Original article

Water relations of adult Norway spruce (*Picea abies* (L) Karst) under soil drought in the Vosges mountains: whole-tree hydraulic conductance, xylem embolism and water loss regulation

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Summary — Drought-induced changes in whole-tree hydraulic conductances *(gL)* were monitored throughout a growing season in a 30-year-old stand of *Picea abies*. gL was derived from concurrent measurements of leaf water potentials and sap flux densities through the trunk. Soil water deficits clearly reduced gL, the reduction being most likely located in the soil–root compartment of the soil–plant sap pathway. The decreases in gL did not result in large decreases in midday leaf water potentials because midday sap flux densities were reduced proportionally to gL. We therefore hypothesized that maximum sap flux densities in *Picea abies* are adjusted under dry conditions according to changes in whole-tree hydraulic conductances with effect of maintaining midday water potentials above the point of xylem dysfunction caused by water stress-induced cavitations.

hydraulic conductance / cavitation / stomatal conductance / drought / sap flux / water potential / *Picea abies*

Résumé — Relations hydriques chez l'épicéa commun (*Picea abies* (L) Karst) soumis à une sécheresse édaphique dans les Vosges : conductance hydraulique totale, embolie du xylème et régulation des pertes en eau. *Les variations de conductances hydrauliques totales induites par une*

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Abbreviations: F: water flow; dF: sap flux density; dF_{midday} and $dF_{predawn}$: dF at midday and predawn, respectively; GL: whole-tree apparent hydraulic conductance; gL: sapwood-area-specific GL; g_s: stomatal conductance for H_2O; K: hydraulic conductance of a xylem segment; K_{init}: initial K; K_{max}: K at saturation; PLC: percent loss of conductivity; Ψ: water potential; Ψ_{soil}: soil Ψ; Ψ_{leaf}: leaf Ψ; Ψ_{midday} and $\Psi_{predawn}$: Ψ_{leaf} at midday and predawn, respectively.

sécheresse ont été suivies tout au long d'une saison de végétation dans une parcelle de Picea abies âgés de 30 ans. gL a été calculé à partir de mesures simultanées de potentiels hydriques foliaires et de densités de flux de sève dans les troncs. Le déficit hydrique dans le sol a réduit nettement gL, cette réduction étant probablement localisée dans le compartiment sol-racine. La chute de gL n'a pas induit de diminution importante du potentiel hydrique minimum parce que les densités de flux de sève maximales ont été réduites proportionnellement à gL. Nous faisons l'hypothèse que les valeurs maximales journalières de flux de sève chez l'épicéa sont ajustées en fonction de la conductance hydraulique totale, ceci ayant pour effet de maintenir le potentiel hydrique minimum au dessus du point de dysfonctionnement xylémique causé par la cavitation des trachéides.

conductance hydraulique / cavitation / conductance stomatique / sécheresse / flux de sève / potentiel hydrique / Picea abies

INTRODUCTION

Severe drought events since the mid-1970s are probably responsible for Norway spruce forest decline observed in the Vosges mountains (eastern France) during the 1980s (Lévy and Becker, 1987; Probst et al, 1990). However, the existence of a causal relationship between drought and spruce decline is still an open question. Water deficits develop in forest soils as a result of an unbalance between water input (precipitation) and water output (mostly tree transpiration). The responses of tree and stand transpiration to long-term soil water deficits are therefore key points in the understanding of spruce decline. It has recently been suggested that xylem dysfunctions due to catastrophic cavitation events (Tyree and Sperry, 1988) may be responsible for crown desiccation and tree dieback (Tributsch, 1992; Auclair, 1993). Cumulative tracheid cavitation impairs the xylem water transport capacity which, eventually, can lead to a complete disruption of the water supply to the leaves. Xylem embolism develops when the xylem tension becomes higher than a threshold value specific of an organ and of a species (Sperry and Tyree, 1988). For Picea abies, this critical tension is around −2.5 MPa when estimated by the leaf water potential (Cochard, 1992).

