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# Transpiration of four common understorey plant species according to drought intensity in temperate forests

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## Abstract

· **Key message** Water use patterns of understorey vegetation are species-dependent. *Calluna vulgaris* showed little or no regulation of transpiration in response to soil water depletion or air vapour pressure deficit, unlike *Pteridium aquilinum*, *Rubus* sp. and *Molinia caerulea*.

· **Context** Evapotranspiration at forest stand scale is the sum of three components: overstorey and understorey transpiration, and evaporation from soil. During periods of soil water shortage, evapotranspiration of trees declines significantly, but the response of understorey vegetation is less well known. Some reports suggest that understorey vegetation can sometimes be the main source of water depletion in a forest stand during drought episodes.

· **Aims** We assessed transpiration in response to decreased soil water content (SWC) and increased vapour pressure deficit (VPD) in the atmosphere for four understorey species with contrasting patterns of resource capture.

· **Methods** Potted plants of *Pteridium aquilinum*, *Molinia caerulea*, *Calluna vulgaris* and *Rubus sect. Fruticosi* were grown under two radiation levels combined with three levels of SWC. Temperature, radiation, VPD and transpiration were monitored.

· **Results** *Calluna vulgaris* displayed a water spender behaviour with little or no regulation of transpiration during soil water depletion and increased VPD, whereas *Pteridium aquilinum* showed a low transpiration rate whatever the conditions. *Rubus sect. Fruticosi* gradually decreased transpiration during soil water depletion and increased VPD, whereas *Molinia caerulea* responded strongly to soil water depletion but only moderately to VPD.

· **Conclusion** This study highlights the importance of adding identity and water use strategy of understorey species to the tree canopy component to establish a reliable forest water balance.

**Keywords** Water use patterns · Vapour pressure deficit · Soil water depletion · Radiation · Potted experiment

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## 1 Introduction

Increases in leaf area (LA) and attendant water demand resulting from increasing radiative forcing, is expected to favour recurrent, more intense drought periods in many parts of the world (IPCC 2013). Water availability in particular may become a limiting factor in some temperate forest ecosystems. Recorded effects of recurrent droughts on forest ecosystems range from growth losses (Barber et al. 2000; Mäkinen et al. 2003), and higher sensitivity to pathogens, pests and insects (Desprez-Loustau et al. 2006; Hogg et al. 2002; Jactel et al. 2012) to forest decline (Allen et al. 2010).

The review of Wullschleger et al. (1998) indicates that the maximal daily water use of 90 % of trees (of average height 21 m) varies between 10 L and 200 L per day according to tree

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species and dimensions. However, trees are not the only forest component that consumes water. Aussenac et al. (1995) and Barbour et al. (2005) point out that forest-stand evapotranspiration (ET) is the sum of soil evaporation, and understorey and overstorey transpiration.

Studies in temperate and boreal forests have shown that understorey transpiration averages out at one-third of total stand ET (Diawara et al. 1991; Granier et al. 1990; Launiainen et al. 2005; Ohta et al. 2001), but can range from as little as 15 % (Constantin et al. 1999; Lindroth 1985; Staudt et al. 2011) to over 90 % (Simonin et al. 2007). Loustau and Cochard (1991) explain that between-study differences in measured ET may be due to different climate demands, vegetation composition, and different development stages resulting in contrasting leaf area index (LAI). Furthermore, understorey vegetation ET is often higher during droughts (Diawara et al. 1991) and before deciduous tree budbreak (Vincke and Thiry 2008).

Although overstorey transpiration is known to be tree species-dependent (Roberts 1983), understorey vegetation is still often considered as a mere layer of vegetation without distinction of species identity. To refine this view, Frochot et al. (2002) and Balandier et al. (2006) grouped understorey species by general plant functional types such as graminoids, heathers, small shrubs and ferns according to how they competed with tree seedlings and saplings. Also, plant functional types summarize general response patterns to environmental conditions (Diaz and Cabido 1997; Friedrich et al. 2012).

The main objective of this study was to characterize the transpiration of understorey species in response to decreased soil water content (SWC) and increased vapour pressure deficit (VPD) in the atmosphere. The species were chosen among common interfering plants in temperate forests that are strongly competitive, in particular towards young tree seedlings (Willoughby et al. 2009). They were also selected according to contrasting functional traits, particularly those linked to resource capture (e.g. root morphology and light interception): *Molinia caerulea* L. for graminoids, *Calluna vulgaris* (L.) Hull for heathers, *Rubus sect. Fruticosi* for small shrubs and *Pteridium aquilinum* (L.) Kuhn for ferns. These species are considered as typically monopolistic with significant foliage cover even in shady conditions (Balandier et al. 2013; Gaudio et al. 2011).

*M. caerulea* is a perennial deciduous grass found in a broad range of wet soils, but able to tolerate dry soils temporarily (Grime et al. 1988). It is known to be highly competitive relative for water (Aerts et al. 1991) and has even been reported as drought-resistant by maintaining constant biomass production during drought and a low enough shoot-root ratio to tolerate low water availability (Friedrich et al. 2012). *P. aquilinum* is a perennial deciduous fern species (Gonzalez et al. 2013) that tolerates moderately waterlogged soils, and is often considered to be a strong competitor for light and to cope with water and nutrient shortage by resource storage in its rhizomes (Dumas 2002; Marrs and Watt 2006). *C. vulgaris* is an evergreen shrub with a low growth rate (Aerts et al. 1991). Britton et al. (2003) showed that its cover percentage, height and biomass production were not dependent on soil water availability, and Gordon et al. (1999b) showed that *C. vulgaris* used more water than *P. aquilinum*. *Rubus* sp. is a group of perennial shrub species with often very dense cover that is able to maintain high water consumption rates during drought periods by increasing root growth (Fotelli et al. 2001).

Based on a greenhouse experiment, the transpiration of the four species was characterized under different levels of soil water depletion. As light availability strongly modulates climate demand, we also evaluated the transpiration of the four plants under two contrasting light levels. We tested the hypothesis that the four species would (1) present different transpiration levels and (2) different response patterns to SWC and/or VPD levels, and that (3) the shaded conditions would interact with soil water depletion and VPD in affecting plant transpiration.

