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Water use of young maritime pine and *Eucalyptus* stands in response to climatic drying in south-western France

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Background: There is increasing interest in developing eucalypt stands in France for biomass energy, but the water requirements of eucalypt coppice are largely unknown.
Aims: We assessed the water use and growth of two 5-year-old managed forest stands: an indigenous maritime pine stand and an introduced eucalypt stand.
Methods: We used a combination of meteorological, sap flow, soil and biomass measurements, between September 2009 and July 2011.
Results: The stand structure was the main driver of both water use and its partitioning between water balance components in each site. The evapotranspiration was high in the eucalypt stand, with a significant contribution of tree transpiration due to high leaf area index of the tree canopy. Under well-watered conditions, both species exhibited a similar stomatal behaviour in relation to vapour pressure deficit and, with high biomass production, the two stands presented a maximal water use efficiency in respect to their local environments and constraints. However, they experienced significant sensitivity to successive early spring and summer droughts. The unexpected prolonged soil water deficit in the eucalypt stand, induced by high water consumption and insufficient water supply, directly impacted leaf shedding and stem secondary growth. In contrast, the pines appeared conservative with respect to soil water deficits and maintained secondary growth.

Keywords: biomass production; drought; *Eucalyptus*; *Pinus pinaster*; transpiration; water deficit; water use

Introduction

Biomass will be increasingly used to meet future renewable energy requirements (IPCC 2011). To meet this growing demand for wood energy, the main management strategies being considered for southern Europe are short (10-year) and very short (< 5-year) rotation eucalypt coppice, and fast-growing coniferous plantations. Indeed, there is increasing interest in developing new forest crop systems in France for biomass energy and to secure the raw material supply to the existing forest industry (Lesgourgues and Drouineau 2009). Indigenous species, e.g. maritime pine (*Pinus pinaster* Aït.)*,* as well as exotic tree species, e.g. species of *Eucalyptus,* are putative species being considered for these purposes. However, the latest IPCC report (IPCC 2007) predicts that southern Europe is likely to experience increased temperatures and reduced precipitation. Climate models consistently forecast an increase in the frequency of summer drought (Déqué 2007; Déqué and Cloppet 2010; Giannakopoulos et al. 2009). Within this climatic context, the impact of new agro-systems on water resources is a major issue. Furthermore, these intensified forest management alternatives are being considered for afforestation or reforestation of large areas that have been damaged by windstorms or fires, and are expected to require significant inputs of resources such as water and

nutrients. However, little is known about the behaviour of these potential replacement species, especially under future climatic and water availability constraints.

Rapid growth of eucalypt trees in Mediterranean-type climates is associated with high water consumption which is mainly derived from winter soil moisture recharge (Pereira De Almeida and Riekerk 1990; Silberstein et al. 2001). In water-limited areas, high rates of water use could lead to the depletion of the water resource, and large-scale afforestation is likely to have significant impacts on streamflow (Jackson et al. 2005). Currently there are no published data that detail the water balance of eucalypt stands at high latitudes. However, there is increasing concern regarding the potential environmental impacts of expanding eucalypt plantations to meet increasing demands for biomass energy at these latitudes (Hardcastle 2006; Leslie et al. 2012). In France, the research that has been conducted into eucalypts has mostly focused on frost tolerance (Lacaze 1962; Cauvin and Potts 1991). In southern France, ca. 1500–2000 ha of a first-generation hybrid of *E. gunnii* Hook. and *E. dalrympleana* Maiden have been planted in the last decade. The parent species are native to the Australian Alps of New South Wales and Victoria, and Tasmania's Central Plateau. Several clones of this hybrid were produced, among which clone N° 821290 is the most

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attractive in terms of productivity and exhibits good frost tolerance. *E. gunnii × dalrympleana* has been successfully planted for almost 30 years in the south-west of France for pulp production, and is now being promoted for its potential to produce biomass for energy production purposes (Melun and Nguyen-The 2006), despite a lack of data on their growth and water use in this area.

Maritime pine is the most widely planted tree species in the forests of south-western Europe (IEFC 2002), for example in the one-million hectare 'Landes de Gascogne' forest that was established more than 150 years ago. The hydrological behaviour of maritime pine has been widely studied (Berbigier et al. 1991, 2001; Granier and Loustau 1994; Delzon and Loustau 2005; Jarosz et al. 2008; Stella et al. 2009; Moreaux et al. 2011). Across this region, annual evaporative demand (Penman's PET: 600–700 mm year^{-1}) is lower than the annual rainfall (750–1150 mm year^{-1}). However, given the uneven seasonal distribution of precipitation, forest stands regularly experience water stress, especially during summer when the imbalance between rainfall and potential evapotranspiration is estimated to be 120 mm, which is larger than the mean value of soil water holding capacity of 60–110 mm (Choisnel et al. 1987).

The present study focused on the water use and growth of two 5-year-old stands (in 2009) with similar stocking densities and growing under similar climatic conditions. The first stand was an exogenous eucalypt stand (*E. gunnii × dalrympleana*) and the second a native maritime pine stand. Experiments were carried out in parallel from January 2010 over 18 months that included an unprecedented drought in the spring of 2011. We addressed the following questions:

- What is the annual and seasonal water use in the eucalypt stand and how is evapotranspiration partitioned among the stand compartments? To what extent does this water use converge or diverge with the indigenous pine stands taking into account differences in environmental conditions?

- How is water use controlled in a young eucalypt stand?
- How does *E. gunnii × dalrympleana* perform with respect to water use and growth under conditions of successive droughts that might be expected to occur in Southern France?

Material and methods

Study sites

The eucalypt plantation was located in the Midi-Pyrenees region, at Montbartier, France (43° 54′ 03.22″ N; 1° 17′ 25.17″ E, altitude: 137 m, Table 1). The climate is a degraded oceanic climate type with a mean (± std) annual rainfall of 725 ± 98 mm and a mean annual temperature of 13.4 ± 0.5 °C (data for the long-term average 1993–2007, obtained from SAFRAN grid point of 8 × 8 km^2 resolution that overlaps the Montbartier site, Vidal et al. 2010). The soils of the Montbartier region are acidic and hydromorphic luvisol-redoxisol (Baize and Girard 2008) in which the mean texture of the top 0.6 m soil is silt–loam, with low fractions of sand and clay. The proportion of clay increases with depth and forms an accumulation layer at a depth of 0.6 m showing redox spots.

The study plot covers 15 ha and was planted with 6-month-old cuttings of *Eucalyptus gunnii × dalrympleana*, clone N° 821290, in October 2004. Fertilisers (150 kg ha^{-1} of P_2O_5) were applied before planting. Trees were planted with a spacing of about 2 m × 4 m (1200 trees ha^{-1}). The understory was controlled for the first 3 years after planting. Typically, these plantations are established for pulp production with rotation lengths of 10 years. In December 2009, the mean height of the trees was 10.2 m with a leaf area index (LAI) of 3.4 m^2 m^{-2} and basal area of 14.5 m^2 ha^{-1} as calculated from inventory data, allometric equations and specific leaf area measurements (init. Melun and init. Nguyen-The, pers. comm.). In 2010, the plot had a homogeneous structure within which

Table 1. Summary of the pine and eucalypt stand characteristics at Bilos and Montbartier sites, respectively. Data are for December 2009, unless specified.

	Bilos	Montbartier
Coordinates	44° 29′ 38.08″ N, 0° 57′ 21.9″ W	43° 54′ 03.22″ N, 1° 17′ 25.17″ E
Altitude (m)	40	137
Tree species	*Pinus pinaster* Aït	*E. gunnii × dalrympleana*
Age (year)*	5.5	5.5
Understory	*Ulex minor* Roth. diverse herbaceous	sparse low grass sparse *Ulex europeaus* L.
Stocking (tree ha^{-1})	1800	1040**
Mean tree LAI (m^2 m^{-2})**	1.15	4.5
Trees		
DBH ± standard deviation (mm) **	51.2 ± 15.7	133 ± 24
H ± standard deviation (m)**	3.19 ± 0.65	15.0 ± 1.5
Basal area (m^2 ha^{-1})**	3.7	14.5
Management (2008–2009)	understory removal (11/09)	–

*in January 2010
**in January 2011

the understory was formed by sparse and low grasses in the inter-row.

