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ORIGINAL ARTICLE

Sap flow and photosynthetic response to climate and drought of *Pinus nigra* in a Mediterranean natural forest

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Abstract

Key message **Drought caused a decrease of water flux and photosynthesis due to stomata closure, typical of drought-avoiding strategy. No photoinhibitory stress was observed.**

Abstract Drought represents an important source of disturbance in Mediterranean ecosystems. For long-term forest management, knowledge of tree responses to climate is essential. To investigate the seasonal functioning of *Pinus laricio* and its tolerance to summer drought in a Mediterranean climate, we carried out a field study in a natural mountainous pine forest over a 2-year period. For the first time for this species, sap flow, chlorophyll fluorescence, and gas exchange were used as indicators of tree vitality. Mild winter did not alter photosynthetic performance while sap flow declined. In spring, increase of sap flow was observed, revealing the end of tree dormancy and the beginning of the growth season. In response to summer drought, stomatal closure caused a reduction of gas exchange and sap flow. At the same time, pines increased their water use efficiency and reduced the limitation of mesophyll conductance. The reduction in CO_2 assimilation was associated with photochemical stability, which might cause an imbalance between light energy input and energy used in photochemistry. The stability of chlorophyll fluorescence parameters indicated the absence of photoinhibitory stress, probably because of the use of photorespiration. The reduction of sap flow and stomatal conductance during drought confirmed the water-saver status of *P. laricio* species.

Keywords Chlorophyll fluorescence · Gas exchange · *Pinus laricio* · Drought · Stress · Mediterranean · Sap flow

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Introduction

Pinus nigra Arnold and its different subspecies represent a substantial proportion of the forest area (3.5×10^6 ha) in the Mediterranean mountains, from Morocco to Turkey (Richardson 2000). This study focused on *P. nigra* Arnold subsp. *laricio* (Poir.) Maire var. *corsicana* (Loudon) or *P. laricio*, whose forests characterize Corsican mountains in the supramediterranean and montane zones (900–1800 m). It is a tree growing up to 50 m tall with a straight trunk and grey to dark brown bark, whose long needles (12–15 cm) are persistent during 3 years. It is very closely related to the variety *calabrica* present in Calabria and Sicily (Rameau et al. 2008). *Pinus laricio* is endemic to Corsica, but due to its widespread use in reforestation, it is now principally present in continental forests (Schabaver 2001; Inventaire Forestier National 2006). Given its high patrimonial and ecological value, *P. laricio* natural habitat is ranked a priority in the "Habitats" Directive (Leone and Lovreglio 2004).

Many cases of forest dieback and tree mortality attributed to drought or heat-induced stress have been reported worldwide over the last few decades (Allen et al. 2010); indeed, the long lifespan of trees prevents them from

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adapting rapidly to environmental changes (Lindner et al. 2010). In the Mediterranean Basin, annual precipitation is expected to decrease by more than 25–30% by the end of the 21st century, probably accompanied by a 4–5 °C rise in average annual temperatures (Christensen et al. 2007; Giorgi and Lionello 2008) and even more so in mountainous areas (Meehl et al. 2007).

Seasonal adjustments in leaf function enable evergreen Mediterranean species to survive annual summer drought (synthesis in Osuna et al. 2015); however, climatic and dendrochronological studies have demonstrated severe impacts of summer drought on *P. nigra* (Herguido et al. 2016; Lebourgeois 2000; Martín-Benito et al. 2008). Nevertheless, we lack basic data on the hydric and photosynthetic functioning of *P. laricio.* These data are essential for the assessment of short-term responses of *P. laricio* to summer drought, and could help us understand how future climatic conditions could affect this species.

Sap flow measurement is used to study water movement in tree trunks (Lu et al. 2004) and transpiration (Delzon and Loustau 2005). It provides accurate responses to seasonal variations in climate and drought. Many studies carried out in mountainous ecosystems show that sap flows are slow in winter (Delzon and Loustau 2005) and show an ability of trees to decrease sap flow during drought period (Anfodillo et al. 1998; Klein et al. 2014a, b; Lu et al. 2004).

Some tree species have highly plastic photosynthetic processes in terms of gas exchange or photochemistry. The responses depend on species, provenance, and stage of development (Repo et al. 2016), and undergo seasonal variations (Lundmark et al. 1998; Ottander et al. 1995; Ogaya et al. 2011). This response is attributed to variations in temperature and water availability. The effects of drought on net photosynthetic rate (A), rate of RuBP carboxylation by Rubisco (V_{cmax}), rate of electron transport driving regeneration of RuBP (J_{max}) and stomatal conductance (g_s) were observed on many species (Avola et al. 2008; Warren and Dreyer 2006; Way and Sage 2008; Xu and Baldocchi 2003). Simultaneous gas exchange and chlorophyll fluorescence measurements showed variations in photosystem II (PSII) and carbon assimilation in a crop plant (*Vigna unguiculata* L.) during a drought period (Souza et al. 2004) and in *Quercus douglasii* Hook. & Arn. during a 3-year survey (Osuna et al. 2015). Simultaneous decreases in sap flow and stomatal conductance were observed in water-stressed *Picea abies* in summertime during a 5-month survey (Lu et al. 1995).

In this study, we investigated the relationships between photosynthetic processes and sap flow in a natural mountainous *P. laricio* forest over a 2-year period. We sought to answer the following questions:

1. What is the seasonal physiological cycle of *P. laricio* in a Mediterranean climate?
2. How does *P. laricio* withstand summer drought?