Our understanding of plant water relations is based on the "tension–cohesion" theory initially developed by Dixon (1914) and on its "Ohm's analogy" formalism proposed by Van den Honert (1948). Water moves from the soil to the leaves along a negative potential gradient caused by hydraulic resistances. The sap mass flow (Fi, kg s^{-1}) through any segment i of sap pathway will, at steady state, only depend on the dynamic water potential drop across the segment (dΨi, Pa) and on its hydraulic conductance (Ki, kg s^{-1} Pa^{-1}):

$$Fi = Ki * d\Psi i$$

Successful attempts have been made to simplify and generalize this equation to the whole water pathway (eg for woody plants, Landsberg et al, 1976; Cohen et al, 1983; Granier et al, 1989):

$$F = GL * (\Psi_{soil} - \Psi_{leaves}) \qquad [1]$$

where F represents the water flow through the whole soil–plant continuum, GL the total apparent hydraulic conductance from the soil to the leaves, Ψ_{soil} the mean soil water potential in the root zone and Ψ_{leaves} the mean leaf water potential. When a water flux density is measured (sap flux per unit conductive sapwood area), then a specific hydraulic conductance gL can be computed.

Equation [1] gives a simple functional relationship between the leaf water status,

the sap flux through the plant, the soil water status and the total hydraulic conductance from the soil to the leaves. It is therefore necessary to analyze the concurrent changes in Ψ_{soil}, GL and F to understand the changes in Ψ_{leaves} and to assess the possible risk of catastrophic xylem cavitation.

In the framework of the French Forest Decline Research Program (DEFORPA), a stand of *Picea abies* was chosen in the Vosges mountains where intensive ecophysiological investigations were undertaken during the 1990 growing season. The seasonal and drought effects on water potential, stomatal conductance and transpiration have been published in a previous paper (Lu *et al*, 1995). This second paper reports results on the hydraulic functioning and dysfunctioning of spruce under drought conditions and its possible implications for regulation of water loss.

MATERIALS AND METHODS

Study site

Measurements were conducted from June to November 1990 in a 30-year-old *Picea abies* (L) Karsten plantation in the Vosges mountains (NE France, 7°15'E, 48°15'N, 1 050 m elevation). Stand density was 2 343 stems.ha^{-1}, mean height 12.6 m and projected leaf area around 5.8 m^2.m^{-2}. Two representative adjacent plots of about 30 trees each were selected in the plantation and equipped with 12-m high scaffoldings to give access to the crown of the trees. The summer drought was increased in the "dry" treatment by restraining external inputs of water from 10 July to 7 September by means of a 1-m deep circular trench all around the plot and a waterproof plastic roof located 2 m above the ground. At the end of this period, this plot was rehydrated by a 40 mm irrigation, and allowed to dehydrate anew. The control "watered" plot was repeatedly irrigated throughout the summer (6 times for a total of 58 mm) but limited soil water deficits could not be fully avoided.

Ecophysiological measurements

Sap flux density (dF, kg.dm^{-2}.h^{-1}) was measured continually throughout the study period on four trees of each plot with sap flowmeters (Granier, 1987) inserted in the trunk at breast height. Total sap flow through the trunk can then be derived by multiplying the sap flux density by the sapwood area at breast height. More details about this technique are given in the previous paper (Lu *et al*, 1995). Leaf water potential (Ψ_{leaf}) was measured on one-year-old leafy twigs with a pressure chamber. For each measurement, three or four sun exposed and shaded twigs were sampled in the upper half of the crown in order to get a good estimation of the average canopy twig water potential.

