

# Different vulnerabilities of *Quercus ilex* L. to freeze- and summer drought-induced xylem embolism: an ecological interpretation

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## ABSTRACT

*Quercus ilex* L. growing in the southern Mediterranean Basin region is exposed to xylem embolism induced by both winter freezing and summer drought. The distribution of the species in Sicily could be explained in terms of the different vulnerability to embolism of its xylem conduits. Naturally occurring climatic conditions were simulated by: (1) maintaining plants for 3 h at ambient temperatures of 0, –1.5, –2.5, –5.0 and –11 °C; and (2) allowing plants to dry out to ratios of their minimum diurnal leaf water potentials ( $\psi_l$ ) to that at the turgor loss point ( $\psi_{tlp}$ ) of 0.6, 0.9, 1.05, 1.20 and 1.33. The loss of hydraulic conductivity of one-year-old twigs reached 40% at –1.5 °C and at  $\psi_l/\psi_{tlp} = 1.05$ . Recovery from these strains was almost complete 24 h after the release of thermal stress or after one irrigation, respectively. More severe stresses reduced recovery consistently. The percentages of xylem conduits embolized following application of the two stresses, were positively related to xylem conduit diameter. The capability of the xylem conduits to recover from stress was positively related to the conduit diameter in plants subjected to summer drought, but not in the plants subjected to winter freezing stress. The ecological significance of the different vulnerabilities to embolism of xylem conduits under naturally occurring climatic conditions is discussed.

**Key-words:** *Quercus ilex* L.; Fagaceae; Holm-oak; hydraulic conductivity; xylem embolism; conduit diameter; winter freezing; summer drought.

## INTRODUCTION

Xylem embolism has been recognized to be the most serious cause of reduction in the productivity of plants subjected to some environmental as well as pathogenic stresses (e.g. drought, freezing and tracheomycoses) (Dimond 1970; Talboys 1968; Zimmermann 1983; Tyree & Sperry 1989; Just & Sauter 1991).

However, both structural and functional features have been developed by plants, to reduce their potential susceptibility to such adversities. For instance, xylem

conduit dimensions have been suggested to be positively related to the vulnerability to embolism of the xylem system (Isebrands & Larson 1977; Milburn 1979; Zimmermann 1983; Lo Gullo 1989). Therefore, short and narrow xylem conduits would be of advantage to plants exposed to xylem embolism, although implying a lower efficiency in water conduction. The concept of 'plant segmentation' has been stated by Zimmermann (1983) on this principle.

Previous studies (Salleo & Lo Gullo 1986; 1989a, b) conducted by us in three plant species, namely *Chorisia insignis* H. B. et K., *Vitis vinifera* L. and *Ceratonia siliqua* L., as well as anatomical measurements reported by Lo Gullo (1989) in the desert plant *Simmondsia chinensis* (Link) Schneider, have confirmed this hypothesis in that wider xylem conduits underwent cavitation at less negative water potentials than narrower ones. In contrast, Tyree & Dixon (1986), did not find such a relation when different species were compared. As an example, greater vulnerability to cavitation was recorded in conifers such as *Thuja occidentalis* L. and *Juniperus virginiana* L. (with xylem composed only of tracheids) than in plants with vessels such as *Acer saccharum* Marsh. However, wider xylem conduits were found to be more vulnerable than narrower ones within each species studied (Tyree & Dixon 1986).

There is evidence (Tyree & Sperry 1989) that it is the pit-membrane pore diameter rather than the conduit diameter that determines vulnerability to embolism of a xylem conduit. This view is in agreement with the 'air-seeding' hypothesis (Zimmermann 1983; Crombie, Hipkins & Milburn 1985; Sperry & Tyree 1990), according to which gaseous emboli would enter xylem conduits through the pit-membrane pores whenever the pressure differences across them are high enough to make the radius of the air-water meniscus smaller than that of the pore. Such an 'exogenous' nucleation of xylem cavitation would occur in plants exposed to drought.

Freezing injury also implies xylem embolism (Zimmermann 1983; Ewers 1985; Hammel 1967; Cochard & Tyree 1990; Just & Sauter 1991). However, this is interpreted to be nucleated by gaseous bubbles forming within the xylem conduits during the transition of water

from the liquid to the ice phase (Sucoff 1969). Therefore, the vulnerability of xylem conduits to freeze-induced embolism should not depend on the pit membrane pore diameter.

There are only a few studies in the literature on the resistance of whole plants to low temperatures in terms of resistance of their xylem conduits to embolism as related to their diameters. The question of whether the adaptation of plants to drought and frost does or does not imply similar xylem structures appears to be of both ecological and evolutionary importance.

Plants growing in some climates are exposed to both drought and freezing injury. An interesting case is that of *Quercus ilex* L., a species of arcto-boreal origin (Kyriakopoulos & Richter 1991) growing throughout the Mediterranean Basin, at elevations which are higher at lower latitudes: in Sicily, the species grows between 700 and 1200 m elevation (Pignatti 1982) and it can be found up to 1800 m on Mount Etna. Therefore, *Q. ilex* is exposed to the typical Mediterranean dry period, usually lasting from mid-April to the end of September, during which only about 60–80 mm rainfall interrupt the dry, hot summer. In the winter, the minimum temperature falls commonly to 0°C and even below zero at the higher elevations.

The natural (i.e. not synanthropic) distribution of *Q. ilex* in Sicily is surprisingly limited. Below and above certain elevations the species is replaced by others, suggesting critical vulnerability of *Q. ilex* to one or both of the environmental stresses to which the species is exposed.

A further problem regarding the vulnerability of plants to environmental stresses concerns their elasticity in recovering from stress (Levitt 1980). In fact, not only the potential vulnerability of a plant is of importance, but also the amount of residual damage which can be considered as 'permanent' after the stress is released (net vulnerability).

Our present work was designed to study the resistance of *Q. ilex* to both drought- and freezing-induced xylem embolism as well as the capability of the species to recover from stress, in terms of the potential and net vulnerability to embolism of xylem conduits of different diameters.