## 2 Materials and methods

### 2.1 Experimental set-up

The experiment was set up in spring 2012 in a greenhouse located at the Irstea Research Centre (Nogent-sur-Vernisson, France, 47°50'06"N 2°45'40"E). The four species were cultivated in 20 L pots. Soil was sandy-clay (74.6 % sand, 13.8 % loam and 11.6 % clay) with an organic matter content of 2.2 % and a $pH_{water}$ of 6.8. C/N ratio was 12.4. Soil fertility was medium ($N_{total}$: 1.05 g kg$^{-1}$, $P_{Dyer}$: 0.361 g kg$^{-1}$, CEC: 8.74 cmol$^+$ kg$^{-1}$).

Two centimetres of siliceous stone was laid on the soil surface to limit soil evaporation, and plants were fertilized with 0.107 g of a trace element mixture (B, Cu, Fe, Mn, Mo, Mg and Zn) (Hortrilon®, Compo®, BASF, Ludwigshafen, Germany) and 0.3 g of NPK fertilizer (Hakaphos® bleu, Compo®, BASF) per pot.

*C. vulgaris*, *P. aquilinum* and *M. caerulea* seedlings were collected in the nearby Orléans forest and *R. sect. Fruticosi* seedlings were collected from the Irstea Research Centre forest stand. A closely similar initial biomass was selected per species and potted in 21 kg of the soil described above. For *C. vulgaris*, we collected plants (root plus stem) and selected those with a mean weight of 1.1±0.4 g. For *M. caerulea*, we collected root and stump parts and selected those with a mean weight of 16.2±3.0 g. For *P. aquilinum*, we selected rhizomes with short 20 cm-long shoots, and sampled rhizomes of mean weight 18.9±4.3 g. For *R. sect. Fruticosi*, we collected plants (root plus one stem) and selected those with a mean weight of 15.1±5.6 g. To limit the effect of the transplantation crisis on

transpiration, plants were cultivated for 1 year under non-limited water supply. The experiment was thus started in summer 2013.

## 2.2 Experimental design

The experiment used a fully replicated design crossing two radiation levels and three SWCs [relative extractable water (REW) of 100 %, 40 % and 20 %]. REW is the ratio of actual to maximal extractable soil water. It was shown that an REW of 40 % is the threshold below which many species begin to reduce transpiration through gradual stomatal closure (Black 1979; Bréda et al. 1995). This threshold is similar for many species and is independent of the soil. REW at a given time $t$ was fixed as identical for all species and calculated using the following equation:

$$REW_t = (SWC_t - SWC_{WP}) \Big/ (SWC_{FC} - SWC_{WP}) \qquad (1)$$

Where

SWC_t     Soil water content at a given time $t$
$SWC_{FC}$     Soil water content at field capacity
$SWC_{WP}$     Soil water content at permanent wilting point

The two radiation levels of 70 % and 20 % PAR (photosynthetically active radiation, as percent incident radiation above the greenhouse) were obtained by greenhouse interception and the addition of a shading net throughout the experiment. Interceptions were measured at the set-up of the experiment by PAR sensors (SKP 215, Skye Instruments, Powys, UK). As a first level, 20 % of incident radiation was chosen to reflect the light conditions usually observed below the canopy of the typical oak (Q. petraea, Q. robur) temperate forests of Central France, with a dynamic thinning regime. The second level of 70 % of incident radiation reflects radiation conditions after a severe thinning designed to favour tree regeneration.

Soil water depletion was applied during three measurement sessions: between days 211 and 214 (30 July–2 August 2013), 217 and 220 (5–8 August 2013) and 260 and 263 (17–20 September 2013), hereafter noted S1, S2 and S3, respectively. Sessions S1 and S2 were in the middle of the growth season and under high climatic demands. The third session at the end of the growth season enabled us to measure transpiration under lower air temperature than during sessions S1 and S2. The week before the measurement sessions, pots with 20 % and 40 % REW levels were left to dry a little below the set REW and then watered the night before the measurement sessions to reach the set REW. The watering was based on a preliminary study where weight of the pots and predawn leaf water potential were monitored during a soil water depletion session. No watering was done over the following days corresponding to the measurement sessions. The rest of the year, pots were watered to field capacity.

The three levels of SWC were applied under the two radiation levels, resulting in six modalities (2 levels of radiation × 3 levels of REW). Each modality was applied to the four plant species plus a bare soil control, and eight repetitions were set up, giving a total of 240 pots in the greenhouse [6 modalities × (4 species + 1 bare soil) × 8 repetitions = 240]. In parallel, three pots per species were installed outdoors (i.e. 100 % radiation) and maintained at field capacity to provide a reference of transpiration under natural climate conditions. During S3, transpiration was not measured outdoors due to rain.

## 2.3 Assessment of plant water stress

SWC (%) and temperature ($T_{soil}$, °C) in the pots were measured every 5 min from June to September using SWC reflectometers (CS616, Campbell Scientific, Logan, UT) and copper-constantan thermocouples, respectively, connected to a datalogger (CR1000, Campbell Scientific). The water content reflectometer measures a wave period (Pa, microseconds). A specific calibration was applied using pot soil texture and $T_{soil}$ corrections according to the manufacturer's equation in order to improve SWC accuracy (Eqs. 2, 3). SWC was measured in one pot per species and per modality for 100 % and 20 % REW levels.

$$Pa_t = Pa + (20 - T_{soil})$$
$$\times \left(0.526 - 0.052 \times Pa + 0.00136 \times Pa^2\right) \qquad (2)$$
$$SWC = -0.07458 \times Pa_t^2 + 5.39265 \times Pa_t - 67.30099 \qquad (3)$$

Predawn leaf water potential ($\Psi_p$) of the plants was measured at the end of each session for each modality. Small stems for C. vulgaris and leaves for the other three species were sampled before sunrise, and water potential was measured in a Scholander chamber (Model 600, P.M.S. Instruments, Albany, OR). The relation between SWC and $\Psi_p$ (Eq. 4) enabled us to determine SWC at the permanent wilting point ($\Psi_p$ at −1.6 MPa according to the literature) (Kirkham 2014) that corresponded to 14 % SWC for the four species in our experiment.

$$SWC = 1 \Big/ \left(0.036007 + 0.028009 \times \sqrt{\left(\left|\Psi_p\right|\right)}\right) \quad r^2 = 0.67^{***} \quad n = 48$$
$$(4)$$

## 2.4 Transpiration measurements

Transpiration measurements were made by weighing the pots over 3 successive days following application of the soil water depletion for each session. ET corresponded to the sum of soil water evaporation and plant transpiration. The layer of

siliceous stone above the soil surface was designed to limit the soil water evaporation component, so that ET would be driven mainly by plant transpiration. Despite this protection, on average, soil evaporation (pot without plant) was not negligible, with $1.02 \pm 0.64$ mm day$^{-1}$ of pot area. However, plant transpiration remained the main source of soil water depletion. Daily transpiration was calculated as the difference between initial pot weight (measured in the morning) and pot weight after 24 h, measured using a dynamometer (HCB50K20, Kern, Balingen, Germany, precision $\pm 20$ g).