The pine plantation at Bilos, France (44° 29′ 38.08″ N; 0° 57′ 22″ W, altitude: 40 m, Table 1) covers 60 ha. The 1993–2007 mean (± std) annual temperature and precipitation were $13.3 ± 0.5$ °C and $917 ± 130$ mm respectively (data obtained from SAFRAN grid point of $8 × 8$ km resolution that overlaps the Bilos site, Vidal et al. 2010). The topography of the stand is flat. The soil is a sandy podzol with a discontinuous layer of iron hard pan at a depth of 0.75 m.

Following clear-cutting in 1999, the site was ploughed to 30 cm depth, fertilised with 60 kg P_2O_5 per ha in 2001, and sown with maritime pine seeds in 2004, tree rows being spaced at 4 m. Measurements of turbulent fluxes of momentum, sensible and latent heat and carbon dioxide using the eddy covariance technique have been made at this site since 2000. In November 2008, the stand (4.5 years old) was thinned and the weedy vegetation cleared so that the soil surface was subsequently covered by woody debris. Weedy vegetation, including gorse and herbaceous plants, re-grew spontaneously and was mechanically destroyed for a second time in November 2009. The LAI was estimated at 1.15 $m^2 m^{-2}$ and the basal area at 3.71 m^2 ha^{-1} in January 2011.

Measurements and models

Meteorological and soil measurements. In the eucalypt stand, an automated meteorological station was installed at 16 m height. Measurements included photosynthetic active radiation, *PAR* (SKY 215; Skye Instruments Limited, Powys, UK) and net radiation, R_n (NR-Lite, Kipp and Zonen, The Netherlands), air temperature, T_a, and relative humidity, *RH* (CS215; Campbell Scientific, Logan, Utah, USA). Incident rainfall, *P* was measured using a tipping bucket rain gauge (SBS500; Campbell Scientific). Wind speed and wind direction were recorded by a wind monitor (RM Young 05103, Campbell Scientific). Soil water content, SWC, was monitored using a network of 14 TDR probes (Time Domain Reflectometry CS616; Campbell Scientific) in three soil profiles: two profiles with sensors at -20, -40, -65, -95 and -130 cm and one profile with probes at -20 ($×2$) -40 and -65 cm. Total water availability of the soil was estimated for the depth of 0–150 cm. Measurements were recorded using a data logger (CR1000; Campbell Scientific, Logan, Utah, USA) at scan rates of 10 s (meteorological and sap flow measurements) or 5 min (SWC), with 30 min averages being recorded.

In the pine stand, the four components of the radiation balance (incident and outgoing shortwave radiations and incident and outgoing longwave radiations, R_g, aR_g, R_a and R_t, respectively) were measured using a net radiometer (CNR4; Kipp & Zonen, The Netherlands). Atmospheric pressure was measured with a CS105 barometric pressure sensor (model PTB101B; Vaisala, Helsinki, Finland). Air temperature and relative humidity were measured at a height of 6 m using a CS215 probe. Precipitation above

the canopy (*P*) was measured with a tipping bucket rain gauge (ARG100; Campbell Scientific, Logan Utah, USA). Wind speed and wind direction were measured by wind monitors (W200P; Vector Instruments, Rhyl, North Wales, United Kingdom). SWC was determined using time domain reflectometry in four pits at six depths: two pits at depths of 15 ($×2$) 30, 45, 60 and 80 cm and two pits at the lower depths of 15 ($×2$), 30 ($×2$), 45 and 60 cm, limited by the presence of a layer of iron pan below. Evapotranspiration, *ET*, was estimated from eddy covariance measurements (see Moreaux et al. 2011). All meteorological data at 6 m were measured every 10 s and half-hourly averages were stored by data loggers (CR1000 and CR23X; Campbell Scientific).

Tree and litterfall measurements. Above-ground biomass including stem wood, bark, branches and leaves, B_t were calculated by using allometric equations. For the eucalypts, we used a relationship specifically developed for this plantation. At the end of 2009, 15 trees covering the height and diameter ranges of the stand were felled and separated into biomass compartments (stem wood, branches and foliage). Allometric equations were then fitted to the observed biomass values:

$$W_i = a_i × \text{DBH}^{b_i} \qquad (1)$$

where, a_i and b_i are parameters, W_i is the biomass of the compartment i (in kg_{DM} tree^{-1}) and DBH is the trunk diameter at the height of 1.30 m (Table 2). We hypothesised that this relation held for the studied period (2010–2011).

A previously established equation was used to estimate the total above-ground biomass for maritime pine (Porté et al. 2000):

$$B_t = 5.395 × 10^{-2} × \text{DBH}^{1.885} × \text{age}^{0.621} \qquad (2)$$

In 2010 and 2011, a 50 m $×$ 50 m plot with 260 eucalypts was inventoried for tree diameter (DBH) and height (*H*). The pine plot inventoried (150 m $×$ 80 m) included 2164 trees for the same measurements.

On the two sites, 20 circular litter traps of 0.716 m^2 area were placed at 20 cm above the herbaceous layer or surface. They were randomly distributed along the tree rows and

Table 2. Parameters of the allometric relations between dry mass (*W*) of each component, *i*, and diameter at breast height (DBH) ($W_i = a_i × \text{DBH}^{b_i}$) DBH is expressed in m and each component biomass in kg_{DM} tree^{-1}. Data were collected from a sample of $n = 15$ trees at 5-year age from the Montbartier site.

Component	a_i (kg.tree^{-1})	b_i	Sum of squares	
			Total	Residual
Foliage	260.6	1.7521	605.1	6.5611
Stemwood	1926.3	2.1646	6355.0	24.3061
Bark	153.9	1.7745	192.9	0.8406
Branch	1276.6	2.4178	1026.0	24.3849
Total B_t	3281.7	2.1143	22527.3	44.3645

inter-rows throughout the stands. The traps were emptied monthly at the eucalypt site, and biweekly in summer and once a month in winter in the pine stand. The dry weight at 65 °C of the foliage and remaining composite fraction (bark, dead branches) were determined separately.

Tree growth. At each site, tree radial growth was monitored by using micro-dendrometers, installed on six trees sampled for sap flow measurements (Table 3). These home-made micro-dendrometers use a high-resolution linear position resistive sensor (RS317-780; Radiospares, France) mounted on a rigid aluminium frame attached to the trunk by two threaded rods. The potentiometer connection avoids considering temperature sensitivities by measuring a resistance ratio. The absolute accuracy of the measurements was estimated at 20 μm. These measurements started at the end of March 2010 on the pine plot.

Sap flow measurement, tree transpiration and water use efficiency. In each stand, tree transpiration was estimated from sap flow measurements on six trees (Table 3). Trees sampled represented the frequency distribution of stem basal area and tree height. The heat dissipation method (Granier 1985, 1987) was used to determine instantaneous sap flow density. The mean sap flow density of the sampled trees was then converted into transpiration (E) using the stocking density and cross sectional area of sapwood at 1.3 m height. Heartwood area was measured on a sample of 10 7-year-old disks of *E. gunnii* × *dalrympleana* cut at 1.3 m height, immersed in water for several hours. It was estimated at 35% of the cross sectional area under bark. The sapwood area for the 5-year-old trees was then extrapolated assuming a constant number of sapwood rings, and a value of 85% of the wood area under bark was obtained. Bark thickness was also estimated at 2 mm at 5 years of age with an increase of 1 mm per year.