Daily courses of Ψ_{leaf} were assessed on two different trees in each plot on seven sunny days throughout the study period. Ψ_{leaf} was measured every 2 h from sunrise to sunset. On the same day, midday stomatal conductances (g_s) were measured on the same trees between 12:00 and 13:00 solar time with a Li-Cor 1600 porometer (Lincoln, NE, USA) on four sunlit and shaded twigs in the upper half of the crown. Predawn water potential ($\Psi_{predawn}$) and midday water potential (Ψ_{midday}) were measured more extensively during sunny days every 2 weeks on all the eight trees equipped with sap flowmeters.

Whole-tree specific hydraulic conductance (gL)

gL was calculated i) as the slope of the least-squares linear regression between the daily courses of twig water potential and sap flux density, and ii) in a simpler way according to equation [1], based only on the predawn and midday twig water potential and the midday sap flux.

Seasonal course of xylem embolism and vulnerability to cavitation

The degree of xylem embolism in leafy branches was measured with the technique described by Sperry et al (1988) and Cochard (1992). One to four-year-old branches from two trees of each plot were sampled early in the morning, wrapped in an airtight black plastic bag to reduce water

losses, and brought to the laboratory where they were analyzed the next day. In the laboratory, branches were rehydrated in tap water and 8 to 15 2–3 cm long segments were randomly excised under water. The hydraulic conductance (K_{init}) of each segment was determined by forcing distilled water through the samples with a 6 kPa pressure head and measuring the resulting flux rate with an analytical balance. The embolism was then resorbed by a series of 30 min 100 kPa pressurization with degassed distilled water. The maximum conductivity (K_{max}) was then measured as described earlier and the degree of embolism estimated as a percent loss of conductance: $100*(1 - K_{init}/K_{max})$. Measurements were performed 7 times throughout the growing season.

Xylem vulnerability to cavitation was assessed as described by Cochard (1992). Seven 1- to 3-year-old branches were randomly sampled in the crowns of the well-watered trees and dehydrated in the laboratory under controlled conditions. After a few hours to a few days of dehydration, 1 branch was chosen, its xylem water potential was measured on leafy twigs with a pressure chamber and the degree of embolism was estimated as described earlier. The percent loss of conductance *versus* minimum xylem water potential represents the "vulnerability curve" of this xylem.

RESULTS

gL estimations derived from the daily sap flux density *versus* leaf water potential relationships were in close agreement with gL values based on the predawn and midday values alone ($n = 24$, $r^2 = 0.91$, slope not different from one at $P = 0.05$) (fig 1). The agreement between the 2 methods resulted from the linearity of the dF/Ψ_{leaf} relationships (see fig 2) observed for most of the trees. Therefore, we include with confidence in this paper the values of gL computed with the second technique.

The changes in the flux/potential relationships during the summer for one tree from the control and one from the dry plot are shown in figure 2. The slope of the regression lines represents $1/gL$ by definition. gL, $\Psi_{predawn}$, Ψ_{midday} and dF_{midday}
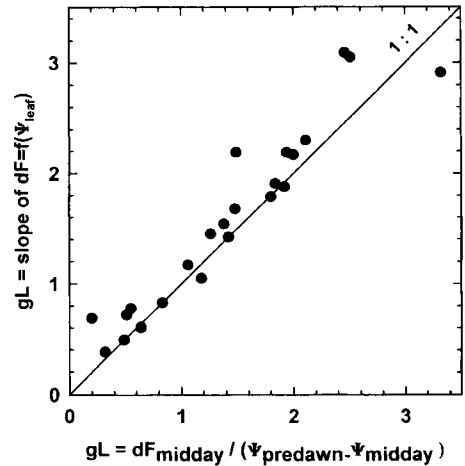

Fig 1. Whole-tree specific hydraulic conductances computed as the slope of a linear regression between the daily variations in Ψ_{leaf} and dF (Y axis) or according to equation [1] based on the predawn and midday values alone. The two techniques yielded comparable results which validates the second method.

remained high for the watered trees throughout the summer although they could be reduced when limited water deficits developed. In contrast, for the nonwatered trees, the water shortage and the drop in $\Psi_{predawn}$ induced a clear reduction in gL. Concurrently, with the decrease in gL, an important reduction in dF_{midday} was observed: from about 2.0 kg.dm^{-2}.h^{-1} to less than 0.5 kg.dm^{-2}.h^{-1} at the end of the drought period. It can also be seen in figure 2 that the decline in Ψ_{midday} was limited and that Ψ_{midday} remained above –2.5 MPa all through the drought period. These general trends noted for the two trees in figure 2 are shown for all the studied trees in more detail in the subsequent figures.