## 2.5 Environmental measurements

Air temperature ($T_{air}$, °C) and relative humidity ($RH_{air}$, %) were measured every 5 min at each radiation level by four USB dataloggers (LOG32, Dostmann Electronic, Wertheim, Germany) under the greenhouse and one USB Datalogger outdoors. $T_{air}$ and solar radiation (SR, kJ m$^{-2}$) were also measured by a copper-constantan thermocouple and a pyranometer (SP1110, Campbell Scientific), respectively, both connected to a datalogger (CR1000, Campbell Scientific). Daily potential evapotranspiration (PET$_{Turc}$, mm, Eq. 5) (Turc 1961) was calculated from mean daily temperature ($T_{air}$, °C) and total daily solar radiation (SR, cal cm$^{-2}$ day$^{-1}$):

$$PET_{Turc} = 0.013 \times (SR + 50) \times (T_{air}/(T_{air} + 15)) \quad (5)$$

Daily air VPD (in kPa) was calculated as the difference between saturated ($P_{sat}$, Eq. 6) and effective water vapour pressure of the air ($P_{air}$, Eq. 7) (cf. von Arx et al. 2013; WMO 2008)

$$P_{sat} = 0.6112 \times exp\left((17.62 \times T_{air})\big/(T_{air} + 243.12)\right) \quad (6)$$

$$P_{air} = P_{sat} \times RH/100 \quad VPD = P_{sat} - P_{air} \quad (7)$$

## 2.6 Allometric relation

To compare transpiration between species of different size and architecture, transpiration was expressed in millimetres of water per day and per square metre of LA of each potted plant. As it was wholly impractical to measure LA on all plants, we used allometric relations between LA measured at the end of the summer and species-specific morphological traits or biomass (based on the better statistical model) established on a subset of plants. Leaf samples (with stem for *C. vulgaris*) were scanned, and LA was measured by an image analysis system (WinFolia, Regent Instruments, Quebec City, Canada).

When differences were found in the allometric relations between leaves from plants established in the two contrasting radiation levels (20 % and 70 % PAR), such as for *M. caerulea* and *C. vulgaris*, different models were established. LA of

*C. vulgaris* was corrected by a coefficient between exact LA (measurement on 160 leaves under a microscope) and LA with stem on the scan. On average, these coefficients were $0.87 \pm 0.07$ and $0.73 \pm 0.10$ for illuminated and shaded plants, respectively. We obtained the following allometric relations:

For *P. aquilinum*:

$$LA = 0.0308\, x^{2.3473} \quad r^2 = 0.93^{***} \quad n = 34 \quad x : frond\ length (cm)$$
$$(8)$$

For *R. sect. Fruticosi*:

$$LA = 2.03x + 1124.54 \quad r^2 = 0.77^{***} \quad n = 20 \quad x : total\ cane\ length (cm)$$
$$(9)$$

For *M. caerulea*:
illuminated plants

$$LA = 164.43\, x^{1.0796} \quad \mathbf{r}^2 = 0.61^{**} \quad n = 11 \quad x : total\ leaf\ biomass (g)$$
$$(10)$$

shaded plants

$$LA = \sqrt{(-553744 + 62538\, x^2)} \quad r^2 = 0.78^{***} \quad n = 10$$
$$x : total\ leaf\ biomass (g)$$
$$(11)$$

For *C. vulgaris*:
illuminated plants

$$LA = 177.11\, e^{x\,0.036} \quad r^2 = 0.99^{***} \quad n = 6 \quad x : total\ biomass (g)$$
$$(12)$$

shaded plants

$$LA = 21.71\, x^{1.13} \quad r^2 = 0.96^{***} \quad n = 7 \quad x : total\ biomass (g)$$
$$(13)$$

To take into account the variation in LA between S1 and S3 for *R. section Fruticosi* and *P. aquilinum*, we made one measurement in mid-summer and another in late summer.

## 2.7 Data analysis

All data were analysed with R software ® (R Development Core Team 2013). In accordance with the experimental plan, the effects of radiation levels, REW levels and species identity on transpiration were tested by nested analysis of variance (ANOVA). The species factor was nested in the REW factor, itself nested in the radiation factor. The time factor (sessions, day of measurements) in the ANOVA was considered as a pseudoreplication (repeated measurements from the same individual). When a result was significant, modalities were compared by a Tukey test. Model postulates (normality,

homoscedasticity) were checked by graphic validation. If postulates were not respected, data were transformed (square root, logarithmic and arctangent of square root). Allometric relations and relations between transpiration and VPD or times were established with linear and non-linear models. The best-model fit was selected on the $r^2$ value when the model was significant. All tests were carried out with a 5 % error risk.

# 3 Results

## 3.1 Climate demand and drought stress undergone by plants

On average, the daylight temperatures were 30 % higher in the greenhouse than outdoors at 30±8 °C during sessions S1 and S2 and 25±9 °C during session S3. In the greenhouse, there was no significant difference in mean daylight temperature between 20 % PAR and 70 % PAR. PET$_{Turc}$ was 2.3 to 2.6 times higher in 70 % than 20 % PAR, and was halved between the first two sessions and the third session (Table 1).

As a whole, $\Psi_p$ was more negative for the 20 % REW level, confirming that our water supplies were adequate (Fig. 1). Unlike *P. aquilinum*, the three other plants reached wilting point or lower $\Psi_p$ values for the 20 % REW level, (Fig. 1a–d). During S1, conditions were not sufficient to reach a low $\Psi_p$, and no difference was observed between the three levels of REW (Fig. 1e). By contrast, for S2 and S3, plants showed a gradual decrease in $\Psi_p$ in relation to watering regime: $\Psi_p$ was close to zero (−0.2±0.1 MPa) at the 100 % REW level, intermediate (−0.6±0.5 MPa) at the 40 % REW level, and lowest (−1.9±1.2 MPa) at the 20 % REW level (Fig. 1f, g).