## MATERIALS AND METHODS

All the measurements were made on one-year-old twigs of 8-year-old plants of *Q. ilex*, growing in pots of 0.125 m<sup>3</sup> in volume. The plants had been grown at 800 m elevation, in a nursery belonging to the Department of Forestry of Messina, Sicily. They were transferred to Messina (at sea level) some months before the experiments.

To estimate the amount of experimentally induced xylem embolism, three different methods were employed: (1) *the acoustic method*, by recording ultrasound acoustic signals (AE), emitted from the wood in

the frequency range of 100–300 kHz (Tyree & Dixon, 1983, Salleo & Lo Gullo 1989a, b); (2) *the hydraulic method*, by measuring the hydraulic conductivity of one-year-old twigs (Sperry, Donnelly & Tyree 1987; Lo Gullo & Salleo 1992); and (3) *the anatomical method*, by measuring the number and internal diameters of both functional and non-functional xylem conduits (Salleo & Lo Gullo 1989) after perfusing the stems with safranin. All three methods (see below), have been described in detail by us previously (Lo Gullo & Salleo 1991).

Two groups of 25 plants were selected and subjected to the following stresses.

### Freezing-induced xylem embolism

All the experiments were conducted between November 1991 and February 1992. Before the experiments, plants were stored outside the laboratory in the open where the minimum temperature was  $+4 \pm 2^\circ\text{C}$  and the maximum was  $+10 \pm 2^\circ\text{C}$ .

The freezing stress was applied by putting single plants into a dark freezing chamber to simulate the low temperature conditions occurring in Sicily at night. The temperature in the chamber was decreased at a rate of  $0.3^\circ\text{C min}^{-1}$  to the desired value which was maintained constant for 3 h. After this period of time, the temperature was raised again at the same rate, to about 18°C. Five temperature values were tested, namely 0,  $-1.5$ ,  $-2.5$ ,  $-5$  and  $-11^\circ\text{C}$ . The first two values occur commonly on Sicilian mountains as pre-dawn winter temperatures, while a minimum temperature, of  $-2.5^\circ\text{C}$  is rare, in Sicily. The two lower temperatures tested,  $-5$  and  $-11^\circ\text{C}$  are never recorded in the southern Mediterranean Basin region, although they occur in the northern Mediterranean area where *Q. ilex* grows such as the Karstic region (Larcher 1981; Mitrakos 1982). Five plants were subjected to each temperature tested.

AE were recorded, on one twig per plant of the five plants tested. An AE transducer (R15, Physical Acoustic Corp., Princeton, NJ, USA) was clamped to the exposed wood (1.5 cm<sup>2</sup>) at 2/3 of the twig length during plant freezing and up to 1 h after the temperature of the chamber had been raised to about 18°C. The AE amplifier (4615 Drought Stress Monitor, P.A.C.) was set at a gain of 52 dB. One one-year-old twig per plant, 50 cm long (i.e. longer than the longest conduits which were about 12 cm long) was cut from five different plants under double-distilled water, pre-filtered through 0.2 µm filters and connected to the equipment for measuring their 'native' hydraulic conductivity (Lo Gullo & Salleo 1991). Maximum conductivity was achieved by repeatedly flushing the twig at a pressure of 175 kPa. Two more twigs per plant from five different plants were connected to pipettes filled with 0.1% safranin, dissolved in a 100 mol m<sup>-3</sup> KCl filtered solution. They were perfused with the dye for 20 h under a gravity-induced pressure gradient of 10 kPa. One to two

internodes at about 2/3 of the twig lengths were cross-sectioned by hand and the number as well as the internal diameters of the stained (functional) and unstained (non-functional) xylem conduits were measured on a computer display connected to a microscope via a telecamera. The conduits nearest to the pith (i.e. the first ones formed during the previous springtime) were found to be permanently blocked and were, therefore, excluded from counting. To test the ability of plants to recover from thermal stress, both hydraulic and anatomical measurements were repeated on one twig per plant after the five plants had been maintained in the open for 24 h under a screen near the laboratory. The external relative humidity of the air was, as is usual in Messina, about 80%.

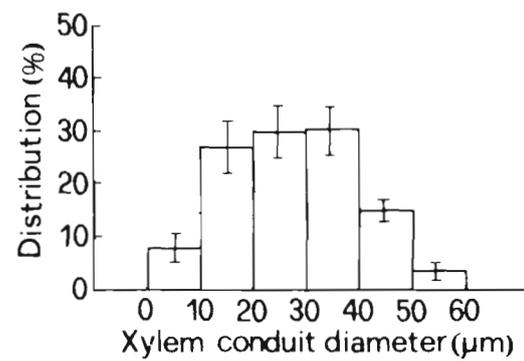
### Xylem embolism induced by simulated summer drought conditions

All the experiments were conducted between February and May 1992. Before and after the experiments, pressure-volume curves were measured using the pressure chamber technique (Scholander *et al.* 1965; Tyree & Hammel 1972; Salleo 1983), on 10 leaves each time (i.e. two leaves per plant on five different plants), so as to derive leaf water potential at the turgor loss point ( $\psi_{tlp}$ ). This was found to be  $-2.95 \pm 0.5$  MPa and to remain constant throughout the experimental period.

Twenty-five plants were put into a room with artificial supplemental lighting provided by mercury halide and high pressure sodium lamps at an irradiance of  $175 \text{ W m}^{-2}$  and photoperiod of 16 h. The room temperature varied between  $22^\circ\text{C}$  at night and  $30^\circ\text{C}$  at 1430 h.

Plants were deprived of irrigation. Leaf conductance to water vapour ( $g_l$ ) was measured on one leaf per plant of five plants at each stress level tested, every day at time intervals of 1 h between 0700 and 1700 h, using a steady-state porometer (LI-1600, LI-COR Inc., Lincoln, NE, USA). Leaf water potential ( $\psi_l$ ) was measured, using a pressure chamber, every day at 0900, 1100, 1430 and 1600 h on three leaves from different plants each time. The drought stress applied was estimated in terms of the ratio of the minimum diurnal  $\psi_l$  (as measured at 1430 h) to  $\psi_{tlp}$ . Five  $\psi_l/\psi_{tlp}$  ratios were tested, namely 0.62, 0.91, 1.05, 1.23 and 1.33. The first two values have been commonly recorded by us in the field in May and August, respectively (S. Salleo and M.A. Lo Gullo, unpublished data). A  $\psi_l/\psi_{tlp}$  ratio of about 0.90 has been reported by Rhizopoulou & Mitraikos (1990) in August, in Greece. The three higher levels of water stress were selected to check the limits of resistance of the species to drought.