Water use efficiency (WUE) was estimated from the annual increment of the above-ground biomass and the annual transpiration measurements described above as their ratio $\Delta B_t \, / \, E$. WUE was estimated using the data collected in this experiment for 2010 and 2011. In addition, we extended this calculation for pine in 2009 using datasets previously reported in Moreaux et al. (2011).

Canopy conductance. At each site, canopy conductance, g_c in m s^{-1}, was estimated from inversion of the Penman–Monteith equation (Equation (3)):

$$\frac{1}{g_c} = \frac{1}{g_a} \cdot \left(\frac{\varepsilon(R_n) + \rho.c_P.g_a \frac{\text{VPD}}{\gamma}}{Tr} - \varepsilon - 1 \right) \qquad (3)$$

Aerodynamic conductance g_a was estimated according to Launiainen (2010) as follows:

$$g_a = \frac{1}{r_a} \quad \text{and} \quad r_a = r_{a,m} + r_b = \frac{\overline{U}}{u^{*2}} + \frac{kB^{-1}}{ku^*} \qquad (4)$$

where:

Tr	W m^{-2}	Transpiration (conversion of the measured transpiration, E)
R_n	W m^{-2}	Net radiation absorbed at canopy level
g_a	m s^{-1}	Aerodynamic conductance
r_a	s m^{-1}	Aerodynamic resistance
$r_{a,m}$	s m^{-1}	Aerodynamic resistance for momentum transfer
r_b	s m^{-1}	Quasi laminar layer resistance
U	m s^{-1}	Horizontal wind speed at measurement height
u^*	m s^{-1}	Friction velocity
k	–	= 0.4, Von Karman constant
kB^{-1}	–	= 2, in the case of forest (Verma 1989)
ε	–	Ratio s/γ
s	Pa K^{-1}	Slope of saturation vapour pressure curve
γ	Pa K^{-1}	= 66, psychrometric constant
ρ	kg m^{-3}	Air density
VPD	Pa	Vapour pressure deficit
c_p	J kg^{-1} K^{-1}	Heat capacity of the air at constant pressure

Assuming a homogeneous canopy, this method is appropriate for relating canopy conductance to climatic and edaphic conditions (e.g. Granier and Loustau 1994; Mielke et al. 1999).

The response of canopy conductance to different meteorological variables (VPD, R_g and T_a) was analysed on a daily basis. The response to soil moisture was also analysed using the soil moisture deficit (SMD), calculated as the ratio of the difference between SWC at field capacity and the actual SWC to available water capacity. We explored these responses using a model of canopy conductance (Equation 5), an adaptation to Jarvis's empirical formulation (Jarvis 1976).

$$g_c = g_{c,\max} \times f(\text{VPD}) \times f(T_a) \times f(\text{SMD}) \times f(PAR) \quad (5)$$

The model was fitted using the data collected from both sites by non-linear regression. This model was parameterised for a subset of data satisfying the following conditions: dry canopy ($P < 0.2$ mm), $R_g > 20$ W m^{-2} and VPD > 0.1 kPa.

Water balance. In the two stands, the water balance at monthly and annual scales was established as follows:

$$\Delta SWC = P - E - I - E_{\text{soil}} - R - D \qquad (6)$$

where ΔSWC represents the change in soil water content on a monthly or seasonal scale. P is the incident rainfall measured above the canopy and E is the tree transpiration deduced from measurements of sap flow density. Rainfall

Table 3.   Initial values of tree dimensions of the individual sampled for sap flow measurements and stem diameter growth at the start of measurements. DBH represents the stem diameter at 1.30 m. Hm and Hs refer to the micro-dendrometer and sap flow probe insertion heights, respectively, and Dm and Ds to the stem diameters at these heights.

Pine	(05/2009)	Micro-dendrometers (04/2010)		Sap flow probes (05/2009)	
Number of the tree	DBH (cm)	Hm (m)	Dm (cm)	Hs (m)	Ds (cm)
1	7.7	1.60	5.9	1.06	7.8
2	2.9	1.05	3.30	0.46	3.9
3	6.5	1.70	5.7	0.77	6.7
4	4.5	1.18	4.6	0.31	6.2
5	5.4	0.95	5.3	0.48	6.2
6	3.3	1.30	3.3	0.59	4.3
Eucalypt	(09/2009)	Micro-dendrometers (09/2009)		Sap flow probes (09/2009)	
Number of the tree	DBH (cm)	Hm (m)	Dm (cm)	Hs (m)	Ds (cm)
1	11.0	–	–	1.29	11.2
2	13.8	0.590	14.9	1.24	14.2
3	10.4	0.658	11.7	1.22	10.7
4	11.5	0.705	12.9	1.19	11.9
5	14.9	0.900	14.8	1.21	15.4
6	12.0	1.185	11.8	1.76	11.4

interception by the crown, I, was not measured on the eucalypt plot. It is very dependent on leaf area (Nizinski and Saugier 1989) and on rainfall intensity. In a number of publications, annual interception by the canopy of eucalypt trees has been found to vary from 10–34% (Whitehead and Beadle 2004). The lowest values recorded correspond to drier climates compared with highest values observed in humid tropical climates. A value of 12% was assumed in this study, based on results obtained in Portugal for *E. globulus* Labill. stands aged from 7–9 years growing under a similar rainfall regime of 700–900 mm (Valente et al. 1997). This value also approximates estimates observed in five natural eucalypt forests in Australia where the rainfall interception by the canopy represented from 13–17% of rainfall (Adams and Attiwill 1991 in Laclau 2001). Interception in the pine plot was measured by using eight systems composed of V-shaped gutters of 2 m in length placed beneath pine crowns and directed into automated rain gauges (Moreaux et al. 2011). Soil evaporation, E_{soil}, was determined using the empirical approach of Penman and Monteith, by determining the energy available at ground level, $R_{n,soil}$, and soil conductance, g_{soil}. $R_{n,soil}$ was deduced from the attenuation of net radiation measured above the canopy according to the Beer–Lambert law. Considering the flat topography of the two sites, surface runoff was not taken into account (see also Pereira De Almeida and Riekerk 1990). In Equation (6) the last term, D, corresponds to the upward or downward movement of water from below the rooting zone. It was assumed to equal the residual of Equation (6) between the sum of the other terms. Positive values of D refer to a downward vertical flow, i.e. the deep drainage, whereas negative values represent an upward capillary rise of water.

Total evapotranspiration, ET, was calculated as the sum of E, I and E_{soil} in the case of the eucalypt plot and was directly measured with eddy covariance

system for the maritime pine stand (see Moreaux et al. 2011). Estimating the contribution of soil evaporation and understory transpiration separately and independently from eddy flux measurements on the pine plot could not be achieved since physical properties for this soil-understory compartment were not measured and using a modelling approach would have increased uncertainty in the final estimation. The reference evapotranspiration, ET_o, estimated from the FAO56-PM equation (Allen et al. 1998) was calculated using site micrometeorological measurements. It defines the potential annual water use in the absence of soil water limitation.

Statistical analysis

Statistical analyses were carried out by using the statistical software SAS 9.2 (SAS Institute Inc., Cary, NC, United States, 2002–2008) using the non-linear regression procedure (NLIN). The best fits were chosen by minimising the sum of squared residuals and assuming a physical/biological consistency. The software R (Faria 2011) was used to fit polynomials for processing sap flow data.

