nd of July 2008 (six, eight, twelve, and fifteen months after the beginning of grazing). In addition, measurements of air temperature and relative humidity were taken at 1.5 m above the ground with a thermohygrometer (*Elka FTM10*, Lüdenscheid, Germany). Incident photon flux density was measured in a clear area with no plants with a *LI-COR* integrating quantum/radiometer/photometer using a *LI-190 SB* quantum sensor cell (Nebraska, USA). These measurements were taken on one occasion (at 12:00) during the ecophysiological measurements (*see* Table 1).

Gas-exchange measurements were taken on random, fully developed leaves (five leaves per plant) from among the nearest to distal ends of secondary branches at midday using an infrared gas analyzer in an open system (*LI-6400, Li-COR Inc.*, Lincoln, NE, USA). Net photosynthetic rate (P_N), intercellular CO_2 concentration (C_i) and stomatal conductance to CO_2 (g_s) were determined at 365 µmol mol^{-1}(CO_2), temperature of 20/25ºC, 50 ± 5% relative humidity and a photon flux density of 1,000 µmol m^{-2} s^{-1}. P_N, C_i and g_s were calculated using standard formulae of von Caemmerer and Farquhar (1981). Photosynthetic area was calculated by superimposing the surface of each leaf over a mm-square paper (Redondo-Gómez *et al.* 2007). Water-use efficiency (WUE) was calculated as the ratio between P_N and transpiration rate [mmol(CO_2 assimilated) mol^{-1}(H_2O transpired)].

Chlorophyll (Chl) fluorescence was measured in random-selected, fully developed leaves (*n* = 10, two leaves per plant) from among the nearest to distal ends of secondary branches using a portable modulated fluorimeter (*FMS-2*, *Hansatech Instrument Ltd.*, King´s Lynn, UK). Light- and dark-adapted fluorescence parameters were measured at dawn (stable, 50 µmol m^{-2} s^{-1} ambient light) and at midday (1,600 µmol m^{-2} s^{-1}) to investigate whether herbivory affected the sensitivity of plants to photoinhibition (Werner *et al.* 2002). Photoinhibition is a common phenomenon in environments with high radiation fluxes, especially when plants are exposed to additional environmental stresses. Photoinhibition can be short-term and reversible (dynamic photoinhibition), as a regulatory process for the controlled dissipation of excessive light energy, or long-term and irreversible as a slowly reversible process that may occur following prolonged exposure to excessive photon fluxes and under environmental stress conditions (chronic photoinhibition; Werner *et al.* 2002).

Plants were dark-adapted for 30 min, using leaf–clips exclusively designed for this purpose. The minimal fluorescence level in the dark-adapted state (F_0) was measured using a modulated pulse (<0.05 µmol m^{-2} s^{-1} for 1.8 µs) which was too small to induce significant physiological changes in the plant. The data stored were an average taken over a 1.6-second period. Maximal fluorescence in this state (F_m) was measured after applying a saturating actinic light pulse of 15,000 µmol m^{-2} s^{-1} for 0.7 s. The value of F_m was recorded as the highest average of two consecutive points. Values of the variable fluorescence ($F_v = F_m - F_0$) and maximum quantum efficiency of PSII photochemistry (F_v/F_m) were calculated from F_0 and F_m. This ratio correlates with the number of functional PSII reaction centres, and dark-adapted values of F_v/F_m can be used to quantify photoinhibition (Krivosheeva *et al.* 1996).

Table 1. Air temperature, air relative humidity and photon flux density (PFD) measurements taken at 1.5 m above the ground at 12 h. PFD was measured in a clear area with no plants.

	Temperature [ºC]	Relative humidity [%]	PFD [μmol m^{-2} s^{-1}]
7th November 2007	21.3	42.5	866
5th January 2008	16.7	36.9	730
6th May 2008	27.7	49.2	1846
22nd July 2008	32.2	53.9	1633

The same leaf section of each plant was used to measure light-adapted parameters. Steady state fluorescence yield (F_s) was recorded after adapting plants to ambient light conditions for 30 min. A saturating actinic light pulse of 15,000 μmol m^{-2} s^{-1} for 0.7 s was then used to produce the maximum fluorescence yield (F_m') by temporarily inhibiting PSII photochemistry.

