



Hydraulic vulnerability, vessel refilling, and seasonal courses of stem water potential of *Sorbus aucuparia* L. and *Sambucus nigra* L.

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Abstract

Differences in the seasonal variation in stem water potential between the two shrub species *Sorbus aucuparia* and *Sambucus nigra* were related with their vulnerability to xylem cavitation. It was also demonstrated indirectly that the two species differ in the extent to which they reverse cavitation. Seasonal variation in stem water potential was investigated during three growing seasons with *in situ* stem psychrometers. *Sorbus* experienced wide water potential variations and reached a minimum of -4.2 MPa during drought. Under the same microclimatic conditions, *Sambucus* experienced consistent stem water potentials with a minimum of -1.7 MPa. The relationship between percentage loss in hydraulic conductivity (PLC) and water potential (hydraulic vulnerability curve) of the two species differed in shape: a flat curve with nearly total loss of conductivity at -6 MPa was found for *Sorbus*. *Sambucus* showed a steep vulnerability curve with 90% loss conductivity at -2.2 MPa. Thus, *Sambucus* is extremely vulnerable to cavitation, but *Sorbus* is an almost invulnerable species. This different cavitation resistance adjusted the ranges of field stem water potential that the species experienced. Finally, seasonal courses of naturally occurring (native) embolism were compared with calculated PLC courses. This comparison indicates that *Sorbus* did not refill embolized xylem vessels whereas *Sambucus* reversed embolism. It was concluded that species which are highly vulnerable to cavitation and drought-induced embolism need refilling of embolized vessels as well as isohydric water potential patterns as two strategies of survival.

Key words: Stem water potential, hydraulic vulnerability curve, refilling of embolism, *Sorbus aucuparia*, *Sambucus nigra*.

Introduction

A continuum of possible drought-resistance strategies exists among vascular plants. At one end of this range there are species facing a wide variation in water potential (anisohydric species), and at the other end there are those that experience consistent xylem pressure (isohydric species). Often, anisohydric species tend to be drought-tolerant whereas isohydric species buffer their water potential on a diurnal and seasonal time scale by different drought-avoidance strategies (Larcher, 1994). The classification of several species to one or the other of these hydroecological types was done early in this century (Müller-Stoll, 1936; Walter, 1960). However, the underlying mechanisms are still a subject of research (Tardieu, 1997; Croker *et al.*, 1998; Loewenstein and Pallardy, 1998a, b; Tardieu and Simonneau, 1998). Moreover, many details of drought avoidance (Davies *et al.*, 1994; Monteith, 1995; Hartung *et al.*, 1998) as well as of drought tolerance (Blum, 1997; Passioura, 1997; Hare *et al.*, 1998) are not yet understood.

According to the widely accepted cohesion–tension theory of sap ascent (Dixon, 1914), xylem sap in the vessels of transpiring plants flows under tension caused by evaporation from the leaves. Therefore, it is possible that the xylem sap columns cavitate. Cavitation is the abrupt change from liquid water under negative pressure to water vapour (under vapour pressure) leading

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to an air-filled (embolized) vessel under atmospheric pressure. The quantity of cavitation events depends on the amount of cavitation-causing factors in the sap or the cell walls. As a result of cavitation and embolism formation, stem hydraulic conductivity is reduced, which may be critical for a plant under drought stress (Pickard, 1981; Zimmermann, 1983).

The air-seeding hypothesis (Zimmermann, 1983) is confirmed by various methods (Crombie *et al.*, 1985; Sperry and Tyree, 1988, 1990; Salleo *et al.*, 1992; Jarbeau *et al.*, 1995; Pockman *et al.*, 1995; Sperry *et al.*, 1996). It states that cavitation occurs when air outside a water-filled conduit is aspirated into the conduit through pores in the pit membranes. These pores will retain an air-water meniscus until the difference between the gas pressure and xylem pressure across the meniscus exceeds the capillary forces holding it in place. These forces are, among others, a function of the pore diameter. The bigger the pore, the smaller the critical pressure difference causing cavitation becomes, and the more vulnerable to cavitation a species is (Sperry and Tyree, 1988; Tyree *et al.*, 1994a; Sperry *et al.*, 1996). The species-specific different vulnerability to cavitation may thus determine the possible variation in xylem pressure a species experiences in the field, i.e. its anisohydric or isohydric performance.