AE were counted on one twig per plant (in the five plants used for each stress level tested), every day between 0700 and 1700 h, continuously so as to get the cumulative number of AE produced by the plants during the entire stress period. AE were recorded from one-year-old internodes at about 2/3 of the twig length. As



**Figure 1.** Distribution of xylem conduit diameters in one-year-old internodes. Vertical bars are standard deviations ( $n = 15$ ). The mean number of conduits per section was  $515 \pm 100$  ( $\pm$  SD,  $n = 15$ ).

the pre-established  $\psi_l/\psi_{tlp}$  ratio was reached, five twigs from different plants were cut under double-distilled, filtered water and tested for hydraulic conductivity as well as for single xylem conduit functionality.

To test the ability of plants to recover from drought, pre-stressed plants were supplied with  $200 \text{ cm}^3$  water per plant, corresponding to a rainfall of approximately 4 mm, typical of the water supply to plants on a rainy summer day in Sicily. Five one-year-old twigs (one for each plant tested) were used for hydraulic conductivity measurements and single xylem conduit functionality, 24 h after the irrigation.

## RESULTS

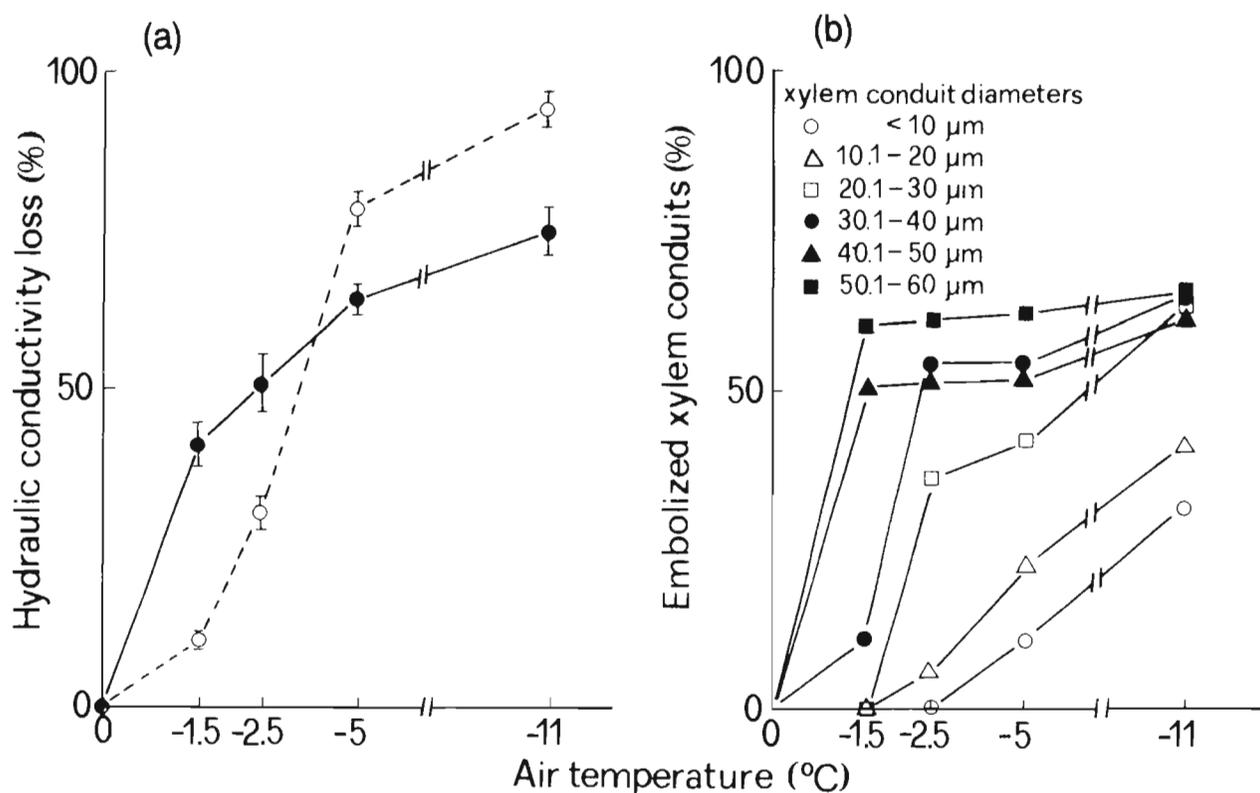
The distribution of xylem conduit diameters in one-year-old internodes of *Q. ilex* is shown in Fig. 1. Xylem conduits wider than  $40 \mu\text{m}$  in diameter were only 18.5% of the total number of conduits per section, while those up to  $20 \mu\text{m}$  in diameter were about 35%. The narrowest conduits measured (up to  $10 \mu\text{m}$  in diameter) appeared as transition forms between fibres and tracheids, distinctly distinguishable from true fibres, however, by their less thick walls.

### Freezing-induced xylem embolism

Plants exposed to an ambient temperature of  $0^\circ\text{C}$  (Fig. 2a) showed no loss of hydraulic conductivity.

A period of 3 h at  $-1.5^\circ\text{C}$ , on the contrary, caused a consistent loss of hydraulic conductivity (about 40%). Such a strain was found to be reversible, in that 24 h after the external temperature was raised above  $0^\circ\text{C}$  the residual reduction of hydraulic conductivity was only 10%.