Using fluorescence parameters determined in both light- and dark-adapted states, the following were calculated: quantum efficiency of PSII [$\Phi_{PSII} = (F_m' - F_s)/F_m'$] and non-photochemical quenching [$NPQ = (F_m - F_m')/F_m'$; Redondo-Gómez *et al.* 2006].

Photosynthetic pigments in fully expanded leaves ($n = 5$, taken randomly) nearest to distal ends of secondary branches from each treatment were extracted using 0.05 g of fresh material in 10 ml of 80% aqueous acetone. After filtering, 1 ml of the suspension was diluted with a further 2 ml of acetone and chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*) and carotenoid (C*x*+*c*) contents were determined with a *Hitachi U-2001* spectrophotometer (*Hitachi Ltd*., Japan), using three wavelengths (663.2, 646.8, and 470.0 nm). Concentrations of pigments were obtained by calculation, using the method of Lichtenthaler (1987).

Statistical analysis: All statistical tests were carried out using *Statistica v. 6.0* (*Statsoft Inc*., Tulsa, OK, USA). Data were analyzed using one-way analysis of variance (*F*-test). Data were first tested for normality with the *Kolmogorov-Smirnov* test and for homogeneity of variance with the *Brown-Forsythe* test. Data were subsequently transformed using $\sqrt{x}$ and arc-tangent functions to improve normality and homogeneity of variance. Significant test results were followed by *Tukey* test for identification of important contrasts. Differences between measurements of fluorescence at dawn and midday and between grazed and nongrazed treatments were compared by the *Student* test (*t*-test).

Results

Gas exchange: P_N was higher for grazed plants of *E. scoparia* and *H. halimifolium* in May (*t*-test, $p<0.05$; Fig. 1*A*). Furthermore, P_N of *H. halimifolium* was substantially reduced for both grazed and nongrazed treatments in July (*ANOVA*, $p<0.001$; Fig. 1*B*). There were not significant differences between grazed and nongrazed plants for *M. communis* ($p>0.05$; Fig. 1*C*).

g_s showed a trend similar to that of P_N (Fig. 1*D–F*); except in grazed plants of *H. halimifolium*, which recorded higher g_s values in November (*t*-test, $p<0.001$; Fig. 1*B*). C_i was also higher for grazed plants of this species in November (*t*-test, $p<0.001$), while it did not show differences between grazed and nongrazed treatments for both *E. scoparia* and *M. communis* ($p>0.05$; Fig. 1*G–I*).

WUE of *H. halimifolium* was higher for nongrazed control in November (*t*-test, $p<0.05$), while there were not differences between grazed and nongrazed treatments for the other two species (Fig. 2*A–C*). In addition, the lowest WUE values for *E. scoparia*, at both grazed and nongrazed treatments, were recorded in July (*ANOVA*, $p<0.0001$ and $p<0.001$ for grazed and nongrazed plants, respectively).

Chl fluorescence: F_v/F_m was always lower at midday and the reductions resulted mainly from lower values of F_m (data not presented) at midday than dawn (Fig. 3). Furthermore, F_v/F_m values at both dawn and midday were significantly lower for grazed plants of *M. communis* in November (*t*-test, $p<0.01$; Fig. 3*C*,*F*). On the other hand, *H. halimifolium* showed the lowest midday F_v/F_m values in July, while *M. communis* recorded the lowest values in January (Fig. 3*E*,*F*) at both dawn and midday, again because of different values of F_m.

Values Φ_{PSII} at dawn were uniformly high (data not presented) at both grazed and nongrazed treatments for all sampling times, varying around 0.80 for all three species. There were no differences of Φ_{PSII} values between grazed and nongrazed treatments at midday for any of the three species (*t*-test, $p>0.05$; Fig. 4*A*,*C*). There were no significant differences of NPQ between grazed and nongrazed treatments (Fig. 4*D–F*).

