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**Water use of
mediterranean
maquis species**

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A whole plant approach to evaluate the water use of mediterranean maquis species in a coastal dune ecosystem

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Received: 1 December 2008 – Accepted: 9 December 2008 – Published: 6 February 2009

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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Abstract

An integrated approach has been used to analyse the water relations of three Mediterranean species, *A. unedo* L., *Q. ilex* L. and *P. latifolia* L. co-occurring in a coastal dune ecosystem. The approach considered leaf level gas exchange, sap flow measurements and structural adaptations between 15 May and 31 July 2007, and was necessary to capture the different response of the three species to the same environment. The complexity of the response was proportional to the complexity of the system, characterized by a sandy soil with a low water retention capacity and the presence of a water table. The latter did not completely prevent the development of a drought response, and species differences in this responses have been partially attributed to a different root distribution. Sap flow of *A. unedo* decreased rapidly in response to the decline of Soil Water Content, while that of *Q. ilex* decreased only moderately. Midday leaf water potential of *P. latifolia* and *A. unedo* was between 2.2 and 2.7 MPa through the measuring period, while in *Q. ilex* it reached a value of 3.4 MPa at the end of the season. *A. unedo* was the only species to decrease the leaf area to sapwood area ratio from 23.9 ± 1.2 (May) to 15.2 ± 1.5 (July), as a response to drought. *A. unedo* also underwent an almost stepwise loss on hydraulic conductivity, such a loss didn't occur for *Q. ilex*, while *P. latifolia* was able to slightly increase hydraulic conductivity, showing how different plant compartments coordinate differently between species as a response to drought. Such different coordination affects the gas exchange between vegetation and the atmosphere, and has implications for the response of the Mediterranean coastal dune ecosystems to climate change.

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1 Introduction

Coastal systems are expected to be exposed to increasing risks, including coastal erosion, over coming decades due to climate change and sea-level rise (Nicholls et al., 2007). Climate change may exacerbate the already limiting environment typical of coastal dunes characterized by low nutrient availability, scarce water retention potential, salinity and aerosols from sea breeze (Alley et al., 2003). In Mediterranean climates, the dune vegetation has also to cope with a prolonged summer drought, which can be partially avoided by deep rooting species if a relatively shallow fresh water table is present. However, Regional Circulation Models predict a decrease of the amount of precipitations in the Mediterranean Basin (IPCC, 2007), with a consequent decrease of the water table resources in this area. The low nutrient availability of dunes may represent a limiting factor with a possible negative effect on plant productivity similar to that of the low water availability. Additionally, a low water availability may alter nutrient availability (Sardans and Peñuelas, 2007).

Moreover, coastal ecosystems are often located in the proximity of anthropogenic pollution sources, and the interaction between maquis vegetation and atmospheric pollutants, particularly photochemical oxidants, is complex and not yet fully understood (Ferretti et al., 2007).

Altogether, these characteristics of Mediterranean dune ecosystems may prevent the possibility to determine the water use strategy of a species: whether a species follows an isohydric or an anisohydric behaviour. Isohydric plants are recognizable from their fairly constant leaf water potential, Ψ_l , independent from the soil water potential Ψ_s , while the Ψ_l of anisohydric plants varies according to the Ψ_s (Tardieu and Simonneau, 1998; Franks et al., 2007). Because of this difference, isohydric plants transpire less water than anisohydric plants as the SWC decreases, a behaviour that reflects the nomenclature of “water savers” and “water spenders”, respectively (Schultz, 2003). However, there is no clear picture of the environmental or evolutionary significance of isohydry or anisohydry, and yet no clear mechanism has been described for either

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(Franks et al., 2007). Moreover, in the presence of a water table, midday water potential (Ψ_{MD} , MPa) and predawn water potential (Ψ_{PD} , MPa) may remain unaltered during the summer even if the soil water content decreases in the top soil, hindering the possibility of determining the strategy. Nevertheless, it is important to understand how the dune vegetation will respond to climate change, where an increasing drought and a possible salt water intrusion are likely to take place.

Given the complexity of the environmental and biotic characteristics of this environment, drought response mechanisms are ought to be investigated at whole plant level, reminding that a mass balance between the liquid phase of water and the vapour phase cannot be avoided:

$$gH_2O_l = gH_2O_v \quad (1)$$

where g is grams, H_2O_l is water in the liquid phase flowing through the sapwood area and H_2O_v is the water transpired by the total leaf surface of the plant. Accepting some simplifications and introducing the Ohm's analogy for the hydraulic circuits, the equation can also be written as:

$$(\Psi_l - \Psi_s) \times K_p = VPD \times LA \times g_s \quad (2)$$

Where Ψ_l and Ψ_s are the leaf and the soil water potential, respectively, K_p is the whole plant hydraulic conductance, LA is the whole plant leaf area, g_s is the stomatal conductance per unit leaf area and VPD is the Vapour Pressure Deficit of air. Given the analogy with the electric circuit, the left term of the equation is equal to the sap flow, while the right side term corresponds to the plant transpiration. The equation can also be rearranged and take the form proposed by Mencuccini (2003) if a term is also added to take idrostatic pressure in consideration:

$$\Psi_l = \Psi_s - \frac{LA \times g_s \times VPD}{K_p} - \rho_w \times g \times h \quad (3)$$

Where ρ_w is the density of water, g is the gravity acceleration constant and h is height. This equation allows to identify which parameters will vary as a response to

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a change of the environmental or physiological conditions. The ratio of leaf area to sapwood area, LA/SA, as well as the leaf area itself is generally lower in arid regions than in more mesic ones (de Lillis, 1991; Mencuccini and Grace, 1995). Plants may control their water consumption by stomatal control, changes in LA/SA (Bucci et al., 2004), changes in xylem vessel dimensions or combination of these factors. Perhaps, all these sectors of the plant system can compensate for one another in order to tend towards homeostasis, but we still lack the ability to predict the physiology of a plant given its hydraulic architecture or vice versa (Gartner, 1995). It is hence important, in plant water relations studies, to concomitantly take into account both leaf and whole plant level responses as well as eventual structural changes.