We hypothesized that *P. laricio*, at the montane level, would show all the signs of dormancy in winter, with a considerable reduction in all physiological parameters. Furthermore, we hypothesized that *P. laricio*, under conditions of summer drought, would reduce sap flow and gas exchange, to the detriment of carbon assimilation. This behaviour would be characteristic of a drought-avoiding/water-saving strategy (Anfodillo et al. 1998; Baquedano and Castillo 2006).

The results will provide the first data on seasonal physiological trends in *P. laricio* and indicate its potential capacity to resist climate change in Mediterranean.

Materials and methods

Site description

Measurements were made in a natural pure 300 m² stand of *P. laricio* located in Corsica, France (42°11′48.5″N 9°05′39.6″E) at 1200 m above sea level, at the edge of supramediterranean and montane levels. The slope is about 70–80%, the basal area is 36.5 m² ha⁻¹, and trees have a northeast exposition. Competition index for all pines was measured using Hegyi's (1974) method (Prévosto 2005). The soil is a low-depth brown with many rocky outcrops on granitic bedrock. This plot has not been exploited for 30 years.

Meteorological measurements

General meteorological measurements were provided by a weather station located in a clearing a few meters from the plot. Temperature, relative humidity (CS215, Campbell Scientific Ltd., Loughborough, UK), and PAR (photosynthetically active radiation) (PAR Quantum Sensor SKP 215, Skye Instruments Ltd., Llandrindod Wells, UK) were measured every 30-s and averaged over 30 min. Rainfall measurements (Rain Gauge 52203, R. M. Young Corporation, Traverse City, MI, USA) were collected every 30 min. Data were recorded using a battery-powered CR1000 data logger (Campbell Scientific Ltd., Loughborough, UK) recharged daily by a photovoltaic power source.

Physiological measurements

Sampling Twelve co-dominant pine trees were randomly selected for continuous sap flow measurements between July 2013 and October 2015. Among them, nine trees were

monitored for chlorophyll fluorescence and gas exchange between December 2013 and July 2015. Characteristics of sampled trees are presented in Table 1. 5–6 m high sun-exposed branches were sampled on the same crown position and orientation (northeast); they were immediately recut under water and stored in this way to avoid cavitation. Preliminary experiments on Corsican pines demonstrated that cutting had no effect on gas exchange or chlorophyll fluorescence for up to 12 h after the cut was made (data not shown). Similar results were observed with other conifers, including *Pseudotsuga menziesii* and *Pinus pinaster* (Warren et al. 2003; Warren 2006). As measurement was time intensive, three branches per day were sampled and analysed, on three consecutive days each month (sampling dates are presented in Table 1 of the Electronic Supplementary Material). To ensure implementation of reliable measures and to avoid senescent needles, measurements were always carried out on current-year needles (Warren 2006; Sperlich et al. 2015), at the end of the branch.

Sap flow Sap flow was measured with thermal dissipation probes (TDP) according to the Granier method (Granier 1985). Either TDP-30 or TDP-50 (Dynamax Inc., Houston, TX, USA) was used, depending on trunk diameter (Table 1). Sensors were installed at breast height with the same exposition (northeast) and protected with reflective insulation. Sap flow was calculated according to Granier and Gross (1987) and expressed as $dm^3\ dm^2\ h^{-1}$; it was monitored between 13 July 2013 and 26 October 2015. During winter, due to the low recharge of battery by solar panels, only 1 tree was monitored. Other TDP were turned off after reduction and stabilization of sap flow (due to winter) and turned on when sap flow increased again. Measurements were taken every 30 s and averaged every 30 min. Data were recorded in a battery-powered data logger (CR3000, Campbell Scientific Ltd., Loughborough, UK) recharged daily by solar panels.

Chlorophyll fluorescence Chlorophyll fluorescence was measured using a PAM 2100 (Heinz Walz GmbH, Effeltrich, Germany) fitted with DLC-8 leaf clips, which permitted dark acclimation. Three measurements per branch were made, on different needles, dark adapted for at least 30 min before measurements. Four parameters were monitored: (a) maximum yield of PSII (F_v/F_m), (b) quantum yield of PSII (Φ_{PSII}), (c) photochemical quenching (qP), and (d) non-photochemical quenching (NPQ) calculated according to Maxwell and Johnson (2000).

Gas exchange Gas exchange was measured using an LI-6400XT Portable Photosynthesis System fitted with a 6400-01 CO_2 Injector and a 6400-22L Lighted Conifer Chamber (LI-COR Inc., Lincoln, NE, USA). Net photosynthesis (A) and stomatal conductance (g_s) were recorded during the first CO_2 step (350 µmol mol^{-1}) because it is the closest to ambient CO_2 concentration. Measurements were made in the same order and the same hour every month. To estimate the maximum Rubisco carboxylation rate (V_{cmax}), the maximum electron transport rate (J_{max}), the rate of triose phosphate export from the chloroplast (TPU), and the mesophyll conductance (g_m), A–C_i curves were fitted with 13 steps of CO_2: 350, 275, 200, 125, 50, 450, 550, 700, 900, 1100, 1300, 1600, and 2000 µmol mol^{-1}.

Other parameters were kept constant (PAR = 1200 µmol m^{-2} s^{-1} with red blue source (ratio: 0.94–0.06), temperature = 25 °C, air flux = 350 µmol s^{-1}, and vapour pressure deficit (VPD) = 1.2 ± 0.05 kPa). Three readings were made with 30-s intervals between them for each CO_2 step.