## 3.2 Plant leaf area

In general, *P. aquilinum* always showed the highest LA per pot, followed by *R. sect. Fruticosi*, and *M. caerulea*, which had similar leaf areas, and *C. vulgaris* with the lowest value (comparison of species for the same modality, Table 2). Only *P. aquilinum* showed a decrease

in LA with increasing radiation ($P<0.001$). On average, the LA of *P. aquilinum* was three times higher under 20 % than under 100 % available solar radiation. Soil water depletion had no effect on LA in any of the species studied here, but the REW modalities were applied only for short periods.

## 3.3 Effect of radiation and soil water content on transpiration

Generally, transpiration decreased when radiation level decreased, and there were significant effects of soil water depletion and species identity nested in radiation levels (Table 3). On average for all species and REW levels, transpiration was 1.2 times lower at 20 % than at 70 % radiation. We note that transpiration measured outdoors was 2.5 times higher than in the greenhouse.

Species showed different transpirations and sensitivities to REW and radiation levels (Table 4). On average for all radiation and REW levels, transpiration of *C. vulgaris* was 2.5, 3.0 and 4.6 times higher than those of *R. sect. Fruticosi*, *M. caerulea* and *P. aquilinum*, respectively. Conversely, *P. aquilinum* often showed the lowest transpiration for a modality. *R. sect. Fruticosi* and *M. caerulea* showed intermediate and similar transpiration in most modalities. Except for *C. vulgaris* and during the first measurement session (S1) where conditions were not sufficient to reach a low $\Psi_p$ (Fig. 1e), transpiration fell significantly and gradually from 100 % to 40 % and 20 % REW (Table 4). On average for all radiation levels, transpiration of *R. sect. Fruticosi*, *M. caerulea* and *P. aquilinum* was divided by 3.4, 2.8 and 2.2, respectively, from 100 % to 20 % REW. Under 20 % PAR and for all species, the coefficient of transpiration reduction from 100 % to 20 % REW was lower than under 70 % PAR. Conversely, *C. vulgaris* transpiration showed few significant differences between REW and radiation levels within a measurement session compared with the three other species.

Under the 20 % REW level, *M. caerulea* transpired significantly more in shaded than in illuminated conditions (S1 and S2, Table 4). At the end of the summer (S3), climatic water demand decreased (Table 1) leading to a concomitant decrease in transpiration (Fig. 2).

## 3.4 Responses of species relative to VPD in interaction with soil water depletion

At field capacity, transpiration by *R. sect. Fruticosi* and *P. aquilinum* fitted a humped model relative to VPD, and peaked at 2.6 and 2.8 kPa, respectively (Fig. 3a). Transpiration by *M. caerulea* and *C. vulgaris* increased linearly with VPD between 0.8 and 3.6 kPa (Fig. 3a). When soil water content became limited (Fig. 3b),

**Table 1** Potential evapotranspiration (PET$_{Turc}$; average ± SD in mm) during the three sessions. Upper and lower case letters indicate statistically significant differences between sessions and between radiation modalities, respectively [analysis of variance (ANOVA), $P<0.05$]

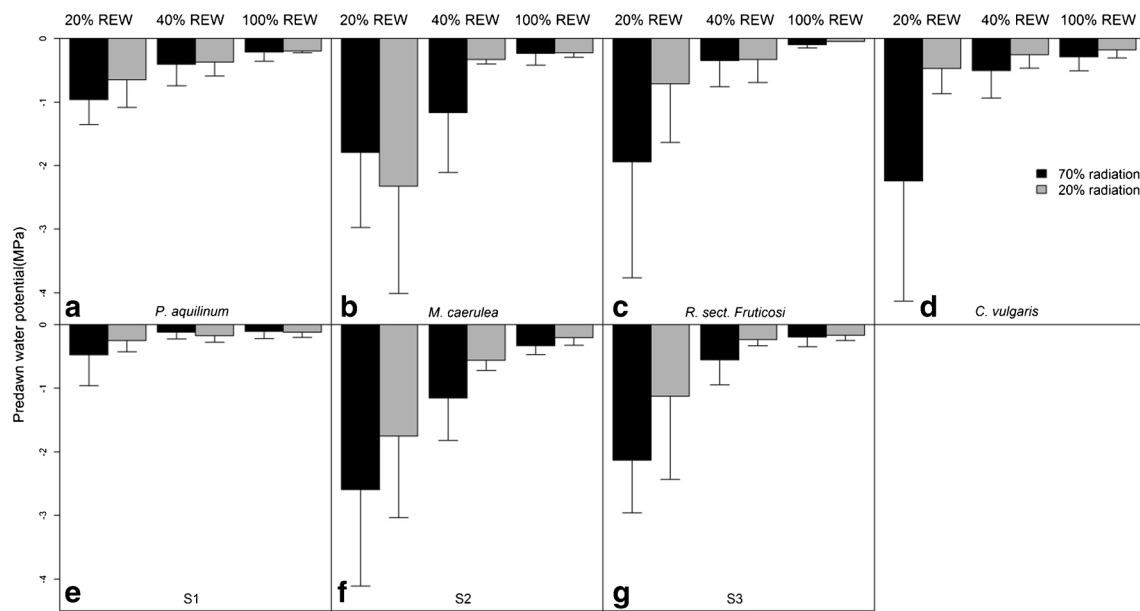|  | Session 1 | Session 2 | Session 3 |
|---|---|---|---|
| 70 % radiation | 3.9±0.9 (a)A | 4.2±0.5 (a)A | 2.1±0.7 (a)B |
| 20 % radiation | 1.5±0.3 (b)A | 1.6±0.1 (b)A | 0.9±0.2 (b)B |

**Fig. 1** Average (± SD, $n$=3) predawn leaf water potential relative to watering regime per species (all sessions together). **a** *Pteridium aquilinum*; **b** *Molinia caerulea*; **c** *Rubus sect. Fruticosi*; **d** *Calluna vulgaris*, and per session for all species **e** S1, **f** S2, **g** S3 under 20 % radiation (*grey*) and 70 % radiation (*black*)

*M. caerulea* and *C. vulgaris* showed a shift in response curves to VPD. Transpiration by *C. vulgaris* fitted a humped model relative to VPD, peaking at 2.3 kPa (2.1 mm day$^{-1}$ m$^{-2}$ LA). Transpiration by *M. caerulea* did not exceed 0.5 mm day$^{-1}$ m$^{-2}$ LA (on average) and did not show any relation with VPD. *R. sect. Fruticosi* and *P. aquilinum* still fitted a humped model relative to VPD, but the amplitude of transpiration was reduced by 62 % and 34 %, respectively (Fig. 3b).