In this paper, we focussed on the whole-plant drought response of *Arbutus unedo* L., *Quercus ilex* L. and *Phyllirea latifolia* L., three evergreen sclerophyllous species co-occurring in the Mediterranean dune vegetation. Many studies have previously been conducted on leaf gas exchanges and ecophysiology of these species (e.g. Tretiach, 1993; Peñuelas et al., 1998; Manes et al., 1997a, 2006; Asensio et al., 2007), with *A. unedo* being described as the least drought tolerant (Ogaya et al., 2003), *Q. ilex* showing an intermediate degree of drought adaptations (Filella et al., 1998), and *P. latifolia* being the most resistant to severe to drought conditions (Peñuelas et al., 2000; Gratani and Varone, 2004). However, the few works (Martínez-Vilalta et al., 2002, 2003) that focused on the water relations of these tree species through an integrated approach, considering gas exchange, sap flow measurements and structural adaptations of plants growing under the same ecological conditions, do not completely confirm this ranking. We argue that a study at different levels in the soil-plant-atmosphere continuum may help to better understand the response of woody plants to changing environmental conditions, in such a complex ecosystem as the coastal sandy dune. The implication of our findings for the quantification of the interactions between Mediterranean vegetation and the atmosphere will be finally discussed, in the frame of the ACCENT-VOCBAS campaign.

2 Material and methods

2.1 Site description and vegetation characteristics

The study site is located inside the Presidential Estate of Castelporziano (Rome, Italy), 100 m from the coastal line, just behind the first dune. The climate is typically Mediterranean, with a pronounced summer drought and rain events concentrated in autumn and spring. Mean monthly temperatures range between a minimum of 6°C and a maximum of 24°C. The proximity of the sea determines a high air humidity (rarely below 50%) that often leads to the formation of dew at night (Pitacco et al., 1992). The soil is a regosol with some organic matter in the first horizon, which is also rich in fine roots. The vegetation of the studied site is composed of patches of Mediterranean maquis and garigue. The latter are *Helichryso stoechadis-Cistetum eriocephali* or *Erico-Rosmarinetum*, characterized by the abundant presence of *Rosmarinus officinalis* and *Erica multiflora*; *Arbutus unedo* and *Phillyrea latifolia* are frequent species (Pignatti, 2001). The site is dominated by *Q. ilex*, with a maximum height of 3 m. For a detailed description of site characteristics and vegetation composition and distribution, see Fares et al. (2009).

2.2 Environmental monitoring

Volumetric Soil Water Content (SWC, %v/v) was measured at four different depths (10, 40, 80 and 100 cm) in three different positions (bare soil, covered soil, partially covered soil) with three TDR probes (soil profiler PR2, DeltaT Devices, UK). Two trenches 1 m wide, 2 m long were excavated, and the water table depth and the maximum root depth were measured on 27 May and 4 August.

A net radiometer (Kipp and Zonen, NL) a PAR meter (190SZ, Licor, UK) and a barometer (PTB101B, Vaisala, FI) were placed at 2 m above the canopy, while three thermohygrometer probes (50Y, Campbell, USA) were placed at 0.1, 1 and 3.5 m height, respectively, on an aluminum scaffold. The VPD (kPa) was calculated based on air tem-

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perature (T_a , °C) and relative humidity (RH, %) by using the Murray's formula (Murray et al., 1967).

All sensors were connected to a CR10 data logger (Campbell, USA) which acquired data from the sensors every minute and stored them as 30 min averages.

5 2.3 Stand structure and structural changes

Plant Leaf Area (LA, m²) to Sapwood Area (SA, m⁻²) ratio (LA/SA, $\times 10^{-2}$ m² m⁻²) was measured in May and July following the protocol described in Fares et al. (2009). Moreover, Specific Leaf Area (SLA, g cm⁻²) was derived by using the same values of leaf area (cm²) and leaf mass (g) used to determine leaf biomass in Fares et al. (2009).

10 2.4 Leaf level measurements

Leaf-level measurements of gas exchange and water potential were performed on *A. unedo*, *Q. ilex* and *P. latifolia*. Gas exchange and microclimatic data were measured during spring and summer 2007, on six different days (25 May; 11, 15, 27 June; 5, 21 July) in the morning (08:00–09:00 and 10:00–11:00 GMT+1), at midday (12:00–14:00 GMT+1) and in the afternoon (16:00–17:00 GMT+1) on sun-exposed, fully developed leaves. Net photosynthesis (A_n , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), leaf transpiration (E_l , $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), stomatal conductance (g_s , $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and sub-stomatal CO₂ concentration (C_i , ppm) were measured simultaneously by a portable open-system CIRAS I (PP Systems, Hitchin, UK). Environmental parameters such as irradiance (PAR, $\mu\text{E m}^{-2} \text{ s}^{-1}$), relative humidity (RH, %), T_a and leaf temperature (T_{leaf} , °C) were also recorded by the instrument; Vapour Pressure Difference between leaf and air was then calculated (VPD_l , mbar) For each measuring day, 27 to 45 leaf measurements were carried out on 3 to 5 representative adult trees for each species.

Midday leaf water potential ($\Psi_{1,\text{MD}}$, MPa) was measured with a Scholander chamber (PMS Instruments, Oregon, USA) during four different days (15, 27 June; 5, 21 July). A minimum of 4 leaves per species was sampled immediately after the gas exchange

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measurements (12 to 20 measures per day).

2.5 Sap flow measurements

Sap flow measurements, based on the Heat Field Deformation system (HFD) (Čermák et al., 2004; Nadezhdina et al., 2004), were performed on four stems of *A. unedo* and *Q. ilex* from 15 May 2007 until 31 July 2007. Sap flow was measured with both radial and single point sensors on the same plants used to measure leaf level gas exchange. Radial profile sensors were inserted in two stems per species with a diameter above 6 cm, allowing to measure sap flow at different depths, i.e. every 12 mm. Single point sensors were placed at 0.5 mm below cambium in stems with a diameter smaller than 5 cm. In all plants, sap flow was observable at all depths. The stem flow for the bigger stems was derived by integrating flows at different depth of each radial sap flow sensor, obtaining flows per section. The total flow of the tree was derived as average flow per section, in agreement with the methodologies described in Čermák and Nadezhdina (1998). For the smaller stems, flow was assumed to be uniform at all sapwood depths.

From the total sap flow of each tree, the mean flow per unit leaf area of the single species (Q_l , $\text{mmol m}^{-2} \text{s}^{-1}$) was derived by dividing it by the mean LA/SA ratio.

All sap flow sensors were connected to a DL2 data logger (Delta-T devices, UK) which acquired data every minute and stored them as 10 min averages. The DL2 was synchronized with the CR10.

