



Age-related decline in stand water use: sap flow and transpiration in a pine forest chronosequence

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Abstract

We investigated changes in the pattern of stand water use in a chronosequence of four even-aged maritime pine stands, differing in age (10-, 32-, 54- and 91-year old) and growing under similar environmental conditions. Extensive sap flow measurements were carried out during a period of 2 years (2001–2002), using thermal dissipation sensors located 1 m below the live crown and corrected for the radial profile of sap flow. We found significant differences in transpiration among stands. Overstorey transpiration, E_T , declined with stand age from 508 mm per year for the 10-year-old stand to 144 mm per year for the 54-year-old stand in 2001. This age-related decline was driven by (i) a decrease in transpiration per unit leaf area (55%), due to a decrease in stomatal conductance in taller trees and (ii) a significant reduction in leaf area index (38%). There was a strong effect of soil moisture deficit on transpiration and an interaction with age. A strong decrease in overstorey transpiration resulted from the prolonged drought in 2002 due to both a lower transpiration rate per unit leaf area and lower leaf area evidenced both by optical and litterfall measurements. The drought effect was greater in the younger stands compared to older stands. In the 32-year-old stand, simultaneous measurements of sap flow and eddy covariance showed that the overstorey transpiration contributed to half of the total ecosystem water loss, E . Moreover, the total ecosystem evaporation estimated for each stand by a water balance approach was not different between stand ages. We suggest, therefore, that the decline in overstorey transpiration with stand age mainly affects partitioning of the components of evaporation between trees, understorey and soil but not the magnitude of total evaporation.

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1. Introduction

Due to forest management, most European forests are composed of even-aged stands and form a spatial mosaic of stands differing in age and tree spacing. This spatial distribution of age classes is the major component of forest landscape heterogeneity. The

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forest age distribution is highly variable due to difference in management practices and the degree of damage from fire and storms. The effects of stand age on mass and energy exchanges are becoming better understood, in particular in the assessment of the forest carbon and water balance (Kowalski et al., 2003, 2004; Law et al., 2001, 2003). The age-related decline in forest net primary production and timber production is well documented and can be explained by the hydraulic limitation of stomatal conductance and photosynthesis (Ryan et al., 1997; Ryan and Yoder, 1997; Yoder et al., 1994). Although this should also affect forest transpiration, the influence and regulatory role that trees play in water movement through forest stands with increasing age are less well documented. The amount of transpiration depends on tree leaf area (Granier et al., 2000; Oren et al., 1999a; Vertessy et al., 1995), and stomatal characteristics (Hogg and Hurdle, 1997; Kelliher et al., 1993). But less is known about how decreases in stomatal conductance as trees grow taller, i.e. hydraulic limitation (Ryan and Yoder, 1997; Schafer et al., 2000), and water relations (e.g. hydraulic lift (Dawson, 1996)) influence stand water use. Whether differences in transpiration with age are compensated by evaporation from changes in evaporation rates from understorey and soil, remains unclear. More studies addressing the size- and age-related effects of trees on stand water use are needed. However, investigating stand water relations in relation to age and size is difficult, because climatic, soil and forest management conditions are rarely similar among stands of different age.

The southwestern European of maritime pine (*Pinus pinaster* Ait.) forests offer optimal conditions for addressing the effect of age on forest water relations. The estate covers 0.9 million hectares and consists of a mosaic of 5–100 ha pine stands of different ages, established in homogenous soil with similar management practices on a flat sandy plateau growing in maritime conditions. Currently, the rotation length is between 45 and 55 years but older stands are still found (up to 100 years of age). Hydrological studies based on eddy covariance and sap flow measurements carried out over the last decade (Berbigier et al., 1996, 2001; Granier and Loustau, 1994; Loustau et al., 1996, 1998) have provided useful information on the environmental and physiological processes regulating transpiration. Moreover, in a

previous study on maritime pine trees, Delzon et al. (2004a) found a decline in stomatal conductance with increasing tree height. Stomatal conductance values of tall (91 years old) trees were 60% lower than those of smaller (10 years old) trees. Lower stomatal conductance maintained a functional water balance, i.e. homeostasis of needle water potential, to compensate for a decrease in leaf-specific hydraulic conductance with increasing tree height. Consequently, we expected a decline in transpiration with stand development. However, the potentially independent effects of the age and size of the trees on stand water use remain almost unknown, and annual stand water use has not previously been quantified for a maritime pine forest.

Our main objectives were (i) to compare the stand water use across a chronosequence of four maritime pine stands growing in relative close proximity, (ii) to identify and quantify the physiological and structural causes inducing the changes in transpiration in relation to stand age, and (iii) to evaluate the year-to-year variation in the relationship between age and water use. We based our investigations on sap flow measurements monitored during two consecutive years under contrasting soil water availability, highlighting drought effects.

2. Materials and methods

2.1. Site description

The experiments were carried out in pure, even-aged stands of maritime pine (*P. pinaster* Ait.) that were 10-, 32-, 54- and 91-year-old trees in 2002. For clarity in this paper, we always refer to the same stand age (age in 2002) both for 2001 and 2002. The chronosequence was located in the “Landes de Gascogne” forest, south-western France, about 20 km southwest from Bordeaux (Table 1). This flat region (altitude = 60 m) has a maritime climate, with a mean annual temperature (1950–2000) of 13 °C and precipitation (1970–2000) of 977 mm (Meteo France, Merignac, France). Understorey vegetation was very dense and consisted mainly of *Molinia coerulea* (L.) Moench. The soil is a sandy humic podzol with a cemented B_h horizon limiting the depth of the root zone to 0.8 m with little variation among stands.