V_{cmax}, J_{max} and TPU were estimated according to the Farquhar, von Caemmerer, and Berry model (Farquhar et al. 1980; von Caemmerer 2000), through the online service presented by Gu et al. (2010) and available from http://leafweb.ornl.gov/. Based on the works of Flexas et al. (2012) and Sun et al. (2014), we chose to estimate mesophyll conductance (g_m) in order to avoid the under-

Table 1 DBH, height, age (in spring 2013), TDP length and competition index of monitored trees

	1*	2*	3	4	5*	6*	7*	8*	9*	10*	11*	12
DBH (cm)	15.0	14.5	13.0	12.5	12.5	13.5	19.0	18.0	21	21.5	20	21.0
Height (m)	11.8	13.1	8.6	6.9	7.3	11.5	8.6	13.5	10.1	8.0	10.1	12.7
Age (years)	45	38	36	29	23	22	29	42	42	42	50	43
TDP length (mm)	30	30	30	30	30	30	50	50	50	50	50	50
Competition index (unitless)	17.8	6.5	9.2	12.0	12.0	12.4	8.2	9.9	6.7	6.3	5.8	16.3

Photosynthetic measurements were realized on trees indicated with an asterisk. For trees 3, 4 and 10, sap flow measurements underwent technical problems

estimation of V_{cmax} and J_{max}. Slope of A/g_s, A/g_m, and g_m/g_s relationships was used to explore variations in CO_2 fluxes and water loss by season (Sperlich et al. 2015).

Statistical analyses

Statistical analyses were conducted using R 3.2.3 for Linux. Statistical differences between measurement dates for gas exchange and chlorophyll fluorescence parameters were tested using one-way ANOVA and Tukey's range test when normality and homoscedasticity were verified (by Shapiro–Wilk and Levene's tests). Otherwise, Kruskal–Wallis and Wilcoxon signed-rank tests were performed. Significant differences were determined at $P \le 0.05$. Linear regression was used to study A/g_s, A/g_m, and g_m/g_s relations. Analyses of covariance (ANCOVA) were used to test statistical differences between slopes and intercepts of regression lines. Dependencies between sap flow and vapour pressure deficit (VPD) were tested using Spearman's rank correlation coefficient.

Results

Meteorological data

Meteorological trends were similar from year to year, with relatively hot, dry summers and mild winters. The year 2015 had the coldest winter (mean minimal temperature: -1.5 °C in February) and the hottest summer (mean maximal temperature: 29.5 °C in July) (Fig. 1a). The end of the summer 2014 was particularly dry, with 41 rainless days (31 July–9 September) and only 14.5 mm of rainfall in September (Fig. 1b). Important daily and seasonal variations of VPD (Fig. 1c) were observed, with notably high values (>2 kPa) during summer.