2.6 Canopy stomatal conductance and whole plant hydraulic conductance

Assuming that sap flow density scaled by the sapwood to leaf area ratio (Q_l , $\text{mmol m}^{-2} \text{s}^{-1}$) is equal to transpiration per unit leaf area, canopy stomatal conductance, (G_s , $\text{mmol m}^{-2} \text{s}^{-1}$) can be derived from sap flow measurements, based on a simplification of the Penman-Monteith equation (Whitehead and Jarvis, 1981; Pataki et

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al., 1998; Martínez-Vilalta et al., 2003):

$$G_s = \frac{\gamma \times \lambda \times Q_l}{\rho \times c_p \times VPD} \quad (4)$$

where γ is the psychrometric constant (kPa K^{-1}), λ is the latent heat of vaporization of water (J kg^{-1}), ρ is the density of air (kg m^{-3}), c_p is the specific heat of air at constant pressure ($\text{J kg}^{-1} \text{K}^{-1}$) and VPD is the vapour pressure deficit (kPa), measured at canopy height. The VPD used for G_s derivation was the VPD calculated at 1 m height. The simplification of the Penman-Monteith equation can be considered valid if G_s is predominant over the boundary layer conductance, G_b (Whitehead and Jarvis, 1981) i.e. when the canopy is strongly coupled with the atmosphere. The Mediterranean vegetation is known to be well coupled to the atmosphere also because of the small size of its leaves (Martínez-Vilalta et al., 2003). g_b was evaluated using the equation proposed by Jones (Jones, 1992):

$$g_b = 6.62 \times \left(\frac{u}{d}\right)^{0.5} \quad (5)$$

Where d is the average leaf size and u is the wind speed. g_b/G_s was always greater than 0.95.

For *A. unedo* and *Q. ilex*, leaf specific whole plant hydraulic conductance, K_p was evaluated by:

$$K_p = \frac{Q_{l,\max}}{\Psi_s - \Psi_{l,\text{MD}}} \quad (6)$$

Where $Q_{l,\max}$ ($\text{mmol m}^{-2} \text{s}^{-1}$) is sap flow per unit leaf area during peak transpiration at midday, $\Psi_{l,\text{MD}}$ is leaf water potential at midday and Ψ_s is the soil water potential (MPa) at 100 cm depth. The latter has been derived from SWC through a soil water retention curve (pF curve), constructed by using 3 soil samples, which describes the relationship between the logarithmic value of the soil water potential, Ψ_s , and the volumetric SWC (Schofield, 1935). For *P. latifolia* instead, K_p could not be estimated since

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the small stem diameter allow for sap flow measurements. As in Magnani et al. (2002), leaf level transpiration at midday ($E_{l,MD}$) was used instead of $Q_{l,max}$ in Eq. (6), to determine leaf specific whole plant hydraulic conductance (K_l).

2.7 Statistical analysis

5 Statistical analyses were made by using Statistica 7 software package (StatSoft, Inc. – Tulsa, OK – USA). Physiological data were analyzed by using a two-way Analysis of Variance (ANOVA, $p < 0.05$), followed by the Newman-Keuls test, taking into consideration species \times day of measurement as discriminant factors. Data were previously tested for normality by using the Levene test at the significance level of 0.05. If vari-
10 ances were unequal, then the Welch-ANOVA was applied (significance level $p < 0.05$). Data in figures and tables are presented as mean value \pm standard deviation.

3 Results

3.1 Environmental monitoring

15 During the experimental period, cloudy or partially cloudy days were rare, hence net radiation remained fairly constant (data not shown). Air temperature showed a generally increasing trend and the mean daily value ranged between 18.3 and 24.8°C (Fig. 1a). Mean daily RH remained in the range 60–80% throughout the campaign, while VPD increased as a consequence of the increase in temperature (Fig. 1a).

20 Soil water content (Fig. 1b) at the beginning of the experimental period, was as low as 2% in the first 10 cm, rich in fine roots. The few mm of rain fallen on 29, 30 and 31 May influenced only this top soil layer, and for a limited time period. Both at 40 and 80 cm, water content dropped to 4.5% on 30 May, while at 100 cm, SWC declined less rapidly, reaching a constant value of $\sim 4.5\%$ from the beginning of July. Ψ_s estimated from the pF curve (Supplementary material 1: <http://www.biogeosciences-discuss.net/>

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6/1713/2009/bgd-6-1713-2009-supplement.pdf) in the first 80 cm of soil was rarely above -3 MPa (data not shown).

3.2 Stand structure and structural changes.

Table 1 shows structural parameters of the three studied species, obtained with the procedure described in Fares et al., 2009. It is worth noting that all species developed new leaves during mid of May, but while *Q. ilex* and *P. latifolia* show significant alteration in the LA/SA ratio, *A. unedo* reduced its value from 23.9 ± 1.2 (May) to 15.2 ± 1.5 (July). Specific Leaf Area (SLA) was lowest in *A. unedo* and highest in *P. latifolia*.

3.3 Leaf level measurements

Both *A. unedo* and *P. latifolia* showed relatively constant values of $\Psi_{I,MD}$ during the experimental period, with no significant difference between the two species in each measurement day ($p=0.64, 0.34, 0.64$ and 0.89 , respectively). *Q. ilex* instead showed decreasing values of $\Psi_{I,MD}$ during the season which became significantly lower than the other two species in the final measurement day ($p=0.0002$ and $p=0.0002$ respect to *A. unedo* and *P. latifolia*, respectively) (Fig. 2).

Figure 3 highlights the different seasonal patterns of An and g_s of the three studied species. *A. unedo* had the highest stomatal conductance at the end of May ($p=0.00004$), with g_s daily mean values as high as $170.5 \pm 71.0 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, and An of $9.2 \pm 2.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Concomitantly with the decrease of SWC at 100 cm, the gas exchanges rates of this species decreased gradually until the end of June ($61.7 \pm 34 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ and $5.5 \pm 2.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for g_s and An , respectively), and remained rather constant during the remaining experimental period (Fig. 3a).

Q. ilex maintained fairly constant gas exchange rates during the whole experimental campaign, although a slight reduction of g_s , not statistically significant ($p=0.06$), occurred on 21 July ($45.5 \pm 30.0 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) (Fig. 3b).

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As for *P. latifolia*, it showed the highest values of g_s and An on mid June (159.2±29.0 mmol H₂O m⁻² s⁻¹ and 11.6±1.5 μmol CO₂ m⁻² s⁻¹, respectively), followed by a 33% reduction in g_s and 12% in An; despite this reduction *P. latifolia* showed, at the end of the experimental period (21 July 2007), the highest gas exchange rates with respect to the other two species (Fig. 3c).