Results

Weather and soil conditions

Mean annual temperature and rainfall for Montbartier and Bilos sites were 12.2 °C and 655 mm and 12.1 °C and 853 mm, respectively. The annual 2010 mean values of VPD, *RH* and R_g were 0.47 kPa, 76% and 4600 MJ m^{-2} respectively, and were similar at both sites. The two sites exhibited a negative anomaly of the mean annual temperature compared with the long-term average of the 1993–2007 period (Figure 1A), explained by an unusually cold winter (January, February and December 2010). Conversely, in April 2010, the two sites displayed a positive

temperature anomaly of $+1.1\ ^{\circ}$C. A negative annual rainfall anomaly was observed at both sites (-75 mm for Bilos and -70 mm at Montbartier). Furthermore, the study period was characterised by enhanced seasonality in rainfall events, compared with the average seasonal pattern (Figure 1B). The pine sites at Bilos experienced a drier spring and summer 2010, with a rainfall deficit of -74 mm and -178 mm, respectively, but this was partly balanced at the annual scale by an excess of $+\ 161$ mm of precipitation during the autumn season. A deficit of rainfall also occurred at the beginning of 2010 at Montbartier (February–May), with a rainfall deficit of -70 mm compared with its long-term average, again, offset at the annual scale by exceptional rainfall events in June 2010 ($+\ 83$ mm). A more pronounced pattern was observed for spring 2011 with a temperature anomaly of $+\ 3^{\circ}$C at both sites in April and a deficit in precipitation between February and May 2011 of -155 mm and -125 mm at the Bilos and Montbartier sites, respectively.

In the pine stand, normalised soil water availability in the rooting zone (0 to -0.8 m) decreased considerably during late spring and summer, reaching values close to zero in August. This period was followed by rapid recharge following autumn rainfall storms in mid-September (Figure 2A). In contrast, the eucalypt stand exhibited a steep increase in SWC in July 2010 due to heavy rainfall followed by an almost continuous decrease for the rest of the studied period. Winter rainfall at this site was not sufficient to replenish the soil water reserves (available water content estimated at 180 mm for the 0–150 m profile) so that a decrease in water content persisted throughout the winter and into the following spring. The SMD of the eucalypt stand was consequently maintained above a value of 0.8 from October 2010 onwards, whereas in the pine plot it became zero in November and during winter (Figure 2B). Unfortunately, the measurements were interrupted at the pine site in February 2011 and resumed only in the following June.
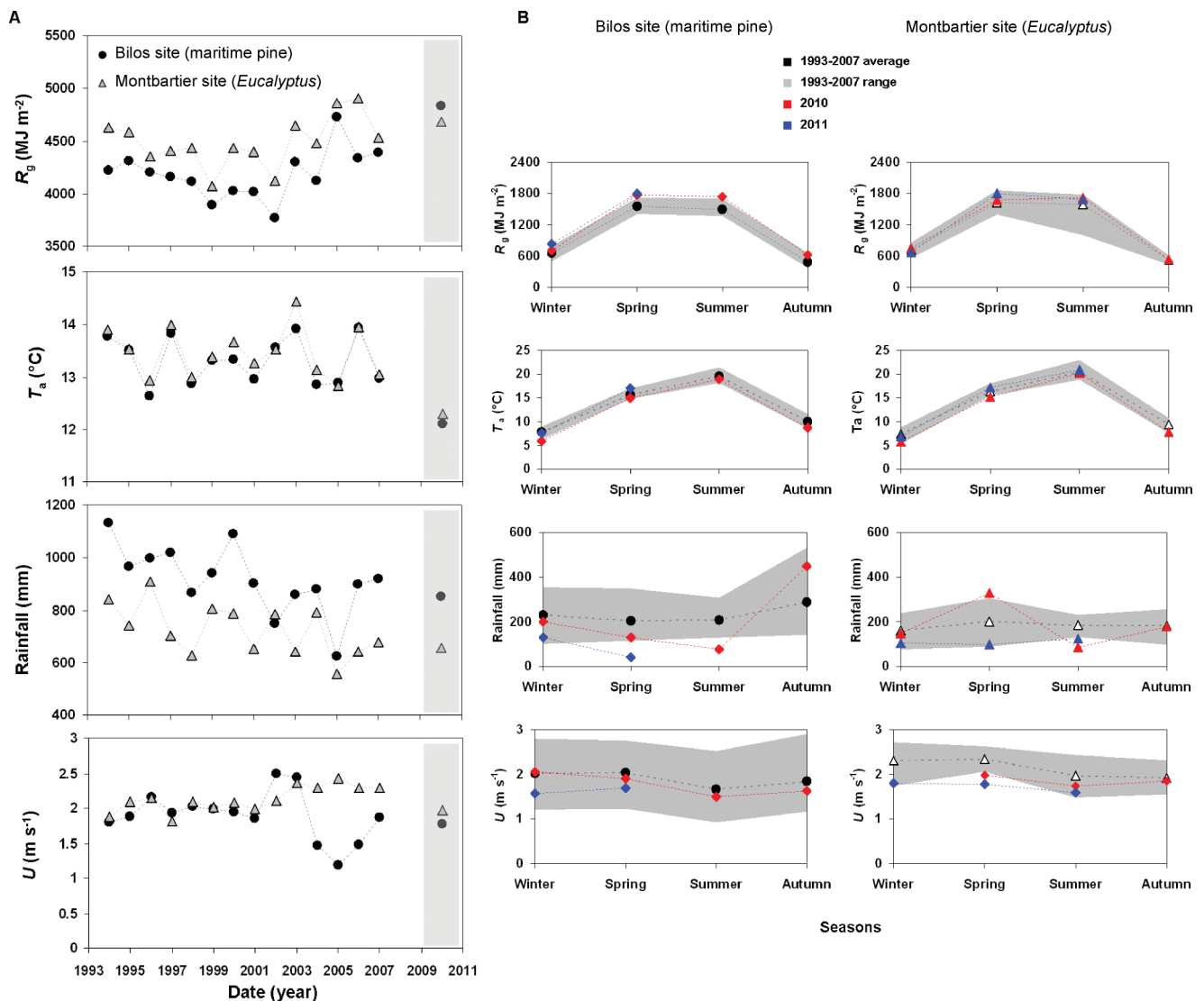

Figure 1.   Time courses of the meteorological variables measured at Bilos and Montbartier sites: A. From 1993 to 2010. The grey zone refers to the 2010 values. B. Seasonal patterns. R_g represents the global radiation, T_a the air temperature and U the wind speed.
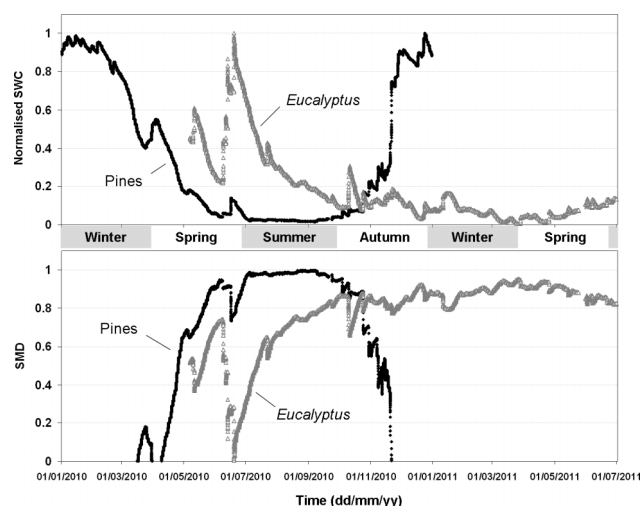
Figure 2. Time courses of the normalised soil water content (SWC) and soil moisture deficit (SMD) for the two plots. The root zone is 0–80 cm for the pine stand and 0–150 cm for the eucalypt stand.

Stand water use and tree transpiration

Monthly and seasonal sums of the water balance components are presented in Table 4. In 2010, stand water use represented 675.8 mm in the eucalypt plantation, which exceeded precipitation by 3%. Tree water use ($E+I$) was the largest component of evapotranspiration in the eucalypt stand and accounted for 75% of annual ET in 2010. The residual term of the water balance is assumed to correspond to drainage below ground (runoff being ignored) and reached annual values of 24 mm. For the maritime pine stand, evapotranspiration was 64% of the total rainfall (542.2 mm). At that site, soil evaporation and understory transpiration were the largest components of ET (60%) and

tree water use ($E+I$) represented 40% of total ET. The value of the annual drainage at this site was estimated at 311.9 mm.