Table 1
 Meteorological instrumentation installed above the canopy in each stand

Stand age	Latitude and longitude	Measurement height (m)	Air temperature and humidity (HMP45AC temperature-humidity probe (Vaisala, Helsinki, Finland))	Net radiation (NR Lite FT006 net radiometer (Kipp and Zonen, Delft, Netherlands))	PAR (LI 190S crystalline silicon cells (LICOR, Lincoln, NE, USA))	Precipitation (ARG100 rain gauge (Young, Traverse City, Michigan, USA))	Wind speed (A100R switching anemometer (Vector Instruments, north Wales, UK))
10 and 54 years ^a	44°44'N, 0°46'W	12	May 2001–December 2002	May 2001–December 2002	January 2002–December 2002	May 2001–December 2002	May 2001–December 2002
32 years	44°44'N, 0°46'W	25	January 2001–December 2002	January 2001–December 2002	January 2001–December 2002	January 2001–December 2002	January 2001–December 2002
91 years	44°37'N, 0°34'W	33	May 2002–December 2002	May 2002–December 2002	May 2002–December 2002	May 2002–December 2002	May 2002–December 2002

PAR = photosynthetically active radiation (400–700 nm).

^a Measurements of air temperature and humidity carried out during 6 months above the canopy for the 54-year-old stand (29 m height) did not show any difference with those measured at the meteorological station 150 m distant in the centre of the 10-year-old stand.

Estimates of stem diameter at 1.3 m (d) in 2001 for each tree in the chronosequence were obtained from circumference measurements. Top height (h) was measured on a sample of 100 trees per stand, stratified according to tree basal area. Both in summer 2001 and 2002, the plant area index (PAI) was measured with an optical method (DEMON, CSIRO, Canberra, Australia). These measurements were always carried out when the angle of the sun to the vertical was close to 57° and along the same transect. The sapwood cross-sectional area below the live crown ($A_{S,LC}$, m^2) and tree leaf area (A_L , m^2) were calculated using the following relationships established across the same chronosequence (Delzon et al., 2004a):

$$A_{S,LC} = 0.3058 d_{LC}^{1.6385} \quad (1)$$

$$A_L = 0.0433 d_{LC}^{2.043} \sigma \quad (2)$$

where d_{LC} (m) is the stem diameter under the live crown and σ ($m^2 kg^{-1}$) the specific leaf area. For calculating $A_{S,LC}$ and A_L , Eqs. (1) and (2) were applied for each stand using d_{LC} values estimated for each individual tree from a linear regression established between d and d_{LC} . Values of d and d_{LC} were measured on a sample of 30 trees per stand (R^2 ranging from 0.95 and 0.98). Then leaf area index (LAI) of each stand was estimated following Chen and Black (1992) as half the total surface leaf area per unit ground area.

2.2. Sap flow measurements

Sap flow was measured for the four stands with a constant heating radial flowmeter according to Granier (1985, 1987). The two probes for each sensor were installed 130 mm apart in the outer 20 mm of sapwood. The upper probe was heated continuously with a constant current of 0.140 A while the lower one was not heated. The sensors were installed on six trees in the 10-year-old stand and seven trees in the other stands on the eastern side of the stems at 1 m under the live crown, which corresponds to 1–18 m above ground level. Sap flow data were collected from April 2001 to January 2003 at the three younger sites and from March 2002 to January 2003 in the 91-year-old stand. Data were recorded every 10 s and averaged every 30 min with dataloggers (model 21X, Campbell Scientific Ltd., Shepshed, UK) and multiplexers (model AM416, Campbell Scientific Ltd., Shepshed,

UK). Sap flow density, Q_s , was calculated using the original calibration coefficients of Granier (1985).

To avoid the natural temperature gradient, the two probes were inserted in the same horizontal plane except when stem diameter was too small or branch insertions were present. In the latter case, the probes were placed one above the other, and the vertical temperature gradient along the stem was accounted for as follows. The natural temperature gradient was measured in each tree during short periods of 3–4 days when the heating was turned off. Using these data, simple empirical models were determined for each tree based on meteorological variables (Do and Rocheteau, 2002a, 2002b; Lundblad et al., 2001). Among the variables tested – solar radiation, air humidity, wind speed and temperature – the most satisfactory statistical correlation for the natural temperature gradient was found with temperature alone. If such a temperature gradient to be ignored, the mean daily sap flux density in the 10-, 32-, 54- and 91-year-old trees would have been overestimated by 3, 6, 6 and 5%, respectively.

We scaled up the measurements of sap flux density to the entire sapwood cross-sectional area as follows. First, following Loustau et al. (1998), azimuthal variations were assumed to be negligible. Second, the radial profile of sap flux density was accounted for applying a correction factor for individual tree sapwood area, C , which depended on d_{LC} ($C = -1.17643 d_{LC} + 1.1936$ with $R^2 = 0.90$ (Delzon et al., 2004b)). Neglecting this radial correction would have led to an overestimate of daily transpiration by 4, 14, 26 and 47% in the 10-, 32-, 54- and 91-year-old stands, respectively.

In accordance with previous studies on sap flow in maritime pine (Loustau et al., 1990, 1996), we found no relationship between Q_s and tree size within stands. Consequently the overstorey transpiration, E_T , was calculated as the product of the corrected sapwood area summed over the stand by the mean sap flux density, such that

$$E_T = \overline{Q_S} S^{-1} \sum_{i=1}^n (A_{S,LC,i} C_i) \quad (3)$$

with $\overline{Q_S}$ is the mean sap flux density under the live crown, $A_{S,LC}$, the sapwood area below the live crown

of tree i , n the number of trees per stand and S the ground area for the stand. Transpiration per unit leaf area, E_L , was calculated by dividing E_T by the leaf area index of each stand.

2.3. Eddy covariance measurements

Latent and sensible heat fluxes were monitored continuously over the 32-year-old stand using the eddy covariance system (Aubinet et al., 2000). The system consisted of a closed-path infra-red gas analyser (IRGA, LiCor 6262, LICOR, Lincoln, NE, USA) and a 3D sonic anemometer (Solent R2, Gill instruments, Lymington, Hampshire, UK). The system was installed in 1996 in the centre of the stand on a 40-m tall tower, 20-m above the canopy. Water vapour exchange rates were estimated and gap-filled as described by Berbigier et al. (2001) to estimate the total ecosystem evaporation (E , mm d^{-1}).

2.4. Needle water potential

The predawn needle water potential ψ_p was measured six times during the 2 years of the experiment in each stand. Measurements were taken on three different whorls of three trees per stand. Needle water potential was measured using pressure chambers on 18 fully expanded needles per stand, sampled from the upper crowns before sunrise.