Plants maintained at  $-2.5^\circ\text{C}$  underwent a larger loss of hydraulic conductivity (over 50%) with a reduced ability to recover from xylem blockage (the residual loss was still about 30%). On exposing plants to lower temperatures ( $-5$  and  $-11^\circ\text{C}$ ), the loss of conductivity increased to 75% and increased further with time (up to 94% after 24 h). This was apparently accompanied by



**Figure 2.** (a) Loss of hydraulic conductivity (expressed as percentage of the maximum) in relation to the external temperature to which plants were exposed for 3 h. Measurements are reported for 1 h (●) and 24 h (○) after the temperature had been raised to 18°C. Vertical bars are standard deviations for  $n=5$ . The samples consisted of one twig per plant from five different plants per each temperature tested. (b) Embolized xylem conduits as a percentage of the total number of conduits per section within given diameter intervals, in relation to ambient temperature.

damage to leaves, which showed necrotic areas over 40% and 80% of the leaf surface area in plants exposed to  $-5$  and  $-11^{\circ}\text{C}$ , respectively. Leaves died and dropped a few days after the end of the experiments.

In terms of vulnerability to freezing-induced embolism, wider xylem conduits were much more vulnerable than narrower ones at all the low temperatures tested (Fig. 2b). After the plants had been maintained at  $-1.5^{\circ}\text{C}$  for 3 h, 50–60% of the conduits between 40 and 60 μm in diameter were found to be embolized by comparison with only 10% of those between 30 and 40 μm in diameter. Conduits less than 30 μm in diameter were all functional.

The percentage of blocked conduits between 40 and 60 μm in diameter was already high at  $-1.5^{\circ}\text{C}$  and increased only slightly at lower temperatures. Equally critical was the loss of conduits between 20 and 40 μm in diameter, at  $-2.5^{\circ}\text{C}$ . Loss of function of conduits narrower than 20 μm increased more gradually as a function of the ambient temperature.

Recovery from embolism as related to xylem conduit diameter is shown in Fig. 3 which shows that the wider a xylem conduit, the lower the likelihood of it being refilled after thermal recovery of plants previously exposed to  $-1.5$  and  $-2.5^{\circ}\text{C}$ . Also, the further loss of xylem conduits as recorded 24 h after thermal recovery in plants maintained at  $-5$  and  $-11^{\circ}\text{C}$ , appears to be positively related to xylem conduit diameter. In other words, not only were the wider xylem conduits more vulnerable to freezing-induced embolism than the nar-

rower ones, but the number of blocked xylem conduits increased with the time.

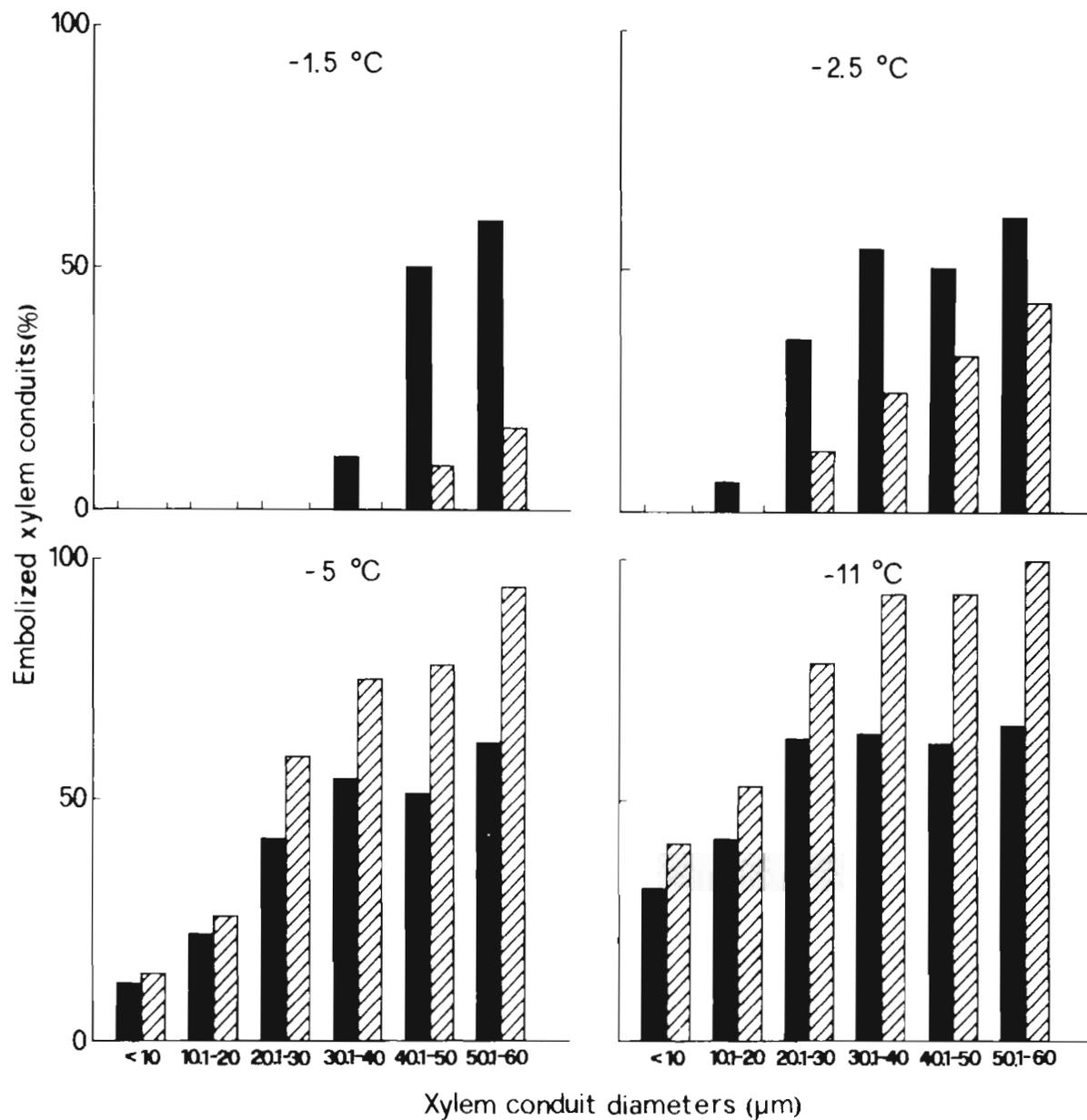
### Xylem embolism induced by simulated summer drought conditions

Plants dried to an average  $\psi_1$  of  $-1.77$  MPa, which corresponds to about 0.6 of  $\psi_{tlp}$ , underwent no loss of hydraulic conductivity (Fig. 4a). In contrast, when the  $\psi_1/\psi_{tlp}$  ratio reached 0.90, corresponding to mid-summer conditions, a loss of hydraulic conductivity of over 30% was recorded. In response to this, leaf conductance to water vapour ( $g_1$ ) decreased from 1.33 to 0.55  $\text{mm s}^{-1}$ , i.e. a decrease of about 59%. However, the decrease in hydraulic conductivity was found to be reversible in that a moderate water supply to plants (corresponding to about 4 mm rainfall) was sufficient for the xylem to recover conductivity almost completely.