The relationship between vapour pressure difference based on leaf temperature, VPD_l, and E_l, was bell shaped for both *Q. ilex* and *A. unedo*, reaching a maximum value at 2.6 kPa; E_l of *P. latifolia* instead rises continuously, even if the slope decreases at 2.8 kPa. This difference is due to a lower leaf temperature, which in turn is due to a higher E_l (Fig. 4).

3.4 Sap flow, canopy stomatal conductance and whole plant hydraulic conductance

The trend of sap flow during the experiment is shown in Fig. 5a, b. Between the mid of May and the end of July, both *A. unedo* and *Q. ilex* showed a decline in $Q_{l,max}$ concomitant with the reduced SWC (Fig. 6) and the higher evaporative demand. As observed from leaf level gas exchanges, $Q_{l,max}$ of *A. unedo* decreased a 41% linearly with the SWC at 100 cm, until the end of June ($R^2=0.88$). However, differently from what observed at leaf level, $Q_{l,max}$ continued to decrease (15%) even when the SWC at 100 cm remained constant at a value of ~4.5%. In *Q. ilex* instead, $Q_{l,max}$ slightly decreased (13%) in the same SWC range ($R^2=0.25$), after which it declined of only another 6%. For this reason, given the constant SWC, it is not possible to correlate $Q_{l,max}$ with SWC for both species after the end of June (Fig. 6).

G_s , estimated from sap flow measurements (Eq. 4) at saturating light intensities (PAR>1000), declined as the VPD increased following an exponential curve in both *A. unedo* and *Q. ilex* (Fig. 7a, b). While in *A. unedo* the relationship changed considerably before and after 20 June, the same relationship changed only slightly in *Q. ilex*, suggesting a higher loss in K_p for *A. unedo* than *Q. ilex*.

The different loss of K_p between the species is confirmed by the K_p values estimated

as in Eq. (6) and (7). In the course of the dry season *Q. ilex* showed a negligible reduction in K_p (from 0.7 ± 0.12 to 0.49 ± 0.08 $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) as compared to the loss in *A. unedo* (from 1.99 ± 0.32 to 0.91 ± 0.15 $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) (Fig. 8). Figure 8 also shows the change in K_l for *P. latifolia* derived from transpiration at leaf level; for this species it is noticeable that K_l increased during the season (from 0.53 ± 0.19 to 1.11 ± 0.13 $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$).

The radial sap flow sensors allowed to measure sap flow at different depth from the cambium, and hence to highlight changes in the radial pattern of sap flow. Changes in the radial pattern of sap flow were strong for *A. unedo* where flow was nearly evenly distributed throughout the xylem in the beginning of the season but, as the season progressed, a larger percentage of the total flow occurred in the deeper xylem (Fig. 9a). In *Q. ilex* instead, the radial pattern change during the season (Fig. 9b).

4 Discussion

The physiological response of the species to increasing drought stress in the period from Spring to high Summer, although adapted to the same environment, was species-specific as observed earlier by Martínez-Vilalta et al. (2003), Ogaya and Peñuelas (2003); Gratani and Varone (2004). Moreover, the seasonal trend of the physiological parameters was similar to that found by other authors, both for sap flow in a Spanish site (Martínez-Vilalta et al., 2003), as for leaf level measurements recorded in Tuscany (Tognetti et al., 2000) and in a nearby site inside the Presidential Estate of Castelporziano (Gratani and Bombelli, 1999). Our LA/SA values, instead, compared with those reported by Martínez-Vilalta et al., 2003, were similar only for *Q. ilex* (24.2 ± 4.2) and considerably lower both for *A. unedo* (9.5 ± 0.5) and *P. latifolia* (8.8 ± 0.3). The Spanish site is known to have more extreme aridity and evaporative demand than our coastal site. It is likely that *A. unedo* and *P. latifolia* respond to this more extreme environment by reducing the LA/SA ratio, hence raising the amount of water available per unit leaf area (Eq. 3). *Q. ilex*, instead, shows the same LA/SA values as in

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the Spanish site, coherently with Sanchez-Vilaz et al. (2007), who report conservative LA/SA ratio in this species despite light environment and genetic differences.

In spite of the similar trend of sap flow, the comparison with the results of Martínez-Vilalta et al. (2003) highlights different relative response of the three species. In our case *A. unedo*, and not *Q. ilex*, was subject to the highest reduction in Q_j (Fig. 5). Our results also differ in terms of $\Psi_{I,MD}$ which, in the Spanish site, was lower than in our site; additionally, while in the Spanish site $\Psi_{I,MD}$ was clearly proportional to the predawn Ψ_j , our $\Psi_{I,MD}$ vary from 15 June to the end of July despite the absence of rainfalls, except for the slight decrease observed for *Q. ilex*. For the latter species, in particular, the values and trend of $\Psi_{I,MD}$ measured in our site were comparable to those reported by Bussotti et al. (2002) in a Tuscan site, where vegetation response to the driest period was influenced by groundwater. Therefore, these difference can be once more explained by the different environmental condition and, in particular, by the presence of a relative shallow water table in the Castelporziano site (Busuoli et al., 2001); hence, the decrease in both canopy conductance, G_s , and leaf conductance, g_s , observed in our study should not be attributed to a prevention of embolism.

Given the presence of a water table, it is not possible to use our data to clearly attribute a water use strategy (isohydric or anisohydric, sensu Tardieu and Simonneau, 1998) to these species. In fact, if roots have unlimited access to the water table, water use by the species should not be limited. In the absence of a water table, instead, a much stronger water stress was to be expected (Bussotti et al., 2002). In our case only a moderate response is observed: $\Psi_{I,MD}$ values are well inside the critical tension for embolism known for these species (Martínez-Vilalta et al., 2002; Corcuera et al., 2004) and above values usually reported for Mediterranean species during drought stress (Manes et al, 2006; Tognetti et al., 2000, Serrano et al., 2005). Nevertheless, a stomatal control and a reduction of sap flow took place concomitantly with a sharp decline in SWC in the top soil layers, a control which is particularly evident for *A. unedo*. In these conditions it becomes more complicated to discuss water availability only in terms of Ψ_s as a proxy of extractable water (Lundblad and Lindroth, 2002).

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The relationship between stomatal control and SWC may be understood taking in consideration the nature of the soil and the root species specific distribution.

Sandy soils are characterized by a pore size distribution, concentrated over a small range and, in this type of soil, the pF curve shows an almost stepwise change of Ψ_s as the SWC diminishes, which also corresponds to an abrupt loss of soil hydraulic conductivity. The particular underground structure of the dune, a water table between 210 and 290 cm depth (Fares et al., this issue) and a rapid variability in SWC in the above layers, operates similarly to a control switch on water availability for the vegetation in this site.