2.5. Litterfall measurements

Litterfall was collected on 1 m × 1 m frames with wire-mesh netting from April 2001 to April 2003 in each stand. Twenty collectors were randomly placed in each stand and litter was collected monthly throughout the summer and every two months the rest of the year. Litter was manually sorted into needles and other plant parts, dried at 65 °C and weighed.

2.6. Meteorological and soil measurements

Local micrometeorological conditions were measured at the top of the canopy in each stand, except in the 54-year-old stand which was 150 m distant from the meteorological station in the 10-year-old stand

(Table 1). The same dataset was used from both stands. Data were measured every 10 s and averaged every 30 min. All sensors were inter-calibrated in the laboratory before installation.

Soil volumetric water content was measured using two techniques, a water content reflectometer system (CS615 water content reflectometer, Campbell scientific LTD, Logan, UT, USA), and a TRASE system (TRASE 6050X1, Soil moisture, Goleta, USA). In the 54- and 91-year-old stands, 20 stainless steel probes CS615, with 300 mm long rods, were inserted horizontally into the soil at 0.15, 0.3, 0.6, 0.9 and 1.3 m depths at four locations in each stand. In the 10- and 32-year-old stands at five and four locations, respectively, 200 mm long TRASE probes were installed horizontally in the soil at depths of 0.15, 0.3, 0.5 and 0.8 m. In each stand, data were collected every 4 h, except in the 32-year-old stand, where collection was once a week. A cross-comparison of the two systems gave satisfactory agreement. In each stand, manual readings of groundwater level were made once a week, and in addition in the 10-year-old stand, groundwater level was monitored automatically every 30 min with a pressure transducer (PDCR 830, Campbell Scientific Ltd., Logan UT, USA). Finally, the soil water content, θ , was calculated in each stand from 0 to 0.8 m depth, corresponding to the depth of the root zone.

2.7. Statistical analysis

Analysis of variance (ANOVA) was performed to test for between-tree differences in monthly sap flux density and the dependence of sap flux on stem size. All statistical analyses were made with SAS procedure GLM-SNK (Student-Newman-Keuls) (SAS Version 8.1, SAS Institute, Cary, NC).

3. Results

3.1. Stand characteristics

Stand basal area obtained from circumference measurements increased until the trees reached 40 years and then decreased slowly (Fig. 1a). Stand sapwood area below the live crown ($A_{S,LC}$) declined with age from $13.1 \text{ m}^2 \text{ ha}^{-1}$ in the 10-year-old stand

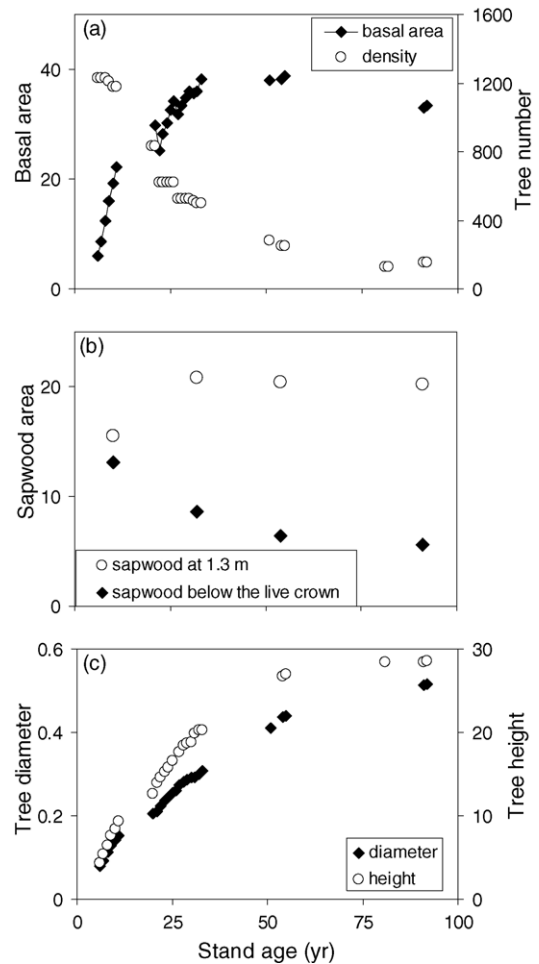


Fig. 1. Changes with age of (a) stand basal area ($\text{m}^2 \text{ ha}^{-1}$) and number of trees per unit area (ha^{-1}), (b) stand sapwood area at 1.3 m above ground and below the live crown ($\text{m}^2 \text{ ha}^{-1}$), (c) mean tree diameter at 1.3 m above ground, d (m) and mean tree height, h (m) for five maritime pine stands in the “Landes de Gascogne” forest. Height and diameter measurements were carried out annually since 1989, 1995, 1998 and 2001 in the 10-, 32-, 54- and 91-year-old stand, respectively. Points linked by lines belong to the same stand.

to $5.6 \text{ m}^2 \text{ ha}^{-1}$ in the 91-year-old stand while stand sapwood area at 1.3 m above ground level increased in the young stages and showed no trend at older stages (Fig. 1b). Due to successive thinnings, tree number per unit area decreased throughout the forest rotation to a final value of 155 tree ha^{-1} (Fig. 1a). Stem diameter at 1.3 m (d) and tree height (h) increased until the trees were 60 years old, then reached a plateau (Fig. 1c).