Transpiration exhibited seasonal dynamics that followed a similar trend between the two sites from the beginning of the study until the end of August 2010 (Figure 3). At both sites, tree transpiration reached a maximum during spring 2010 and subsequently declined until the end of August, interrupted only by rainfall events that substantially restored the transpiration rate for the following days. The sensitivity of transpiration to these rainfall events was particularly pronounced in the eucalypt site, with a high amplitude of the signal from a minimum to a maximum. During autumn 2010, patterns of transpiration at each site diverged. The eucalypt stand received less rainfall than the pine stand (184 mm versus 415 mm from mid-September to November), and this was not sufficient to restore its transpiration capacity. During the winter of 2011, pine tree transpiration rates were higher than those measured in the eucalypt, but trees at both sites followed a parallel trend. The gap was increased within early spring 2011 when pine transpiration reached its highest value (1.1 kg$_w$ m$^{-2}_{LEAF}$ d^{-1}). In contrast, eucalypt transpiration rates remained low (0.4 kg$_w$ m$^{-2}_{LEAF}$ d^{-1}). At the end of the study period, the unusual drought observed in spring 2011 severely impacted E in every site.

On a ground area basis, the mean transpiration rate of eucalypt trees, E, varied from 1.05 mm day^{-1} to 1.70 mm day^{-1} in September and July, respectively, with maxima and minima of 2.45 mm day^{-1} in spring and 0.30 mm day^{-1} for a late summer dry day. Transpiration for the pine trees was much lower, with an average of 0.48 and 0.40 mm day^{-1} for May and August, respectively. During the growing season, the minimum and maximum values were 0.25 and 0.65 mm day^{-1} (Table 4).

Table 4. Components of the water balance (mm) for different periods of the study year and annual water use efficiency (kg$_{DM}$ m^{-3}) at the Bilos (*Pinus pinaster* Aït.) and Montbartier (*Eucalyptus gunnii* × *dalrympleana*) sites.

Water use	P	ET_o	ET	E	D
Pine					
Spring (A, M, J) 2010	129.2	327.5	216.8	36.2	6
Growing season (M J J A S) 2010	180.8	548.6	301.2	64.8	−93.8
Annual (01/2010−12/2010)	**853.1**	854.6	**542.2**	**128.4**	311.9
Eucalypt					
2010					
Spring (A, M, J) 2010	243	338.4	236.3	154.7	−
Growing season (M, J, J, A, S) 2010	289.8	585.7	362.2	226.4	−10.3
Annual (01/2010−12/2010)	**654.8**	−	**675.8**	**425.5**	−
2011					
Spring (A, M, J) 2011	80.4	354.7	156.4	109.1	−105
Annual (05/2010–04/2011)	**591.3**	883.8	**638.4**	**410.9**	23.9
Water use efficiency	**2009****		**2010**	**2010–2011***	
Pine	1.57		2.42	−	
Eucalypt	−		3.78	1.64	

*05/2010-04/2011
**for comparison. Calculated from data obtained from the same site and published in Moreaux et al. (2011).
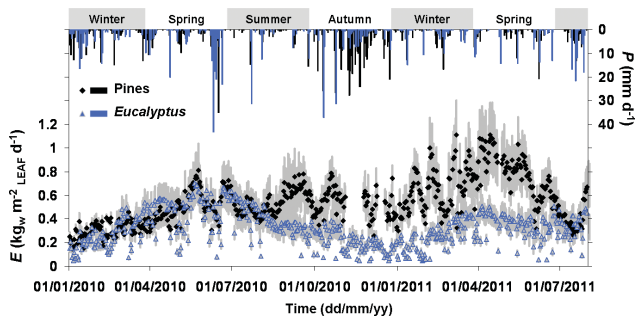
Figure 3. Time course of the transpiration E (kg_w m^{-2} LEAF AREA day^{-1}) over the whole period. Rainfall patterns are also represented on both sites.

Environmental and physiological controls of tree water use

VPD explained a significant component of the variation in calculated canopy conductance g_c. The effects of other potential drivers, such as incident radiation, soil moisture or air temperature, were not significant (Figure 4). Thus the g_c model could be written as a non-linear relation with only VPD, as follows, the k_0 and k_1 values being given in Figure 4:

$$g_c = f\,(\text{VPD}) = \frac{k_0}{1 + \frac{\text{VPD}}{k_1}} \qquad (7)$$
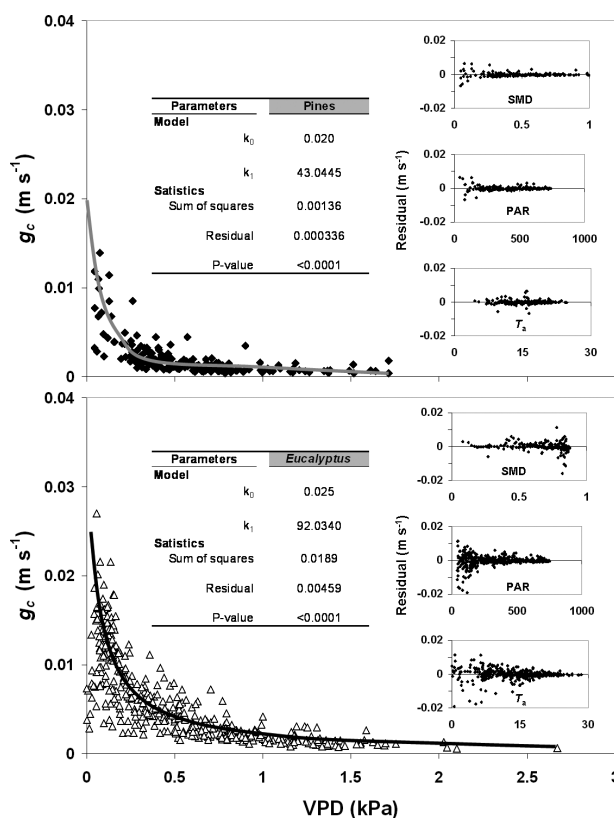
Figure 4. Canopy conductance response to vapour pressure deficit (VPD) for each site (symbols). Modelled g_c is also represented (lines) with respective statistical analysis (tables). Residual g_c is plotted against other environmental parameters in respective inset plots.
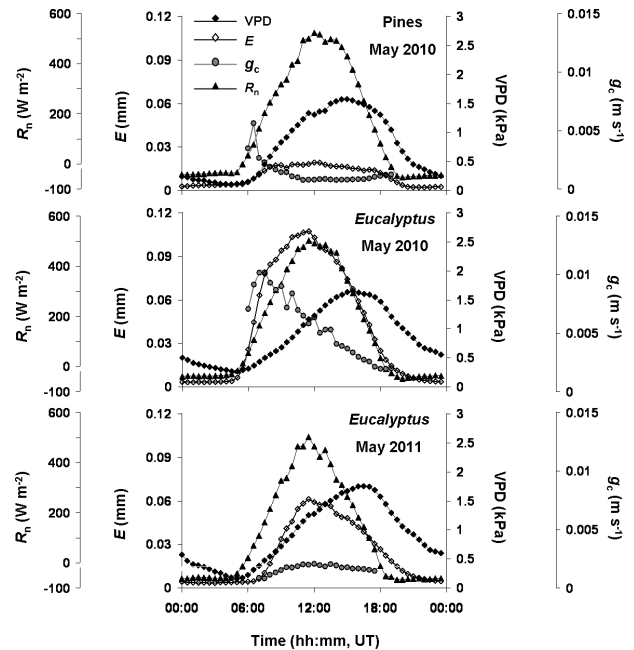

Figure 5. Diurnal patterns of net radiation (R_n), transpiration (E), vapour pressure deficit (VPD) and canopy conductance (g_c) obtained as a 10-day average during the growing season (May 2010) for the two sites. The 2011 period is also represented for the eucalypt plot.

