

# Water relations of climbing ivy in a temperate forest

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**Abstract** Ivy (*Hedera helix*) is the most important liana in temperate European forests. We studied water relations of adult ivy in a natural, 35 m tall mixed deciduous forest in Switzerland using a construction crane to access the canopy. Predawn leaf water potential at the top of climbing ivy ranged from  $-0.4$  to  $-0.6$  MPa, daily minima ranged from  $-1.3$  to  $-1.7$  MPa. Leaf water potentials as well as relative sap flow were held surprisingly constant throughout different weather conditions, suggesting a tendency to isohydric behaviour. Maximum stomatal conductance was  $200 \text{ mmol m}^{-2} \text{ s}^{-1}$ . The use of a potometer experiment allowed us to measure absolute transpiration rates integrated over a whole plant of  $0.23 \text{ mmol m}^{-2} \text{ s}^{-1}$ . Nightly sap flow of ivy during warm, dry nights accounted for up to 20% of the seasonal maximum. Maximum sap flow rates were reached at ca. 0.5 kPa vpd. On the other hand, the host trees showed a less conservative stomatal regulation, maximum sap flow rates were reached at vpd values of ca. 1 kPa. Sap flow rates of ivy decreased by ca. 20% in spring after bud break of trees, suggesting that ivy profits strongly from warm sunny days in early spring before budbreak of the host trees and from mild winter days. This species may

benefit from rising winter temperatures in Europe and thus become a stronger competitor against its host trees.

**Keywords** Global warming · Granier method · *Hedera* · Lianas · Sap flow · Stomatal conductance · Leaf water potential

## Abbreviations

A	Sap wood area
b	Reference conductance at 1 kPa
$g_s$	Stomatal conductance
$g_c$	Canopy conductance
m	Vpd sensitivity
PAR	Photosynthetically active radiation
SF	Sap flow
vpd	Vapour pressure deficit
WSD	Water saturation deficit
$\alpha$	Fitting parameters for the non-linear fit between SF and vpd
$\beta$	Fitting parameters for the non-linear fit between SF and vpd
$\psi$	Leaf water potential

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## Introduction

Lianas contribute greatly to forest biodiversity and affect many aspects of forest dynamics. Lianas compete with their host trees for resources like light, water, nutrition and space, and it has been shown that they may be particularly successful in open, disturbed forests (Zhu and Cao 2010). By using their host as a climbing frame, they save resources that otherwise would have to be invested in massive stems and roots (Putz and Holbrook 1991).

The weight of lianas and the additional leaf area exposed to wind can enhance forest dynamics, particularly through wind throw (Clark and Clark 1990; Schnitzer and Bongers 2002; Schnitzler and Heuzé 2006). Once lianas have reached the top of their host tree crown, they often suppress tree growth and regeneration (Putz 1984). In the case of Ivy (*Hedera helix* L.), the most abundant liana in temperate forests of Europe (and a key invader in North America, e.g. Biggerstaff and Beck 2007; Ringold et al. 2008), many of the adverse influences on trees attributed to lianas do not apply. Ivy is neither particularly aggressive, nor does it overgrow healthy tree crowns, but usually remains in the subcanopy (Mitchell 1975). Its distribution in Europe is limited to the north and east by the  $-25^{\circ}\text{C}$  minimum isotherme (Iversen 1944; Parker 1962; Andergassen and Bauer 2002). The largest individuals show diameters  $>25$  cm and can be over 60 years old (Heuzé et al. 2009).

Ivy is quite robust and able to cope with many different light, temperature and water regimes, with a strong potential of phenotypic adaptation (see Metcalfe 2005). A single tree often hosts various clones of ivy, intermingled and physically connected (anastomosis). Massive evergreen canopies up to 30 m above ground are often maintained by only a few thin stems, and severing some of them does not harm the plant as long as a single vine links to the ground (personal observation). This means that the water conducting tissue must be extremely efficient (low Huber value, i.e. cross-sectional xylem area to supplied leaf area) and able to avoid cavitation. In contrast, ivy has intermediate maximum leaf conductance ( $113\text{ mmol m}^{-2}\text{ s}^{-1}$ ) and low transpiration rates ( $1.0\text{ mmol m}^{-2}\text{ s}^{-1}$ , Carter and Teramura 1988). Elias (1979) also reports low transpiration rates combined with low maximum water saturation deficit (WSD) and high water holding capacity for *H. helix*. Apart from the cited literature on data mostly from small or potted plants, little information is available on the ecology of *H. helix* in situ, and there is a striking gap in our knowledge of in situ water relations, partly due to difficult crown access of adult individuals.

Because ivy relies on the host tree to provide structural support, it is not only able to conduct water very efficiently, but it also saves in structural tissue, allowing it to grow fast. Recent studies suggest that lianas take exceptional advantage from atmospheric  $\text{CO}_2$  enrichment during their juvenile life stage in deep shade (Granados and Körner 2002) and therefore may become more competitive (Körner 2004; Mohan et al. 2006). This is also true for ivy both in the juvenile and adult stages (Hättenschwiler and Körner 2000, 2003; Zotz et al. 2006). Fischer and Feller (1994) have further shown that photosynthetic proteins in ivy are conserved throughout winter and are activated rapidly during warm spells. Therefore, ivy may additionally profit from milder winters when light availability is

ample in deciduous forests. This hypothesis is supported by a recent dendrochronological study on ivy (Heuzé et al. 2009), which reports increased growth rates during years with exceptionally warm winters.