Photosynthetic pigments: Pigment concentrations were affected by grazing in *E. scoparia* and *M. communis* (Fig. 5). Significant differences between grazed and nongrazed plants of *E. scoparia* were found in May, with

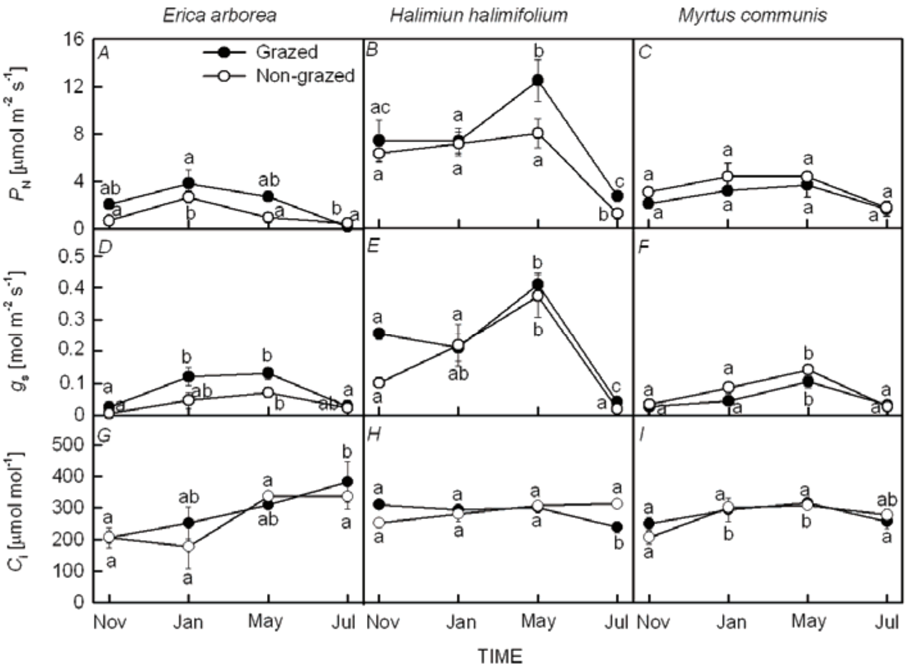

Fig. 1. *A–C*: Net photosynthetic rate (P_N), *D–F*: stomatal conductance (g_s), and *G–I*: intercellular CO_2 concentration (C_i) in *Erica scoparia*, *Halimium halimifolium*, and *Myrtus communis* in response to grazed (•) and nongrazed (o) treatments along a year. Values represent mean ±SE of five replicates.

lower Chl *b* and C*x*+*c* in grazed plants (*t*-test, $p<0.05$; Fig. 5*D*,*G*). In *M. communis*, nongrazed plants recorded higher pigment concentrations in July (*t*-test, $p<0.01$; Fig. 5*C*,*F*,*I*).

On the other hand, *H. halimifolium* and *M. communis* had marked seasonal patterns of variation for both Chl *a* and *b* values, showing the lowest values for both grazed and nongrazed plants in July and January, respectively for each species (*ANOVA*, $p<0.05$; Fig. 5).

Discussion

Grazing by domestic goats (*Capra hircus*) had different effects on the three Mediterranean shrubs studied, and these effects changed seasonally. P_N only showed significant differences for *E. scoparia* and *H. halimifolium* in May; P_N values of both species were markedly enhanced by grazing. Increased leaf-level photosynthetic activity following herbivore damage has been described as a mechanism of tolerance (Strauss and Agrawal 1999, Castro *et al.* 2003) and it may compensate for the lost leaf area and support the synthesis of induced chemical defenses (Karban and Baldwin 1997). According to Maschinski and Whitham (1989), plants are more likely to compensate if the damage occurs early in the growing season, before the reproductive phase has started. However, *E. scoparia* increased its photosynthetic activity after flowering and *H. halimifolium* during the flowering time. This suggests that in these two species phenological stage is not a factor affecting photosynthetic response to grazing.