At both sites, g_c declined in response to increasing VPD. Maximum daily values of g_c reached 2.5 cm s^{-1} in the eucalypt plot and 2 cm s^{-1} in the pine plot.

The daily pattern of transpiration and canopy conductance is illustrated in Figure 5 by representing the mean diurnal pattern observed in May 2010 at both sites. The patterns for May 2011 are also provided in the eucalypt stand. In the pine stand, maximum stomatal conductance was observed in early morning (6.30 am). In contrast, transpiration E increased with the available energy until 10–12 am. As canopy conductance decreased and VPD increased, E tended to level off. At the eucalypt site, the diurnal course of E reflected the diurnal patterns of net radiation in May 2010. The observed decrease in g_c associated with increasing VPD did not strongly regulated E. Peak values of E and R_n were reached at about noon. In 2011, under similar R_n and VPD conditions, the diurnal courses of g_c and E were strikingly different. Transpiration was reduced by half and lagged 2 h behind the net radiation, whereas g_c was lower and exhibited dampened variation during the day with no clear maximum, revealing the impact of SMD on stomatal conductance.

In spring 2010, the daily ratios of E/ET_o of the eucalypt and pine stands were 0.40 and 0.15, respectively. This ratio reached a maximum value of around 0.80 in the eucalypt stand during the winter of 2010–2011. There was a marked decline in E/ET_o after March 2011, related to the increasing evaporative demand and high SMD. Between May 2010 and May 2011, E/ET_o was reduced by 50% on the eucalypt site, to a value of 0.2 (Figure 6).
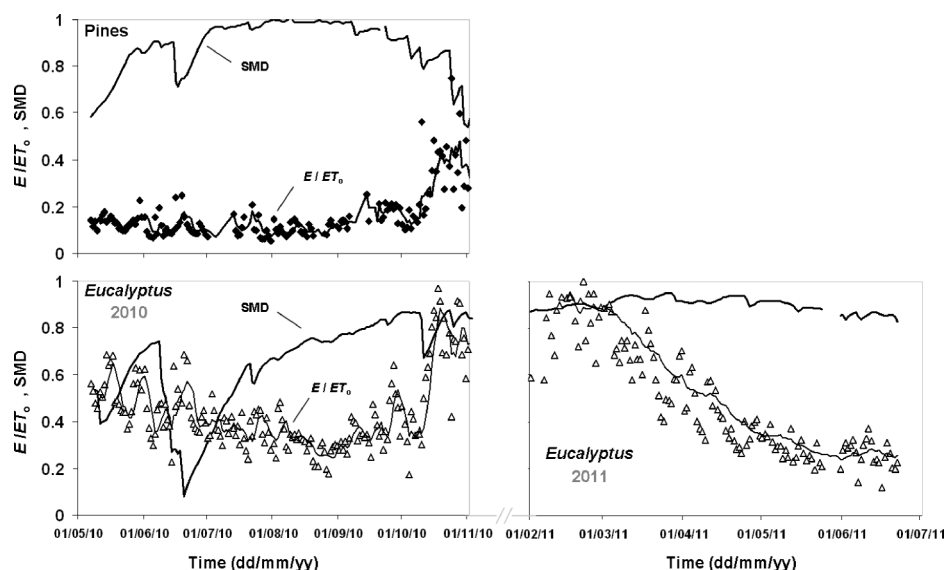
Figure 6.   Time courses of E/ET_o ratio and soil moisture deficit (SMD) obtained for the 2010 growing season on the two sites. The same curves are shown for the 2011 growing season on the eucalypt site. For a better observation, the thin black lines of the E/ET_o courses refer to a 5-day moving average.

Tree growth and water use efficiency

During 2010, the growth of the eucalypts exhibited two distinct phases. The first growth phase was initiated on 20 February and continued until late June. Growth then ceased until October 2010, when a second phase began, following the rainfall in autumn. From 15 November 2010, eucalypt growth ceased again for a period of 3 months. However, in February 2011, low growth rates were observed. Over the period considered (1 March 2010–30 June 2011), eucalypt DBH increased by an average of 1.5 cm. Throughout the period studied, the eucalypt stem diameter responded quickly to rainfall events, as was also the case for transpiration. The rainfall events recorded in May 2010, June 2010, July 2010, early September and early October 2010 all preceded an observed increase in stem diameter (Figure 7). Over the whole period, the total stem diameter growth in the pine stand was, on average, 1.59 cm.

On a daily time scale (inset 1, from 25/06 to 27/06, in Figure 7), the stem diameter at both sites reached a maximum between 6.30 am and 8.30 am following night-time replenishment of elastic tissues. During the day, the diameter decreased to a minimum at 3 pm. In October (inset 2, Figure 7), these two phases were no longer visible in the eucalypt trees, which were continuously enlarging. This behaviour corresponded to a decrease in demand for transpiration. During this period, pine transpiration was still substantial so that stem shrinkage remained visible (12/10 and 13/10).

Leaf shedding events occurred between July and September 2010 in the pine stand and from May to October 2010 and April 2011 in the eucalypt stand. On an annual scale, from May 2010 to April 2011, litterfall from eucalypt trees corresponded to a LAI fraction of 2.31 $m^2 m^{-2}$, half of which occurred in April 2011. In the

pine stands, litterfall corresponded to a LAI fraction of 0.43 $m^2 m^{-2}$.

In the pine stand, WUE increased between 2009 (1.57 kg_{DM} m^{-3}) and 2010 (2.42 kg_{DM} m^{-3}) due to lower water use and higher biomass production in 2010. For the eucalypt site, the 2010 value of WUE was the highest of the period studied (3.78 kg_{DM} m^{-3}). Conversely, when the 2011 early drought period was included in the calculation, the eucalypt WUE value (1.64 kg_{DM} m^{-3}) was severely reduced (Table 4).