Table 2

Seasonal average values of mean, minimum and maximum air temperatures (T_{mean} , T_{min} and T_{max}), maximum vapour pressure deficit (D_{max}) and downward photosynthetically active radiation (PAR) by stand during the experiment

Year	Season	Stand age	T_{mean} ($T_{\text{min}} - T_{\text{max}}$) (°C)	D_{max} (Pa)	PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
2001	Spring	10 and 54 years	15.8 (10.1–21.2)	1446.1	735.5
		32-years	16.5 (11.5–21.4)	1454.3	780.2
	Summer	10 and 54 years	19.2 (13.4–25.0)	1742.2	687.9
		32 years	20.0 (15.2–25.3)	1723.1	734.0
	Autumn	10 and 54 years	9.9 (5.5–15.0)	739.7	399.7
		32 years	10.7 (6.7–15.5)	744.6	391.4
2002	Winter	10 and 54 years	9.1 (5.3–13.9)	669.6	334.6
		32-year	9.7 (6.1–14.1)	645.7	330.3
	Spring	10 and 54 years	13.9 (8.3–19.9)	1313.9	655.0
		32 years	14.6 (9.6–19.8)	1332.7	670.4
		91 years	14.1 (8.36–20.1)	1401.4	667.0
	Summer	10 and 54 years	18.5 (13.1–24.4)	1594.6	667.7
		32 years	19.2 (14.5–24.4)	1661.1	721.6
		91 years	19.1 (13.8–24.9)	1700.5	660.3
	Autumn	10 and 54 years	11.6 (7.5–17.2)	827.2	338.5
		32 years	12.3 (8.8–16.5)	826.8	372.1
		91 years	11.6 (8.1–16.2)	745.0	312.7

3.2. Weather and soil water content

During the 2 years of the experiment, air temperature, daily maximum vapour pressure deficit, D_{max} , and photosynthetically active irradiance, PAR, showed minor differences between stands (Table 2). D_{max} spring and summer values in 2002 were 100 Pa lower compared with those of 2001. However, there was no noticeable difference in D between years, July 2001 values being slightly lower than 2002 while August values showed an opposite pattern (Fig. 4c).

Rainfall in autumn 2000 and winter 2000–2001 reached a value of 905 mm, which was higher than the 1950–2000 average for the same period (548 mm) and so the water table remained close to the ground surface. Consequently, in 2001, soil water content was high in spring, then decreased in mid-summer below the threshold value corresponding to soil drought expected in this area (85 mm, corresponding to a soil moisture deficit of 40% (Granier and Loustau, 1994)). At this time of the year, the onset of soil drought was simultaneous in all stands (Fig. 4b). By contrast, the cumulative rainfall during autumn 2001 and the following winter was exceptionally low (289 mm, i.e. 259 mm below the 1950–2000 average) and the water table remained below the root zone depth. Consequently, θ in spring and early summer 2002 was lower than in 2001 and differed among stands. In particular,

soil water content was markedly lower in the 32-year-old stand during spring and summer 2002, due likely to agricultural practices close to this site (irrigation and pumping groundwater). In 2002, the threshold value for the onset of soil drought and stomatal closure was reached on April 20th, June 20th, June 23rd and July 27th in the 32-, 54-, 10- and the 91-year-old stands, respectively. Measurements of predawn needle water potential accordingly showed that trees were stressed both in summer 2001 and 2002 ($\Psi_p < -1$ MPa). Further, in mid-summer 2002, Ψ_p of the 32-year-old stand was lower than that in the other stands, reaching a minimum value of -2.0 MPa (Delzon et al., 2004a), when transpiration rate was zero and $\theta = 40$ mm.

3.3. Sap flux density variations

The daily pattern of sap flux density was roughly similar between trees, but the magnitude of the mean sap flux density differed between stands (Fig. 2). The between-tree variability of Q_s was greater in young stands than in older stands and Q_s was independent of stem size ($P > 0.05$) within each stand. In 2001, sap flux density per unit sapwood area was lower for the 54-year-old stand than for the 10- and 32-year-old stands, at least for the period April to August when sap flux density was the highest ($P > 0.05$, Fig. 3a). Conversely,

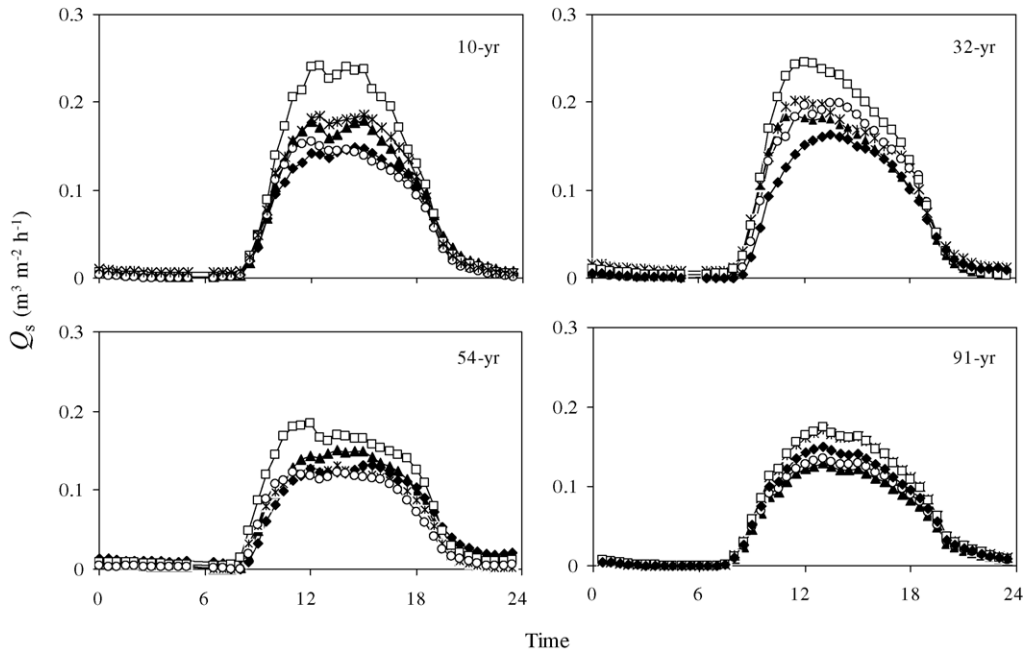


Fig. 2. Diurnal variation of sap flux density, Q_s , of individual trees measured in four stands along the maritime pine chronosequence. The four plots show a typical clear day on 26th April 2002 with a $D_{max} = 1342$ Pa and maximum PAR = $1845 \mu\text{mol m}^{-2} \text{s}^{-1}$ with soil water availability not limiting ($\theta = 150 \text{ kg m}^{-2}$). Each symbol corresponds to a single tree.

in 2002, sap flux density was not significantly different between stands except for the 32-year-old stand (Fig. 3b), where sap flux density was lower and water soil deficit from June to August was higher.

3.4. Overstorey transpiration

For all stand ages, the annual course of transpiration, E_T , followed the same seasonal pattern (Fig. 4a).