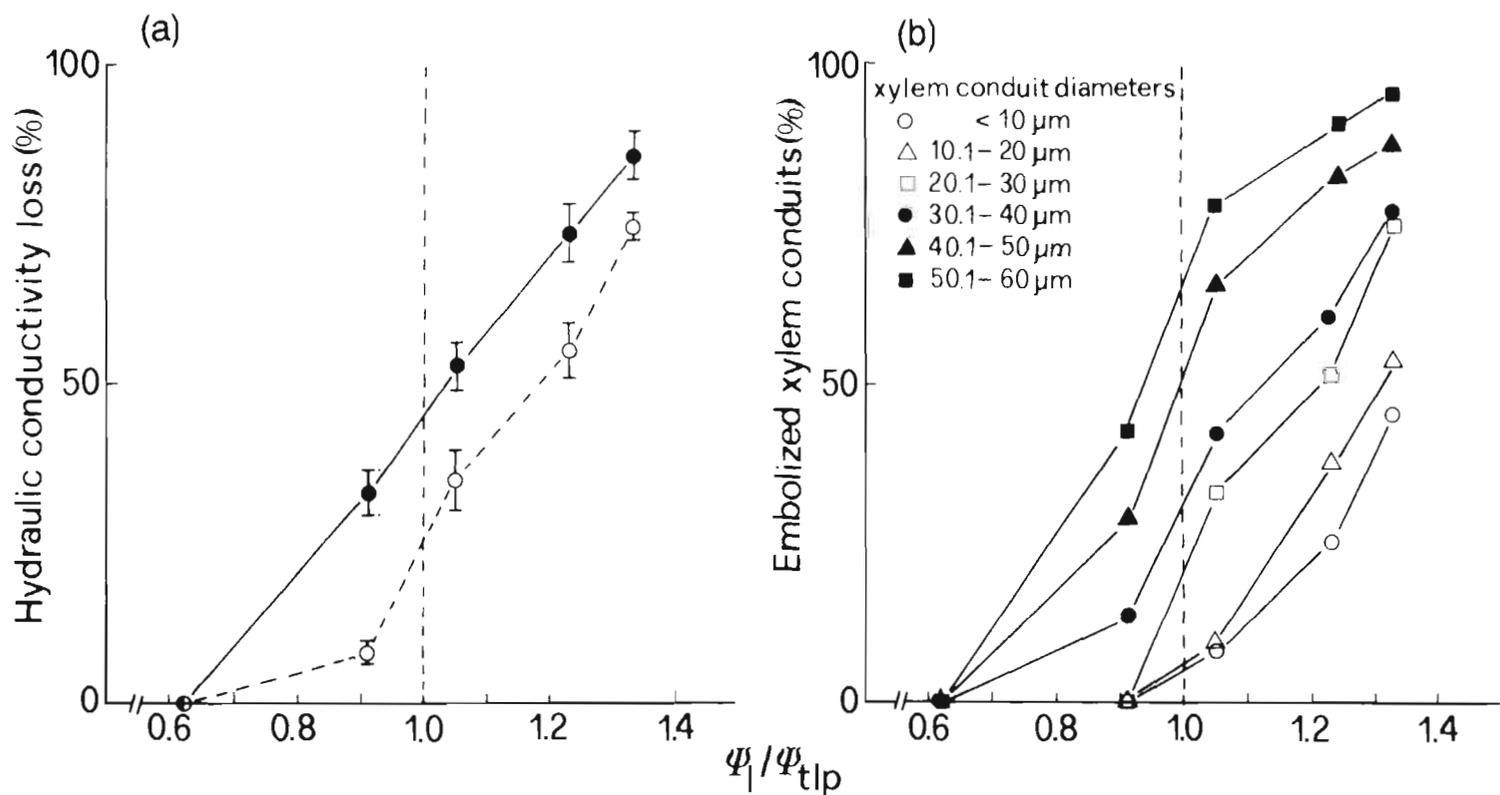
A  $\psi_1/\psi_{tlp}$  ratio very close to unity (1.05) caused a more consistent loss in hydraulic conductivity (53%), a further decrease in  $g_1$  (Fig. 6) and also a large reduction in recovery from the strain (i.e. a recovery of only one-third was recorded).

Higher  $\psi_1/\psi_{tlp}$  ratios, up to about 1.3, not only caused larger losses of hydraulic conductivity (up to 85%), but also reduced the capability of the xylem conduits to recover from embolism, although  $g_1$  further decreased almost to cuticular values (Fig. 6).

Once more, the vulnerability of xylem conduits to embolism increased with their diameters (Fig. 4b).