The aim of this study was threefold. (1) We wanted to fill in a gap in fundamental knowledge on in situ water relations of mature ivy. (2) We systematically compared ivy water relations with water relations of host trees before and after tree leafing to test the hypotheses that ivy takes advantage of warm, sunny winter days. (3) We assessed the possibility of using Granier-type heat-dissipation probes in ivy, and suggested a calibration for their use in this species. To achieve these goals, we used standard methods for monitoring water relations (sap flow and leaf water potential measurements, porometry, and a potometer approach) and the Swiss canopy crane (SCC) to provide access to the upper canopy.

## Materials and methods

### Site description

The experiment was located at the SCC research site in a diverse mixed deciduous forest on a gentle north slope about 12 km south of Basel, Switzerland ( $47^{\circ}28'\text{N}$ ,  $7^{\circ}30'\text{E}$ , elevation: 550 m a.s.l.). The forest is approximately 100 years old with tree heights between 30 and 38 m. Stem density (diameter at breast height  $\geq 10$  cm) in the stand is ca.  $415\text{ trees ha}^{-1}$ . The stand has a total basal area of  $46\text{ m}^2\text{ ha}^{-1}$ , a leaf area index of ca.  $5\text{ m}^2\text{ m}^{-2}$  in the experimental area and is dominated by *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. Also present as companion species are *Carpinus betulus* L., *Tilia platyphyllos* Scop., *Acer campestre* L. and *Prunus avium* L.. Furthermore, there is a strong presence of conifers (*Abies alba* Mill., *Picea abies* L., *Pinus sylvestris* L. and *Larix decidua* Mill.). The understory is dominated by *Lonicera xylosteum*, *Corylus avellana* and *Daphne laureola* as well as young trees (especially *Acer pseudoplatanus*, *Fraxinus excelsior* and *Fagus sylvatica*). Ivy (*Hedera helix* L.) plays a prominent role on the forest floor (juvenile life phase) as well as in the canopy. With stems up to 15 cm diameter at breast height, ivy reaches over 25 m in height in some trees and occupies a significant fraction of the forest's sub-canopy. Nearly all *Larix* and *Picea* trees and most of *Quercus* and *Carpinus* trees at this site host large ivy individuals.

The climate is a typical humid temperate zone climate with mild winters and moderately warm summers. The mean temperatures during January and July are 2.1 and  $19.1^{\circ}\text{C}$ , respectively. The long-term total annual precipitation for the region averages 990 mm, of which two-thirds fall during the growing season ranging from the end of April

until the end of October. The soil is a silty-loamy rendzina on calcareous bedrock with a pH of 5.8 in the top 10 cm of soil profile. The accessible profile depth is ca. 30 cm.

#### Plant material and canopy access

A 45-m tower crane with a gondola on a 30-m jib provided access to tree canopies over an area of 2,800 m<sup>2</sup>. The experimental design (see below) required access to individuals of *Hedera helix* at two measuring heights (upper and lower canopy; 12 and 23 m height above ground). Therefore, appropriate host trees infested with adult *Hedera helix* reaching at least 23 m in height were selected. The multiple infestations of host trees with different stems of *Hedera helix* and the countless intersections of stems and branches prevented the identification of single individuals over the whole height gradient. Therefore, it was not possible to ensure that readings on the two measuring heights were always taken from the same genet. Readings of leaf conductance, light exposure and leaf water potential (see below) were taken from ‘individuals’ of *Hedera helix* on six different host trees (two *Larix decidua*, one *Picea abies* and three *Quercus petraea* individuals).

#### Environmental data

Wind speed, photon flux density, rainfall, air temperature and relative humidity were measured above the tree canopy using a weather station located at the top of the crane (anemometer AN1, quantum sensor QS, tipping bucket rain gauge RG1, shielded temperature and relative humidity probe RHA 1, Delta-T Devices Ltd., Cambridge, UK). A self-made wet and dry bulb aspiration psychrometer attached to the crane mast at ca. 30 m was used to calculate vapour pressure deficit (vpd) at canopy height. All data were recorded as 10 min means with a data logger (DL2e, Delta-T Devices Ltd.). Soil water content was obtained from hourly measurements of seven theta-probes (ML2x, Delta-T Devices Ltd.) connected to another data logger (DL2e, Delta-T Devices Ltd.).

#### Leaf conductance, photon flux density and leaf water potential measurements

Measurements were taken during five clear, sunny days from May to September 2004 (12 May, 10 June, 22 July, 2 August and 2 September) from mature leaves of different branches of the current year. Leaf conductance ( $g_s$ ) was measured with a portable diffusion-porometer (AP4, Delta-T Devices Ltd.) and data were recorded as soon as the readings were constant. Photosynthetically active radiation (PAR) was measured in the direction vertical to leaf blade orientation using a photodiode integrated in the measuring unit of

the diffusion-porometer. Following each porometer measurement, leaf water potential ( $\Psi$ ) of the same leaf was recorded using a pressure chamber (SKMP 1400, Sky Instruments, Powys, UK). To prevent water loss after cutting the leaf, samples were wrapped with sticky tape and measured immediately after cutting them off.

Daily courses of  $g_s$  and  $\Psi$  in adult ivy were measured at 12 and 23 m above the ground. For a single time slot, three to four readings of leaf conductance, light exposure and leaf water potential were taken at both heights, which took ca. 2 times 15 min. In order to eliminate diurnal bias, measurements at both heights were repeated immediately in opposite order. These four data sets (two for each height) were then pooled and averaged to represent the mean for a certain time of day with similar environmental conditions. This procedure was repeated for other individuals in random order. For the comparison between ivy and host trees, the data set of Keel et al. (2007) on stomatal conductance of trees in the same area (both host trees and surrounding trees) were used. The values shown represent means of measurements on bright days with similar soil moisture status and history from all six deciduous species present in the area (see above, for details see Keel et al. 2007).