The increase in E_T at the beginning of the growing season coincided with the period of needle expansion, while the summer decline in E_T coincided with the drought period ($\theta < 85 \text{ mm}$). The highest transpiration rates, $E_{Tmax} = 3.8, 2.3$ and 1.1 mm d^{-1} for the 10-, 32- and 54-year-old stands respectively, occurred in June 2001 due to high vapour pressure deficit and PAR. The annual course of transpiration was dramatically different between the 2 years of

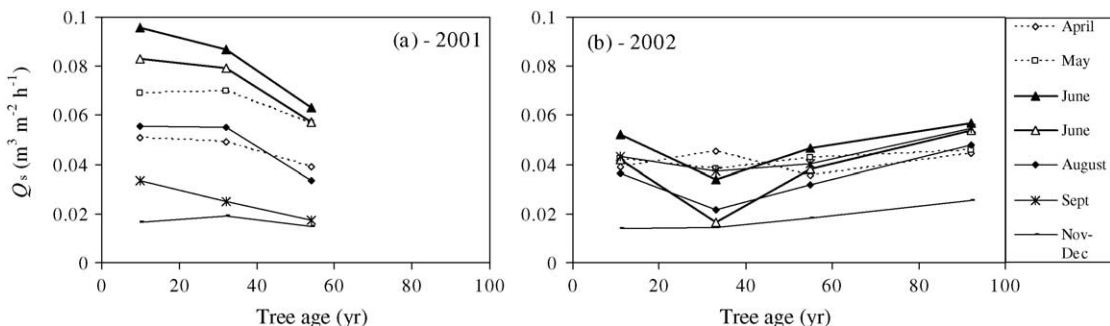


Fig. 3. Changes in mean monthly sap flux density, Q_s , with stand age in 2001 (a) and 2002 (b). Each point corresponds to the mean of all sample trees per stand during one month.

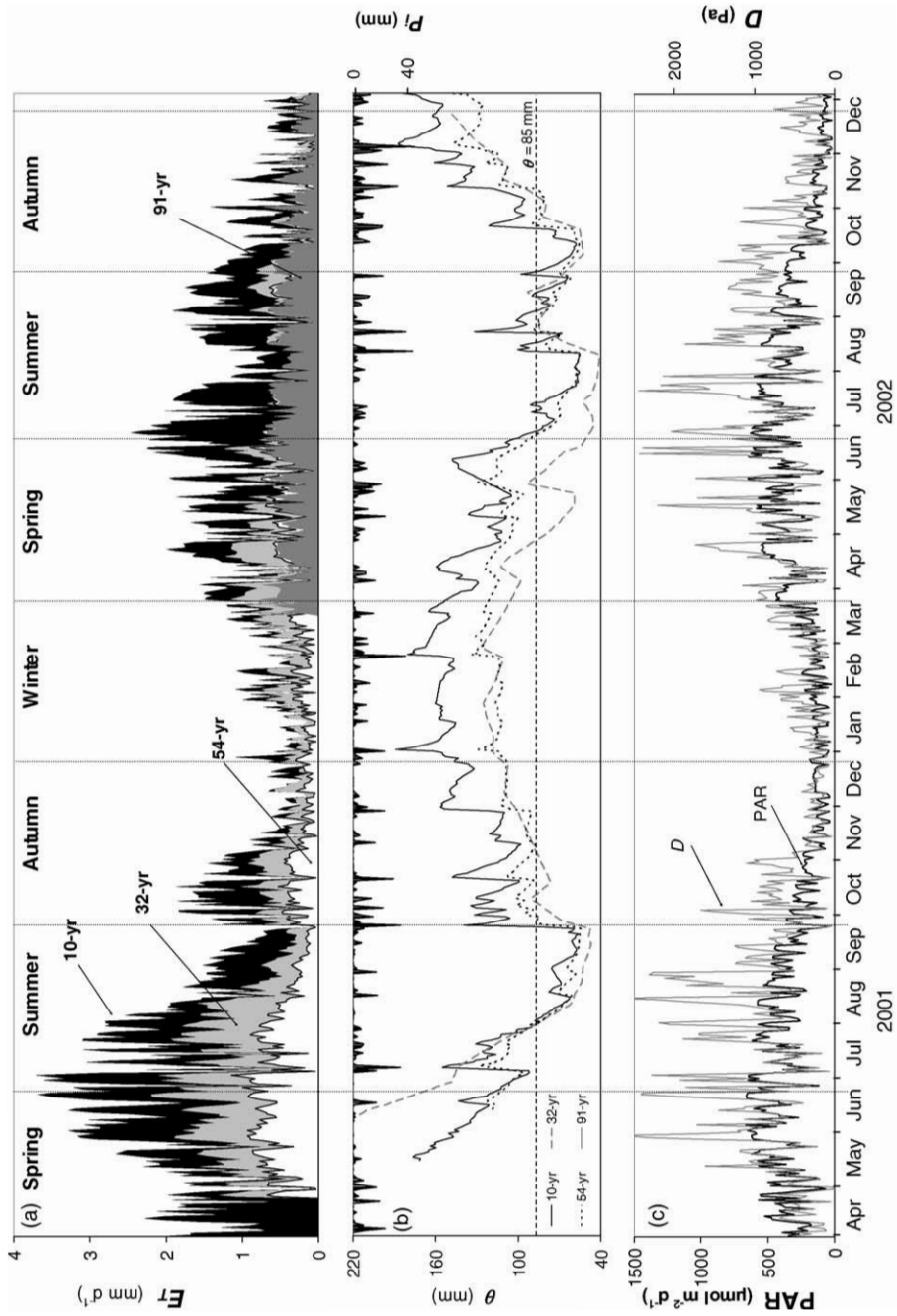


Fig. 4. Seasonal course of (a) overstorey transpiration, E_t , (b) soil water content from 0 to 0.8 m depth, θ , rainfall, P_i (vertical bars), and (c) photosynthetic active radiation, PAR, and daily mean vapour pressure deficit, D , of the four stands over the 2 years of the experiment (2001–2002). For clarity, P_i , PAR and D are only shown for the 10-year-old stand. Seasonal periods are bounded by solstices and equinoxes.

measurements (2001 and 2002). Transpiration rates remained at very low values throughout spring–summer 2002 in all stands compared to values in 2001, and it is unlikely that the minor differences in vapour pressure deficit observed between the two growing seasons could explain these differences.