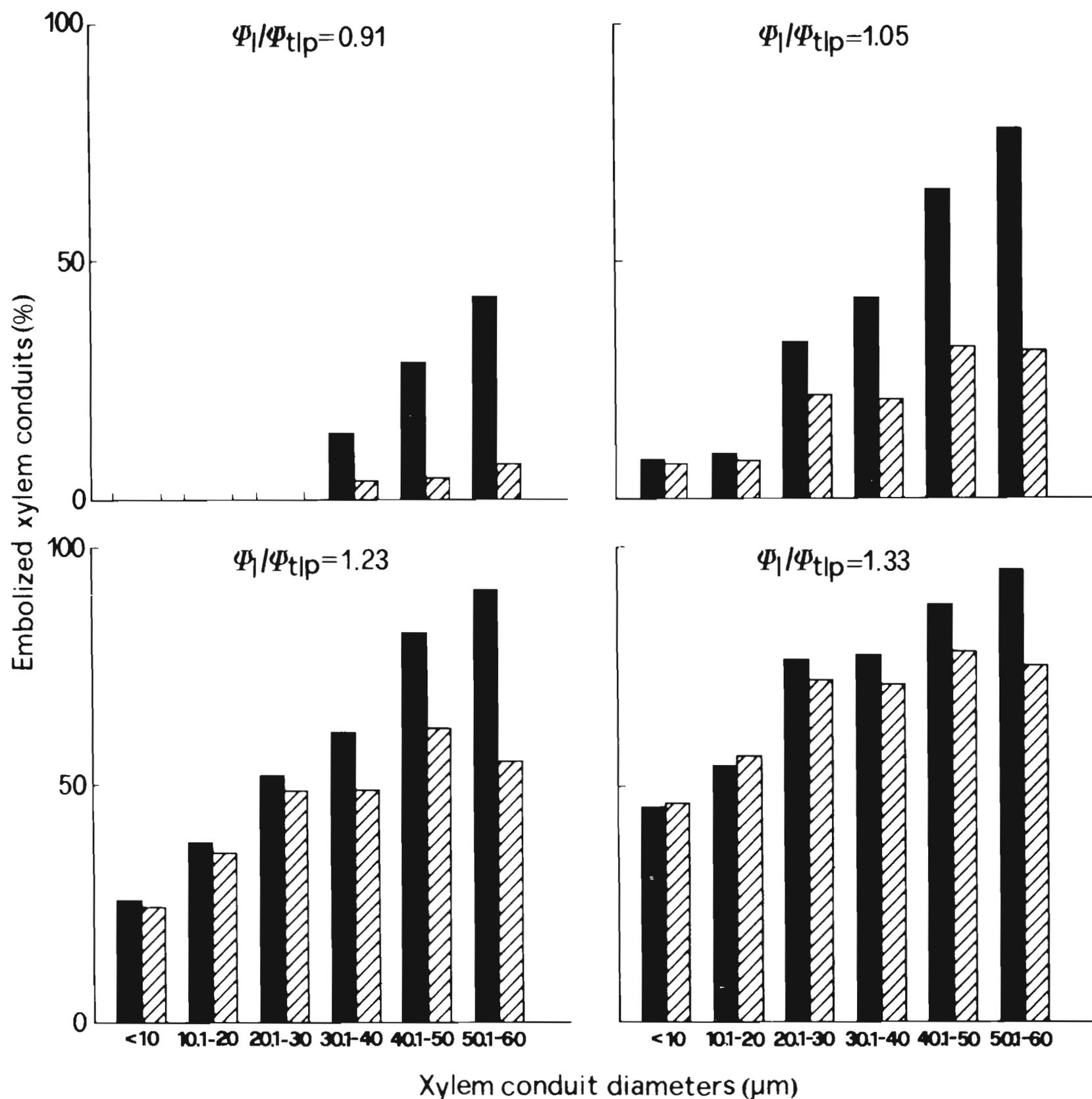


**Figure 3.** Embolized xylem conduits as a percentage of the total number of conduits per section within given diameter intervals measured 1 h (■) and 24 h (▨) after the ambient temperature was raised to 18 °C.



**Figure 4.** (a) Loss of hydraulic conductivity (expressed as percentage of the maximum) in relation to the water stress applied (expressed as the ratio of the minimum diurnal leaf water potential ( $\psi_l$ ) to  $\psi_l$  at the turgor loss point ( $\psi_{t1p}$ ), 1 h (●) and 24 h (○) after one irrigation. Vertical bars are standard deviations for  $n = 5$ . The samples consisted of one twig per plant from five different plants per each stress level tested.

(b) Embolized xylem conduits as a percentage of the total number of conduits per section within given diameter intervals, in relation to the water stress applied.



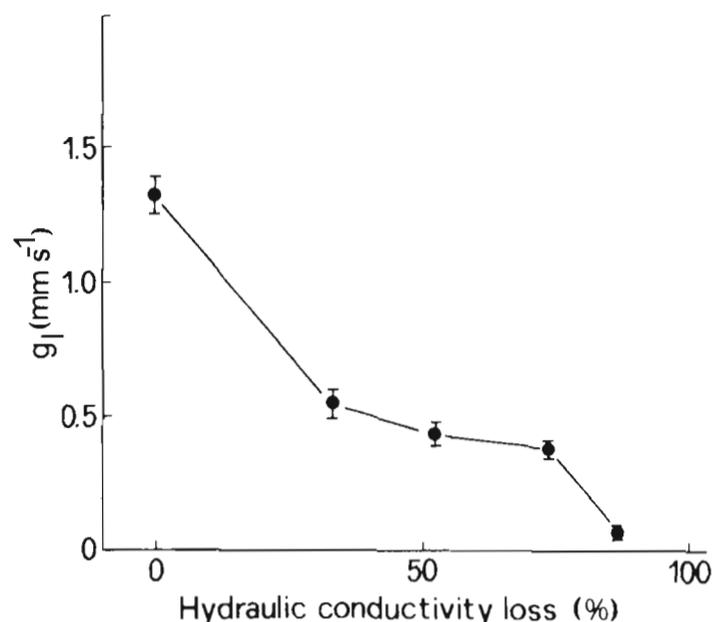
**Figure 5.** Embolized xylem conduits as a percentage of the total number of conduits per section within given diameter intervals, measured 1 h (■) and 24 h (▨) after one irrigation.

Plants dried to a  $\psi_1$  value very close to  $\psi_{t1p}$  ( $\psi_1/\psi_{t1p} = 1.05$ ) lost conductivity of 65–78% of their widest xylem conduits (40–60  $\mu\text{m}$  in diameter) while only 10% of the narrowest ones (up to 20  $\mu\text{m}$ ) were lost. Intermediate percentages of embolized xylem conduits were found for conduits between 20 and 40  $\mu\text{m}$  in diameter. In comparison with the analogous graph (Fig. 2b) showing the vulnerability of xylem conduits to freezing-induced embolism, more gradual loss of conductivity was found as a function of both the level of the stress applied and the conduit diameter at equal stress levels.

