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Soil water dynamics in an oak stand

I. Soil moisture, water potentials and water uptake by roots

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Abstract

Soil water dynamics under a mixed stand of mature sessile and pedunculate oaks were studied both under natural conditions and during imposed water shortages in a lysimeter. Root densities of each species were described in situ by counting roots in the trench surrounding the dry plot. Soil water contents and potentials, and pre-dawn leaf water potentials (Ψ_{wp}) were monitored during three successive years. Soil water retention characteristics were obtained from field measurements of water potential and water content. The decreasing rooting density with depth was strongly related to soil physical properties. The root system was separated into two compartments by a layer with a high clay content. The deepest soil compartment was mainly explored by fine roots. Neutron probe measurements allowed the detection of variations in water content down to a depth of 2.00 m. The distribution of water uptake among the different soil layers changed when drought increased. Water was extracted from the deepest reservoir, and capillary rises even occurred after partial water depletion in the upper part of the soil. Seasonal trends of pre-dawn leaf water potential generally matched those of soil water potential in the wettest rooted zone, which was at −140 cm. In the upper, dry, horizons, the sharp loss of soil hydraulic conductivity reduced water transport to roots leading to impossible equilibrium between roots and soil at pre-dawn. Finally, Ψ_{wp} presented a low sensitivity to variations of total soil water content between 40% and 100% of extractable water. Below this threshold, Ψ_{wp} decreased sharply to a minimal value of about −2.0 MPa.

Introduction

Sessile (*Quercus petraea* (Matt) Liebl.) and pedunculate (*Quercus robur* L.) oaks are European oak species that grow together in many places in France. Although previous studies have established that sessile oak has a clear competitive advantage over pedunculate (Lévy et al., 1992), in situ ecophysiological measurements have shown no major difference among both species under natural conditions (Bréda et al., 1993b); both species are tolerant to water stress, as shown by their ability to maintain significant transpiration and assimilation during water shortage. Nevertheless, differences in rooting depth of co-occurring sessile and pedunculate oaks may be involved in their efficiency of soil water uptake, leading to a different competitive achievement in mixed stands. For a given species, the actual water available to trees primarily depends upon root density and distribution (Crombie et al., 1988; Callaway, 1990). Water uptake by roots also depends upon the nature of the soil and on water potential gradients across three components of the root-soil system in series: the soil, a root-soil air gap and the root (Nobel, 1991).

Since it is difficult to directly measure root xylem potential, pre-dawn xylem water potential has been interpreted as a measure of the effective soil potential at the surface of the root system (Aussenac and Granier, 1978; Ritchie and Hinckley, 1975). The interpretation of the pre-dawn potential measurements still remains difficult especially for deeply-rooted forest species, because roots are non uniformly distributed in soil layers that differ in water content and hydraulic conductivity. Aussenac et al. (1984) showed that the pre-dawn water potentials of Douglas fir matched to the soil water potential at increasing depths during a progressive drought. Some authors compared the tolerance to water stress of species markedly differing in their rooting depth (Cermak et al., 1980; Goulden, 1991) and concluded that they displayed contrasting patterns of access and utilisation of water, leading to differences in sensitivity to drought. The changes of pre-dawn water potential over a growing season are strongly related to the effective depth where the maximum of root absorption occurs. Nevertheless, little data is yet available to illustrate this pattern during increasing drought, soil rehydration or under various stand densities.

The dynamics of root absorption have to be analysed in relation to soil water vailability. Two different approaches may be used, both quantifying changes in soil water content and plant water uptake: direct measurement, or modelling. A number of models describing the water flux in the soil from the Darcy-Richard equation combined with an extraction term accounting for root water uptake are available (Molz, 1981). In these models, the root distribution throughout the soil profile is the essential parameter for the description of water uptake from different horizons. Thus, most of the studies on plant and soil water relationships have involved root system descriptions and water uptake measurements (Gardner, 1960). Nevertheless, some work combined both water uptake and soil water potential measurements (Rambal, 1984)

In this paper and its companion (Barataud et al., 1994), we describe observations and measurements of responses of adult trees in a mixed oak stand, under contrasting soil moisture conditions. Here we analyse (1) the rooting profile, (2) the seasonal pattern of soil water potentials and soil water content and (3) the pattern of root water uptake during drying cycle. The significance of the measured pre-dawn water potential is also discussed. The objective of the second part (Barataud et al., 1994) is to develop a model from these field data to quantify the soil-root impedance and its variations with drought.

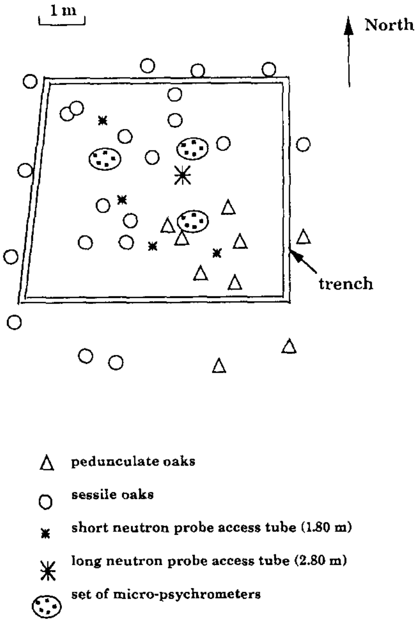

Fig. 1. Map of the dry plot delimited by a trench, showing the distribution of oaks from both species, and location of soil water content (neutron probe access tubes) and potential (micro-psychrometers) measurements.