We modelled the vpd– $g_s$  relationship using the model that was favoured in a comparison study of several models (Oren et al. 1999):

$g_s = -m \cdot \ln(\text{vpd}) + b$ , where  $m$  represents the vpd-sensitivity and  $b$  is the reference conductance at 1 kPa.

#### Sap flow measurements

The constant heat-flow technique described by Granier (1985) was used to measure the sap flow in the xylem. Each sensor (UP, Kolkwitz, Germany) consisted of two 20 mm long, 2 mm diameter probes. Each probe was equipped with a copper-constantan thermocouple and wrapped with a heating wire. The two probes were inserted in radial holes in the sapwood at breast height (holes lined with a thin aluminium tube).

Sap flow readings were recorded between 1 April and 25 September in 2004 on six mature ‘individuals’ of *Hedera helix* as well as on 9 trees (three *Quercus petraea*, three *Fagus sylvatica* and three *Carpinus betulus* individuals.). To protect sap flow sensors from rain and atmospheric thermal fluctuations, each sensor pair was covered with an aluminium box filled with polyester wool. Readings were taken at 30-s intervals and recorded as 10-min means with a data logger (DL2e, Delta-T Devices Ltd.). Because nightly minimum sap flow rates were approximately constant, no trend removal was necessary.

We used relative sap flow values (seasonal maximum set to 1, not occurring during the shown periods), because the sapwood of *Hedera helix* remains active for many years and

even central parts of the stem can support sap flow. Thus, the 20-mm-long probes did not capture the complete cross-sectional sap flow in any stem exceeding a diameter of 4 cm (plus phloem layer). Furthermore, *Hedera helix* produces a multitude of interconnected stems (anastomosis), making it impossible to infer absolute flow per unit leaf area. Accordingly, we could not calculate absolute whole-canopy conductance, but rather estimated relative canopy conductance ( $g_c$ ) by dividing the 95th percentile relative sap flow values of each vpd class by the corresponding vpd value. This represents a unit-less form of the inverted Penman–Monteith equation applied for example in Pataki et al. (1998). This allowed us to fit the same model to sap flow data as to the stomatal conductance data, and compare  $e^{b/m}$ , the (hypothetical) value of complete stomatal closure (Monteith 1995). A non-linear model used for photosynthesis-light curves was fitted to the 95th percentile sap flow (SF)–vpd curves:  $SF_{95th\ percentile} = SF_{max} \times (1 - \exp(-\alpha \times vpd / SF_{max})) - \beta$  with  $\alpha$  and  $\beta$  parameters to be fitted. Vapour pressure deficit values were binned in 0.1 kPa classes.

#### Potometer experiment

In an attempt to determine absolute transpiration per unit leaf area, we constructed an in situ potometer experiment. The experiment also allowed us to calibrate the Granier sap flow sensors for ivy. We selected an individual that had only one climbing stem (ca. 24.5 m total plant height), which was cut off under distilled and degassed water (in order to prevent embolism) ca. 0.5 m under the two inserted sap flow sensors. Water consumption was then monitored (10 min intervals) by refilling a glass cylinder from which the stem drew water. Nocturnal water supply was ascertained by connecting the cylinder with a second, larger water reservoir. Total nocturnal water consumption was then measured the next morning and all following readings were taken in intervals of 10 min as before. The colouring of the water at the end of the experiment showed that the whole stem xylem area (14.6 cm<sup>2</sup> at breast height) conducted water and supplied a total leaf area of 54 m<sup>2</sup> (sap wood to leaf area ratio =  $2.8 \times 10^{-5}$  m<sup>2</sup> m<sup>-2</sup>). At the end of this experiment, we harvested all leaves in height intervals of 5 m. For each interval, we took five subsamples of 10–60 g to measure leaf weight and leaf area (LI-3100 AreaMeter, LI-COR, Lincoln, NK, USA) in order to calculate the specific leaf area (SLA). The leaf area index (LAI) of this individual was about 10 if we refer to the estimated projected area of all shoots at ground level.

#### Data analysis

The free software package ‘R’ (version 2.10.1, R Development Core Team 2009) was used to fit the non-linear

models (package nlme, generalised least squares model, function ‘gnls’). All graphics were drawn using R.