The capability of xylem conduits to recover conductivity after moderate resupply of water to the plants is shown in Fig. 5. As expected, this was negatively related

to the water stress applied. It is of interest to note that recovery, even if small, occurred also in xylem conduits of heavily stressed plants like those at  $\psi_1/\psi_{t1p} = 1.33$ . This did not occur in plants exposed to  $-5$  and  $-11^\circ\text{C}$ . Furthermore, the capability of xylem conduits to recover from summer drought-induced embolism appeared to be positively related to their diameters at all the levels of water stress tested. As an example, in plants at  $\psi_1/\psi_{t1p} = 1.05$ , xylem conduits less than 20  $\mu\text{m}$  in diameter did not recover in practice, while about 50% of the lost conduits between 20 and 40  $\mu\text{m}$  in diameter did and 50–60% of the lost widest conduits (up to 60  $\mu\text{m}$ ) were found to be functional, 24 h after the irrigation.

The two stresses applied, namely freezing and



**Figure 6.** Minimum diurnal leaf conductance to water vapour ( $g_l$ ) in relation to the loss of hydraulic conductivity (expressed as percentage of the maximum) of one-year-old twigs on plants subjected to simulated summer drought conditions. Vertical bars are standard deviations for  $n = 5$ . The samples consisted of one leaf per plant from five different plants.

summer drought stress, both led to consistent losses of hydraulic conductivity (Figs 2a & 4a) and presumed xylem blockage by embolism. However, the origin of the emboli was in the two cases, apparently different. Under summer drought conditions, hydraulic conductivity decreased with the stress applied as a result of xylem cavitations, as shown in Fig. 7 where the cumulative AE, counted every day after the suspension of irrigation, increased linearly with the loss of conductivity. The fairly high correlation coefficient between the two variables ( $r = 0.977$ ) suggests that water cavitation occurred mainly in the xylem conduits.

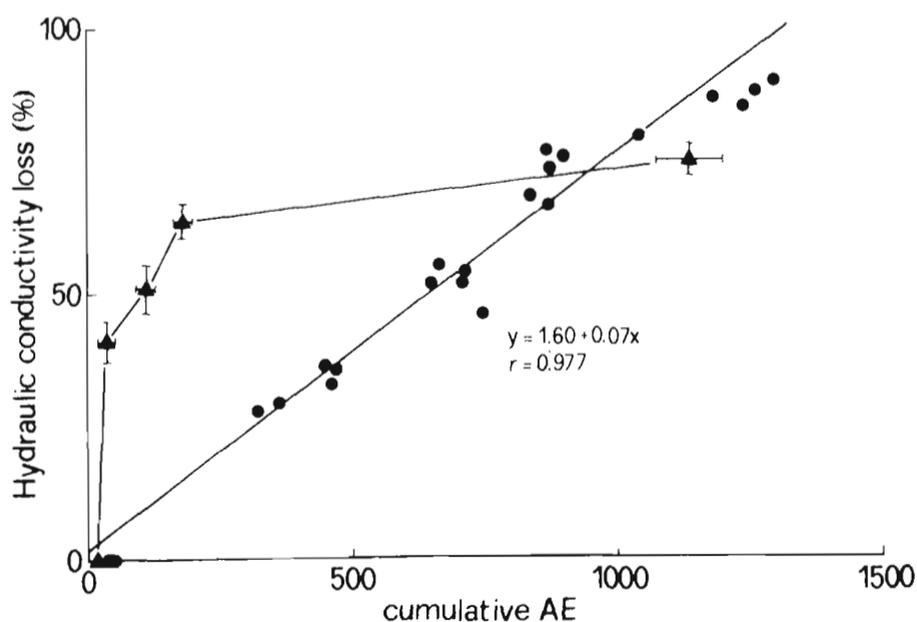
Such a good linear relationship between loss of conductivity and AE was not observed by Cochard &

Tyree (1990) in *Q. rubra* and *Q. alba*. We feel that this may depend on the number of xylem fibres as well as on their vulnerability to cavitation, i.e. the larger their number or their vulnerability to cavitation, the higher the AE counts at equal losses of conductivity, and therefore, the less good the linearity of such relationship.

In contrast, under freezing stress, a large loss of hydraulic conductivity occurred with only a few AE. For example, a loss of conductivity of 40% was measured when plants were exposed to an ambient temperature of  $-1.5^\circ\text{C}$ , with only about 30 AE. A comparable loss of conductivity resulting from simulated drought was associated with over 600 AE. The large increase in the number of AE counted at  $-11^\circ\text{C}$  (1150 AE) was probably the result of the combined effects of emboli spreading into fibres and of damage to other leaf tissues.

## DISCUSSION

The xylem architecture of one-year-old twigs of *Q. ilex*, consisting of only a small percentage (18.5%) of conduits between 40 and  $60\ \mu\text{m}$  in diameter, together with over 80% of narrower conduits (Fig. 1), was able to resist xylem embolism as caused by the two environmental stresses to which the species is exposed in Sicily. Xylem conduits 40– $60\ \mu\text{m}$  in diameter were more heavily damaged than narrower ones by both the stresses applied (Figs 2a & 4a). Since emboli caused by freezing stress develop *within* the xylem conduits and do not enter them from outside, as happens in plants subjected to summer drought, the major vulnerability to embolism of the wider xylem conduits in both cases confirms that they are *intrinsically* more vulnerable than the narrower ones, at least in Angiosperms (Isebrands & Larson 1977; Zimmermann 1983; Salleo & Lo Gullo 1986, 1989a, b).



**Figure 7.** Loss of hydraulic conductivity (expressed as percentage of the maximum) in relation to the cumulative number of acoustic emissions (AE) in one-year-old twigs of plants subjected to freezing ( $\blacktriangle$ ) and summer drought ( $\bullet$ ) stresses. Linear regression of the hydraulic conductivity loss to the number of AE ( $\bullet$ ) is shown. Vertical and horizontal bars ( $\blacktriangle$ ) are standard deviations for  $n = 5$ . The samples consisted of one twig per plant from five different plants for each temperature tested.