However, compensation in July could be limited by summer drought; it is consistent with the lower WUE recorded for *E. scoparia*, and with stomatal closure and lower pigments concentrations and F_v/F_m values recorded for *H. halimifolium* in both grazed and nongrazed plants in July, which provide an explanation for the concomitantly declining photosynthetic assimilation rates.

Tschaplinski and Blake (1989) suggested that, when enhancement of photosynthesis occurs after defoliation, this indicated that leaves were operating below their maximum photosynthetic potential before defoliation. In a similar vein, Thomson *et al.* (2003) reported that the increase in carbon demand induced plants to use their absorbed light more efficiently, recording a decrease in NPQ, or energy lost as heat, in the leaves of herbivore-damaged plants. However, a reduction of NPQ was not found in our experiment, although lower Chl *b* and C*x*+*c* were recorded in grazed plants of *E. scoparia* in May, as compared to the nongrazed plants. Nevertheless, there were no significant effects on F_v/F_m or Φ_{PSII} values, with no differences between grazed and nongrazed plants of *E. scoparia* and *H. halimifolium* in May. This agrees with the results presented by Macedo *et al.* (2007), who found a lack of significant effects of any defoliation treatments on any of the Chl *a* fluorescence parameters measured in wheat. In contrast, Layne and Flore (1992) found that photosynthetic enhancement of individual leaves to leaf-area reduction was caused by increased photochemical and carboxylation efficiencies and RuBP regeneration rate on *Prunus cerasus*. Thus, the lack of alteration of g_s in *H. halimifolium* in May could indicate that carboxylation efficiency and RuBP regeneration may have been enhanced. In contrast, this species showed

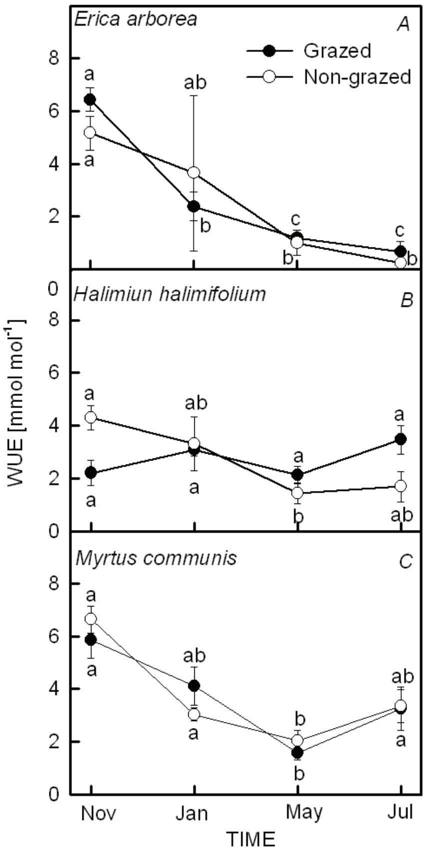

Fig. 2. Water-use efficiency (WUE) in *Erica scoparia* (*A*), *Halimium halimifolium* (*B*) and *Myrtus communis* (*C*) in response to grazed (•) and non-grazed (o) treatments along a year. Values represent mean ±SE of five replicates.

higher g_s values for grazed plants, a fact that led to a higher C_i in November, although it did not correspond with changes in P_N. On the other hand, the lower stomatal control of grazed plants led to a reduction in WUE.

In the case of *E. scoparia,* g_s in grazed plants was higher than that in nongrazed plants in May. Consequently, enhanced g_s in spring appeared to provide an explanation for the concomitantly enhanced photosynthetic assimilation rate. A similar result was obtained by Macedo *et al.* (2007) in wheat, where, after defoliation, injured leaves did not close their stomata. Furthermore, same as in our experiment, they found that the lack of a significant effect of grazing on other photosynthetic parameters such as C_i and WUE suggested that water loss was not a limiting factor for photosynthesis in the leaves of the grazed plants.