## Results

### General characterisation of water use in *Hedera helix*

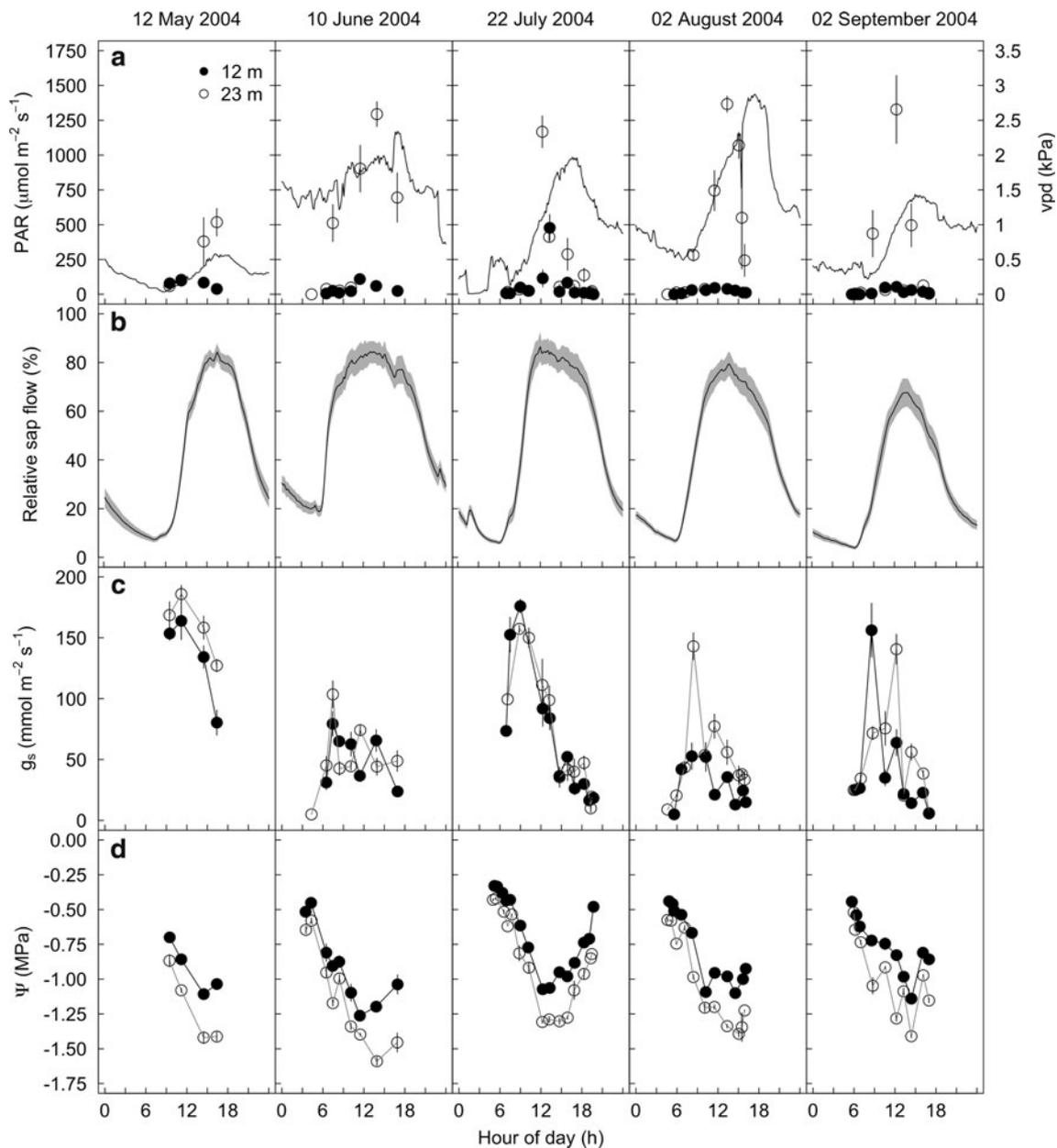
During the five measuring days, mean predawn leaf water potentials ( $\Psi$ ) ranged from about  $-0.33$  to about  $-0.48$  MPa in 12 m height above ground, and from about  $-0.43$  to about  $-0.63$  MPa in 23 m height above ground (Fig. 1). Soil moisture was moderate to high during all five measuring days with soil water content never falling below 29% vol. When accounting for the 0.11 MPa difference in hydrostatic pressure the readings between the two sampling heights did not differ significantly ( $t$  test,  $n = 6$ ,  $P = 0.50$ ). Diurnal courses in leaf water potential ( $\Psi$ ) showed values from  $-1.1$  to  $-1.4$  MPa at 12 m height above ground, and from  $-1.3$  to  $-1.7$  MPa in 23 m height. Leaf water potential dropped faster during the day at 23 m than at 12 m above ground, and differences of daily minimum  $\Psi$  between heights were larger than expected from the hydrostatic difference alone (Fig. 1).

The diurnal course of leaf conductance was highly variable both within and between measuring heights (Fig. 1). Most leaves were at least partly shaded; therefore, these values do not represent physiological maxima. Light conditions at the studied leaves varied a lot, with a median of  $37 \mu\text{mol m}^{-2} \text{s}^{-1}$  at 12 m and  $45 \mu\text{mol m}^{-2} \text{s}^{-1}$  at 23 m (between 9 and 18 h). There was no significant difference in mean maximum leaf conductance at the two measuring heights ( $t$  test,  $n = 6$ ,  $P = 0.11$ ).

The daily amplitudes of relative sap flow density remained more or less unaffected throughout very different vpd conditions (Fig. 1). Overcast, cool weather conditions yielded similarly high sap flow rates than bright days. Relative sap flow reached 50% of the seasonal maximum even during days when vpd did not exceed 0.33 kPa. Out of 166 days of continuous sap flow data, only 14 days had a mean maximum relative sap flow below 50% of the seasonal maximum. In contrast to ivy, the amplitude of relative sap flow of trees was very responsive to changing weather conditions (data not shown).

### Comparison between water relations of ivy and host trees

Stomata of ivy responded very sensitively to vapour pressure deficit, resulting in a strong down-regulation of leaf conductance and hence sap flow, as vpd exceeded ca. 0.5 kPa (Intersection of linear fit through first six 95th percentiles of vpd classes with the maximum, dashed



**Fig. 1** Diurnal course of **a** light conditions at the leaves (PAR) and vapour pressure deficit (vpd, *solid line*), **b** mean sap flow (relative to seasonal maxima not shown here,  $n = 6$ , *grey area* indicates one standard error of standardised series), **c** stomatal leaf conductance ( $g_s$ )

and **d** leaf water potential ( $\Psi$ ) of *Hedera helix*. *Open circles* are data measured at 23 m above ground, *filled circles* are data measured at 12 m above ground. *Error bars* represent one standard error

vertical line in left top panel of Fig. 2). Trees were less conservative and stomatal downregulation started at ca. 0.8 kPa (vertical dashed line in right top panel of Fig. 2). The conservative water use of ivy compared with that of trees is also illustrated by fitting the model  $g_c = -m \ln(\text{vpd}) + b$  ( $g_c$  = relative canopy conductance computed from sap flow, top panels of Fig. 2) and  $g_s = -m \ln(\text{vpd}) + b$  (for direct stomatal conductance measurements, bottom panels of Fig. 2). The hypothetical vpd

value at which  $g_c$  or  $g_s$  is zero ( $e^{b/m}$ ) is 2.7 versus 5.9 kPa in ivy and trees, respectively ( $g_c$ ), and 9.6 versus 18.1 kPa in ivy and trees, respectively ( $g_s$ ). Ivy thus showed a much higher vpd-sensitivity than the host trees.