In such a vertical and time limited distribution of the water resource, it is likely that the water use of the species will depend on their below ground root distribution (Bréda et al., 2006). Plants with prevalently superficial roots are to suffer drought during summer, while, on the other side, plants with a dependence on a reliable water resource are likely to respond weakly to summer drought. A third situation may be represented by plants with roots distributed between the superficial layers and the water table: these may show a dual behaviour, as the changes in the vertical distribution of the water resource will be reflected in a change in the absorbing surface. The observed radial pattern profiles of sap flow (Fig. 9) suggest that *A. unedo* and *Q. ilex* have a different root distribution. In fact, according to Nadezhdina et al. (2008), superficial roots of *Quercus suber* are mainly connected with the outer xylem, while the deep roots are preferentially connected with the inner xylem. The observed change in the radial pattern of *A. unedo*, but not of *Q. ilex*, hence suggests that *A. unedo* should have more evenly vertically distributed roots, being able to use both water resources (superficial water, when present, and water table), while *Q. ilex* should draw most water from a reliable water resource (water table). The different root distribution and the different used water resource is confirmed by Alessio et al. (2004). By using isotopic O_2 ratios, these authors were able to describe the provenience of water, superficial (typically coming from late spring-summer precipitation) or water table (that is constituted by the abundant autumn-winter and early spring precipitation) used by *A. unedo*, *Q. ilex*, and

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P. latifolia in the same site of our study. Their results show clearly that while *Q. ilex* and *P. latifolia* both prevalently draw water from the water table, *A. unedo* uses both superficial and deep waters, i.e. the roots of *Q. ilex* and *P. latifolia* are prevalently distributed in the deeper layers, while the roots of *A. unedo* are distributed both in the top and deep soil layers. From the same work, it is also deductible that *P. latifolia* is the species that draws water almost exclusively from the deeper water resources, i.e. the species with the deepest rooting system. The advantage of a different root distribution is not clear, one possible explanation could be that the nutrients distribution in the soil profile is not qualitatively homogeneous and that the root distribution reflects the known different nutrient requirements of the species (Sardans and Peñuelas, 2007).

As already noticed, the different root distribution implies a different change in absorbing root surface as the SWC progressively declines from the superficial layers; i.e. the absorbing surface will be reduced the most for *A. unedo* and the least for *P. latifolia*. K_p , especially in the absence of embolism, is strongly dependent on root conductivity, which in turn depends on the root surface and on the permeability of both the apoplast and the simplast. Because of this, the largest loss of K_p during summer is expected for *A. unedo*, less for *Q. ilex* and null for *P. latifolia*, an expectation that is confirmed by our data (Figs. 7 and 8). Noticeably, *P. latifolia* increased K_l , this cannot be explained solely by a negligible loss in root absorbing surface, but it implies an increase in root permeability.

Plants may strongly modify root permeability by rapid changes in aquaporines concentrations in cell membranes (Kaldenhoff et al., 2008). A loss in root surface (lower K_p), could hence be compensated with an increase in permeability (higher K_p), of the remaining roots. Changes in permeability may also compensate for a reduced water availability, allowing to a certain extent, to keep a constant Ψ_l independently from the SWC. This mechanism has been reported for a *Vitis* hybrid (Galmés et al., 2007) and allows for an adequate water supply even at low SWC.

Recalling Eq. (3) to summarize the different coordination mechanisms of the species, it emerges that *A. unedo* is the species that responds more drastically to the environ-

mental changes and it does so by modifying both physiological and structural parameters: a reduction in transpiration by a strong stomatal control and a reduction of the LA/SA ratio in order to keep Ψ_l inside the critical value for embolism. *Q. ilex* instead is the only species that compensates for the slight loss in K_p by lowering its $\Psi_{l,MD}$, allowing to keep an almost constant transpiration during the course of the season. The decline in G_s of *Q. ilex* can be attributed mostly to an increase in VPD, in fact the G_s vs. VPD plot shows a unique relationship as opposed to that of *A. unedo*. Finally, *P. latifolia* not only compensates for the loss in root surface by increasing root permeability, but increases K_l in order to allow for a high g_s even when the transpirative demand increases. This response seems in agreement with its known drought tolerance (Serrano and Peñuelas, 2005), and in accordance with its afro-tropical origin (Quézel, 1985). *P. latifolia* is in fact considered a residual element of the Paleo-Mediterranean vegetation, that has evolved under the tropical Pliocenic climate (Blondel and Aronson, 1995); the *Arbutus* and *Quercus* genera instead, are described as Neo-Mediterranean elements, that have evolved under strictly Mediterranean climatic conditions (Raven, 1973; Quézel et al., 1980).

5 Conclusions

Coastal dune ecosystems are often characterized by strong time and space variability of the water resources, an environmental characteristic to which species may adapt differently. In this complex environment, it appears that the water use strategies of the maquis species cannot be described solely in the frame of the isohydric/anisohydric behavior. Our results showed that a whole plant approach highlights more complex mechanisms, and that adaptation to different environments may bring to an inversion of the ranking of species in terms of responses to drought, as shown by the comparison with previous studies (e.g. Martínez-Vilalta et al., 2003). Moreover, it is interesting to notice that the species with the most constant transpiration (*Q. ilex*) is also the one that presents the most conservative structure both in time (i.e. during the sea-

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son) and in space (when compared with other sites) (Manes et al., 1997b), while the other two species, known to be mid-successional species, present more variability in transpiration and in structure in response to environmental conditions (Bazzazz, 1979; Castro-Díez and Montserrat-Martí, 1998). In particular, we found that, for *A. unedo*, the rapid adaptation to environmental variability implies both physiological and structural adjustments, making it highly competitive in the Mediterranean plant community (Vitale and Manes, 2005).

In the frame of the ACCENT-VOCBAS field campaign, the present work has contributed to a better understanding of the complexity of environmental, physiological and structural factors influencing the behaviour of sandy dune plants, particularly in terms of gas exchange with the atmosphere through stomata. Finally, given that abrupt, non-linear changes in the water table resources of the dune ecosystem, that may occur through variations in rainfall patterns and intrusion of sea water, we may also argue that the dynamism of the Mediterranean maquis phytocenosis may be directly affected by Climate Change and sea-level rise.