We then examined the differences in transpiration rates between stands of different age. From spring 2001 to summer 2002, transpiration decreased gradually with age in the 10-, 32- and 54-year-old stands whereas in summer and autumn 2002, transpiration was only greater in the 10-year-old stand than the other ones. Transpiration in the 91-year-old stand was measured only after winter 2002, and was similar to that of the 54-year-old stand. The largest difference was observed in spring–summer 2001 when E_T of the 10-year-old stand was three times that of the 54-year-old stand. Through spring and summer 2002 when soil water content fell, the decrease in transpiration was larger for the 10-year-old stand than the 54-year-old stand, i.e. the seasonal change in transpiration was more pronounced for the young stand.

A comparison between total ecosystem evaporation (E) and overstorey transpiration (E_T) was done in the 32-year-old stand in 2001–2002 is shown in Fig. 5. Both E and E_T reached maxima at the end of spring, decreased in September 2001 and remained lower throughout 2002. Annual ecosystem water loss was less in the second year (333 mm) than in the first year (543 mm). For calculating annual sums of stand transpiration, linear relationships were established

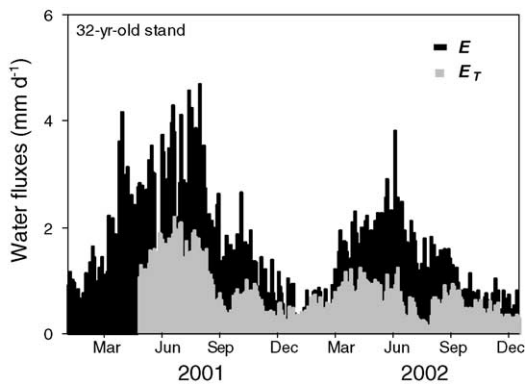


Fig. 5. Seasonal variation of the daily sums of overstorey transpiration, E_T , measured by sap flow, and total ecosystem evaporation, E , measured by eddy covariance in the 32-year-old stand during the two years of the experiment.

Table 3

Annual values of the overstorey transpiration, E_T , for the four stands in 2001–2002

Stand age	E_T (mm year ⁻¹)	
	Year 2001	Year 2002
10 years	508	344
32 years	296	177
54 years	144	124
91 years	–	127

Annual rainfall was 808 mm and 762 mm for 2001 and 2002, respectively.

between E_T and E to extrapolate estimates of stand transpiration at the beginning of 2001 when sap flow sensors were not installed and to further extent the data of transpiration for the 10- and 54-year-old stands. Annual overstorey transpiration markedly and gradually declined with stand age both in 2001 and 2002 (Table 3), E_T being approximately 70% lower in the two older stands compared to the youngest stand.

3.5. Transpiration per unit leaf area

In 2001, we observed a significant decrease in transpiration per unit leaf area, E_L , with stand age classes, E_L being systematically lower for old stands (Fig. 6a). Differences between ages were greater at high transpiration rates. Maximum values of E_L were lower for older stands, 0.08 and 0.05 at 32- and 54-year, respectively, versus 0.12 kg m⁻² leaf d⁻¹ in the 10-year-old stand. Not surprisingly, in 2002, differences in E_L between stand age classes were lower because of greater soil water stress conditions (Fig. 6b).

3.6. Leaf area index

Leaf area index decreased with stand age as did plant area index measured in summer 2001 and 2002 (Fig. 7a). It is noteworthy that PAI in 2002 was systematically lower than in 2001. The seasonal course of litterfall during both years 2001 and 2002 showed similar patterns for the five stands of different age (Fig. 7b). Furthermore, as a consequence of the higher leaf area index, annual litterfall was greater for young stands compared to old stands (for 2002, 0.361, 0.312, 0.290 and 0.251 kg m⁻² year⁻¹ for the 10-, 32-, 54- and 91-year, respectively). However, the seasonal pattern of litterfall was different between 2001 and 2002, showing one high peak in 2001 and two peaks in

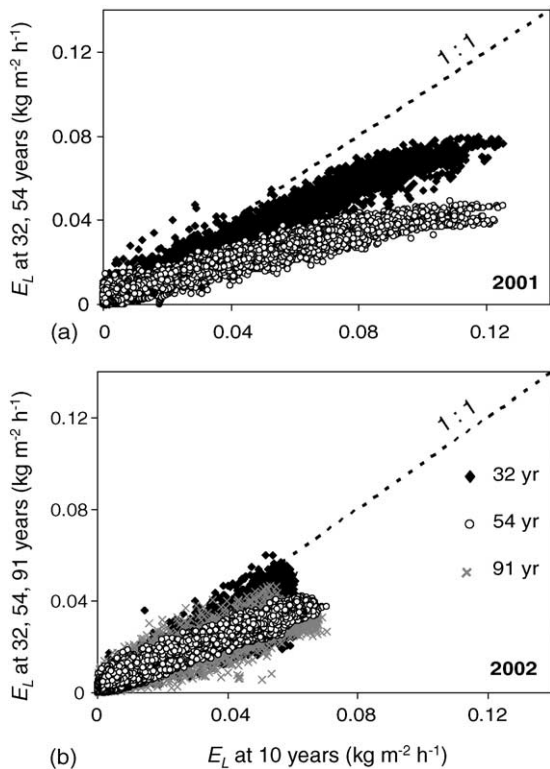


Fig. 6. Transpiration per unit leaf area, E_L , in the 32-, 54- and 91-year-old stands vs. transpiration in the 10-year-old stand in 2001 (a) and 2002 (b).

2002. Annual litterfall increased by 16, 20 and 5.6% in 2002 compared to 2001 for the 10-, 32- and 54-year-old stands, respectively. In 2002 for each stand, trees lost a significant quantity of needles early in the season (March), which is unusual, and may be due to the severe water stress that occurred in the previous summer 2001. This unusual needle mortality was observed at all sites, and corresponded to reductions in LAI of 0.3, 0.46 and 0.65 for the 32-, 54- and 10-year-old stands, respectively. These results were corroborated by inter-annual differences in PAI.