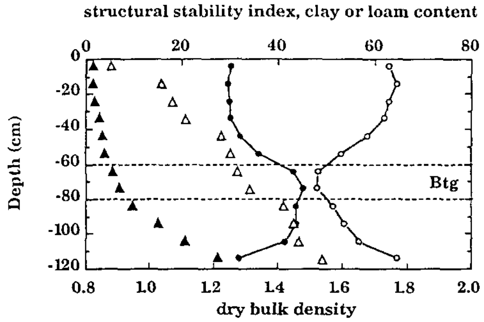

Fig. 2. Pedological description of the soil: granulometric composition in percent (clay: solid circles, loam: open circles), structural stability index (solid triangles) and bulk density profile determined using direct sampling on cylinders (open triangles).

Material and methods

Forest site and experimental design

The study was carried out in a 30 to 40 yr-old oak stand in the Champenoux forest, France (48°44 N, 6° 14 E, elevation: 237 m). Sessile (*Quercus petraea* (Matt) Liebl.) and pedunculate oaks (*Quercus robur* L.) were co-occurring, the former being more abundant than the latter. A simplified lysimeter covered by a water-tight roof was built to apply an artificial drought to both

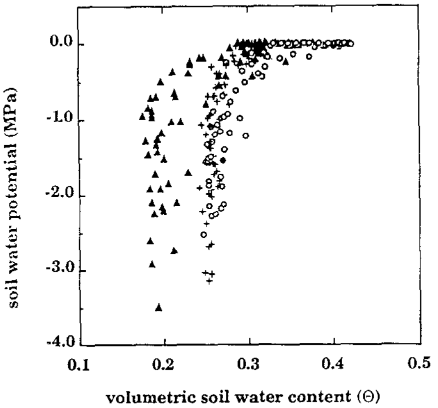

Fig. 3. Soil water retention curves established in situ by using simultaneous measurements of soil water potential (tensiometers and micro-psychrometers) and soil water content (neutron probe) at five depths (−25 cm: solid triangles, −50 to −80 cm: open circles, −110 to −140 cm: crosses). Each point represents paired observations taken using micro-psychrometre and neutron probe, on a single day. Data were obtained during 1992 and 1993 while water content fell during drought.

species. It consisted of a 5 × 5 m square including 17 trees and was surrounded by a 1.60 m deep trench (Fig. 1). This experimental plot has been extensively described in Bréda et al. (1993b). The two species were not intermixed inside this dry plot, but naturally separated into two groups. The comparative study was done during three successive growing seasons from 1991 to 1993. Concurrently to this drought experiment, another experiment was performed to analyse the effects of thinning on the water relations and on stand water balance of sessile oak. The study area was divided in two sub-plots 0.15 ha each, one a control, the other thinned, with basal areas of 24.6 m^2 ha^{-1} and 17.6 m^2 ha^{-1} respectively (see Bréda et al., 1995 for a description of this experiment).

Soil description

The oak stand was grown on a luvisol (F.A.O.), developed on a deep loam. The top horizons, consisting of a silty clay loam, presented a crumb structure. Hydromorphic spots appeared below 30 cm. A clay enriched horizon (B_{tg}), with a clay content of about 45%, bordered this upper compartment between 60 and 80 cm depth (Fig. 2). Below 1 m depth, the clay content decreased while bulk density, determined using direct sampling with cylindrical samples, increased continuously to 1.55 at 1.15 m depth. The structural stability index of the soil was measured using an aggregate breakdown procedure by different liquids (Henin et al., 1956); it increased slightly between 0 and −60 cm, and much more below (Fig. 2). It indicated a good stability between 0–30 cm, that fell into instability as the bulk density increased, to become unstable below 90 cm.

Root densities

The vertical distribution of the root system for both species was described in situ during June 1991. Roots were counted on the vertical face of the trench, using a 10 × 10 cm grid. This grid was applied and fixed on the observation walls, after roughening the soil surface using a wire brush in the top horizons or a dagger in the deeper and more compact ones, in order to clear the roots along 1 or 2 cm. Exposed roots were classified into five diameter classes: < 3 mm, from 3 to 5 mm, from 5 to 10 mm, from 10 to 20 mm, and > 20 mm. Root diameter was measured using a calliper. No attempt was made to measure bigger roots, which are assumed not to be involved in the water uptake. Each root count was 160 cm deep × 120 cm large, i.e. a 1.92 m^2 surface. Three replicates were on the east side of the lysimeter where pedunculate oaks were located, and three on the west side for the group of sessile oaks (Fig. 1). Root density was expressed as number of roots m^{-2}. Another root counting was made in a pure sessile oak plot from the same stand in a 17 m long and 140 cm deep trench, using an identical description. Finally, soil samples were taken deeper, every 10 cm until 200 cm using a borer, in order to detect the presence of deep roots.