The negative effect of soil water depletion on transpiration response to VPD increased with increasing VPD (up to a VPD of 3.1 kPa), again except for *C. vulgaris*, which seemed insensitive (Fig. 4). Soil water depletion had little influence on plant transpiration when VPD was low.

## 4 Discussion

### 4.1 Comparison of transpiration between species

*C. vulgaris* showed higher transpiration per unit LA (mm day$^{-1}$ m$^{-2}$ LA) than the three other species (*C. vulgaris*>*M. caerulea*=*R. sect. Fruticosi*>*P. aquilinum*, Table 4). These results support our first hypothesis: transpiration was dramatically different between the four studied species: transpiration of forest understorey vegetation depends on species identity and vegetation composition. Gordon et al. (1999b) also found that *C. vulgaris* consumed more water than *P. aquilinum*. Transpiration of *M. caerulea* was lower than that of *C. vulgaris*, but higher than that of *P. aquilinum* (Table 4). These results are in line with those of Loustau and

**Table 2** Leaf area (LA; average±SD in m$^2$ per pot) of the four species under different levels of relative extractable water (REW) and radiation. Lowercase and uppercase letters indicate statistically significant differences between modalities for a species and between species for the same modality, respectively (ANOVA, $P$<0.05). Outdoors treatment was not included in the analysis

|                | | Pteridium aquilinum | Rubus sect. Fruticosi | Molinia caerulea | Calluna vulgaris |
|----------------|-----------|---------------------|-----------------------|------------------|------------------|
| 70 % radiation | 100 % REW | 0.49±0.13 (abc)A | 0.34±0.05 (a)B | 0.27±0.05 (a)BC | 0.16±0.11 (a)C |
|                | 40 % REW | 0.39±0.12 (bc)A | 0.30±0.05 (ab)AB | 0.26±0.06 (a)B | 0.10±0.06 (a)C |
|                | 20 % REW | 0.33±0.09 (c)A | 0.29±0.02 (ab)A | 0.25±0.06 (a)A | 0.11±0.07 (a)B |
| 20 % radiation | 100 % REW | 0.72±0.22 (a)A | 0.33±0.11 (ab)B | 0.24±0.06 (a)B | 0.09±0.03 (a)C |
|                | 40 % REW | 0.64±0.14 (a)A | 0.28±0.05 (ab)B | 0.27±0.08 (a)B | 0.07±0.04 (a)C |
|                | 20 % REW | 0.58±0.19 (ab)A | 0.25±0.02 (b)B | 0.20±0.05 (a)B | 0.12±0.06 (a)C |
| Outdoors       | 100 % REW | 0.23±0.15 | 0.29±0.07 | 0.20±0.07 | 0.07±0.01 |

**Table 3** Results of the ANOVA: effects of radiation levels, REW levels and species identity on transpiration ($P<0.05$). Time factor (sessions, day of measurements) was considered as pseudoreplication and the measurements of transpiration outdoors were not taken into account

|  | Df | Sum Sq | Mean Sq | F value | Pr(>F) | |
| --- | --- | --- | --- | --- | --- | --- |
| Radiation levels | 1 | 4.24 | 4.241 | 4.0734 | 0.04373 | * |
| Radiation levels: REW levels | 4 | 117.46 | 29.366 | 28.2078 | <2.20x10-16 | *** |
| Radiation level: REW level: species | 18 | 643.6 | 35.756 | 34.3452 | <2.20x10-16 | *** |
| Residuals | 1624 | 1690.69 | 1.041 | | | |

Cochard (1991) and Roberts et al. (1980), who give *M. caerulea* transpiration at 0.89 mm day$^{-1}$ (LAI of 1.2 in *Pinus pinaster* stands) and *P. aquilinum* transpiration at 0.51 mm day$^{-1}$ (LAI of 1.1 in *Pinus sylvestris* L. stands), respectively, despite different environmental conditions between these two studies. Like *M. caerulea*, *R. sect. Fruticosi* transpiration also lay between those of *C. vulgaris* and *P. aquilinum* (Table 4). *R. sect. Fruticosi* transpiration under 100 % radiation and 100 % REW conditions was 2.4 mm day$^{-1}$ m$^{-2}$ LA, and comparable to the transpiration of *Rubus idaeus* L. (2 mm day$^{-1}$ m$^{-2}$ LA) measured by Neocleous and Vasilakakis (2007).

## 4.2 Specific species responses relative to REW and VPD

In line with the second hypothesis, transpiration response to REW and VPD levels presented quite different patterns between the four species. *C. vulgaris* tended to emerge as a water spender with little or no regulation of transpiration relative to REW and VPD levels. Unlike *C. vulgaris* and consistent with the findings of Fotelli et al. (2001), *R. sect. Fruticosi* strongly regulated its transpiration rate according to both REW and VPD levels. *P. aquilinum* was more sensitive to VPD than soil water depletion, whereas *M. caerulea* responded more to soil water depletion than VPD.

**Table 4** Species transpiration [average±SD in mm day$^{-1}$ m$^{-2}$ leaf area (LA)] for the different modalities of radiation and REW levels and the three sessions. Lower case and upper case letters indicate statistically significant difference between modalities for the same session and between species for the same modality, respectively (ANOVA, $P<0.05$). Outdoors treatment was not included in the analysis