Sap flow

The daily (Fig. 2) sap flow patterns were roughly similar between trees. Nevertheless, the magnitude of the mean sap flow differed for each one, independently of age, height,
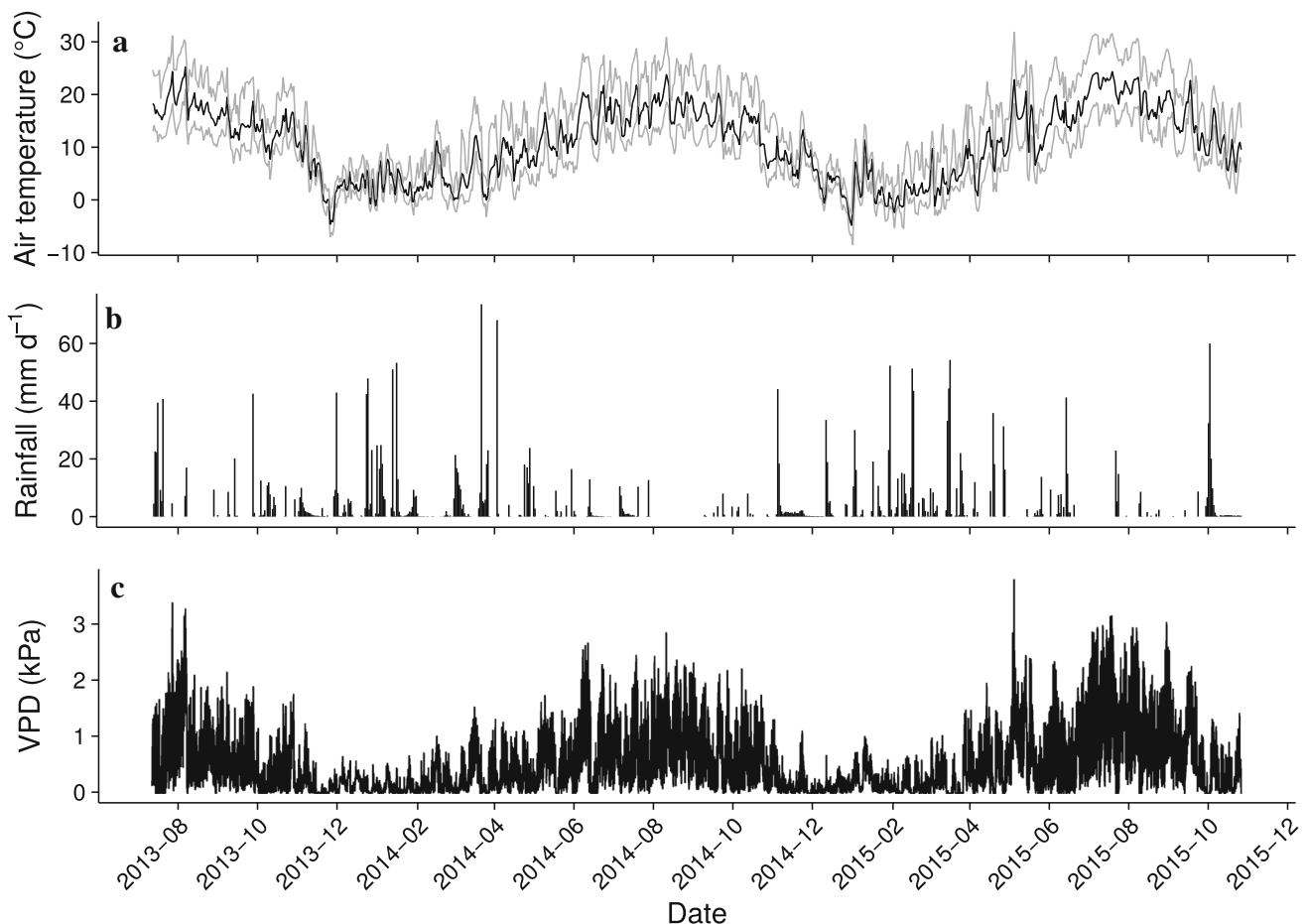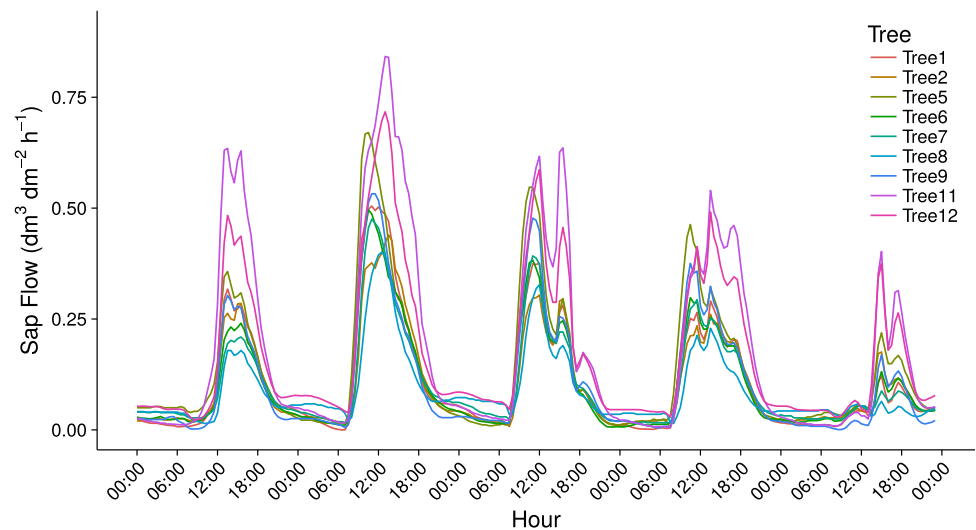

Fig. 1 Daily mean (*black line*), minimum and maximum (*grey lines*) air temperature (°C) (**a**), daily total rainfall (mm d^{-1}) (**b**) and continuous VPD (kPa) (**c**), between 13 July 2013 and 26 October 2015

Fig. 2 Daily variations of sap flow ($dm^3\ dm^{-2}\ h^{-1}$) between the 10 and the 14 July 2014 for all trees. *X*-axis represents hour of the day

DBH, and position in the stand ($P > 0.05$). Sap flow (Fig. 3) values were lowest during winter ($<0.15\ dm^3\ dm^{-2}\ h^{-1}$), and highest in early summer (up to $0.84\ dm^3\ dm^{-2}\ h^{-1}$ in July 2013). A temporary sap flow slowdown occurred at the end of each summer ($\leq 0.33\ dm^3\ dm^{-2}\ h^{-1}$ in September, each year). Spearman's rank correlation coefficient, run using diurnal values, showed strong positive correlations (>0.7) between sap flow and VPD during high sap flow periods (Electronic Supplementary Material, Table 2).

Chlorophyll fluorescence

Φ_{PSII} (Fig. 4a) was relatively stable (maximum value ca. 0.6), and lower values were observed in March 2014 (0.48). Lower F_v/F_m (Fig. 4b) values (0.79) were observed in winter and early spring (January–April) of 2014 and 2015; it was stable during the other months (0.84). qP (Fig. 4c) showed maximal values in spring (max. 0.81 in April 2014), and lower values were observed in summer (0.73 in July 2014 and 0.74 in July 2015). NPQ (Fig. 4d) followed a different trend from the other parameters: higher values (1.38) were observed in winter 2014 (January) and lower values (0.47) in May 2014.

Gas exchange

Maximum values of *A* (ca. 4 µmol $m^{-2}\ s^{-1}$) were observed during winter-spring 2014 and spring 2015. A significant decrease in photosynthesis (from 3.45 to the lowest value, 0.65 µmol $m^{-2}\ s^{-1}$) was observed between July and September 2014 (Fig. 5a). Significant reductions of g_s (Fig. 5b) and g_m (Fig. 5c) (82.5 and 76.0%, respectively) were observed during summer 2014 (between July and

September). V_{cmax}, J_{max}, and TPU (Fig. 5d–f) showed few seasonal variations.