Soil water content

Volumetric soil water content was monitored using a neutron probe (Nordisk Elektrisk Apparatfabrik, Denmark). Counts were logged every 10 cm for the upper 100 cm, and every 20 below. A polyethylene shield was used for the measurements at −10 cm. The lysimeter contained 5 access tubes, four 1.80 m long and one central tube of 2.80 m (Fig. 1). Tubes in the control (3 replicates) and in the thinned plots (13 replicates) were 1.40 and 1.60 m long, respectively. Each treatment included one 2.60 m access tube. Measurements were performed every week during the growing season. Soil moisture profiles are expressed as volumetric water content (Θ) at different depths, and were used to compute the variation of water reserve (ΔR) between dates t_1 and t_2 calculated for a given soil layer using Equation [1]:

$$\Delta R = [\Theta \times z]t_2 - [\Theta \times z]t_1 \qquad (1)$$

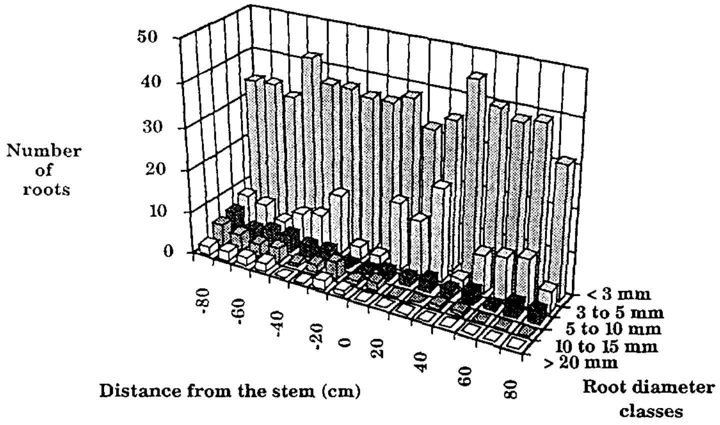

Fig. 4. Lateral distribution of the number of roots from each side of the stem of a sessile oak. The description was made every 10 cm from the stem (reference distance 0). Roots are divided into five diameter classes (< 3 mm: light grey bars, 3 to 5 mm: grey bars, 5 to 10 mm: heavy grey bars, 10–20 mm: black bars, > 20 mm: white bars).

where z is the thickness of soil layer expressed in mm or relative extractable water (REW) of the total soil depth using Equation [2]:

$$REW = (R - R_{min})/(R_{max} - R_{min}) \qquad (2)$$

where R is the actual soil water content, R_{min} the minimum soil water content observed in the dry plot during the experiments, R_{max} the soil water content at field capacity. Total soil extractable water ($R_{max} - R_{min}$) was 165 mm.

Soil water potential was measured in situ with ceramic soil micro-psychrometers (Wescor, Logan, UT). Readings were done in the psychrometric mode using a Wescor HR-33T dew point micro-voltmeter. Probes were fixed at the end of PVC tubes and vertically inserted into access holes bored using an extended masonry bit (diameter 1 cm). Five depths were studied, as defined by the soil horizons: −25, −50, −80, −110, −140 cm. Measurements from micro-psychrometers with zero offsets exceeding $3\mu V$ were rejected. Three sets of micro-psychrometers were installed in the dry plot, two sets in both control and thinned plots. Measurements were made early in the morning, from May to October during each field season.

Water retention curves were established using direct field measurements, coupling water content and tensiometry or micro-psychrometry. The water retention curves of 5 horizons established in situ are shown in Figure 3. All the horizons below −25 cm showed comparable curves characterised by a critical value of soil water content of about 0.30, below which water potential suddenly dropped; minimal soil water content was about 0.25. The top horizon (−25 cm) exhibited a more progressive decrease in soil water potential, minimal value of soil water content being about 0.20.

Leaf water potential. Three scaffolding towers (one in each treatment: dry, control and thinned) gave access to the tree crowns. Pre-dawn leaf water potentials (Ψ_{wp}) in the upper part of the crowns were measured weekly on 2 leaves per tree from two trees in both control and thinned plots using a pressure chamber. Diurnal courses of leaf water potentials were also measured (5 leaves per tree) along six bright days during the drought. Two or three trees from both species were measured in the dry plot. To allow a direct comparison with soil water potentials, tree water potentials were corrected for the gravimetric potential corresponding to the height of trees (0.16 MPa for 16 m). This corrected pre-dawn water potential was denoted by $\Psi_{wp}*$.

Stand transpiration, T, was computed from continuous sap-flow records (Granier, 1987) on 2 droughted trees of both species (Bréda et al., 1993a, b). This technique allows measurement of tree sap flux density, *i.e.* flow per unit of sapwood area (1 dm^{-2} h^{-1}). In the present study, results were expressed as mean daily transpiration (mm day^{-1}), by taking into account the trees sapwood area per unit of soil surface area (17.5 m^2 ha^{-1}). Sap flow measurements started on June 25 (day of year 177) and were stopped at the end of October (day of year 304).