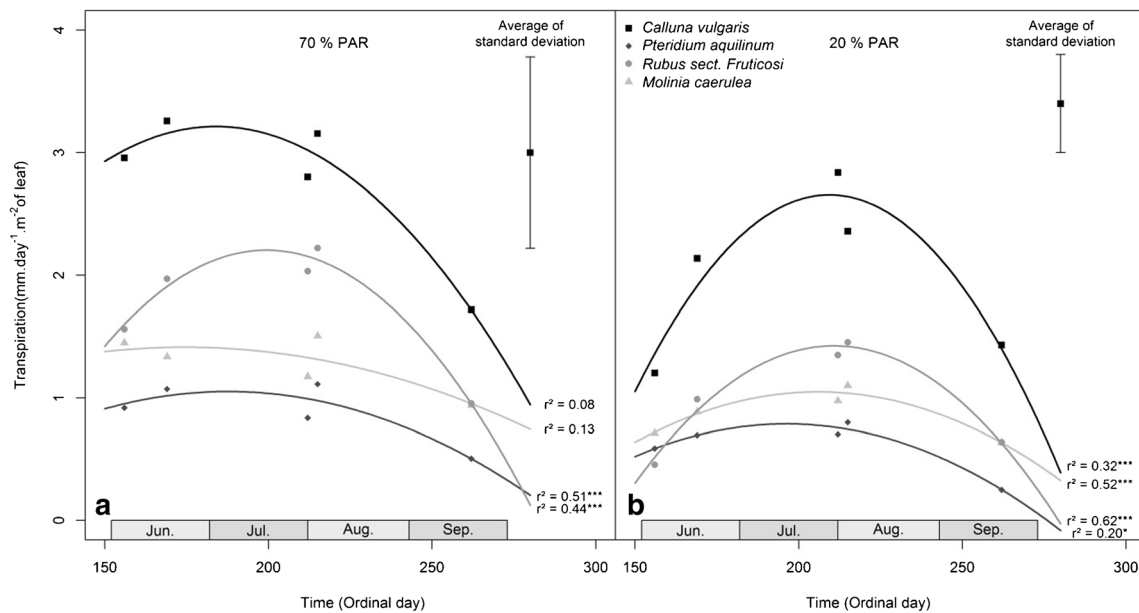| | | | *Calluna vulgaris* | *Molinia caerulea* | *Rubus sect. Fruticosi* | *Pteridium aquilinum* |
| --- | --- | --- | --- | --- | --- | --- |
| S1 | 70 % radiation | 100 % REW | 2.8±2.4 (a)A | 1.2±0.4 (a)B | 2.0±0.8 (a)A | 0.8±0.3 (a)B |
| | | 40 % REW | 3.7±2.7 (a)A | 1.0±0.3 (ab)B | 1.2±0.7 (b)B | 0.5±0.2 (b)C |
| | | 20 % REW | 2.6±2.2 (a)A | 0.5±0.3 (c)C | 1.2±0.7 (b)B | 0.5±0.3 (b)C |
| | 20 % radiation | 100 % REW | 2.8±2.2 (a)A | 1.0±0.4 (ab)B | 1.4±0.8 (b)B | 0.7±0.7 (a)B |
| | | 40 % REW | 2.5±1.9 (a)A | 0.9±0.6 (ab)B | 1.1±0.5 (b)B | 0.5±0.3 (b)C |
| | | 20 % REW | 2.8±4.7 (a)A | 0.8±0.3 (b)B | 0.9±0.5 (b)B | 0.4±0.3 (b)C |
| | Outdoors | 100 % REW | 4.4±1.5 | 1.4±1.3 | 2.4±0.6 | 2.3±1.6 |
| S2 | 70 % radiation | 100 % REW | 3.2±2.3 (a)A | 1.5±0.4 (a)B | 2.2±0.7 (a)A | 1.1±0.3 (a)B |
| | | 40 % REW | 2.9±2.2 (a)A | 0.7±0.3 (cd)B | 0.8±0.4 (c)B | 0.4±0.3 (cd)B |
| | | 20 % REW | 1.5±1.7 (b)A | 0.3±0.2 (e)C | 0.3±0.3 (d)C | 0.5±0.2 (bc)B |
| | 20 % radiation | 100 % REW | 2.4±0.9 (ab)A | 1.1±0.3 (ab)BC | 1.5±0.7 (b)B | 0.8±0.6 (b)C |
| | | 40 % REW | 2.4±1.4 (ab)A | 0.8±0.6 (bc)B | 0.8±0.4 (c)B | 0.4±0.2 (cd)C |
| | | 20 % REW | 1.6±0.8 (ab)A | 0.5±0.4 (d)B | 0.4±0.4 (d)BC | 0.2±0.2 (cd)C |
| | Outdoors | 100 % REW | 4.4±1.1 | 1.9±0.6 | 2.4±0.8 | 2.4±1.1 |
| S3 | 70 % radiation | 100 % REW | 1.7±1.7 (a)A | 0.9±0.3 (a)A | 1.0±0.4 (a)A | 0.5±0.2 (a)B |
| | | 40 % REW | 1.6±2.0 (ab)A | 0.5±0.2 (bc)B | 0.5±0.4 (b)B | 0.3±0.2 (b)B |
| | | 20 % REW | 0.7±0.9 (ab)A | 0.3±0.2 (cd)AB | 0.2±0.3 (c)B | 0.2±0.2 (bc)B |
| | 20 % radiation | 100 % REW | 1.4±1.4 (ab)A | 0.6±0.3 (b)B | 0.6±0.6 (b)B | 0.2±0.2 (bc)B |
| | | 40 % REW | 1.1±0.9 (ab)A | 0.5±0.3 (bc)B | 0.4±0.3 (bc)BC | 0.2±0.1 (bc)C |
| | | 20 % REW | 0.5±0.6 (b)A | 0.2±0.2 (d)AB | 0.4±0.4 (bc)AB | 0.2±0.2 (c)B |

**Fig. 2** Transpiration (average in mm day$^{-1}$ m$^{-2}$ LA, $n$=8) for the three sessions at 100 % REW under **a** 70 % and **b** 20 % incident radiation for the four species studied (*black squares C. vulgaris, dark grey diamonds* *P. aquilinum, grey circles Rubus sect. Fruticosi, light grey triangles M. caerulea*). Performances of the models are expressed by $r^2$ and $P$ value: ***<0.001, **<0.01, *<0.05

*C. vulgaris* transpiration increased linearly with VPD, suggesting that a peak of transpiration could be reached at a VPD over 4 kPa under non-limiting soil water content (Fig. 3a). However, under the 20 % REW level, *C. vulgaris* fitted a humped model, but with a relatively high transpiration at a VPD of 2.3 kPa compared with the other species (about 2 mm day$^{-1}$ m$^{-2}$ of LA). The transpiration response of *Gaultheria shallon* Pursh (another heather) to VPD also fitted a humped model, but its transpiration peaked at a lower VPD

than *C. vulgaris* (Tan et al. 1978). The general resistance of *C. vulgaris* to drought could be linked to the sclerophyllous nature of its leaves (Gordon et al. 1999a).