The slope of A/g_s (Fig. 6a) was significantly higher ($P < 0.05$), and the intercept was lower in summer 2014 and 2015 and autumn 2014. In winter 2015, the intercept was lower than in other seasons except summer 2014 and 2015 and autumn 2014. The intercept of A/g_m (Fig. 6b) was also significantly lower in summer 2014 and 2015 and autumn 2014, while the slope was higher only in summer and autumn 2014. Regarding g_m/g_s (Fig. 6c), the slope was significantly higher in summer 2014 and 2015 and autumn 2014 (Equations, R^2, and *P* values of linear regressions are presented in Table 3 of the Electronic Supplementary Material, and results of ANCOVA are presented in the spreadsheet ESM_ANCOVA).

Discussion

This long-term study on a natural stand of *P. laricio* permitted, for the first time, a seasonal analysis of light use, carbon assimilation, and water status in this species.

In winter, photochemistry and carbon assimilation parameters were fairly stable compared to those of other species. The maximal photochemical efficiency of PSII (F_v/F_m) was very stable in winter due to temperatures (largely $>0\ °C$) experienced in the stand. Indeed, low temperature can induce marked decline of PSII activity in both angiosperms and coniferous tree species (Baquedano and Castillo 2006; Lundmark et al. 1998; Ottander et al. 1995). Significant variations in all chlorophyll fluorescence parameters were observed, but slight decreases in F_v/F_m values (maximum 5%) and the relative stability of other photochemical parameters (Φ_{PSII}, qP, and NPQ; Fig. 4)

Fig. 3 Seasonal variations of sap flow ($dm^3\ dm^{-2}\ h^{-1}$) from 13 July 2013 and 26 October 2015. Mean of values of all tree monitored
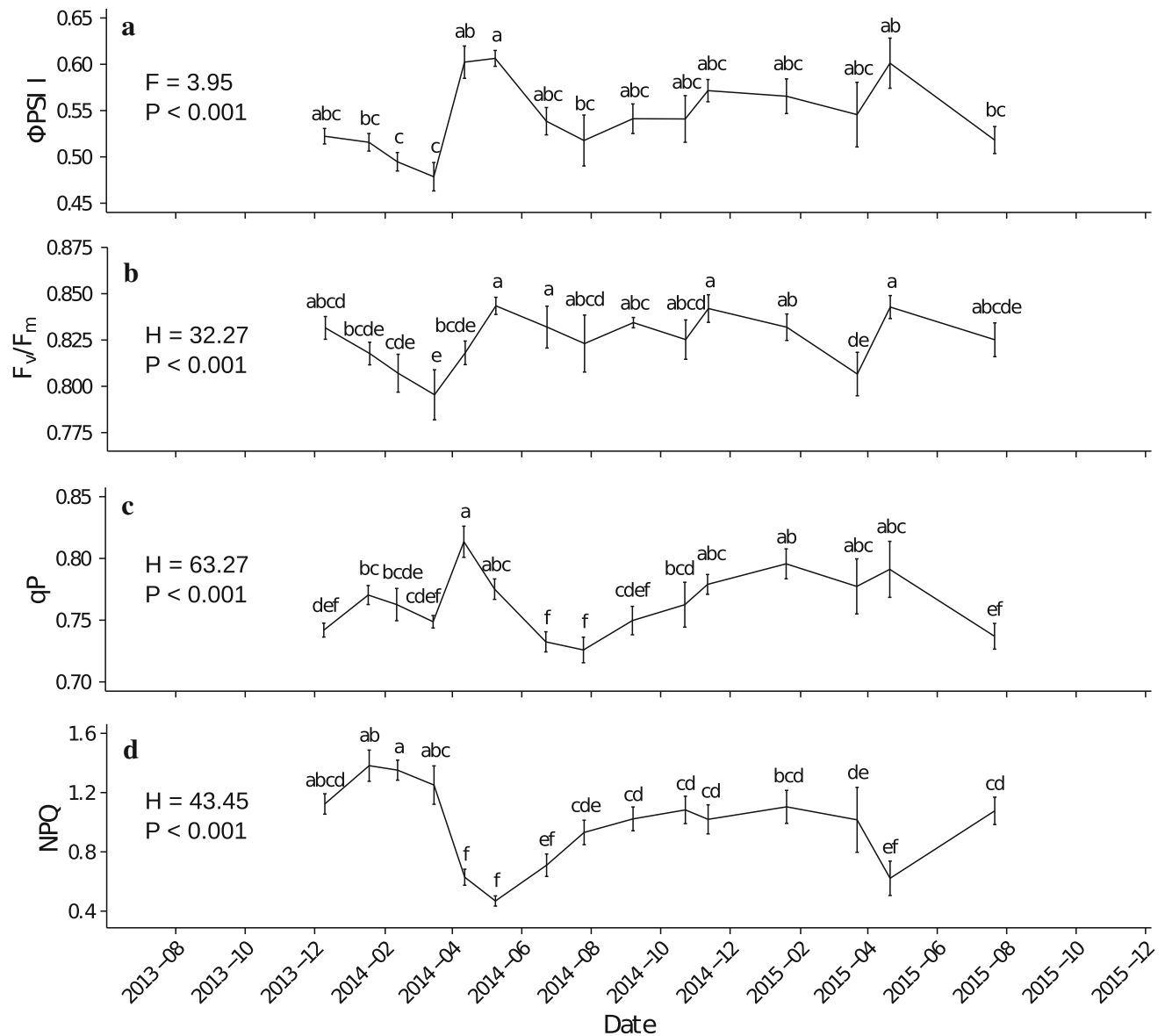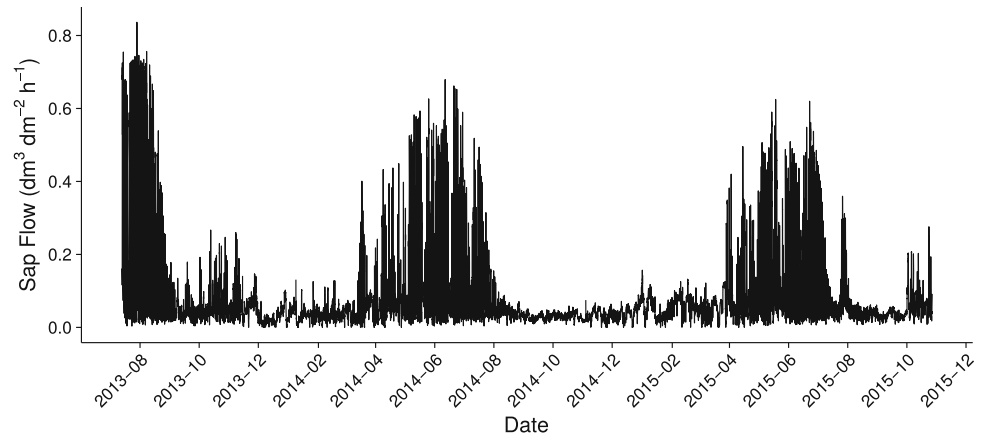