Canopy greening during the last week of April strongly influenced water relations of ivy despite consistently high soil moisture. Daily maxima of relative sap flow were ca. 50% higher at vpd < 0.3 kPa and up to 20% higher at vpd > 0.3 kPa before than after the canopy leafing (Fig. 3).

Relative sap flow of ivy was the highest of the whole season shortly before canopy closure. Maximum relative sap flow was reached at much lower vpd before than after the canopy leafing (Fig. 3).

#### Potometer experiment

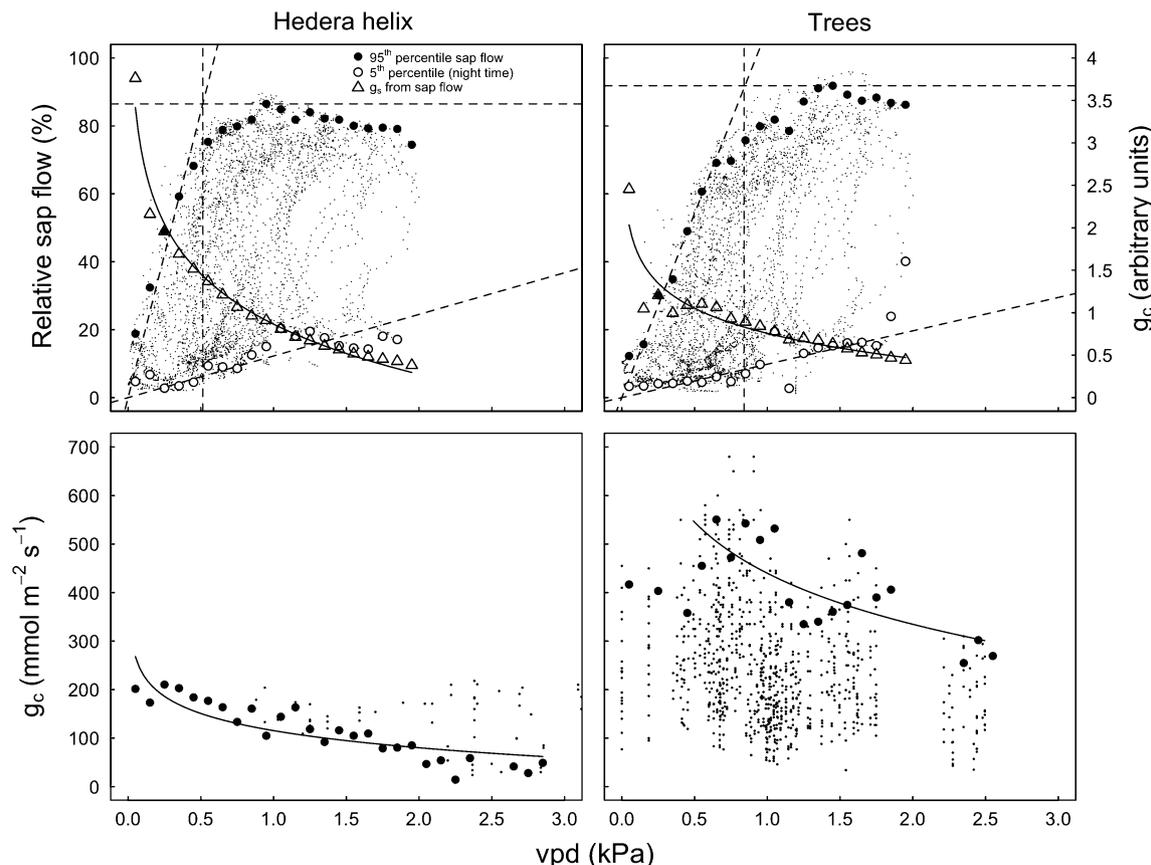
Immediately after separating the stem from its below ground supplies, sap flow rate rose abruptly (presumably as a result of the instantly reduced hydraulic resistance), leading to a relaxation in stem water potential (partial refilling of parenchymal stem water storage). Disregarding this initial peak, maximum water consumption of the whole plant was  $13.5 \text{ ml min}^{-1}$  (i.e.  $1.5 \times 10^{-4} \text{ m}^3 \text{ m}^{-2} \text{ s}^{-1}$  sap flow density with  $14.6 \text{ cm}^2$  sap wood area), corresponding to a mean transpiration rate of  $0.23 \text{ mmol m}^{-2} \text{ s}^{-1}$  (per unit leaf area). Maximum leaf transpiration rate estimated on the basis of  $g_s$  and vpd (disregarding aerodynamic components of conductance) reached  $1.87 \pm 0.05 \text{ mmol m}^{-2} \text{ s}^{-1}$  at a

vpd of ca. 1.6 kPa. Therefore, mean transpiration across all leaves was ca. eight times lower than maximum leaf transpiration of fully sun-exposed leaves. This discrepancy includes self-shading as well as aerodynamic effects, the latter a composite of leaf boundary layer phenomena plus canopy effects (lower effective vpd than assumed from mid-canopy measurement).