F_v/F_m showed a significant reduction at midday compared to dawn values, which is indicative of photoinhibition associated with an over-reduction of PSII. This photoinhibition is most likely to have been caused by a lower proportion of open reaction centres (lower values of F_m) resulting from a saturation of photosynthesis by light. In our experiment, photoinhibition was clearly dynamic, since the low midday values recovered completely by dawn to optimal values for unstressed plants (Björkman and Demmig 1987); except in the case of grazed plants of *M. communis* in November, where these values remained lower than in nongrazed control plants at dawn, indicating a chronic photoinhibition. Therefore, it can be stated that grazing represents a biotic stress factor for *M. communis* in the short term, since plants had been grown for five years without livestock grazing. Hayashi *et al.* (2007) explained that when a plant is exposed to herbivory pressures that differ from the original pressure, the observed performance is a consequence of a fixed strategy that has adapted to the original conditions; in this case, we examined the short-term response. In addition, both grazed and nongrazed plants of *M. communis* showed lower F_v/F_m values at both dawn and midday in January. In this regard, Gratani *et al.* (2008) found a limitation in photosynthetic activity of *M. communis* by low temperatures (minimum air

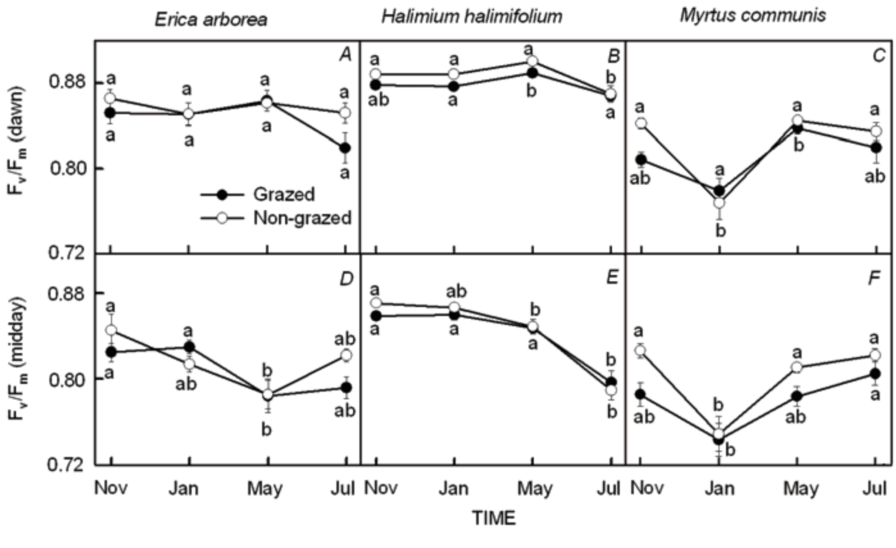

Fig. 3. Maximum quantum efficiency of PSII photochemistry (F_v/F_m) at dawn (*A–C*) and midday (*D–F*) in *Erica scoparia* (*A,D*), *Halimium halimifolium* (*B,E*), and *Myrtus communis* (*C,F*) in response to grazed (•) and nongrazed (o) treatments along a year. Values represent mean ±SE of ten replicates.