Discussion

The two stands studied here differed in important characteristics related to their respective water balance. First, soils at the pine and eucalypt stands were quite different, characterised by the podzolic sandy soils with a shallow ground water table and low water-holding capacity at the pine site and a silt-clay soil with no water table and larger water-holding capacity under the eucalypt stand. Second, rainfall and its distribution varied between sites during the 2010 and 2011 spring and in the autumn of 2010. Thus, it is not unexpected that the patterns of evapotranspiration differed between the two stands during the study period. Nevertheless, both species showed high sensitivity to drought during the study. This is particularly interesting as the climatic conditions observed during the 2010–2011 study period may be representative of future climate scenarios for this region, represented by regionalised ARPEGE Meteo-France model (Loustau et al. 2005). We also stress that this is the first report of the water use of *Eucalyptus* species in Europe at this latitude. Therefore, the parallel analysis of pine and eucalypt growth and water use in response to soil water availability and climate is particularly relevant.
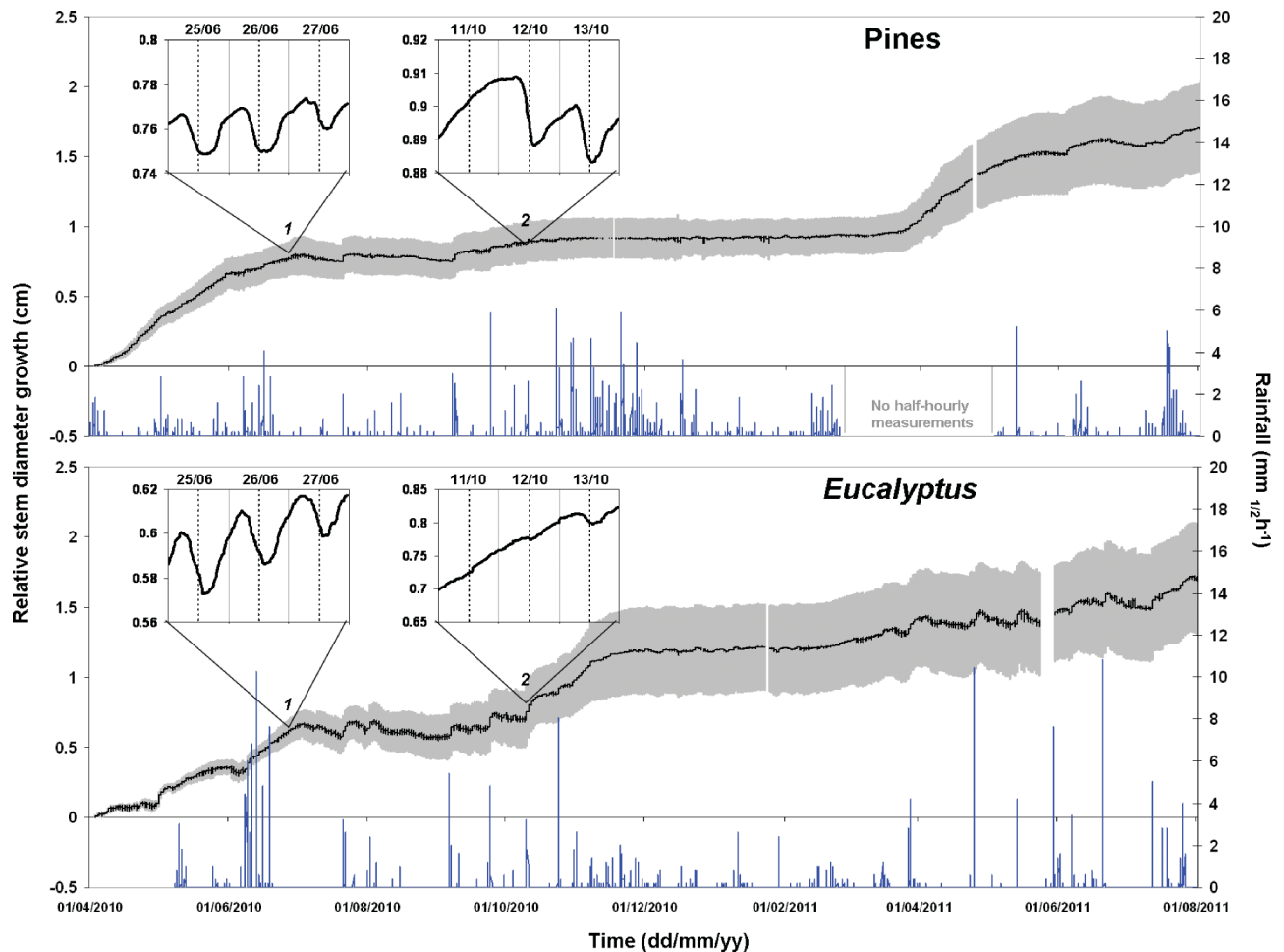
Figure 7.   Time courses of the relative stem diameter growth from April 2010 on the two plots. Two periods are magnified to show the diurnal patterns under different conditions.

Total water use

LAI represented the main driver controlling stand water use at both sites. The eucalypt canopy studied here had a LAI > 4 and approached canopy closure. In contrast, the pine canopy was far from reaching its full expansion, individual crowns being separated by gaps. Under similar evaporative environments, and despite lower rainfall over the study period, the outcome that the eucalypt stand *ET* (675.8 mm) was only 25% more than the maritime pine stand (542.2 mm) was unexpected, considering their different canopy characteristics. In stands of similar age growing under similar climatic conditions, it has been assumed that the forest evapotranspiration should be relatively conservative across different forest types. This has previously been demonstrated in European forests, with a range of forests showing similar stand evaporation rates (Roberts 1983), and this conservative behaviour is attributed to the sensitivity of the stomatal conductance to VPD (Roberts 2007). In contrast, although we found that both species had similar transpiration rates per unit leaf area in well-watered conditions, evapotranspiration from the eucalypt stand was much higher, highlighting that the differences in evapotranspiration between stands were mainly

driven by higher eucalypt LAI. The putative differences between species in their ecophysiological characteristics would consequently play a secondary role in the regulation of evapotranspiration. Indeed, confirming Roberts' hypothesis, annual *ET* in the eucalypt stand approached the evapotranspiration from a pine stands with a similar LAI studied by Moreaux et al. (2011) at an age of 5 years and by Berbigier et al. (2001) or Delzon and Loustau (2005) at older stages.

At the eucalypt site, annual water use (*ET*) exceeded the water supplied by rainfall and resulted in SWC remaining close to the wilting point from summer 2010 until the end of the period studied. Eucalypt stands tend to be profligate water users, and productivity and water use are tightly coupled (Whitehead and Beadle 2004). For example, under non-water-limiting conditions, Almeida et al. (2007) showed that *ET* of a *Eucalyptus grandis* W.Hill ex Maiden stand in Brazil represented approximately 95% of total rainfall over 7-year rotation, including 3 years during which evapotranspiration exceeded rainfall. In the same area, using a modelling approach, Soares and Almeida (2001) estimated annual *ET* to be 1345 mm compared with 1396 mm of rainfall. Furthermore, Cabral et al. (2010)

recently estimated that *ET* represented 82% and 96% of total annual rainfall over 2 years and in a 8-year-old *E. globulus* stand growing in Portugal. Pereira et al. (2007) found that *ET* was equal to rainfall, which agrees with our observation, especially considering the similarity in climatic conditions (annual rainfall of 709 mm in their case) with our site.

In contrast, the annual water use represented 64% of annual rainfall for the maritime pine stand. For a 12-month water balance between June 2009 and May 2010, Moreaux et al. (2011) found that in the same maritime pine site water use was 672.3 mm, which corresponded to 72% of the rainfall. The difference between these annual values is mainly linked to patterns of *ET* in the summer months (July and August) during which water use was reduced by 40% in 2010 relative to 2009, as a result of the drier spring in 2010 compared with 2009. However, *ET* measured in 2010 was within the range of values previously reported for adult maritime pine stands in this area (Berbigier et al. 2001; Kowalski et al. 2003; Delzon and Loustau 2005).

Partitioning of evapotranspiration

Our results highlight the dominant role of the tree canopy LAI on the partitioning of evapotranspiration. This was in accordance with Granier et al. (2000) who showed that LAI is a critical parameter regulating the exchange of energy and water from forest canopies. In the eucalypt stand, most of the water lost via evapotranspiration was from the tree canopy through transpiration and wet canopy evaporation (75%). Eucalypt transpiration alone contributed a significant fraction of *ET* (63%). Soil evaporation was also a significant component of *ET* and was estimated to be 25% of annual water use, a percentage within the range reported for other eucalypt stands. For example, Lane et al. (2004) found a similar contribution of soil evaporation to *ET*, demonstrating that E_{soil} varied between 16–26% of total evapotranspiration in 3- to 4-year-old *E. urophylla* plantations in China. They highlighted the importance of this contribution to total evapotranspiration, particularly in plantations where weeds and understory are removed, leaving areas of bare soil. Similarly, Silberstein et al. (2001) estimated that E_{soil} contributed 9% (spring) and 16% (summer) of *ET* in a eucalypt stand of a mean height of 25 m growing with a 8 m height understory in south-western Australia. We assumed a canopy interception of 12%, based on the studies of Pereira et al. (2007) in Portugal, which is at the low end of values that have been previously reported (Whitehead and Beadle 2004). However, given that measured transpiration was 63% and soil evaporation represented 25% of *ET*, we believe that this assumption was reasonable. As a result, deep drainage within the eucalypt stand was relatively low, and this is consistent with previous observations of these soil profiles (Bouzigues and Vinas 1989).

In contrast, in the pine stand, the dominant term of water use was the combination of understory transpiration and soil evaporation, representing 60% of *ET*. Tree-scale evapotranspiration (*E+I*) contributed 40% of total *ET*. These percentages were similar to those previously reported for maritime pine stands (Moreaux et al. 2011). The contribution of the trees to total *ET* was lower than that previously observed for an older stand in which the trees had reached full canopy expansion (Delzon and Loustau 2005), again highlighting the importance of LAI in regulating the exchange of water between the canopy and the atmosphere.