Table 1. Mean number of roots per square meter, averaged along a 17 m long trench in a sessile oak plot

Depth (cm)	Class of roots diameter <3 mm	3–5 mm	5–10 mm	10–20 mm	>20 mm	total
0–70	270	31	17	13	10	348
70–140	60	4	2	0	0	66
Total	336	35	19	13	10	414
%	81%	8%	5%	3%	2%	

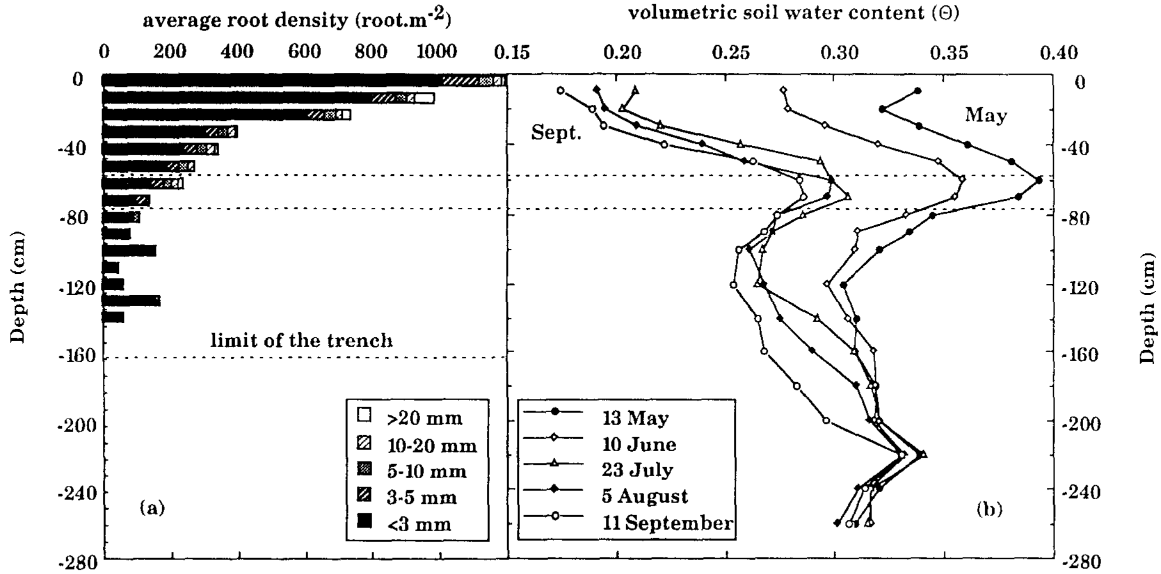

Fig. 5. (**a**) Rooting profile with depth based on root counts. The five diameter classes of Figure 3 are shown. (**b**) Volumetric soil water content (Θ) profiles computed from neutron probe data at different dates (1992) during drying in the lysimeter. Pre-dawn leaf water potential of oaks corresponding to the successive drying profiles were −0.41, −0.62, −1.20, −1.74 MPa. The clay enriched horizon (B_{tg}) is delimited with dotted lines.

Table 2. Root densities (root.m^{-2}, mean values and standard deviation) for the two oak species calculated over all soil profiles for each horizon; asterisk indicates significant differences between both species ($p < 0.1$)

Depth (cm)	Sessile oak	Pedunculate oak	Between species differences
total 0–120	330 (23)	447 (47)	P>S *
0–45	720 (89)	978 (46)	P>S *
45–85	174 (26)	229 (48)	NS
85–120	97 (6)	54 (15)	NS

Results and discussion

Rooting patterns of sessile and pedunculate oaks. The lateral distribution of the rooting averaged over 120 cm depth on both sides of a sessile oak is shown in Figure 4. As no effect of the distance from the stem was apparent, we assumed that the horizontal distribution of roots was homogeneous. This observation was consistent with the low spatial variability of water content among replicates (variation coefficients ranging from 2 to 5%, depending on the treatment) and can probably be ascribed to the high stand density. In contrast, a clustered distribution of old roots (oak and birch) was found by Bédéneau and Auclair (1989), but their root observation window was more than 1 m away from any stem. Nnyamah et al. (1978) found that the root density was highest close to the trunk and declined away from the trunk of Douglas fir. The heterogeneous root distribution of Nnyamah et al. (1978) may be related to the low stocking densities of the stands in both cases and

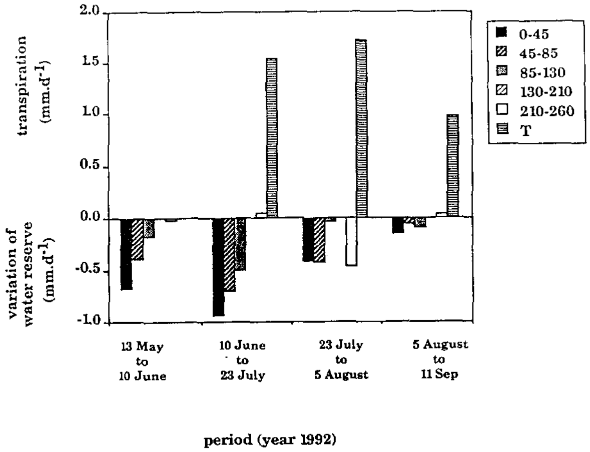

Fig. 6. Mean daily variation of soil water reserve (mm day^{-1}) computed over periods ranging between the two dates of soil water profiles presented on Figure 4. The soil was separated into five soil layers (0–45 cm, 45–85 cm, 85–130 cm, 130–210 cm and 210–260 cm). Mean daily transpiration (T, mm day^{-1}) of both species is also shown.

to the root system architecture. Moreover, coniferous trees are known to develop spreading root systems.