Under freezing stress, the embolism of conduits wider than a given diameter, appeared to occur critically at given air temperatures (Fig. 2b). As an example, in plants exposed to  $-1.5^{\circ}\text{C}$ , 50–60% of the conduits over  $40\ \mu\text{m}$  in diameter were lost while all the others were still functioning. The same occurred at  $-2.5^{\circ}\text{C}$  to conduits over  $20\ \mu\text{m}$  in diameter. A possible explanation is that the formation of emboli occurs, in this case, during xylem sap freezing which is the critical event. After a freezing-thawing cycle, sufficient for emboli to develop in the sap within the wider xylem conduits, only those conduits were functional where water was maintained in the liquid state (i.e. in the narrower conduits). In fact, narrow conduits are likely to contain water at lower free energy, and therefore, with a lower freezing point. The duration of the period at temperatures less than  $0^{\circ}\text{C}$  of 3 h was probably insufficient to cause complete freezing of water in the twigs (Just & Sauter 1991). This freezing period was chosen to be approximately as long as in natural conditions.

In summer drought conditions (Fig. 4b), on the other hand, the loss of xylem conduits increased much more gradually both as a function of the stress applied and of the conduit diameter at equal stress levels. Such a gradual loss of function suggests that a relation may exist between the pit membrane pore diameter and the conduit diameter. If this is the case, at equal pressure gradients across the pit membrane pores, emboli would enter xylem conduits through wide pores more easily than through narrow ones.

The capability of xylem conduits to recover from freezing or to recover from summer drought stress (Figs 3 & 5), was quite different in the two cases. The recovery from freezing-induced xylem embolism in conifers has been found to occur to a smaller extent, than we have recorded here in *Q. cerris* (Borghetti *et al.* 1992; Tyree & Sperry 1989). A possible explanation, in our case, is that xylem tensions were reduced after release of thermal stress by low transpiration rates (resulting from ambient temperatures to 10 to  $12^{\circ}\text{C}$  and high air relative humidities of 80% or more) and high water content of the soil. The resulting increase in root water absorption might have contributed to the redissolution of air in the sap. After exposure to lower temperatures ( $-2.5^{\circ}\text{C}$ ), the larger number of embolized conduits and/or the larger air volumes developed in them as a result of more complete water freezing, may be the cause of consistent reduction in their recovery.

The recovery of xylem conduits from drought-induced embolism, on the contrary, was probably because a number of conduits remained in the cavitated state (i.e. filled with water vapour). Recovery from the cavitated state can occur at much lower pressures than recovery from the embolized state. It is likely that, as the drought stress level increased, i.e. the pressure difference across the interconduit pit membranes increased, transition of the cavitated state into the embolized one occurred more rapidly.

While under freezing stress the percentage of xylem conduits that recovered, with respect to the percentage lost, was negatively related to conduit diameter, under drought stress the reverse occurred. It is probably more difficult for large bubbles to be expelled from wider xylem conduits, especially when tensions in the xylem are raised again during diurnal transpiration. Such large emboli have been reported to persist to an extent proportional to their diameter both in xylem conduits (Hammel 1967; Just & Sauter 1991) and in glass capillaries (Ewers 1985), and may trigger runaway embolism leading to catastrophic xylem dysfunction (Tyree & Sperry 1988). This was actually observed in *Q. ilex* plants exposed to  $-5$  and  $-11^{\circ}\text{C}$  where, in addition, necrosis of leaves increased the damage to the water conducting system. In contrast, an even moderate water supply to plants subjected to summer drought might lead to increase in reduced root permeability to water (Kramer 1983) and generate a root pressure that would help embolized xylem conduits to be refilled (Sperry *et al.* 1987). The high resistance to flow of narrow conduits might make the root pressure developed, insufficient to refill them. This could also explain why once the very narrow conduits in the leaf petioles are cavitated, they cannot be refilled and the leaves fall, even after repeated irrigations (Salleo & Lo Gullo 1993).

At the low temperatures and summer drought stresses most commonly occurring in Sicily, one-year-old twigs of *Q. ilex* showed sufficient resistance to xylem embolism. Although, at  $-1.5^{\circ}\text{C}$  and at  $\psi_l/\psi_{tlp}$  ratios of about 0.90, losses of hydraulic conductivity as high as 40 and 35%, respectively, were recorded, the xylem system was able to recover within 24 h from release of the stress. However, in terms of actual resistance in the field to the two stresses, *Q. ilex* appeared to be potentially more sensitive to summer drought than to winter freezing. Since the diurnal winter temperatures in Sicily are above  $0^{\circ}\text{C}$ , the species can recover from xylem embolism, completely during the day. Even residual damage to the hydraulic conductivity of about 30%, like that recorded 24 h after the plants had been exposed to  $-2.5^{\circ}\text{C}$  (Fig. 2a), would not cause damage to plants because of the low rate of winter transpiration.

In the summer, on the contrary, the time interval between two subsequent rainy days can be of several weeks so that loss of hydraulic conductivity, like that recorded at  $\psi_l/\psi_{tlp} = 0.90$  (35%), cannot be recovered from rapidly and can only be contained by a substantial reduction in  $g_l$  (Fig. 6).

Unlike other Mediterranean species such as *C. siliqua*, *Olea oleaster* Hoffmgg. et Link or *Q. suber* L. which can tolerate  $\psi_l$  values well below the turgor loss point with minor losses of hydraulic conductivity (Salleo & Lo Gullo 1993), *Q. ilex* not only showed losses of hydraulic conductivity of over 50% at  $\psi_l = \psi_{tlp}$  but its capability to recover from embolism also declined consistently (Fig. 4a). This is in agreement with the arcto-boreal origin of the species, in spite of its subse-

quent adaptation to warmer and drier climates. The distribution of the Sicilian ecotypes of *Q. ilex* within given elevation ranges can also be explained on the basis of our data. At minor elevations these ecotypes are damaged by drought stress, causing  $\psi_l$  to approach or become more negative than  $\psi_{tlp}$ , while at higher elevations, the water conducting system would become embolized without any possibility of spontaneous recovery.

The well-known adaptation to freezing stress of *Q. ilex* ecotypes growing in the northern Mediterranean Basin region deserves more study.

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Received 7 July 1992; received in revised form 4 January 1993; accepted for publication 5 February 1993

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