In figure 3 we plotted dF_{midday} and gL as a function of $\Psi_{predawn}$. The decreases of gL and dF_{midday} for the droughted trees were of an exponential type, ie, the most significant decrease was noted at the beginning of the
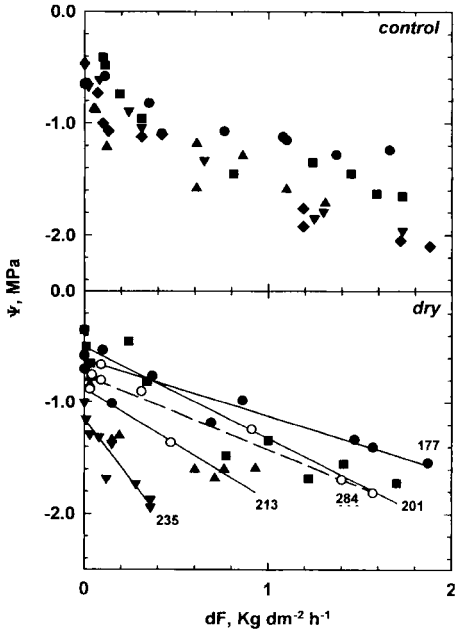
Fig 2. Summer changes in the daily variations of dF and Ψ_{leaf} for 1 control tree (upper) and 1 droughted tree (lower). Different symbols represent different days (figures on the graph). Day 284 is 14 days after rewatering of the dry plot (open circles and dotted line). Lines are first-order regressions.

Fig 3. Relationships between midday sap flux density (dF_{midday}, upper), whole tree specific hydraulic conductance (gL, lower) and predawn water potential ($\Psi_{predawn}$). Open circles represent watered trees; closed circles, dry trees; dotted open squares and dotted circles, trees 1 and 14 days after rehydration of the dry plot, respectively. Lines are third-order polynomial regressions (dry trees only).