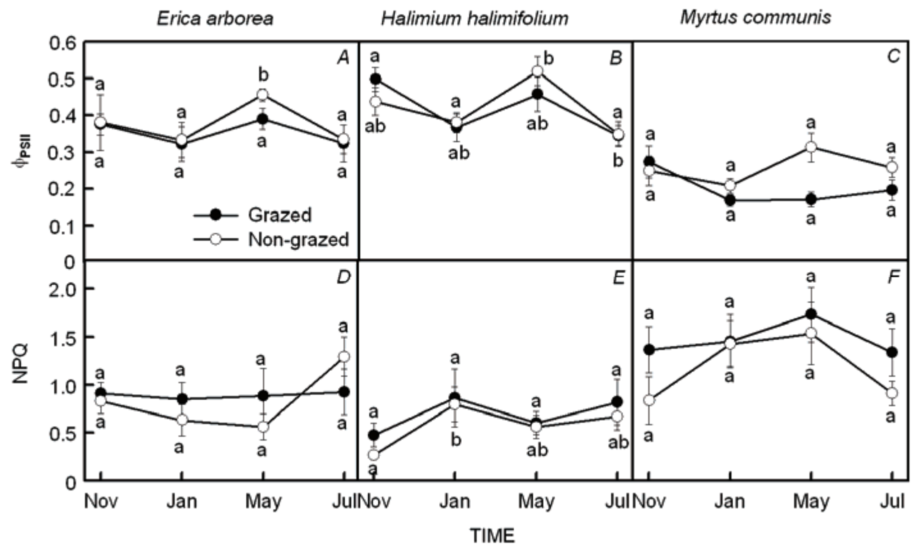

Fig. 4. *A–C*: Quantum efficiency of PSII (Φ_{PSII}), and *D–F*: non-photochemical quenching (NPQ), at midday in *Erica scoparia*, *Halimium halimifolium*, and *Myrtus communis* in response to grazed (•) and non-grazed (o) treatments along a year. Values represent mean ± SE of ten replicates.

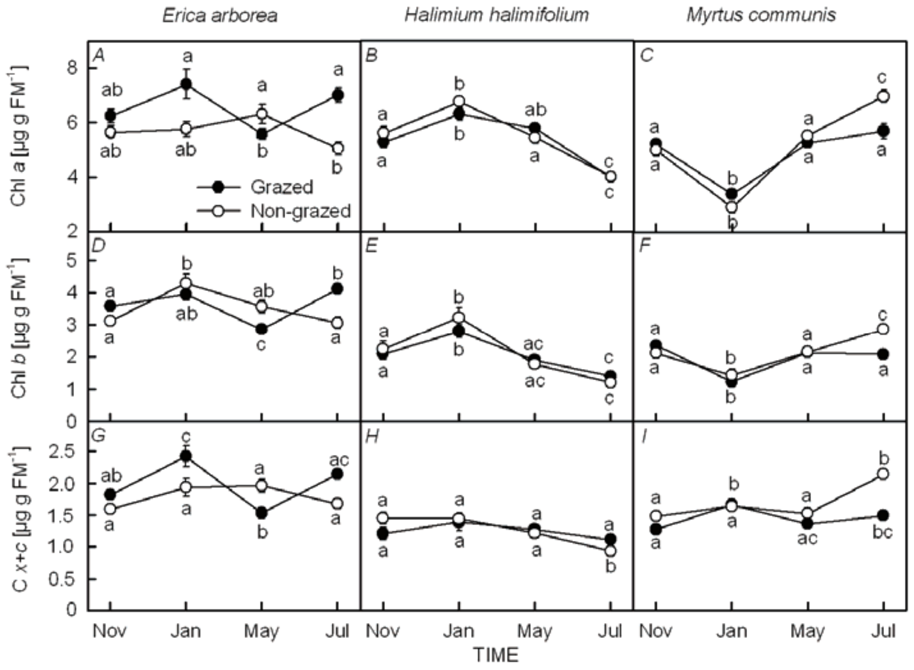

Fig. 5. Chlorophyll (Chl) *a* (*A–C*), Chl *b* (*D–F*), and carotenoid, C*x+c* (*G–I*) concentrations in *Erica scoparia*, *Halimium halimifolium* and *Myrtus communis* in response to grazed (•) and nongrazed (o) treatments along a year. Values represent mean ± SE of five replicates.

temperature 8.8ºC). In our experiment, this decrease could have been caused by a lower proportion of open reaction centres (lower values of F_m), which could be attributed to a decrease in Chl contents or increase in its degradation. Monnet *et al.* (2001) found that destruction of antennae pigments may disturb F_v/F_m. In contrast, the decrease in pigment concentrations recorded for grazed plants of *M. communis* in July did not lead to a significant decline in the photochemistry of PSII of these species. Ni *et al.* (2002) also found significant loss of chlorophylls and carotenoids as a result of Russian wheat aphid infestation, mediated by increased Mg-dechelatase activity.