Acknowledgements. The authors wish to thank De Michelis, Head of the Castelporziano Estate, and Tinelli whose assistance was essential in providing logistical co-ordination. This research was supported by Accademia delle Scienze detta dei XL grants, and Ateneo “Sapienza” MIUR grants.

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Table 1. Structural parameters of *A. unedo*, *Q. ilex* and *P. latifolia*, obtained as described in Fares et al. (2009). Leaf area to Sapwood Area (LA/SA, $\text{m}^2 \text{m}^{-2}$) was measured in May and July, while Specific Leaf Area (SLA, g cm^{-2}) measured only in May.

Parameters	<i>A. unedo</i>	<i>Q. ilex</i>	<i>P. latifolia</i>
LA/SA, May ($\times 10^{-2} \text{m}^2 \text{m}^{-2}$)	23.9±1.2	21.9±1.8	15.7±2.0
LA/SA, July ($\times 10^{-2} \text{m}^2 \text{m}^{-2}$)	15.2±1.5	24.0±1.3	16.4±1.8
LMA, May (g cm^{-2})	0.0168±0.003	0.0198±0.003	0.0236±0.005

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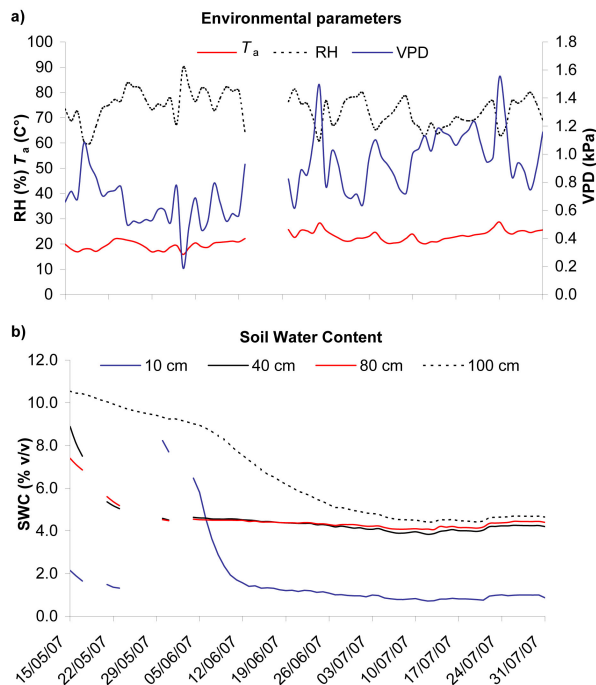


Fig. 1. Trend of environmental parameters, measured from 15 May 2007 to 31 July 2007. **(a)** Air temperature (T_a , °C), Relative air Humidity (RH, %) and Vapour Pressure Difference (VPD, kPa), at canopy height; **(b)** Soil Water Content (SWC, % v/v), measured at four different depths (10 cm, 40 cm, 80 cm and 100 cm); data are daily means of three TDR probes, placed in different positions (bare soil, covered soil, partially covered soil). Missing data are due to data logging interruption.

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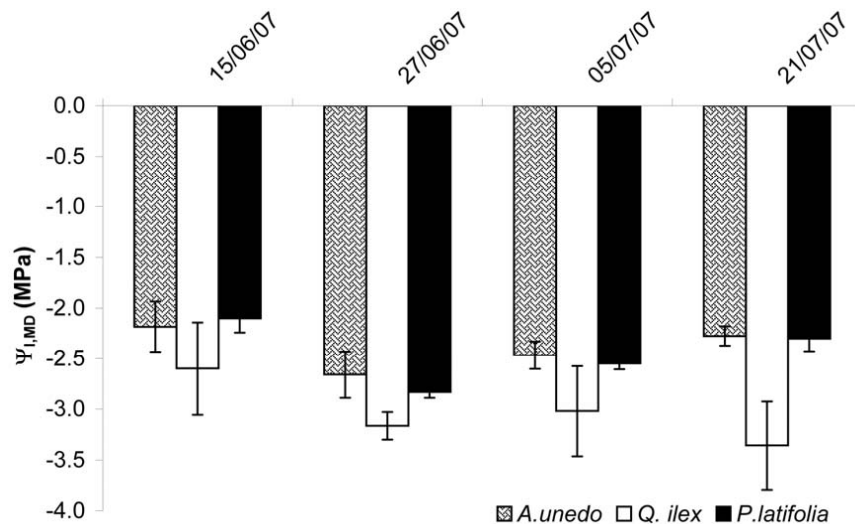


Fig. 2. Trend of midday leaf water potential ($\Psi_{I,MD}$, MPa) measured in four sampling dates on *A. unedo*, *Q. ilex* and *P. latifolia*. Data are means \pm standard deviations, $12 \leq N \leq 20$.

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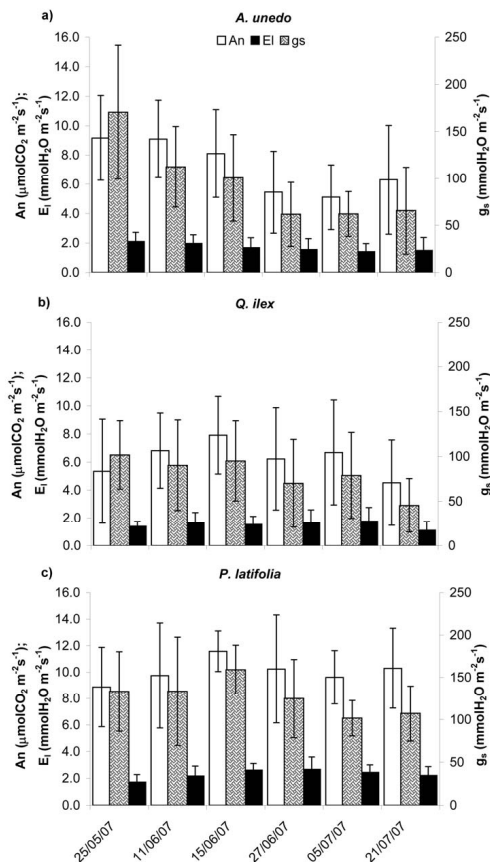


Fig. 3. Daily average of net photosynthesis (An , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), stomatal conductance (g_s , $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and leaf transpiration (E_i , $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) measured on *A. unedo* (a), *Q. ilex* (b) and *P. latifolia* (c). Data are means \pm standard deviations, $27 \leq N \leq 45$.