Several papers have shown refilling during the growing season in different species, for example, in *Plantago* (Milburn and McLaughlin, 1974), *Zea mays* (Tyree *et al.*, 1986) and *Rhapis excelsa* (Sperry, 1986). Refilling is explained by predawn water potentials rising to near zero (Tyree *et al.*, 1986), rainy periods (Sperry, 1986) and root pressure (Milburn and McLaughlin, 1974; Pickard, 1989). Recent studies, however, indicate that embolism removal may be concurrent with transpiration and with considerable negative water potentials in intact nearby vessels (Salleo *et al.*, 1996; Borghetti *et al.*, 1998; McCully, 1999; Tyree *et al.*, 1999; Melcher *et al.*, 2001). It has also been hypothesized that vessel embolism is a reversible phenomenon made possible by the interaction of xylem parenchyma, vessel wall chemistry, and the geometry of intervessel pits (Holbrook and Zwieniecki, 1999).

The aim of the investigation was to find out whether differences in the seasonal variation in stem water potential between the two shrub species *Sorbus aucuparia* and *Sambucus nigra* are related with their vulnerability to xylem cavitation. *In situ* stem psychrometers were installed to measure the stem water potential continuously under field conditions (Dixon and Tyree, 1984). The relationship between percentage loss in hydraulic conductivity (PLC) and water potential (hydraulic vulnerability curve) characterized the species-specific vulnerability to cavitation. On the one hand, *Sorbus* experienced wide water potential variations during drought

(anisohydric type), and its flat hydraulic vulnerability curve indicates that this species is more or less invulnerable to cavitation. On the other hand, *Sambucus* experienced consistent xylem pressure (isohydric type), and showed a steep hydraulic vulnerability curve, an indication of its extreme vulnerability to xylem cavitation.

Finally, the seasonal development of naturally occurring (native) embolism rates was measured and compared with theoretical seasonal courses of native percentage loss of conductivity to find out if refilling of embolized vessels occurred in the shrub species studied. The theoretical courses were calculated from the minimal stem water potentials and the hydraulic vulnerability curves. It is shown indirectly that *Sorbus* and *Sambucus* differed in the extent to which they reversed cavitation. In *Sambucus*, embolism removal occurred in autumn 1995 and during the rainy growing season 1996. This refilling was most probable due to predawn water potentials rising to near zero. No refilling of embolized xylem vessels was determined in *Sorbus*.

It was concluded that the different cavitation resistances of *Sorbus* and *Sambucus* adjusted the ranges of field stem water potential these species experienced. Furthermore, the results indicate that refilling of embolized xylem vessels is species-specific and may be related to the hydroecological type and cavitation resistance of a species.

Materials and methods

Plant material and site

Experiments were carried out on different individuals of *Sorbus aucuparia* L. and *Sambucus nigra* L. growing in the Botanical Garden in Düsseldorf, Germany. Both shrub species are native to Germany and are diffuse-porous. Measurements of stem water potential were conducted during the growing season of 1994 (June–October), 1995 (April–October), and 1996 (May–October) on three individual shrubs of each species. Each year a different pair of shrubs was studied. Plants were 2–5 m tall and had not been watered during the dry periods of 1994 and 1995. Hydraulic vulnerability curves and seasonal levels of native embolism were measured on twigs of several adult shrubs of both species, different from that used for the water potential measurements.

Microclimate

Precipitation was measured with a rain gauge (ARG 100, Driesen & Kern, Germany) and air temperature and humidity with a shaded humidity–temperature meter HMP 31 UT (Vaisala, Finland). Data were recorded every 15 min with a 12-bit data logger (SquirrelTM, Grant, UK).