*M. caerulea*, like most graminoids, has morphological and physiological plasticity (Aerts et al. 1991; Taylor et al. 2001), e.g. leaf rolling to reduce transpiration (Renard and Demessemacker 1983). *M. caerulea* also has a low shoot:root ratio, with a dense fasciculated root system and high water uptake efficiency (Aerts et al. 1991; Coll et al. 2003). Its
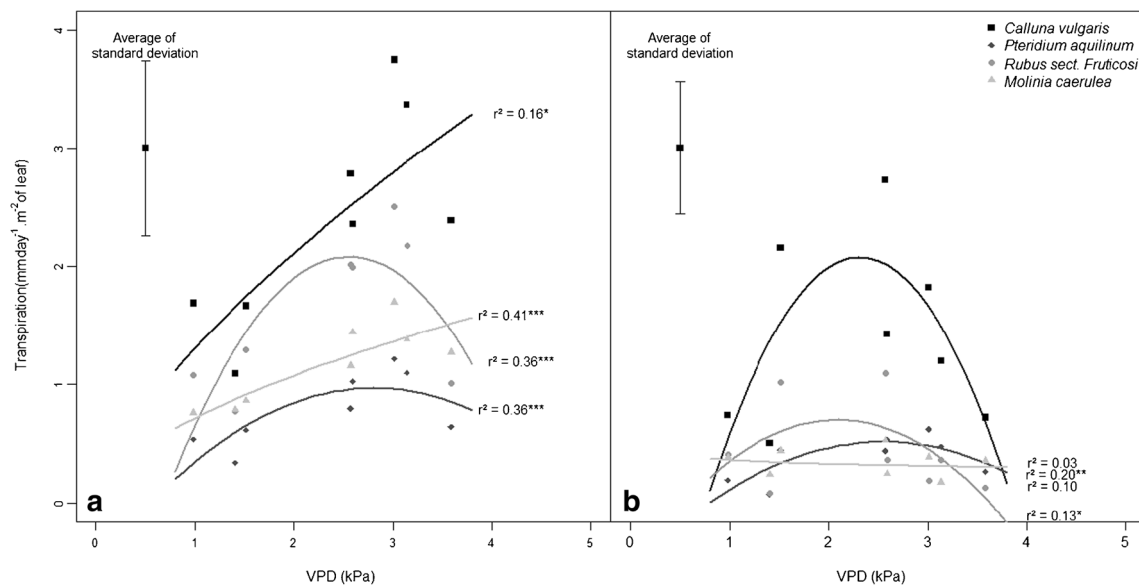


**Fig. 3** Transpiration (average in mm day$^{-1}$ m$^{-2}$ LA, $n$=8) under 70 % radiation as a function of VPD at **a** 100 % REW and **b** 20 % REW for the four species studied (symbols as in Fig. 2). Performances of the models was expressed by $r^2$ and $P$ value: ***<0.001, **<0.01, *<0.05

transpiration response to VPD changed from a linear increase at soil water field capacity to no response under the 20 % REW level (Fig. 3b). The pattern change is also consistent with a $\Psi_p$ close to −2 MPa in a soil water depletion condition at the end of the measurement session, i.e. a relatively negative water potential, but without plant damage, indicating stomatal closure before any dramatic loss in water conductivity. Loustau and Cochard (1991) report that stomatal conductance by *M. caerulea* stays insensitive to VPD when it is lower than 3 kPa. Other studies have shown that *M. caerulea* decreases stomatal conductance exponentially with VPD over 1 kPa by closing their stomata (Otieno et al. 2012). According to several authors (Roberts et al. 1984; Waring and Schlesinger 1985; Wherley and Sinclair 2009), stomatal conductance decreases when VPD increases.

According to Roberts et al. (1980), stomatal conductance by *P. aquilinum* is mildly sensitive to VPD, in contrast to SWC (Hollinger 1987). Thus, the $\Psi_p$ of *P. aquilinum* never fell below −1 MPa (Fig. 1a). Hollinger (1987) and Marrs and Watt (2006) claim that *P. aquilinum* is relatively drought-tolerant owing to its thick cuticle and pinnae rigidity. *P. aquilinum* also has the ability to store up to 6 mm water in the rhizome (Smith 1986 cited in Gordon et al. 1999b). During a drought, *P. aquilinum* is able to increase its water use efficiency, unlike *C. vulgaris*, which continues to consume a lot of water (Gordon et al. 1999b). Despite these traits, *P. aquilinum* still showed signs of wilting at low $\Psi_p$, possibly due to in greenhouse temperatures, as *P. aquilinum* is not thought to tolerate high temperature (Marrs and Watt 2006; Miller and Gates 1967).

Iida et al. (2009) showed that the VPD below the tree canopy was the main factor controlling understorey transpiration.
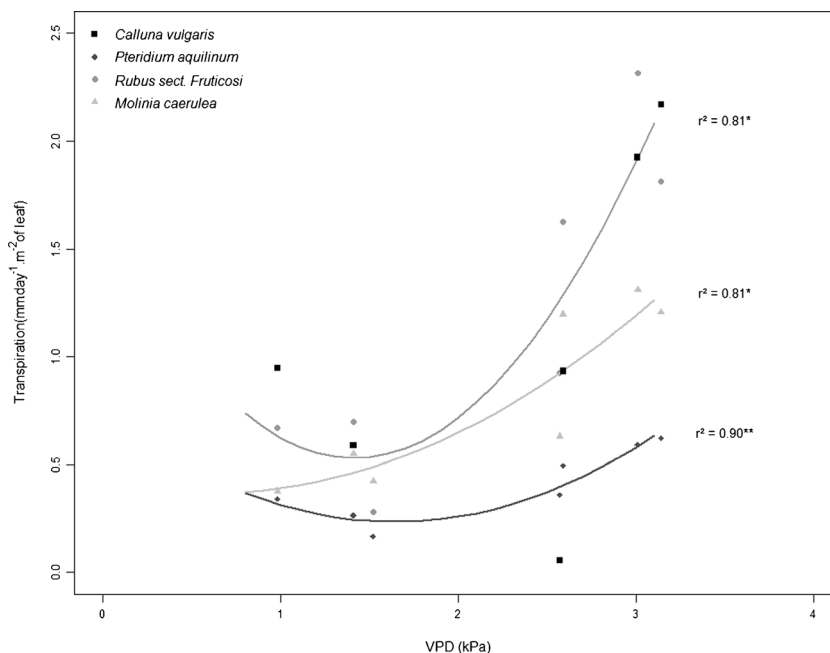
Transpiration by understorey species appeared more sensitive to VPD than SWC, the difference between the highest transpiration and the lowest transpiration along the VPD gradient or between 100 % and 20 % REW being almost twice higher (mean=1.8) for VPD than for REW levels (Fig. 4).