drought when $\Psi_{predawn}$ was still high. The first day after the rehydration of the dry plot, $\Psi_{predawn}$ came back to very high values but both gL and dF_{midday} remained low. Watering of the upper layers of the soil was probably enough to rapidly restore $\Psi_{predawn}$ but because roots in the deeper layers were not yet watered, gL remained low. Thirteen days after rewatering, when the drought was developing anew, gL and dF_{midday} recovered, but for two trees, values for a same $\Psi_{predawn}$ were higher than during the first drought cycle. Data for the control trees were much more scattered than for the droughted trees. This probably resulted from the successive dehydration/rehydration episodes that the trees experienced during the study period that may have caused pat-terns similar to those described earlier for the droughted trees.
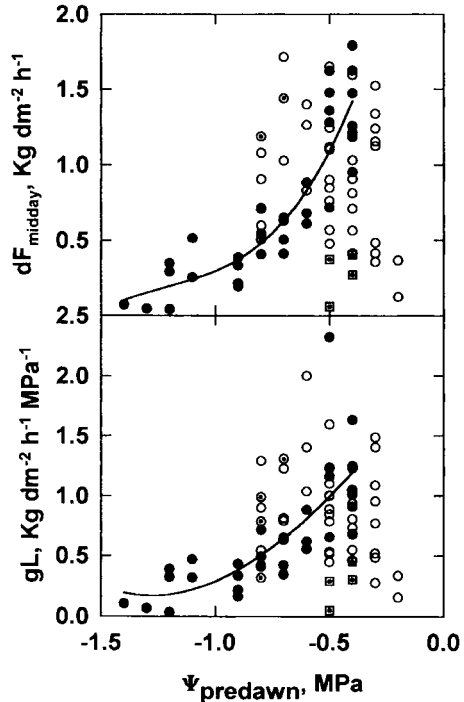
A linear relationship was found between gL and dF_{midday} ($r^2 = 0.78$, $n = 83$) (fig 4). A unique relation was observed for dry, control and rehydrated trees. The midday leaf stomatal conductance (g_s) was not correlated with gL ($r^2 = 0.04$, $n = 29$) (fig 5), but a better relationship was found ($r^2 = 0.51$, $n = 29$) when g_s values were multiplied by the midday vapor pressure deficit (ie the conductance converted to a flux density). However, the correlation remained weak, prob-
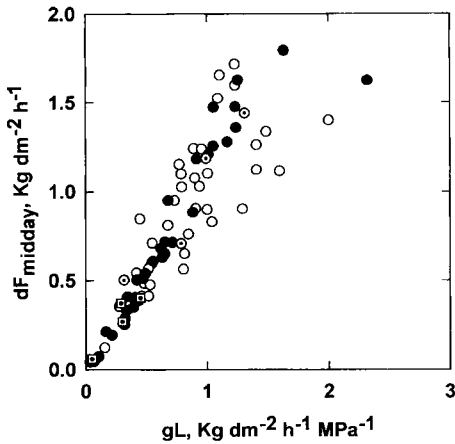
Fig 4. Relationship between midday sap flux density (dF_{midday}) and whole-tree specific hydraulic conductance (gL). Symbols as in figure 3.

ably because g_s was measured in the upper part of the crown and may not be representative of the whole tree.

The vulnerability of *Picea abies* tracheids to cavitation is shown in figure 6. On this same graph, we replotted data from Cochard (1992) on the same species. We also added the data on the seasonal evolution of embolism, the water potential values being the midday leaf water potentials recorded on the days the samples were collected. The degree of embolism in leafy branches of *Picea abies* submitted to natural drought always remained below 10% throughout the study period. Cavitation events in the tracheids were not provoked by the development of the drought nor by the first winter frost. Embolism significantly developed in bench dehydrated branches of *Picea abies* when Ψ_{leaf} became less than a threshold potential of *ca* –2.5 MPa, 50% loss of conductance being noted for Ψ_{leaf} close to –3.5 MPa. It is clear from this graph that embolism did not develop in the branches of the field droughted trees because their minimum water potentials always remained above the threshold potential.
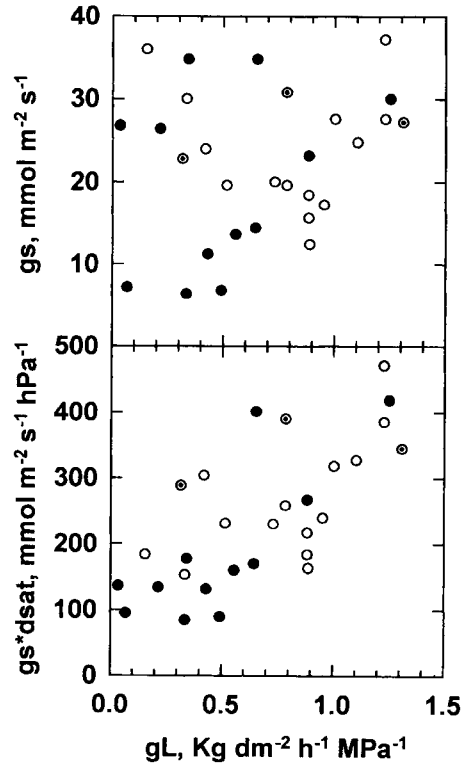

Fig 5. Leaf stomatal conductance (g_s) and g_s*dsat *versus* whole-tree specific hydraulic conductance (gL). Symbols as in figure 3.