During the experiment, sap flow was monitored with two Granier sensors installed about 50 cm above the cut end (Fig. 4a). SF was calculated from  $\Delta T$  using the standard calibration for trees:

$$\text{SF}_{\text{Granier}} = 0.714 \cdot \left( (\Delta T_{\text{max}} / \Delta T) - 1 \right)^{1.231} \cdot A \quad (1)$$

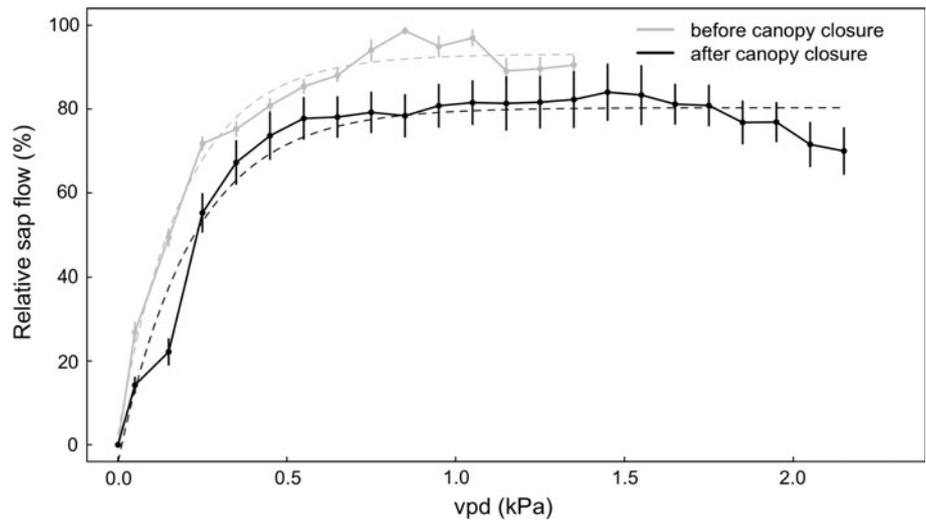
(in  $\text{ml min}^{-1}$ , see Granier 1985), with the sap wood area  $A$  of  $14.6 \text{ cm}^2$  in our case. With this equation, we underestimated water uptake by a factor of ca. 2 (Fig. 4b). Nevertheless, relative values of sap flow and potometer water consumption fitted highly significantly for both sensor couples installed ( $r_{\text{adj}}^2 = 0.993$  for sensor 1 and



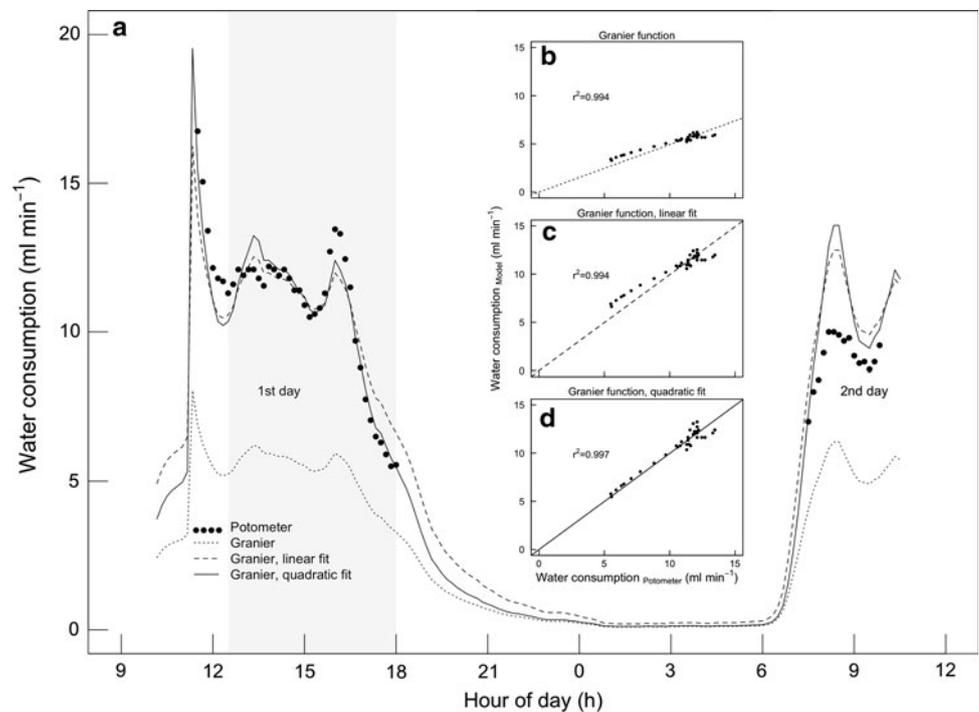
**Fig. 2** Top panels mean sap flow (from 14 June to 8 August, relative to seasonal maximum,  $n = 6$  for ivy,  $n = 9$  for trees) to vapour pressure deficit (vpd). 95th percentiles for vpd (class width 0.1 kPa), marked as black points; solid lines show slope (linear regression through first 6 data points), maximum and the break point (intersection of slope and maximum). 5th percentiles of night-time data (between 11 p.m. and 4 a.m.) for vpd (class width 0.1 kPa) are

marked as open circles; dashed lines show linear regressions. Triangles show  $g_c$  (canopy conductance) estimated from sap flow, with a non-linear regression model fitted (see text). Bottom panels response of stomatal leaf conductance ( $g_s$ ) to vpd, 95th percentiles (class width 0.1 kPa) are marked as black symbols, with a non-linear model fit (see text). Values of stomatal leaf conductance of trees are from Keel et al. (2007)

**Fig. 3** Response of 95th percentiles of mean sap flow (relative to seasonal maximum,  $n = 6$ ) to vapour pressure deficit (vpd, class width 0.1 kPa). Periods of 13 days before (early April, grey line) and after canopy closure (mid-May, black line) are shown. Error bars represent one standard error



**Fig. 4** Water consumption of adult ivy on a clear day in 2004 (points) and calculated sap flow measured with Granier-type sensors using three different models. Subpanels b–d show the fit of those models (water consumption vs. calculated water flow based on sensors)



$r^2_{adj} = 0.995$  for sensor 2;  $P < 0.001$  for both sensors). We adjusted Eq. 1 for estimating absolute flow rates in ivy with the best linear fit ( $SF = 2.018 SF_{Granier}$ , Fig. 4c) and the best quadratic fit ( $SF = 0.016 SF^2_{Granier} + 1.139 SF_{Granier}$ , Fig. 4d) based on data obtained during the first day (ignoring the initial 30 min after cutting).