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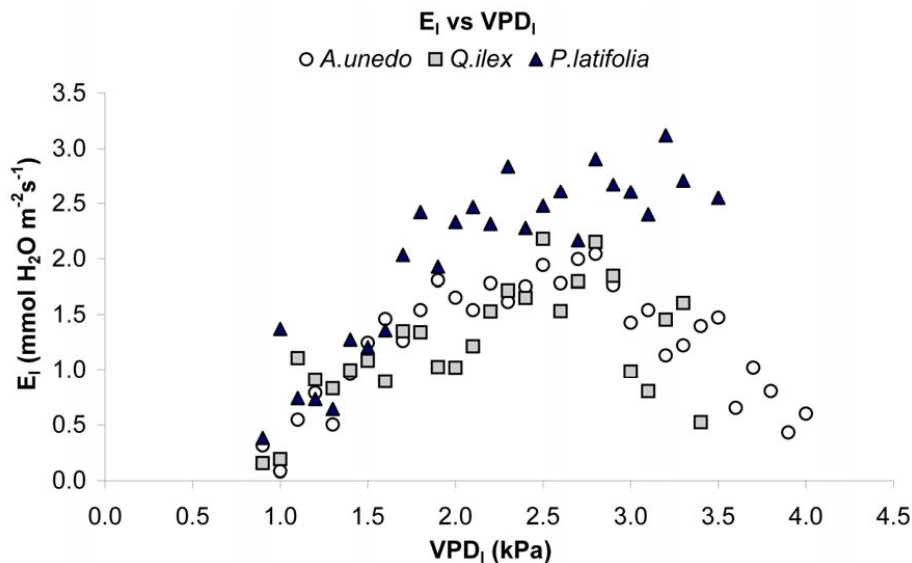


Fig. 4. Relationship between mean Vapour Pressure Difference based on leaf temperature (VPD_i, kPa) and mean leaf transpiration (E_i, mmol H₂O m⁻² s⁻¹) for *A. unedo*, *Q. ilex* and *P. latifolia*. 27 ≤ N ≤ 45.

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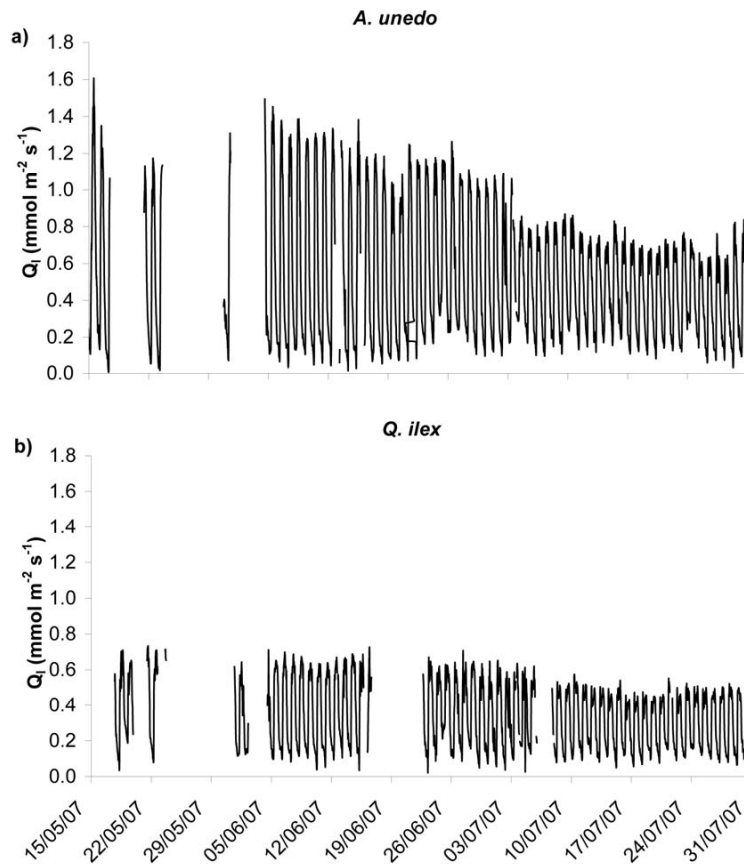


Fig. 5. Seasonal trend of Sap flow (Q_i , $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$) of *A. unedo* (a) and *Q. ilex* (b), measured from 15 May 2007 to 31 July 2007. Missing data are due to data logging interruption.

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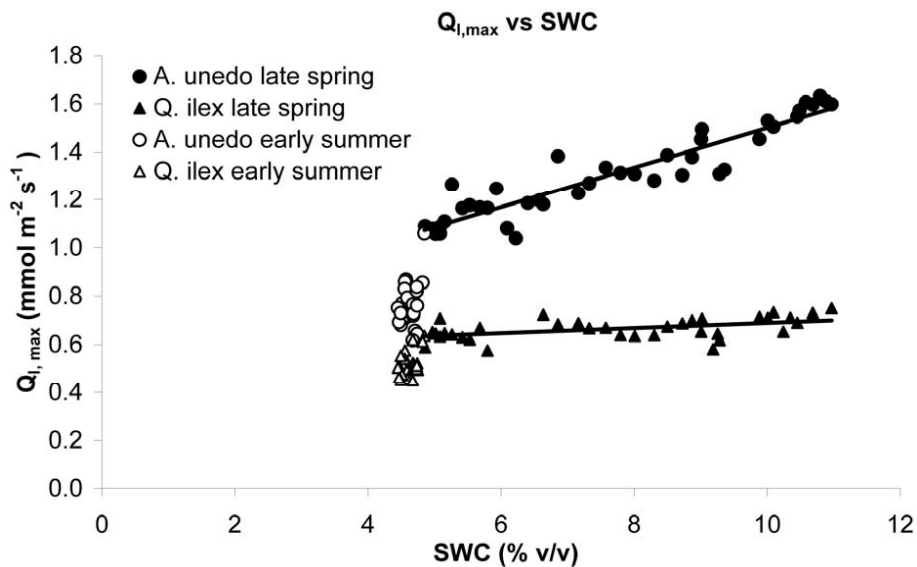


Fig. 6. Relationship between Soil Water Content (SWC, %v/v) and daily maximum Sap flow ($Q_{l,max}$, $\text{mmol m}^{-2} \text{s}^{-1}$) for *A. unedo* and *Q. ilex*. Closed symbols: before 20 June; open symbols: after 20 June.