4. Discussion

4.1. Evidence of decline in overstorey transpiration with age

Maritime pine stands of different age had a similar seasonal course of water use. Transpiration rates were

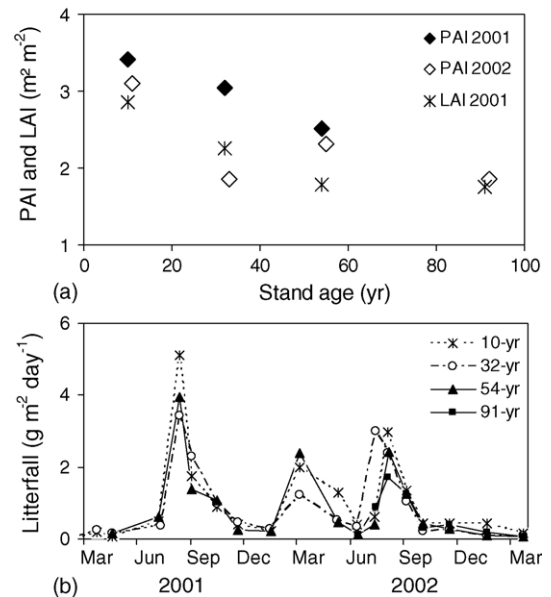


Fig. 7. (a) Relationship between plant and leaf area index (PAI and LAI) and stand age across the chronosequence. PAI was estimated from measurements of total light interception using an optical method (DEMON) and LAI was estimated using allometric relationships. (b) Seasonal course of litterfall in the four stands in the chronosequence.

slightly lower than those found for an 18-year old maritime pine stand where $E_{Tmax} = 3.9 \text{ mm d}^{-1}$ (Loustau et al., 1990) and for a 64-year-old maritime pine stand in Portugal where $E_{Tmax} = 2.6 \text{ mm d}^{-1}$ (Loustau et al., 1996), compared to 1.1 for the 54-year-old stand in the present study. Apart from differences in rooting depth and soil properties, this may be explained by the fact that no correction for radial profile of sap flow was taken into account in these two earlier studies. This may have led to overestimation of whole-tree transpiration, especially in older stands.

Our study showed a significant decrease in stand transpiration with age and it is unlikely that the negligible differences observed in vapour pressure deficit can explain this effect. At the extreme, annual transpiration for the 54-year-old stand was about 70% less than that for the younger stand in 2001. Declines in transpiration with age have been observed in other species, e.g. *Picea abies* where transpiration was about 40% less in 40-year-old stands compared with 140-year-old stands (Alsheimer et al., 1998; Köstner, 2001). Vertessy et al. (2001) reported annual

transpiration values for 15- and 240-year old *Eucalyptus regnans* stands of 733- and 249 mm year⁻¹, respectively (66% decrease). Dunn and Connor (1993) observed a gradual decrease in transpiration with stand development, from 679 mm year⁻¹ at age 50 to 296 mm year⁻¹ at age 230 (56% decrease) for this species and Roberts et al. (2001) observed the same trend for *Eucalyptus sieberi*. In contrast, transpiration of Siberian *Pinus sylvestris* forests increased with increasing age from 28- and 64-year before declining in older stands (Zimmermann et al., 2000), and no decline was found for *Pinus ponderosa* (Irvine et al., 2002) with increasing age. However, in the latter study, no difference in transpiration was found between 14- and 250-year-old stands due to higher LAI in the old stand (2.1 m² m⁻²) than at the young stand (1.0 m² m⁻²).

4.2. Relative role of factors inducing decreases in overstorey transpiration

The observed age-related decline in overstorey transpiration can be explained by (i) the decrease in leaf area index with increasing stand age and also by (ii) the fact that old and tall trees (54- and 91-year-old stand) had lower overall rates of transpiration per unit foliage area than young and small trees (10- and 32-year old). This is because water must be transported 20 m higher in the older trees than the young ones, increasing hydraulic constraints. To maintain functional water transport, homeostasis in the water potential gradient occurs, by decreased stomatal conductance and consequently lower transpiration as reported previously (Delzon et al., 2004a). Regulation of transpiration in small and tall maritime pine trees by stomatal conductance has an important impact on the water use by stands of different ages. A similar decrease in transpiration per unit of leaf area has been observed in various species with increasing tree height and may explain part of the decline in transpiration observed for European beech (Schafer et al., 2000), Ponderosa pine (Hubbard et al., 1999; Ryan et al., 2000) and Norway spruce (Alsheimer et al., 1998; Köstner, 2001; Köstner et al., 2002). Roberts et al. (2001) reported a decline in water use for *Eucalyptus sieberi* stands, with rates of transpiration per unit leaf area of 0.71, 0.36 and 0.22 mm m⁻² d⁻¹ for 14-, 45- and 160-year-old stands, respectively.

With regards to the relative role of changes in transpiration per unit leaf area (via decreased stomatal conductance) and in stand leaf area with forest age, we expressed transpiration and leaf area index of each stand relative to the values in the 10-year-old stand. These ratios were calculated for each stand under similar conditions of soil water availability in 2001. Ratios of transpiration per unit leaf area for the 32- and 54- to 10-year-old stands were equal to 0.73 and 0.45, respectively, whereas the respective ratios of transpiration per unit ground area were 0.58 and 0.28 and the leaf area index ratios were 0.79 and 0.62. In other words, E_L and LAI decreased by 55 and 38%, respectively, between the 10- to 54-year-old stands. In conclusion, the decrease in stomatal conductance and transpiration per unit leaf area with increasing tree height and age was an even more important factor in explaining the decline in water use. In contrast, Law et al. (2001) found for Ponderosa pine that LAI differences were the most likely factor influencing changes in ecosystem water loss.