Fig. 4 Mean Φ_{PSII} (**a**), F_v/F_m (**b**), qP (**c**) and NPQ (**d**). All parameters are unitless. *Error bars* represent the standard errors of the mean. Differences between dates are indicated by dissimilar *letters* ($P < 0.05$)

indicate good photosynthetic performance and the absence of stress. Indeed, it is important to specify that these statistical differences of F_v/F_m values have no biological effect, as values stay very close to the optimal F_v/F_m value [around 0.83 (Maxwell and Johnson 2000; Müller et al. 2001; Sperlich et al. 2015]. Stable A, V_{cmax}, J_{max}, and TPU (Fig. 5) demonstrate continuous carbon assimilation and conductance during mild winters. Photosynthesis was 25% lower during winter 2015 than winter 2014, possibly due to the lower temperatures during winter 2015 (2.6 °C in 2014 and 1.5 °C in 2015, during measurement periods). This could explain the low intercept of the A/g_s regression line during this season (Fig. 6a), i.e. the absence of change of slope indicating stability of the A/g_s ratio.

The seasonal sap flow (Fig. 3) trend observed in *P. laricio* is consistent with previous reports. High level of coupling between canopy and the atmosphere was demonstrated in coniferous stands by Anfodillo et al. (1998). VPD is known to be a major factor determining sap flow, but the strength of this coupling depends on species strategy (drought-avoiding/drought-tolerance) and crown morphology (Anfodillo et al. 1998; Baquedano and Castillo 2006). During winter, sap flow and VPD (Fig. 1c) were both low but their variations were not correlated. Correlation coefficient between these parameters was low (<0.5). This weak correlation might be explained by wintertime tree dormancy (low photoperiod, PAR, and temperatures). High photosynthetic rate associated with low xylem sap flow may not cause imbalances in glucose production and transportation since phloem flow does not seem to be correlated to, or influenced by, xylem flow (Peuke et al. 2001).

Between March and April 2014, the increase in PSII efficiency was due both to an increase in the proportion of open PSII centres (Φ_{PSII} and qP) and to a reduction in non-chemical quenching (NPQ) (Maxwell and Johnson 2000). Similar values were observed for all chlorophyll fluorescence parameters in spring 2014 and 2015. Photosynthetic activity remained high during spring, then it declined slightly in early summer (ca. −15% between March and July for 2014 and 2015). At the same time, an increase of sap flow, probably due to the increase of VPD (Anfodillo et al. 1998), was observed.

Mediterranean climate is defined by a combination of thermal and hydric criteria, and it is characterized by hot dry summers (Quézel and Médail 2003). This affects plant physiology and is frequently responsible for drought stress (Gulías et al. 2002; Klein et al. 2014a, b; Maseyk et al. 2008). In Corsica, the end of summer 2014 was particularly dry, with 41 successive rainless days and only 14.5 mm of rainfall in September. Our results (Table 2 of the Electronic Supplementary Material) show that the correlation between VPD and sap flow was not constant. Sap flow and VPD were highly correlated during late spring and early summer (correlation coefficient >0.7), but less correlated during summer (September 2013 and August 2014 and 2015), especially for the latter 2 years when the correlation was <0.2. The reduction in sap flow despite high VPD could be explained by severe drought and high temperatures in 2014 and 2015. Rainfall influences soil water content and water availability for a tree; in this way, it determines stress conditions (Anfodillo et al. 1998; Klein et al. 2014b). Similar effects of drought on sap flow were observed in other coniferous species (Anfodillo et al. 1998; Klein et al. 2014a; Lu et al. 1995). Sap flow reduction might result from the closure of stomata to reduce transpiration. Significant decreases in g_s (82.5%) and g_m (76%) were observed between July and September 2014. These phenomena are more significant in conifers than other trees (Sperlich et al. 2015; Warren et al. 2004), and are a characteristic of water-saver (drought sensitive) species (Anfodillo et al. 1998; Baquedano and Castillo 2006). Indeed, drought-acclimated species may have higher photosynthetic capacity for compensating lower C_i (due to stomata closure) to maintain photosynthetic performance (Flexas and Medrano 2002). Drought-tolerant species (e.g. *Quercus ilex*), as far as they are concerned, maintain high g_s during a drought period (Sperlich et al. 2015).