In conclusion, grazing by domestic goat affected differently the photosynthetic activity of the Mediterranean shrubs *E. scoparia*, *H. halimifolium* and *M. communis*. P_N of *E. scoparia* and *H. halimifolium* were enhanced by grazing in May, while P_N of *M. communis* was unaffected. Stimulation of the carboxylation capacity of *E. scoparia* by grazing was mediated by enhanced g_s and higher contents of Chl *b* and carotenoids. In the case of *H. halimifolium*, enhancement of photosynthetic rate with the lack of alteration of g_s could indicate that carboxylation efficiency and RuBP regeneration may have been enhanced. Grazing has little overall effect on the photochemical (PSII) apparatus, although grazed plants of *M. communis* showed chronic photoinhibition in the short term. Further ecophysiological studies associated with these three shrubs are needed to reach a more thorough understanding of specific and seasonal differences.

References

Alonso, C., Herrera, C.M.: Seasonal variation in leaf characteristics and food selection by larval noctuids on an evergreen Mediterranean shrub. – Acta Oecol. **21**: 257-265, 2000.

Anten, N.P.R., Ackerly, D.C.: Canopy-level photosynthetic compensation after defoliation in a tropical understorey palm. – Funct. Ecol. **15**: 252-262, 2001.

Belski, A.J.: Does herbivory benefit plants? A review of the evidence. – Amer. Nat. **127**: 870-892, 1986.

Björkman, O., Demmig, B.: Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77K among vascular plants of diverse origins. – Planta **170**: 489-504, 1987.

Castro, H., Nabais, C., Alados, C.L., Freitas, H.: Effects of cessation of grazing on leaf-level photosynthesis of *Periploca laevigata*. – Appl. Veg. Sci. **6**: 255-260, 2003.

Gratani, L., Varone, L., Catoni, R.: Relationship between net photosynthesis and leaf respiration in Mediterranean evergreen species. – Photosynthetica **46**: 567-573, 2008.

Hayashi, M., Fujita, N., Yamauchi, A.: Theory of grazing optimization in which herbivory improves photosynthetic ability. – J. Theor. Biol. **248**: 367-376, 2007.

Karban, R., Baldwin, I.T.: Induced Responses to Herbivory. – Univ. Chicago Press, Chicago 1997.

Kotanen, P.M., Rosenthal, J.P.: Tolerating herbivory: does the plant care if the herbivore has a backbone? – Evol. Ecol. **14**: 537-549, 2001.

Krivosheeva, A., Tao, D.L., Ottander, C., Wingsle, G., Dube, S.L., Öquist, G.: Cold acclimated and photoinhibition in Scots pine. – Planta **200**: 296-305, 1996.

Larson, K.C.: The impact of two gall-forming arthropods on the photosynthetic rates of their hosts. – Oecologia **115**: 161-166, 1998.

Layne, D.R., Flore, J.A.: Photosynthetic compensation to partial leaf area reduction in sour cherry. – J. Amer. Soc. Hort. Sci. **117**: 279-286, 1992.

Layne, D.R., Flore, J.A.: End-product inhibition of photosynthesis in *Prunus cerasus* L. in response to whole-plant source-sink manipulation. – J. Amer. Soc. Hort. Sci. **120**: 583-599, 1995.

Lichtenthaler, H.K.: Chlorophylls and carotenoids - pigments of photosynthetic biomembranes. – Methods Enzymol. **148**: 350-382, 1987.

Macedo, T.B., Peterson, R.K.D., Dausz, C.L., Weaver, D.K.: Photosynthetic responses of wheat, *Triticum aestivum* L., to defoliation patterns on individual leaves. – Environ. Entomol. **36**: 602-608, 2007.

Mancilla-Leytón, J.M., R., Martín Vicente, A.: [Análisis de la apetencia del ganado caprino por las especies de matorral en el Espacio Natural de Doñana.] – Sociedad Española para el estudio de los pastos **48**: 643-648, 2009. [In Spanish.]