4.3. Drought impacts on transpiration for different stand ages

We investigated the possible causes of inter-annual differences in transpiration, with water use remaining low in all stands during 2002. Two reasons could explain these differences between years. First, the needle fall occurred in March 2002 reduced substantially the leaf area index (lower PAI in 2002, Fig. 7) throughout the year and so restricted transpiration compared to those of 2001. Lower transpiration rates, which accompany reductions in leaf area, should reduce the drought effect, maintaining water potentials at a safe margin above critical values. Second, in late spring and summer 2002 the lower soil water content may contribute further to the inter-annual difference in transpiration, especially in July when the average value of θ was about 70 mm compared to 115 mm in July 2001 at the 10-year-old stand. The low transpiration per unit of leaf area (Fig. 6) confirmed that a stomatal closure occurring under drought also contributed to transpiration's decline.

To understand if drought has a similar impact on the stand water use at different ages, we compared only the 10- and 54-year-old stands where sap flow was monitored throughout the 2 years. We excluded the

32-year-old stand from the analysis because of the extreme soil water deficit which occurred in this stand and induced a steeper decrease in water use between 2001 and 2002 compared with the other stands. Our results show that transpiration in the 54-year-old stand decreased less as a result of drought than in the younger stand, i.e. soil water deficit had a greater impact on the rate of transpiration in the younger stand. Three hypotheses may explain this behaviour: (i) stomatal conductance in young trees is more sensitive to drought than that for old trees (Oren et al., 1999b), (ii) a hydraulic lift can occur, so reducing soil water deficit (Dawson, 1996), and (iii) leaf area dynamics in young trees is more affected by drought than that for old trees. Delzon et al. (2004a) demonstrated that the decrease in stomatal conductance was steeper for small (10 years) than tall maritime pine trees (54 and 91 years) with increasing water stress. Consequently differences in transpiration rate per unit leaf area between tree sizes decreases under limited soil water availability. These results support the first hypothesis. Then, similar courses of soil water content occurred during night-time and day-time between stands (data not shown), suggesting the absence of hydraulic lift. For all tree ages, root systems extended no further than a depth of 0.8 m because of the existence of a cemented layer. Therefore, trees do not have access to ground water under drought periods. This means that the second hypothesis did not apply in our chronosequence, because same amount of available water and hydraulic lift were available for trees of different age or size and this can not explain the smaller decrease in water use under drought conditions for old stands. Tree spacing is significantly higher in old stands compared with young stands and it is known that thinning has a positive effect in reducing tree water stress (Medhurst et al., 2002) with more pronounced needle fall in stands with more stems per unit area (Aussenac and Granier, 1988; Cutini, 1996). On the other hand, cavitation risk, inducing needle fall, could be more important in conditions of water stress for tall trees (old stands) as critical water potential is reached sooner due to the larger gravitational gradient. We cannot therefore accept or reject the third hypothesis without further investigation focusing on inter-annual variations in LAI to determine whether leaf area of young trees decreases more due to higher needle loss

and/or lower rates of needle expansion in response to water stress.

4.4. Overstorey contribution to total ecosystem water loss

In the 32-year-old stand, we were able to quantify the contribution of trees to the total ecosystem evaporation from simultaneous measurements of forest evaporation (E) and overstorey transpiration (E_T), estimated by eddy covariance and sap flow techniques, respectively. The water loss from the overstorey accounted for approximately half of the total transpiration, overstorey/ecosystem transpiration ratios being 0.55 in 2001 and 0.53 in 2002. Similar results were found for a Siberian pine forest, where stand transpiration was also about 50% of the ecosystem water loss (Kelliher et al., 1998; Zimmermann et al., 2000).

Does the contribution of overstorey transpiration to ecosystem water fluxes remain constant throughout our chronosequence? To estimate total ecosystem evaporation in all stands, we used a water balance approach, such that:

$$P_i - \Delta\theta = E + R \quad (4)$$

where P_i is rainfall, $\Delta\theta$ the change in soil water storage, E the total water loss by the ecosystem (soil evaporation plus transpiration and interception by both the overstorey and the understorey) and R drainage. Values of E were calculated for each stand as the residual of Eq. (4) only for a period of conditions of low and constant soil water content (summer 2001 only) allowing the assumption of negligible drainage from the root zone. Values of E were 134, 150 and 137 mm for the 10-, 32- and 54-year-old stands, respectively (eddy covariance measurements in the 32-year-old stand during the same period gave similar values, evaporation rates were about 130 mm). No age-related change in E was found throughout the chronosequence, even though overstorey transpiration decreased significantly from 106 to 25 mm between the 10- and 54-year-old stands at the same time, i.e. the overstorey contribution to the total ecosystem evaporation decreased with stand age. Consequently, the compensating effects of increased evaporation from the other components of E , i.e., understorey and soil surface

evaporation occurred in the older stands. Moreover, there was some evidence in our chronosequence that the understorey, consisting only of gramineous species, became an increasingly important component of the forest water use with increasing forest age. We observed an increase in understorey leaf area index in relation to increasing light availability as stands aged (20% increase from 32- to 54-year, Delzon, unpublished data). Loustau and Cochard (1991) reported high rates of understorey transpiration and this was an important contribution (33% of stand transpiration) to total evaporation for an 18-year old maritime pine stand. Consequently, we assume that an increase in understorey transpiration may compensate for the decrease in overstorey transpiration as stands become older. In coniferous forests, the understorey has been found to counterbalance the decrease in tree transpiration with increasing age for *Pinus nigra* (Mencuccini and Grace, 1996) and *Picea abies* (Köstner, 2001) because forest management practices induced more available energy to be transmitted by tree canopy and, consequently, a higher development of understorey leaf area (Kelliher et al., 1990; Whitehead et al., 1994). Moreover, Roberts et al. (1982) showed that the lower transpiration from Scots pine compared to the Corsican pine was offset by greater losses from the understorey.

5. Conclusion

Our extensive measurements of sap flow showed a marked decline in stand transpiration with age in maritime pine forests due to decreases in both stomatal conductance and leaf area. We showed the impact of inter-annual variation in LAI on water use and the need to understand the effect of drought on needle fall. The quantification of age-related changes in overstorey transpiration in this study will be very useful to better estimate regional-scale water use. In addition, our findings suggest that the total ecosystem water loss remains constant in ageing forests due to an increase in understorey leaf area, thus increasing understorey transpiration. However, further investigation is needed to quantify the contribution of each ecosystem component to the total ecosystem water loss with increasing stand age.

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