In response to a weak g_s, *P. laricio* increased its intrinsic water use efficiency (higher slope and lower intercept of A/g_s in summer 2014, 2015, and autumn 2014; Fig. 6a) and reduced its limitation of g_m (higher slope and lower intercept of A/g_m; Fig. 6b; Sperlich et al. 2015). The non-significant variations of the slope of A/g_m during the summer of 2015 could be explained by the higher rainfall than in the previous summer. Nevertheless, the low intercept is consistent with a slight decrease of A. Despite the decline in water and CO_2 use efficiency (higher g_s and g_m), A decreased in September 2014. The reduction of photosynthesis in response to water stress was probably caused by the reduction of g_s (i.e. stomatal closure) rather than the reduction of g_m (Cornic 2000; Warren et al. 2004; Lawlor and Tezara 2009). This is confirmed by the higher slope of g_m/g_s during summer 2014, 2015, and autumn 2015 (Fig. 6c). Non-significant reductions in V_{cmax}, J_{max}, and TPU were observed during this period. Between July and September 2014, the fluorescence remained constant. PSII activity seemed to be less sensitive to drought than sap flow and gas exchange, and similar results were observed by Souza et al. (2004).

Photosynthetic responses to drought may differ according to plant strategy concerning water stress. The declines in photochemical efficiency are greater in drought-tolerant species (*Quercus coccifera* L., *Q. ilex,* and *Juniperus phoenicea* L.) than in drought-sensitive species (*Pinus halepensis* Mill.; Martínez-Ferri et al. 2000). PSII activity
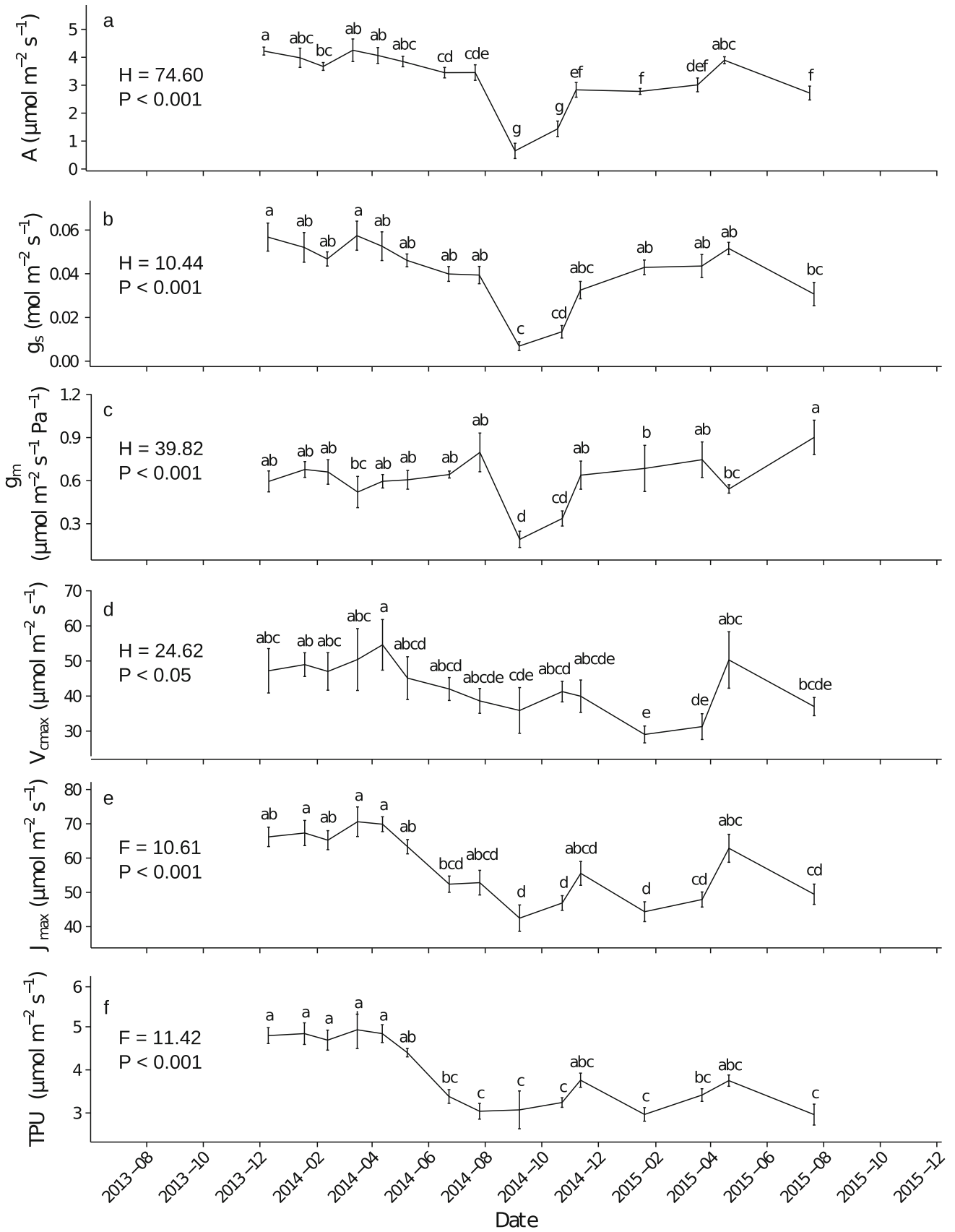
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produces ATP and NADPH, which are used in carbon fixation (Calvin cycle). Reducing carbon assimilation may result in excesses of ATP and NADPH, and thus generation of an oxidative stress (Murata et al. 2007; Damour et al. 2010). These two compounds may be consumed via photorespiration (Martínez-Ferri et al. 2000; Osuna et al. 2015). The stability of photochemical efficiency observed in our study confirms the status of *P. laricio* as water-saver species.