Maschinski, J., Whitham, T.G.: The continuum of plant responses to herbivory: the influence of plant association, nutrient availability and timing. – Amer. Nat. **134**: 1-19, 1989.

Midoko-Iponga, D., Krug, C.B., Milton, S.J.: Competition and herbivory influence growth and survival of shrubs on old fields: implications for restoration of renosterveld shrubland. – J. Veg. Sci. **16**: 685-692, 2005.

Monnet, F., Vaillant, N., Vernay, P., Coudret, A., Sallanon, H., Hitmi, A.: Relationship between PSII activity, CO_2 fixation, and Zn, Mn and Mg contents of *Lolium perenne* under zinc stress. – J. Plant Physiol. **158**: 1137-1144, 2001.

Ni, X., Quisenberry, S.S., Heng-Moss, T., Markwell, J., Higley, L., Baxendale, F., Sarath, G., Klucas, R.: Dynamic change in photosynthetic pigments and chlorophyll degradation elicited by cereal aphid feeding. – Entomol. Exp. Appl. **105**: 43-53, 2002.

Redondo-Gómez, S., Wharmby, C., Castillo, J.M., Mateos-Naranjo, E., Luque, C.J., de Cires, A., Luque, T., Davy, A.J., Figueroa, M.E.: Growth and photosynthetic responses to salinity in an extreme halophyte, *Sarcocornia fruticosa*. – Physiol. Plant **128**: 116-124, 2006.

Redondo-Gómez, S., Mateos-Naranjo, E., Davy, A.J., Fernández-Muñoz, F., Castellanos, E.M., Luque, T., Figueroa, M.E.: Growth and photosynthetic responses to salinity of the salt-marsh shrub *Atriplex portulacoides*. – Ann. Bot. **100**: 555-563, 2007.

Retuerto, R., Fernández-Lema, B., Obeso, J.R.: Changes in photochemical efficiency in response to herbivory and experimental defoliation in the dioecious tree *Ilex aquifolium*. – Int. J. Plant Sci. **167**: 279-289, 2006.

Riba, M.: Effects of intensity and frequency of crown damage on resprouting of *Erica arborea* L. (Ericaceae). – Acta Oecol. **19**: 9-16, 1998.

Ronel, M., Malkiel, H., Lev-Yadun, S.: Quantitative characterization of the thorn system of the common shrubs *Sarcopoterium spinosum* and *Calicotome villosa*. – Isr. J. Plant Sci. **55**: 63-72, 2007.

Strauss, S.Y., Agrawal, A.A.: The ecology and evolution of plant tolerante to herbivory. – Trends Ecol. Evol. **14**: 179-185, 1999.

Thomson, V.P., Cunningham, S.A., Ball, M.C., Nicotra, A.B.: Compensation for herbivory by *Cucumis sativus* through increased photosynthetic capacity and efficiency. – Oecologia **134**: 167-175, 2003.

Tschaplinski, T.J., Blake, T.J.: Photosynthetic reinvigoration of leaves following shoot decapitation and accelerated growth of coppice shoots. – Physiol. Plant. **75**: 157-165, 1989.

Van Staalduinen, M.A., Anten, N.P.R.: Differences in the compensatory growth of two co-occurring grass species in relation to water availability. – Oecologia **146**: 190-199, 2005.

Vila, M., Lloret, F.: Herbivory and neighbour effects on the sprout demography of the Mediterranean shrub *Erica multiflora* (Ericaceae). – Acta Oecol. **17**: 127-138, 1996.

Von Caemmerer, S., Farquhar, G.D.: Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. – Planta **153**: 376-387, 1981.

Welter, S.C.: Arthropod impact on plant gas exchange. – In: Bernays, E.A. (ed.): Insect-Plant Interactions, Vol. 1. Pp.135-150. CRC, Boca Raton 1989.

Werner, C., Correia, O., Beyschlag, W.: Characteristic patterns of chronic and dynamic photoinhibition of different functional groups in a Mediterranean ecosystem. – Funct. Plant Biol. **29**: 999-1011, 2002.