**Night-time transpiration**

Night-time sap flow of ivy was strongly vpd-dependent (Fig. 2 top left panel; linear regression through the 5th percentiles of night-time data, between 11 pm and 4 am, for vpd classes of 0.1 kPa,  $r^2_{adj} = 0.92$ ). During warm and dry

summer nights when vpd exceeded 1 kPa, relative sap flow did not fall below 20% of the seasonal maximum. Hence, ivy loses substantial amounts of water at night during periods of high soil moisture. Night-time transpiration of trees was lower (ca. 10% of seasonal maximum at 1 kPa).

**Discussion**

This study for the first time presents a comprehensive data set on water relations of the most important European liana, *Hedera helix*. Our study suggests that (1) *Hedera helix* exerts a tight control over its water use, ensuring high

leaf water potentials irrespective of climatic conditions (isohydric behaviour relative to their host trees). This control over plant water use is accomplished by an early down-regulation of leaf conductance in response to increasing vapour pressure deficit (and/or transpirational flow rate itself), which results in sap flow maxima reached at very low vpd (0.5 kPa). (2) Canopy leafing of deciduous trees in spring strongly influences the water relations of climbing ivy, causing a considerable reduction of maximum sap flow in response to vapour pressure deficit. Ivy may strongly profit from mild days before canopy leafing causes strong light interception. (3) Granier sensors cannot be used for ivy applying the standard calibration for trees; instead, we suggest a specific model calibration for ivy.

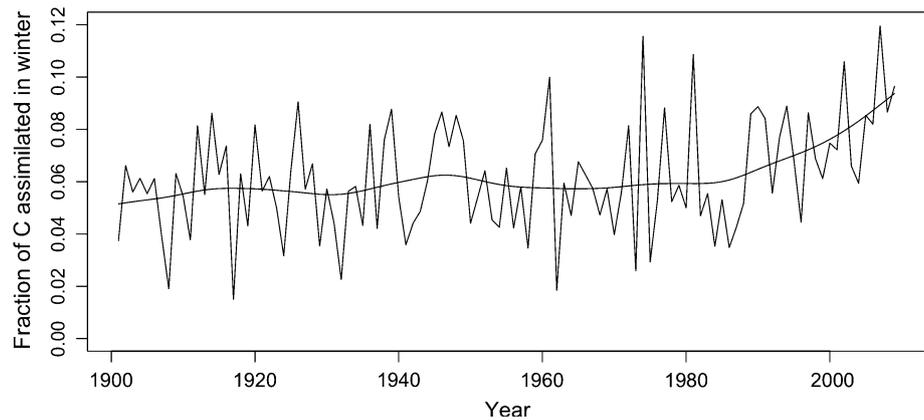
Differences in predawn  $\Psi$  at the different heights above ground were caused by differences in hydrostatic water potential only. Host trees showed similar predawn  $\Psi$  at comparable soil water status in the previous year (Leuzinger et al. 2005). The faster reduction of diurnal leaf water potential in 23 compared with 12 m is probably related to significantly higher light intensities and thus stomatal conductance in the upper canopy. However, this could not be verified as the light regime was changing too rapidly and concurrent measurements of  $\Psi$  and  $g_s$  were not possible from the crane gondola. Diurnal  $\Psi$  at the same height was much lower in host trees ( $<-2$ MPa at ample soil moisture, Leuzinger et al. 2005), and stomatal down-regulation occurred later, which points to a comparatively anisohydric water use as opposed to the more isohydric behaviour by ivy. This difference between ivy and its host trees is further evidenced in Fig. 2, where both a steeper initial slope and an earlier break point in the relative SF–vpd plot are apparent for ivy compared with its host trees. A possible explanation for this is the strong atmospheric coupling of the host trees, while this was much less the case for *Hedera helix* with its dense canopies. The  $g_c$ –vpd model fit is not representative in absolute terms as the  $g_c$  data are an estimate based on relative sap flow, not considering the unknown sap wood-to-leaf area ratio and storage. However,  $e^{b/m}$ , the hypothetical vpd threshold of complete stomatal closure, ranks among the very lowest in a comparison of several tree species reported by Oren et al. (1999), suggesting a particularly high stomatal sensitivity as is known for other broad-leaved evergreen species from humid environments (e.g. Körner and Bannister 1985). The model fit to the  $g_s$  data (Fig. 2, bottom panels) yields higher  $e^{b/m}$  values for both ivy and trees (consistent with data summarised in Oren et al. 1999), but ivy remains ca. 50% lower than trees, again emphasising its strong stomatal sensitivity. Because of the large xylem vessels of lianas (Ewers et al. 1991), cavitation events should have a relatively large impact on conductivity of ivy stems. The highly conservative flow control may have evolved as an

adaptation to the high vulnerability of ivy to cavitation. The benefit of the large vessels may be the low resistance to sap flow, which allows high transpiration rates at low vpd conditions and thus optimal nutrient and carbon acquisition during winter months (Fischer and Feller 1994). This view is supported by the highly consistent water consumption throughout bad weather conditions with low vpd ( $<0.5$  kPa) and low light (peaks of  $<500$   $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ).