Fine roots (< 3 mm) represented 81% of the total; the proportion of the other classes (3 to 5 mm, 5 to 10 mm, 10 to 20 mm and > 20 mm) was 8%, 5%, 3% and 2% respectively (Table 1). The root system as observed along a 17 m trench could be divided into two vertical compartments separated by the clay enriched horizon (B_{tg}) (Fig. 5a): (1) the upper −70 cm of soil contained 85% of the fine roots and roots of all diameter classes, and (2) the deep compartment, quite exclusively composed of fine roots ranging from −80 cm to 1.60 m where measurements were stopped. The root density of each soil layer was inversely correlated to the structural stability index (Fig. 2) ($r^2 = -0.97$) or bulk density ($r^2 = -0.85$), and to a lesser extent to clay content ($r^2 = 0.45$). Table shows the decrease of fine root density according to the depth for the two oak species. The mean root density (all classes) on a 1.20 m deep profile was statistically higher for pedunculate oak than for sessile oak ($p = 95\%$): 416 ± 13 roots.m^{-2} for pedunculate against 330 ± 23 roots.m^{-2} for sessile oak. An horizon-to-horizon comparison of rooting of both species showed a significantly higher root density for pedunculate than for sessile oak in the upper horizons (0 to 45 and 45 to 85 cm). No significant differences could be found in the deepest soil layer (85–120 cm). The exponential decline in root densities with depth has been commonly described (Bédéneau and Auclair, 1989), and was in good agreement with the observations of Lucot and Bruckert (1992) on pedunculate oak growing on a deep colluvial soil. The vertical distribution of root diameter classes showing only fine roots below the clay enriched layer, is also consistent with their results.

Soil water profiles and water uptake during an increasing drought

Volumetric soil water content profiles recorded during 1992 for the 2.80 m long access tube in centre of the lysimeter between the two species are shown in Figure 5b. Because both species lay close together (inside a 5 m square), the patterns of water uptake during the drying cycle were not analysed separately for each species. Successive profiles were selected to illustrate the soil drying pattern. The wettest profile was observed on May 13, but also during other years in spring after drainage, so we assumed to be the field capacity. It showed a maximal water content ranging from 35% to 40% depending on the soil layers. Temporal variation of soil water content was measured down to −200 cm, corresponding to the bottom of the root system, deeper fine roots being observed on cores down to −200 cm. The deep vertical extension of the oak root system is well known (Abrams, 1990). On moist soils without limiting factors such as rock or a solidified soil level, a rooting depth of 1 to 5 meters has been reported by work carried out in Czechoslovakia cited by Cermak et al. (1980), or more recently by Lucot and Bruckert (1992). Nizinski and Saugier (1989) also mentioned the possible penetration of sessile oak roots inside limestone slab cracks. Bouten et al. (1992) described in a mixed oak and beech stand a decreasing root density with depth with a clear extra amount on top of a boulder clay. Our rooting description was limited by the depth of the trench. But it is possible to assess the probable depth of roots from our water uptake measured by using the neutron probe.

Comparing the soil water profiles observed on May 13 and on June 10 shows that the water content mainly decreased above the clay horizon (B_{tg}). Pre-dawn leaf water potentials were around −0.1 MPa, indicating a high water supply. Later, the profiles revealed a deeper water uptake: −160 cm on July 23, −200 cm on August 5 and September 11. Almost no water content variation was recorded in the upper part of the soil during this time. This pattern was observed every year in all treatments. During mid-September, the water content was strongly reduced in all zones containing