DISCUSSION

Whole-tree hydraulic conductances of *Picea abies* under good soil water status were comparable to that reported by other authors for conifer (Granier et al, 1989; Loustau et al, 1990) or broadleaved trees (Bréda et al, 1993) using similar methods. When water availability is reduced in the soil, an important decrease of gL is observed. Our results suggest that the change in conductance was located in the soil-trunk compartment because no xylem embolism was detected in the terminal branches. This is consistent with the fact that the minimum water potential remained above the threshold water
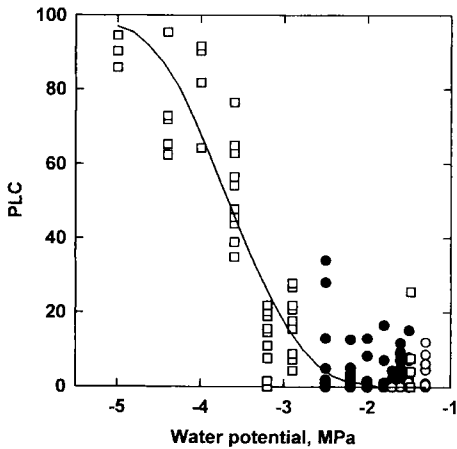
Fig 6. Vulnerability curve of *Picea abies* stems (open squares) and natural level of embolism *versus* minimum water potential for watered trees (open circles) and droughted trees (closed circles).

potential inducing cavitation. It is also unlikely that cavitation occurred in the upstream part of the xylem tissue because water potential is higher in the trunk and the roots. This supposes that the vulnerability of these organs is comparable to that of the branch, which may not be the case (Sperry and Saliendra, 1994). Tracheids in conifers are known to be irreversibly embolized because pit membranes are sealed to the pit pores after cavitation (Sperry and Tyree, 1990). The fact that gL was rapidly restored after rehydration suggests that if cavitation did occur in the roots, it was probably very limited. The changes of gL were therefore not due to changes in xylem hydraulic properties. These reversible modifications in hydraulic conductance were most likely located in the root cortex, in the soil–root interface and in the soil itself (Nobel and Cui, 1992).

An important objective of this study was to analyze the stomatal responses of spruce to soil water deficits. Stomata are known to close in the presence of a drought, thereby limiting leaf water stress. According to equation [1], leaf water stress (estimated by Ψ_{leaf}) results from a static water stress (soil water potential estimated by $\Psi_{predawn}$) and a dynamic water stress equal to $gL*F$. Drought is known to affect water transport in the soil–plant continuum by increasing the static water stress (decrease in the soil water potential). Stomatal responses to $\Psi_{predawn}$ have been discussed in the previous paper (Lu et al, 1995) and we concluded that $\Psi_{predawn}$ was a poor indicator of water stress actually experienced by trees. The consequences of an increase in static water stress may therefore be rather limited. On the other hand, the important variation in soil–plant hydraulic conductance (gL) found in this study implies that a more significant effect of drought would be a potential increase in the dynamic water stress caused by the water flow. The linear relationship between gL and dF_{midday} found in spruce and other species (Reich and Hinckley, 1989; Meinzer and Grantz, 1990; Sperry and Pockman, 1993; Brisson *et al*, 1993; Cochard et al, 1996) suggests that gL may actually be a critical parameter of the soil–plant continuum limiting maximum transpiration rates. It will be noted that although gL is derived from dF_{midday} values, this relationship is more than apparent because i) the dF/Ψ_{leaf} daily variations were linear in our study, which proves that gL is independent of dF_{midday} and ii) gL was also linearly related to independent measurements of water flow in the gas phase at the leaf level (g_s*dsat). Spruce trees cope with the drop in gL by actively controlling their water losses and hence limiting the dynamic water stress.