Physiological and edaphic controls

At both sites, our results show that stomata efficiently control tree transpiration under soil drought (see Figure 5 for the eucalypts). Strong stomatal regulation of transpiration has already been documented for both eucalypt (e.g. Whitehead and Beadle 2004) and pines species (e.g. Berbigier et al. 1991; Granier and Loustau 1994; Loustau et al. 1996) and underlies the capacity of trees to maintain water potential above critical thresholds and prevent catastrophic embolism in response to drought. The simultaneous reduction of tree transpiration at both sites (Figure 3) occurred earlier (May 2010) than in previous observations (Loustau et al. 1990). The decline in canopy transpiration occurred even earlier in spring 2011 and was dramatically pronounced at both sites by the beginning of April 2011 (Figure 3). The comparatively reduced canopy transpiration during these periods was difficult to reconcile as the crop factor (either E/ET_o or ETR/ET_o) showed little response to SMD, suggesting that these plantations were potentially obtaining water from elsewhere in the soil profile than in the zone assessed by our measurements. The available soil water at the eucalypt site was estimated at 180 mm for a soil depth of 0–150 cm, and this value was used for the calculation of SMD. This value is consistent with the range of values reported for similar soil structures within the region (Favrot 1970; Calvet et al. 1998; Calvet and Noilhan 2000). Assuming that this value represents a good estimation of SWC, it is likely that water was taken up by tree roots elsewhere, especially after September 2010.

It was surprising that such a high E/ET_0 ratio (>0.6) was observed in winter in the eucalypt stand, despite the high SMD. Even though lower ET_o were recorded in winter, the high ratio indicates that eucalypt could maintain a certain level of transpiration *E* ($E > 60\%$ of ET_o until April 2011). There are a number of possible explanations for this. One hypothesis is that small rainfall events fully satisfied water demand during winter. Thus, trees use water that infiltrates the first few centimetres of the soil profile after rainfall, although such increases in water availability would not be observed by our sensor at 20 cm depth. Alternatively, a second hypothesis is that water extracted from below the measurement zone could maintain low transpiration rates. Even though there was an obvious clay barrier in this soil at 50 cm depth, many studies have highlighted the possibility that eucalypt roots are able to reach depths deeper than the studied sampling zone, whatever the soil structure, climate region, species and age (Dye 1996; David et al.

1997; Feikema et al. 2010; Duursma et al. 2011). This clay layer could also potentially act as a capacitor that provides a steady upward flux of water in response to water potential gradients generated within upper soil horizons that may help to maintain low rates of transpiration of this period (Macinnis-Ng et al. 2010). Under water-stressed conditions and during tree growth periods, larger proportions of biomass are allocated to below-ground root systems. For example, Silva et al. (2004) observed root extension in *E. globulus* trees in Portugal under water-stressed conditions, suggesting that trees are able to maintain transpiration by progressively exploiting a larger volume of soil (in our case during spring 2011).

The root systems of trees in the pine stands are probably less developed. The prospecting area for understory and pine roots is limited by the presence of the permanent groundwater table at an average depth reaching −1.8 m in summer to −0.2 m in winter (Achat et al. 2008). In addition, the presence of a hard pan at 50–80 cm limits root extension to deeper soil layers (Bakker et al. 2006). At the pine site (data not shown), 90% of fine roots (diameter < 2 mm) were found in the top 0.5 m. In the young and open stand studied here, where understory was destroyed, it is likely that the pine tree root systems explored more of the soil volume horizontally, the presence of the water table at a depth of 60 cm in winter limiting vertical root expansion in that site. To a lesser extent than observed in the eucalypt stand, water might also be taken up during drought from a superficial soil zone not accounted for by the measurements. Thereby, tree transpiration could be sustained, for example in September 2010, without significant changes in soil moisture measurements.

Water use and growth response

In the present study, *Eucalyptus gunnii × dalrympleana* showed similar ecophysiological behaviour, with regards to water use, as that reported by other authors and reviewed in Whitehead and Beadle (2004), highlighting the functional convergence displayed by species of *Eucalyptus*. Canopy conductance was highly reduced under high VPD, providing tight control of water loss, especially under water-stressed conditions. Eucalypts however, employ a number of strategies for regulating plant water use. *Eucalyptus* species have the capacity to develop deep root systems, which are a crucial part of their drought-avoidance strategy and help to explain their profligate water use and associated high productivity (around 15 t ha^{-1} year^{-1}). Furthermore, the reduction of LAI by ca. 40% in April 2011 may be regarded as an adaptive trait. Many *Eucalyptus* species demonstrate strong seasonality in LAI to avoid water stress (Battaglia et al. 1998; O'Grady et al 1999; Nouvellon et al. 2010). Such high variability in leaf area was not observed in the pine stand, where the main control of transpiration was associated with the reduction in canopy conductance.

Water use efficiency of the eucalypts, being 1.6 times higher than that of the maritime pine stand, was within the range (1–5 g$_{DM}$ kg^{-1}) reported in a previous review of different *Eucalyptus* species (Whitehead and Beadle 2004). When soil water was not limiting, water use efficiency was high on the eucalypt site, but the high rates of water use raise questions about the sustainability of eucalypt stands in this region under forecast future climate scenarios. Indeed, water supply strongly limits the productivity of eucalypt stands (Stape et al. 2010). For the study site, the 2011 winter precipitations, despite being in the normal range for this area, were not sufficient to restore the soil water reserve, which led to a significant decrease in tree growth and productivity in the following spring. This raises doubt about the long-term sustainability of the high productivity of eucalypt stands in south-western France under a changing climate.

Conclusion

This study highlighted the important role played by LAI in the observed differences in water use between the two sites. Timing and extent of environmental stress also played a major role in the control of water use and tree growth. We found that the water use strategies of the hybrid eucalypt stand studied here are consistent with other *Eucalyptus* species. Water use by the tree canopy represented the main contributor to evapotranspiration. The eucalypt site underwent a prolonged soil drought that directly affected tree growth in 2011. Despite autumn and winter rainfalls in the range of the long-term average, soil water recharge was low and soil water reserves in the eucalypt site were not replenished. We show that the climatic water availability regime is a critical determinant for tree productivity. In 2011, the entire Midi-Pyrenees and Atlantic regions of France were affected dramatically by the spring drought. In that sense, the pine site also experienced successive droughts but the processes involved in water use regulation and their impacts on growth were different from those in the eucalypt stand due to the inter-site and between-species differences. At the pine site, soil water replenishment and the groundwater rise in autumn and winter provides enough water at the beginning of the growing season. Therefore, growth was less impacted at the beginning of the growing season in 2011, than at the eucalypt site. However, water availability remained low at that time, and growth quickly induced soil drying and a decrease in available SWC. As a result, the transpiration slumped to a higher degree compared with the eucalypt stand that was already affected by prolonged soil drought.

Consequently, during the study period, the SMD was the main limitation of tree transpiration and growth, as evidenced through stomatal closure (both sites) and leaf shedding (eucalypt site). In recent years (1993–2007), the annual evaporative demand (ET_o) has exceeded rainfall by a mean value of 85 mm. However, this deficit between ET_o and rainfall has been increasing during the 1993–2007 period (data not shown), peaking at 292 mm over the 2010–2011 study period (Table 4). It is likely

that this region will experience an increase in summer drought duration and intensity over the next few decades (Loustau et al. 2005; Déqué and Cloppet 2010). Under such a scenario, the potential productivity and profitability of *E. gunnii × dalrympleana* may be reduced significantly across the area.

Notes on contributors

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Denis Loustau is a scientist with interests focusing on understanding the fluxes of carbon and water, mostly in forest ecosystems. He is involved in major European projects devoted to climate change impacts on forests and has participated in the IPCC.

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