The reduction in relative maximum sap flow following canopy closure in spring was most likely due to increased shading from trees and the altered canopy boundary layer property (less wind, Fig. 3). The reduction of the initial slope of the relative SF–vpd curve following bud break is probably also due to reduced light availability and less atmospheric coupling. The time window before canopy closure could represent a temporal niche during which ivy plants gain substantial advantage in carbon assimilation over their host plants.

To estimate the increasing advantage ivy may have over its host trees with warmer winter temperatures, we propose a (coarse) estimate for C-assimilation using sap flow as a proxy. The argument is based on the fact that ultimately, sap flow (transpiration) is intimately coupled to C-assimilation (Körner et al. 1979, see their Fig. 3) and that photosynthetic proteins are active during warm spells (Fischer and Feller 1994). We therefore assume that C-assimilation is approximately proportional to sap flow throughout the year as long as temperature and light are non-limiting. Using a simple temperature-dependence (growth is zero at  $T \leq 6^\circ\text{C}$  and increases linearly until  $T = 20^\circ\text{C}$ , no temperature limitation at  $>20^\circ$ ), we estimated C-assimilation for pre- and post leafing SF–vpd curves (mean growing season length 202 days, Asshoff et al. 2006), with vpd data from a 109-year climate data series nearby (Tank et al. 2002). Because ivy achieves 90% of maximum photosynthesis at  $360 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Carter and Teramura 1988), and because light is strongly correlated with both vpd and  $T$ , we did not include explicit light limitation. Our estimation of the fraction of carbon assimilated during winter shows an almost 50% increase from 1980 to 2009 (6% in 1980 vs. 10% in 2010, Fig. 5). Therefore, if carbon assimilation in summer remained constant, and under the assumption that growth in the subcanopy is carbon limited, ivy showed an increase in carbon gain over the past 30 years. This may explain the increased diameter growth in years with warm winters reported by Heuzé et al. (2009). With winter temperatures expected to rise between 1.5 and  $5^\circ\text{C}$  compared to 1990 in the studied area (OcCC 2008), this trend could continue. A lengthening of the growing season may slightly counteract this trend, but most deciduous host trees' phenology at this site is not solely controlled by temperature but exhibits photoperiod control, in particular beech (Körner and Basler 2010).

**Fig. 5** Estimate of the fraction of carbon assimilated in winter versus summer based on sap flow using a 109-year climate data set from a nearby site. The smooth line is a spline function (function 'smooth.spline', smoothing parameter 0.7, R Development Core Team 2009)



Sap flow was calculated using the standard calibration factor for trees (Granier 1985). The underestimation of sap flow by a factor of ca. 2, however was surprisingly high. The reason for this could be the relatively large xylem vessels of ivy. Steppe et al. (2010) showed that this can lead to an underestimation of sap flow with the constant heat sensors. We propose to use a specific model for ivy by replacing the standard sap flow density calibration factor of 0.714 in Eq. 1 by an adjusted factor of 1.441. Our results confirm the often encountered difficulty to infer absolute flux rates from sap flow signals (Leuzinger and Körner 2007), particularly in ring porous species (Bush et al. 2010). Because relative sap flow correlated well in all three models in Fig. 4, an alternative may be to assume a reasonable seasonal maximum transpiration rate against which sap flow data can be calibrated, particularly under field conditions and when little information on the sap wood area is available. The average sap flow density measured for ivy (volume of water per unit area per second,  $1.5 \times 10^{-4} \text{ m}^3 \text{ m}^{-2} \text{ s}^{-1}$ ) was higher by an order of magnitude than sap flow densities estimated for trees at the same site (ca.  $2 \times 10^{-4} \text{ m}^3 \text{ m}^{-2} \text{ s}^{-1}$ , Cech et al. 2003). The missing root resistance in the potometer experiment probably only accounts for a small fraction of this large difference and ivy certainly has very high sap flow density.

Night-time sap flow was in the upper range (up to 20% of seasonal maximum) of values reported for other plants (Caird et al. 2007). In our case, night-time sap flow could have been caused by (1) actual night-time transpiration, (2) compensation of phloem basipetal flux or (3) sap flow induced by the refilling of stem and leaf reservoirs. Night-time transpiration alone is an insufficient explanation because sap flow was also observed during rainy nights when vpd was close to 0 kPa (data not shown). The potometer experiment showed a maximum transpiration rate of  $13.5 \text{ ml min}^{-1}$  for a total leaf mass of about 13 kg. To refill 10% of the total water content of leaves (at 85% water content) during the night, maximum sap flow rates during almost 1.5 h would have been required. Therefore,

refilling of plant water reserves likely contributed to the flux at night, but a combination of all three mentioned phenomena is most likely. Night-time transpiration may be advantageous for nutrient acquisition (Tanner and Beevers 2001), but this is not true for all species (Christman et al. 2009) and the phenomenon awaits general clarification (Cramer et al. 2009).

In conclusion, we argue that *Hedera helix* has evolved a very conservative, in tendency isohydric water use strategy that is strongly adapted to optimally use light before bud break of surrounding trees and after leaf fall in autumn. Its high transpiration rates at low vpd are possible through minimising stem resistance at the cost of early stomatal downregulation to avoid cavitation. With winters getting milder, we expect ivy to firstly suffer less from severe frosts. Second, ivy may grow more vigorously as a larger proportion of carbon may be assimilated during warming winters (at constant summer assimilation rates) while its host trees are dormant, still not accounting for CO<sub>2</sub>-fertilisation effects as evidenced by Zotz et al. (2006). Both winter-time warming and CO<sub>2</sub>-fertilisation in low light conditions could speed up temperate forest succession due to increased presence of ivy.

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