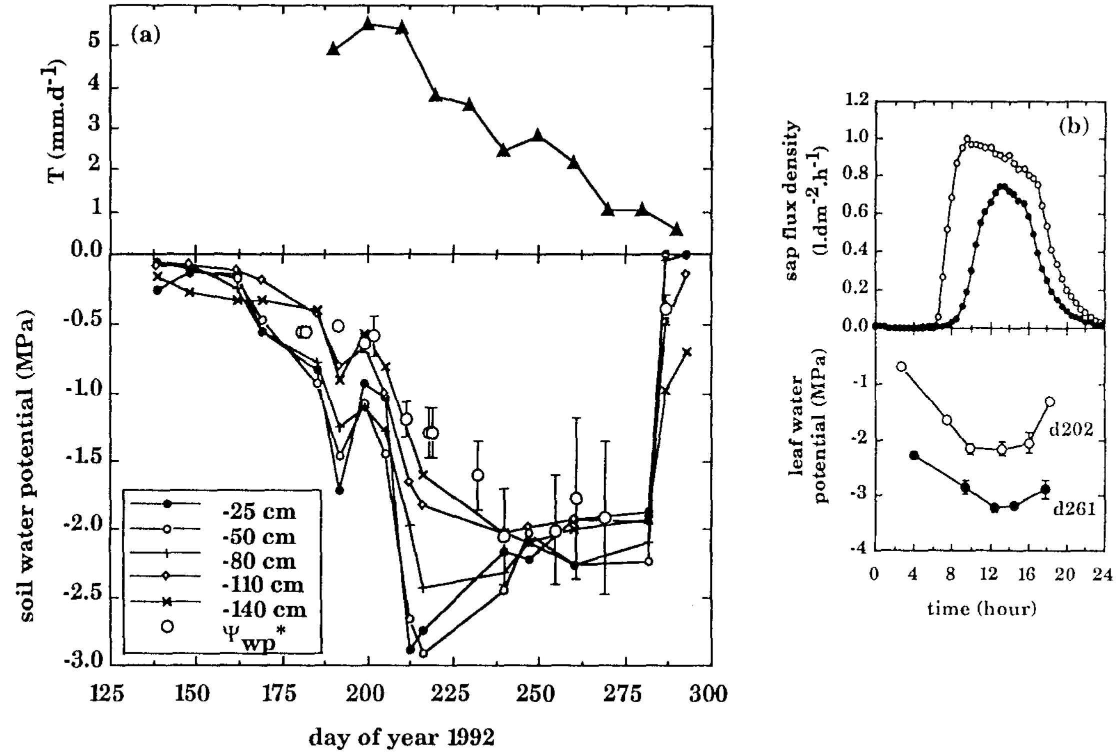

Fig. 7. (a) Seasonal variation during 1992 of: mean daily transpiration averaged over a 10-d period for sessile oaks in the dry plot (top), and of (bottom) soil water potentials measured using micro-psychrometers at five depths in the centre of the dry plot. Course of pre-dawn water potential measured on 3 surrounding sessile oaks expressed at the soil level reference ($\Psi_{wp}*$, MPa, open circles) is also shown. Vertical bars indicate standard error. (b) Example of diurnal courses of sapflux density (top) and of leaf water potential (bottom) during two bright days. These days correspond to high (d202) and low (d261) soil level availability conditions.

roots, and the trees experienced a severe water stress ($\Psi_{wp} = -1.74$ MPa on day 255, September 12). Soil water uptake showed a gradual downward shift as the soil dried. The deeper soil compartment was then the major supply zone, despite lower root densities than in the upper compartment. Similar observations have been made on young *Prunus persica* (Garnier et al., 1986) or on *Quercus coccifera* (Rambal, 1984). In our experiment, the shallow soil compartment located above the B_{tg} was emptied as early as mid-July; it should be noted that radial tree growth was stopped and gas exchange reduced from this date on (Bréda, 1994). The variations of water content in the 220–260 cm layer, probably unrooted, could be ascribed to capillary rises, allowing the maintenance of significant transpiration rates at maximal drought. Such a result was also observed by Bouten et al. (1992): an increasing water uptake in the lower part of the root zone (around -1.5 m) was measured although the root density did not increase with depth. They concluded that the amount of water from capillary rise was sufficient to maintain suitable conditions for water uptake in this zone.

In order to quantify water uptake during the periods described above, we calculated the variation of water reserve (ΔR) between successive dates for five soil layers using Equation 1, assuming that vertical flows of water were negligible. Soil layers were defined as follows: 0–45, 45–85, 85–130, 130–210 and 210–260 cm. During the two spring periods, the contribution of the upper layer (0–45 cm) was the most important (Fig. 6). More than 75% of water uptake was located above the B_{tg} horizon. No water uptake was detected in the two deepest layers. The mean daily sap measured over the period of 10 June to 23 July was about 1.6 mm day^{-1}; this was less than the sum of soil water depletion in each soil layer (2.2 mm day^{-1}), probably because of soil evaporation from both soil surface and vertical faces of the lysimeter. Between July 23 and August 5, water uptake was similar in all soil layers excepted in the B_{tg} that contained no more available water. The mean daily transpiration was about the same

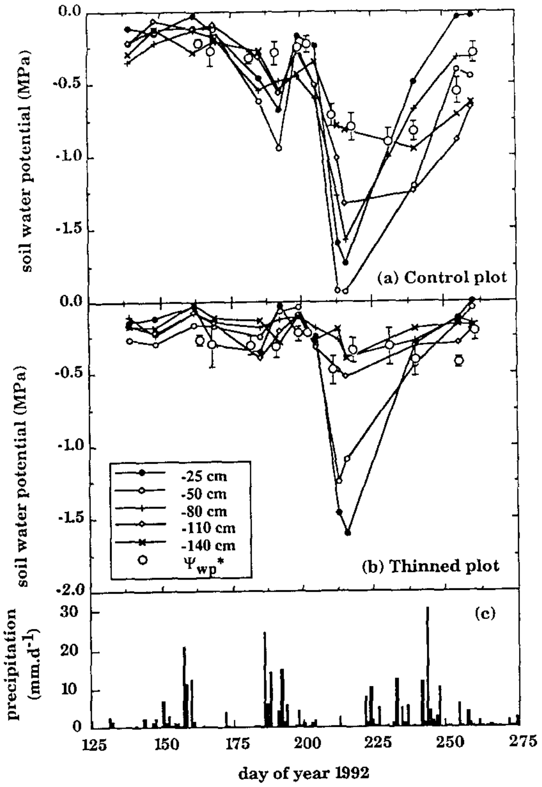

Fig. 8. Time-courses of soil water potentials in the thinning experiment. The data points represent the mean value from the two sets of micro-psychrometers at 5 depths as observed during the 1992 season. Pre-dawn water potential at the soil level reference (Ψ_{wp}*, MPa) of sessile oaks from the control plot (**a**) and from the thinned treatment (**b**) are over plotted (mean and standard error calculated from 2 trees from each plot). (c) Rainfall distribution during summer 1992.