How stomata may respond to changes in gL remains an open question. Stomatal conductance is known to be very dependent on air vapor pressure deficit and light, but these factors cannot explain alone the stomatal behavior in our study. Meinzer and Grantz (1990) suggested that in sugarcane a signal is mediated by hormones produced

in roots and that their production and composition are modified by changes in gL. Sperry and Pockman (1993), by inducing embolism in branches, demonstrated the in *Betula*, stomata were capable of responding to variations in gL independently of changes in soil water status. Our data suggest that it is not the stomatal conductance which is regulated but more precisely the water flux through the stomata $g_s^* dsat$. In other words, transpiration, not stomatal conductance, is being balanced against gL. This result is in agreement with the findings of Meinzer and Grantz (1991) in sugarcane (see also Mott and Parkhurst, 1991).

Stomatal closure reduces assimilation rate in the short term, which may lower plant growth and competition in the long term. Furthermore, stomatal closure may alter leaf integrity by increasing leaf surface temperature. Therefore, there must be some strong short-term ecophysiological benefit for stomatal closure. We suggest that for spruce trees in this study, one of the major benefits of the observed stomatal closure was the maintenance of the xylem integrity. We know from the xylem vulnerability curve and the midday twig water potential measurements that the droughted trees were operating close to the point of xylem dysfunction. We can quantitatively assess this fact by computing, for each tree and given any value of $\Psi_{predawn}$ and gL, the critical dF value that could experience the xylem without developing embolism:

$$dF_{cavitation} = gL * (\Psi_{predawn} - \Psi_{cavitation})$$

where $\Psi_{cavitation} = -2.5$ MPa

In figure 7, we expressed the actual dF_{midday} value *versus* the computed critical $dF_{cavitation}$ values. It is clear from this graph that dF_{midday} was lower but close to $dF_{cavitation}$ and that the "safety margin" was reduced when drought developed. We calculated that for the driest trees (lowest dF_{midday} values), the difference between
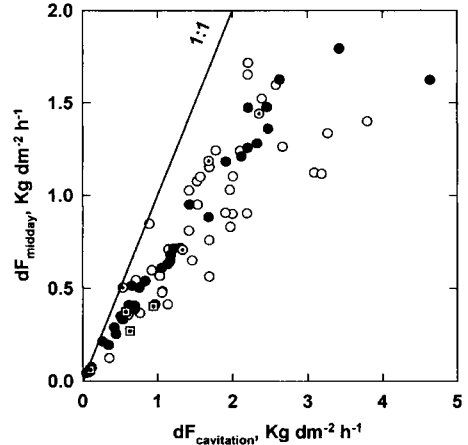

Fig 7. Midday sap flux density (dF_{midday}) *versus* sap flux density inducing xylem embolism $dF_{cavitation}$. Symbols as in figure 3. Solid line is first bissectrice. See text for details.

$dF_{cavitation}$ and dF_{midday} could represent less than a few percent of the observed dF_{midday} prior to the onset of the drought. The maximum transpiration rate seemed therefore remarkably regulated for the control of xylem embolism. Straightforward computations (data not shown) also demonstrate that in the absence of water loss regulation (dF_{midday} of the dry plot set equal for each day to dF_{midday} of the control plot), the Ψ_{midday} would have reached values far lower than $\Psi_{cavitation}$ with predictable shoot desiccation caused by "runaway embolism" (Tyree and Sperry, 1988).

Thus we conclude that, because Norway spruce trees are operating close to the point of xylem dysfunction caused cavitation, drought-induced changes in whole-tree hydraulic conductance put a physiological limitation on midday maximum transpiration rate and hence on CO_2 assimilation rates and growth. A study of water loss regulation in the oak tree *(Quercus petraea)* yielded very similar conclusions (Cochard et al, 1996). Hydraulic functioning of trees

proves to be critical in the understanding of their water relations and growth, but further research is needed for assessing possible impacts on forest decline.

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