The stability of chlorophyll fluorescence parameters indicates the absence of photoinhibitory stress (Murata et al. 2007). After the drought period, g_s, g_m, and
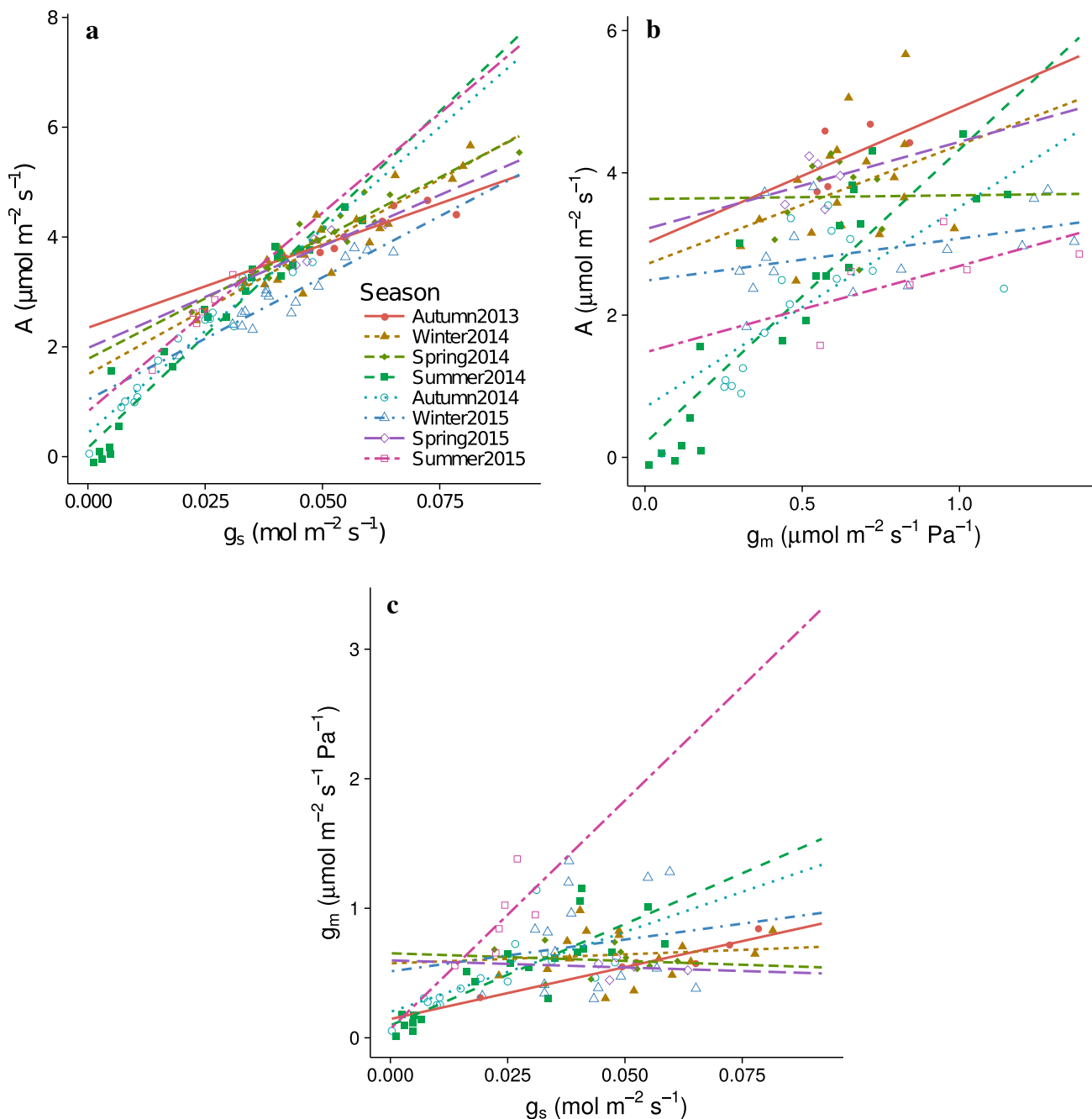
Fig. 6 Change between A (µmol m^{-2} s^{-1}) and g_s (mol m^{-2} s^{-1}) (**a**), A and g_m (µmol m^{-2} s^{-1} Pa^{-1}) (**b**) and g_m and g_s (**c**) by season

A returned to their previous values, suggesting that photosynthetic processes were either slightly damaged or not damaged at all.

Conclusion

This long-term survey provided the first information regarding *P. laricio* physiology in a Mediterranean climate. Various parameters did not show the same sensitivity to seasonal changes. Sap flow was particularly sensitive to meteorological parameters during all seasons, as were *A*, g_s, and g_m. Photochemical parameters, V_{cmax}, J_{max}, and TPU showed some stability throughout the year. The association of these parameters demonstrated good performance (photochemistry, continuous carbon assimilation, and conductance) of *P. laricio* in winter, due to mild conditions, despite low sap flow. *P. laricio* withstands summer drought due to a reduction of sap flow and g_s associated with the stability of photochemical efficiency, which is characteristic of the water-saving strategy. These new findings show that *P. laricio* could undergo physiological adjustments to resist climate change. Moreover, these results serve as an important basis to further understand ecophysiological responses to environmental factors.

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