Importantly, the VPD gradient was not obtained at a constant temperature. VPD and temperature were positively correlated, which means that any decrease of transpiration at high VPD could be linked or co-linked to a temperature inhibition effect. The decrease in transpiration at high VPD could not be linked to a water deficit problem but to a too-high temperature (supra-optimal) for many physiological processes (and particularly photosynthesis), leading to a decrease in transpiration. According to Marrs and Watt (2006), the temperature optimum for *P. aquilinum* ranges between 10 °C and 25 °C. When temperatures exceed this optimum, the decrease in transpiration could depend on a temperature stress rather than a direct VPD effect. Temperature stress could partly explain the transpiration responses of *R. sect. Fruticosi*, and *P. aquilinum* in a humped model relative to VPD without soil water depletion (Fig. 3a).

### 4.3 Responses of species to radiation levels

Radiation level had effects on transpiration (Table 3). For *R. sect. Fruticosi*, *M. caerulea* and *P. aquilinum*, transpiration increased with increasing radiation. In general, radiation drives temperature and air relative humidity (Barbier et al. 2008). However, under our greenhouse conditions, we recorded similar average temperature and air relative humidity between the two radiation levels. The climatic demand expressed by $PET_{Turc}$ was significantly lower at 20 % than



**Fig. 4** Difference between transpiration (average in mm day$^{-1}$ m$^{-2}$ LA) at 100 % REW and at 20 % REW under 70 % radiation as a function of VPD (0.8−3.1 kPa) for the four species studied (symbols as in Fig. 2). Performances of the models was expressed by $r^2$ and *P*-value: *** <0.001, ** <0.01, * <0.05. We found no significant model fit for *C. vulgaris*

at 70 % radiation (Table 1) as PET$_{Turc}$ was nevertheless calculated from radiation. However, we note that the interpretation of PET effects is not totally independent of the calculation method. For example, PET calculated by the Thornthwaite (1948) method based only on temperature would not have shown a difference between radiation levels. Conversely, the Penman-Monteith (Monteith 1965) method based on aerodynamics and energy balance would have shown more significant differences between radiation levels. In true forest conditions, shading, together with lower temperature and higher relative humidity, would be likely to reduce understorey vegetation transpiration even further. Our results support the third hypothesis, i.e. that shade conditions reduce understorey vegetation transpiration, and the intensity of the negative effect of soil water depletion on transpiration.

### 4.4 Implications for forest water balance

Species identity and the composition of the understorey vegetation could change the contribution of understorey vegetation to total stand ET and competition with trees for water.

High SWC and understorey VPD could prevail in forests at the beginning of the growth season when the tree canopy, particularly that of deciduous trees, has a low LAI. During this period, understorey vegetation transpiration will peak (Bréda and Peiffer 1999; Iida et al. 2009; Wilson et al. 2000), exacerbating the risk of water shortage for the rest of the growing season, especially for *C. vulgaris* and *M. caerulea*, which rapidly increase their transpiration with increasing VPD when soil water is not limited (Fig. 3a).

Despite an REW less than 40 %, all four understorey species studied here continued to transpire, and the transpiration rate of *C. vulgaris* evolved little or not at all with the REW level (Table 4). Also, the understorey species *P. aquilinum* and *M. caerulea* have been reported as less sensitive to high VPD than trees (Diawara et al. 1991; Hollinger 1987; Roberts et al.

1984). These results suggest that the prime contribution to total stand ET could be the understorey vegetation when trees adjust their transpiration during drought periods (Hamada et al. 2004; Jarosz et al. 2008; Lüttschwager et al. 1999; Roberts et al. 1980). For example, the transpiration of *Gaultheria shallon* represented on average 45 % of total stand ET (*Pseudotsuga menziessii* stand) and up to 70 % under drought conditions (Tan et al. 1978).

Few studies have measured the maximum daily transpiration in trees per unit LA. Here, in optimal conditions (100 % radiation at field capacity), the average transpiration of the four species was 2.8±1.2 mm day$^{-1}$ m$^{-2}$ LA, higher than the transpiration of some trees (Table 5).

Besides the transpiration patterns of species, the forest water balance should include the ability of understorey vegetation to form a dense cover. According to some authors, the LAI of understorey vegetation represents a large share of whole-stand LAI, and often equals or surpasses the LAI of overstorey (tree) vegetation (Blanken et al. 1997; Gonzalez et al. 2013; Hamada et al. 2004; Iida et al. 2009). The cover of understorey vegetation, and in particular the four species used in this experiment, may prove very large with high LAs, even under shade conditions (Balandier et al. 2013; Gaudio et al. 2011). For example, *M. caerulea*, *P. aquilinum* and *C. vulgaris* showed a cover higher than 75 % at only 20 % PAR (Gaudio et al. 2011) and *R. sect. Fruticosi* can reach a cover of 43 % below 20 % PAR (Balandier et al. 2013). Under these conditions, the high LAI and transpiration of understorey species can explain the large contribution of understorey to whole-stand ET.

## 5 Conclusion

The four species studied here did not show the same response to soil water depletion and VPD. Our findings extend current

**Table 5** Maximum recorded daily transpiration of tree per unit LA. Methods used were either weighing lysimeters and large-tree potometers (L/P) or thermal balance and heat dissipation methods (TM)

| Species | Method | Height (m) | Diameter (cm) | LA (m$^2$) | Water use (kg day$^{-1}$) | Transpiration per leaf area (mm day$^{-1}$ m$^{-2}$ LA) | References[a] |
|---|---|---|---|---|---|---|---|
| *Abies amabilis* | TM | 18 | 40 | 151 | 98 | 0.6 | Martin et al. (1997) |
| *Picea abies* | TM | 25 | 36 | 447 | 175 | 0.4 | Herzog et al. (1995) |
| *Pinus radiata* | L/P | 6 | \ | 265 | 150 | 0.6 | Edwards (1986) |
| *Pinus radiata* | TM | 25 | 42 | 300 | 349 | 1.2 | Teskey and Sheriff (1996) |
| *Populus x euramericana* | L/P | 5 | \ | 26 | 109 | 4.2 | Edwards (1986) |
| *Salix fragilis* | TM | \ | \ | 42.5 | 103 | 2.4 | Èermák et al. (1984) |
| *Salix matsudana* | L/P | 5 | \ | 28 | 106 | 3.8 | Edwards (1986) |

[a] All literature data cited in Wullschleger et al. (1998)

knowledge on transpiration by understorey species, and highlight the importance of integrating understorey species identity and water use in addition to understorey LAI into forest ecosystem ET models exploring water balance.

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