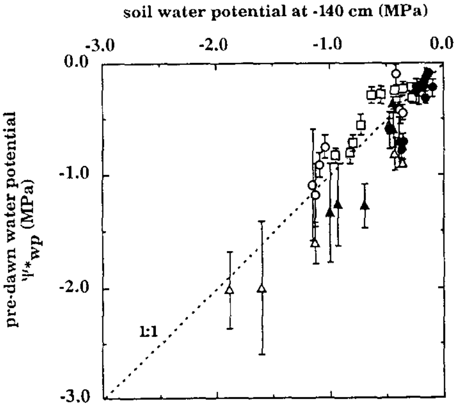

Fig. 9. The regression between measured soil water potential at −140 cm and pre-dawn water potential at soil level reference (Ψ_{wp}*, MPa) during dry periods from control plot (solid circles) and dry plot (open circles). Each point corresponds to a day, pre-dawn water potential is a mean value from 2 or 3 trees per treatment. Replicates for soil potential measurements are distinguished by using different symbols (data from 1992 and 1993 campaigns).

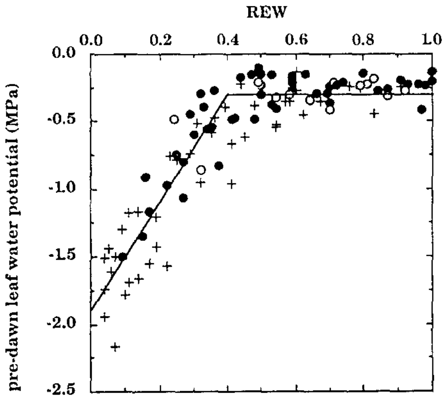

Fig. 10. Relative extractable water (REW) plotted against pre-dawn leaf water potential (Ψ_{wp}, MPa). Data are from drying periods for all treatments and years (solid circles: control plot from 1989 to 1993, crosses: dry plot from 1990 to 1993, open circles: thinned plot during 1992 and 1993). Each point is the average over 3 to 13 neutron probe measurements and Ψ_{wp} is measured on 2 or 3 trees (see material and methods). Mean value of Ψ_{wp} is −0.30 MPa for REW $\leq$ 0.4, and the linear regression below this threshold is $\Psi_{wp} = -1.90 + 3.98$ REW, $r^2 = 0.76$.

as during the previous period, 1.7 mm day^{-1}, while water depletion was 2.0 mm day^{-1}. In late summer, extraction was mainly located between the −140 and −200 cm soil layers, whereas water supply from the upper compartment was strongly reduced. Total water uptake was 0.7 mm day^{-1} and daily sap flow rate was 1.0 mm day^{-1}.

Soil and tree water potentials and reduction of transpiration during drought progression

A large variability of soil water potential was observed among sets of measurements, clearly related to the crown classes of neighbouring trees: the soil water potentials decrease much more in the vicinity of the dominant trees. Much smaller differences among neutron tubes were found for soil water content measurements, due to the sharp decrease of the soil water potential / Θ curves reported in Figure 2. Nevertheless, the water potential gradients were comparable among replicates. Figure 7a shows soil water potentials observed with the set of micro-psychrometers located in the centre of the dry plot. It shows that the soil water depletion occurred in to separate areas. Soil water potentials from −25 to −80 cm followed the same pattern as those of water content with a sharper and earlier decrease than in the deepest ones. Pre-dawn water potentials of trees were close to the soil water potential at −140 cm (Figs. 7 and 9). Only limited variations of tree and soil water potentials were observed during September (day of year 240 to 280); at this time, the trees experienced a severe water stress (−2.0 MPa). Transpiration was then reduced (Fig. 7a) as well as water uptake (see Fig. 5). This drought induced transpiration decrease was also observed on diurnal courses of sap flux densities at the tree scale; diurnal leaf water potential variations followed an inverse pattern (Fig. 7b). This daily data will be used for the calibration of the model presented in part II.

Time courses of soil water potential during 1992 in the two plots of the thinning experiment are shown in Figure 8. 1992 was characterised by a summer drought. In the control plot (Fig. 8a), a decrease of soil water potential from −0.15 to −0.63 MPa was observed in all the horizons since the end of June (day of year 175). After a short rainy period from day 186 to day 194 (71 mm, Fig. 8c), soil water potentials in the upper layers were restored to −0.25 MPa. The following dry period induced a large decrease of soil water potential in all horizons. The minimal value, observed between −25 to −80 cm, was below −1.5 MPa, while the soil water potential observed at −140 cm remained the less negative. As previously pointed out, pre-dawn tree water potential in the dry plot were close to the −140 cm soil water potential (Fig. 9); the variability of Ψ_{wp} among trees increased under maximal drought (Figs. 7a and 9). Another interesting feature is the delay in restoration of deep water potentials after re-watering (day 215): when soil water potential in the upper layer was about −0.1 MPa, it remained below −0.5 MPa in the deepest horizon. On the other hand, the thinned plot (Fig. 8b) showed such a sharp soil water potential decrease in the upper horizons (till −1.5 MPa at −25 cm) slightly later (after mid July, day of year 200), while the soil layers ranging from −80 to −140 cm remained above −0.5 MPa and stable all through the season.