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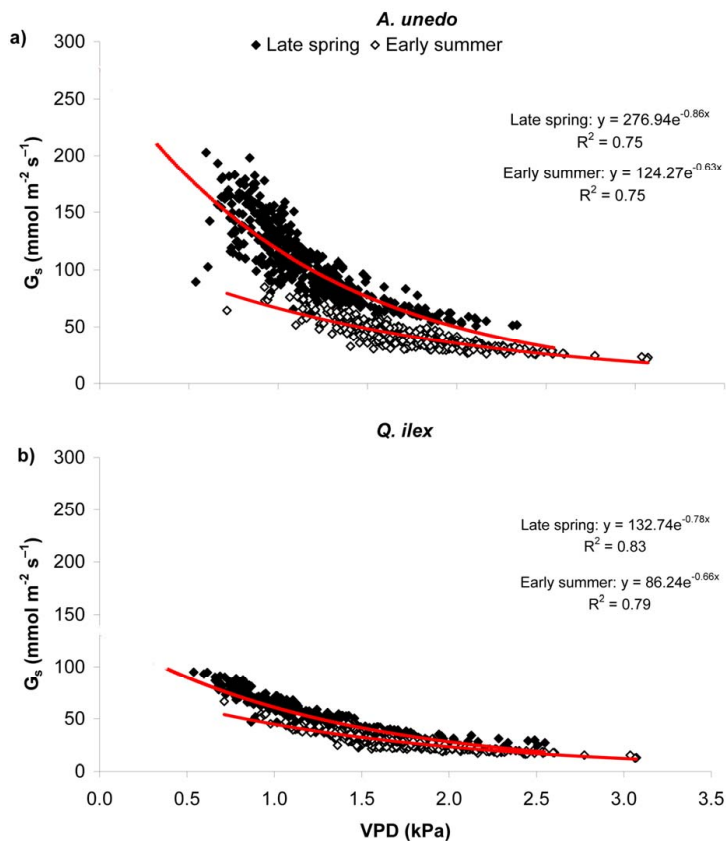


Fig. 7. Relationship between canopy stomatal conductance (G_s , $\text{mmol m}^{-2} \text{s}^{-1}$), estimated from Sap flow measurements at saturating light intensities ($\text{PAR} > 1000$), and Vapour Pressure Difference (VPD, kPa), measured at canopy level for *A. unedo* (a) and *Q. ilex* (b). Closed symbols: before 20 June; open symbols: after 20 June.

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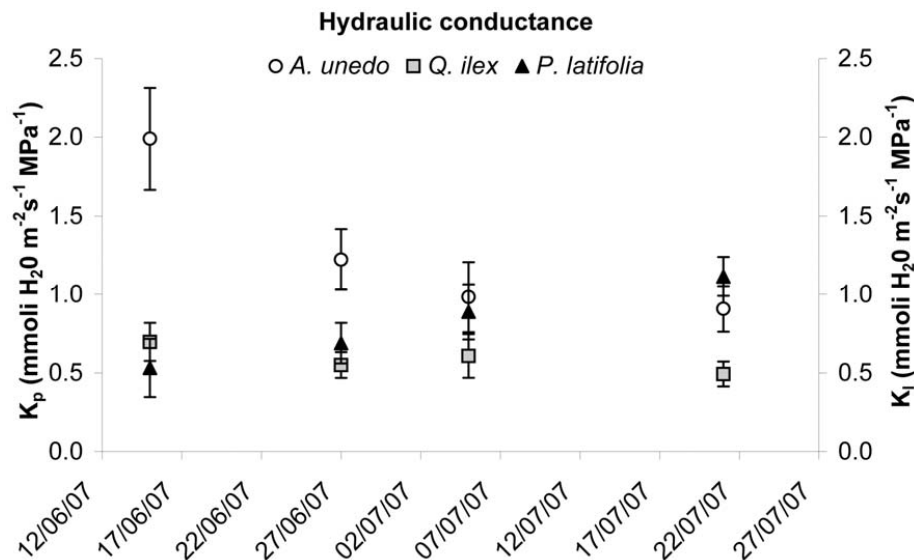


Fig. 8. Leaf specific whole plant hydraulic conductance (K_p and K_i , $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) calculated for *A. unedo*, *Q. ilex* and *P. latifolia*. K_p of *A. unedo* and *Q. ilex* were derived from sap flow measurements, while K_i for *P. latifolia* was derived from leaf level gas exchange measurements. Values are not quantitatively comparable because of upscaling reasons.

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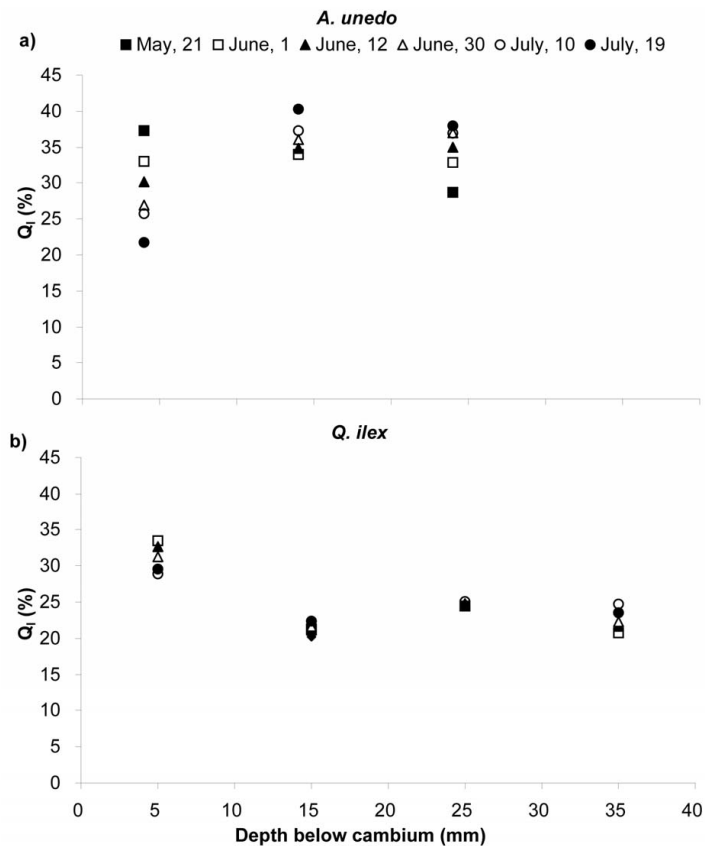


Fig. 9. Changes in the radial profile of *A. unedo* (a) and *Q. ilex*. (b), during the experimental period. Data points indicate the percentage contribution of each depth to the total stem flow. Each value represents the mean of two stem per species, which were chosen with similar diameter: 32–35 mm for *A. unedo* individuals, and 39–43 mm for *Q. ilex* individuals.

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