Furthermore, pre-dawn leaf water potential of the trees never dropped below this threshold of −0.5 MPa, suggesting a higher water availability in the thinned plot. We plotted the pre-dawn leaf water potential Ψ_{wp} against the soil water potential (Ψsoil) measured at −140 cm, in the different treatments and years (1992 to 1993) (Fig. 9); a correlation was found. No differences among years and treatments were detected in this relationship. The regression was: $\Psi_{wp} = 0.79 \times \Psi_{soil}(-140)$, $r^2 = 0.74$. At pre-dawn, water potential is generally assumed to approach equilibrium within plants as well as between the plant and the soil surrounding the plant roots (Reich and Hinckley, 1989). This general assumption does not hold for tree species submitted to a drought, because roots exist in soil layers at a large range of soil water potentials. The good correlation between Ψ_{wp} and Ψ_{soil} at −140 cm is a consequence of the physical equilibrium of potentials occurring in the rooted level showing the highest soil water potential measured (−140 cm); extrapolation of retention curves at −160 cm from Θ (measurements led to a similar correlation. Aussenac et al. (1984) have also reported on Douglas fir that pre-dawn water potential was similar to soil water potential of the wettest, still rooted, soil layer; this species was characterised by a shallow rooting (0–60 cm). An interesting point in both experiments is that the equilibrium at dawn seems to be sustained by a few roots, while during the night the shallow roots are probably not able to absorb water, due to a high hydraulic resistance developed as soon as the soil dries. In the absence of root water potential measurements, this point will be tested using a modelling approach in part II (Barataud et al., 1994).

Nevertheless, new fine roots might be regenerated during the growing season and be involved in equilibrium at dawn, especially in the wettest horizon. Unfortunately, our experimental set-up was not suitable for a dynamic view of the rooted zone. If such an hypothesis is correct, our spring counting could underestimate the root density in this soil layer when the summer water stress occurred. Bédéneau and Auclair (1989) have observed a strong root growth activity during spring till July, followed by a period of reduced growth from August to September. Dynamic change in absorption capacity and variation in root lengths have also been observed on *Quercus rubra* (Johnson et al., 1984). The high growth rate of the young roots (more than 1 cm per day), at least for young oaks (Pagès, 1992), reinforces the hypothesis of lack of new roots in our root density estimate. Nevertheless, Reich et al. (1980) have noticed on mature trees (*Quercus alba*) that root growth was continuous from early March to late August, until soil water potential became limiting; they observed a significant decrease of root growth when Ψ_{soil} dropped below −1.0 MPa; root growth resumed later, following the recharging of soil moisture during fall.

A relationship was also observed between pre-dawn water potential and REW, with no difference between treatments, as shown in Figure 10. Pre-dawn water potential remained in the range of high relative extractable water from 1.0 to 0.4, it decreased strongly and linearly below the threshold of 0.4. Pre-dawn water potential thus appears to be insensitive to a decrease of the soil water content from field capacity to a 40% reduction of the soil water availability. Observations obtained from control, thinned or dry plots, and for different years were gathered on a single close relationship between Ψ_{wp} and relative extractable water. Both transpiration and Ψ_{wp} decreased below the same threshold of REW of 0.4 (Bréda et al., 1995). This value was also reported by Sucoff et al. (1974) in a dense red pine plantation and in an oil palm stand (Dufrêne et al., 1992). With *Pseudotsuga menziesii*, Black (1979) observed the same value (0.4) and Granier (1987) found 0.3 for a control as well as a thinned plot. This threshold of 30–40% of the maximal available water thus appears to be a general feature for trees, independent of the species or soil type, even if the sharp decrease of Ψ_{wp} below this value could have different consequences on tree physiology and growth, depending upon the drought sensitivity of the species. As we observed that Ψ_{wp} was similar to Ψ_{soil} (-140), it should be concluded that the REW(Ψ_{wp}) relationship is an equivalent representation of $\Psi_{soil}(\Theta)$ curve for the -140 cm layer. The threshold of 0.4 may be considered as a typical value for forest soil. For herbaceous species, reduction of transpiration appears much earlier, the threshold of REW being close to 0.6–0.7 (Schulze, 1986). For trees, the early reduction of relative extractable water (REW ranging from 1 to 0.4) had no consequence on the bulk leaf water potential of the trees, because of the large amount of deeper roots were able to maintain sufficient water supply. In other respects, it is known that many physiological variables (especially stomatal conductance and specific hydraulic conductance) are already reduced at low water deficits (Bréda et al., 1993a). Hence pre-dawn leaf water potential is a parameter that is unable to detect early stages of soil drying (Bréda, 1994).

Conclusion

Soil and rooting descriptions, soil water content and potential profiles under various drought conditions were analysed, and interpreted in terms of water uptake. The limitations when studying trends in water transfer resistance using only soil and leaf water potential measurements, are that the relative importance of soil-root resistance is uncertain in such a hierarchised soil-root system. In order to quantify the dominant water transfer resistances, depending on the soil conditions, a model describing the water uptake and the soil-root impedance is developed in the following paper (Barataud et al., 1994). This model is calibrated with the data of diurnal sap flux density and leaf water potential variations.

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