Stem water potential

The stem water potential was measured with *in situ* stem psychrometers (Plant Water Status Instruments, Canada) in

conjunction with autosamplers (Plant Water Status Instruments, Canada) and 12-bit data loggers (SquirrelTM, Grant, UK). The autosamplers steered the measuring process and carried out all temperature corrections. Two stem psychrometers per shrub were used each year. Stem water potentials were recorded at 15 min intervals. Calibration of the instruments was carried out with 0.1, 0.3, 0.5, 0.7, and 0.9 molal (mol kg^{-1}) NaCl solutions of known water potential (Lang, 1967) at 25 °C. During calibration the stem psychrometers remained in an insulating box. With each solution and psychrometer, six values were taken at 15 min intervals. The mean of the last four values was estimated for a calibration line. Calibration was conducted at the beginning of each season and after thermocouple repair. Care was taken to install the psychrometers on the shady side of the stem to minimize temperature gradients, and maintenance of the instruments was carried out frequently. Single predawn shoot water potentials and, in 1994 and 1995, diurnal courses of leaf water potential were measured with a pressure bomb (Scholander *et al.*, 1965) to check the stem psychrometers. If necessary, the instruments were cleaned and reinstalled. To account for thermal gradients, the values of the first 3 h after installation were not used.

Vessel length and hydraulic vulnerability curve

The vessel lengths of *Sorbus aucuparia* and *Sambucus nigra* were estimated from preliminary experiments where air at *c.* 0.05–0.1 MPa pressure was blown into the cut end of branches while cutting off the branch tips under water. Bubbles were blown through when the branch length was shorter than the longest vessel. Thirty branches each were investigated.

Percentage loss of hydraulic conductivity (PLC) achieved by xylem embolism was expressed as a function of the minimal water potential reached during dehydration. This relationship was referred to as a hydraulic vulnerability curve which was measured as follows (Sperry *et al.*, 1988a). At predawn,

branches were cut from the shrubs. Sampling occurred randomly across individuals to account for the population-level variation. The branches were immediately wrapped in plastic bags to prevent further desiccation, brought to the laboratory, and were allowed to dry on the bench over different periods until the desired water potentials were approximately reached. Then, the branches and wet towels were wrapped in plastic bags for 1–2 h (wet branches) (Sperry and Saliendra, 1994) or overnight (dry branches) to equilibrate. Afterwards, the water potential was remeasured with a pressure bomb (Scholander *et al.*, 1965) on at least three leaves or small twigs. The branches included the stem segments on which the hydraulic conductivity measurements were carried out. Investigations were conducted on 164 stem segments of *Sorbus aucuparia* and 132 segments of *Sambucus nigra*. The youngest segments large enough to be measured were between 80 and 100 mm long and 5–8 mm in diameter. Thus, 14% of all *Sorbus* stem segments were 1-year-old, 73% 2-years-old, and 13% 3-years-old. Because of its wider pith 85% of the stem segments of *Sambucus nigra* were 1 year and only 15% 2-years-old. Segments were cut free under water to avoid causing additional embolism, shaved on both ends with a razor blade, and fitted to a 'Sperry tubing apparatus' (Fig. 1) filled with filtered (0.2 μm) water. Segments were located far enough from the original branch cut end to ensure that few to no vessels, embolized by branch removal, extended into the segment.

Hydraulic conductivity was defined (Tyree and Ewers, 1991) as mass flow rate of solution through a stem segment (kg s^{-1}) divided by the pressure gradient along the segment (MPa m^{-1}). Measurements were carried out under a gravity gradient with a maximal pressure head of 0.009 MPa. On diffuse porous shrub species this is low enough to prevent displacement of air from vessels running through the segment. The use of three-way stopcocks allowed the conductivity of 15 segments to be measured in turn. Segments were perfused with filtered (0.2 μm) water which was not acidified (Hacke and Sauter, 1995). An electronic balance (Chyo JL-180, YMC Europe,

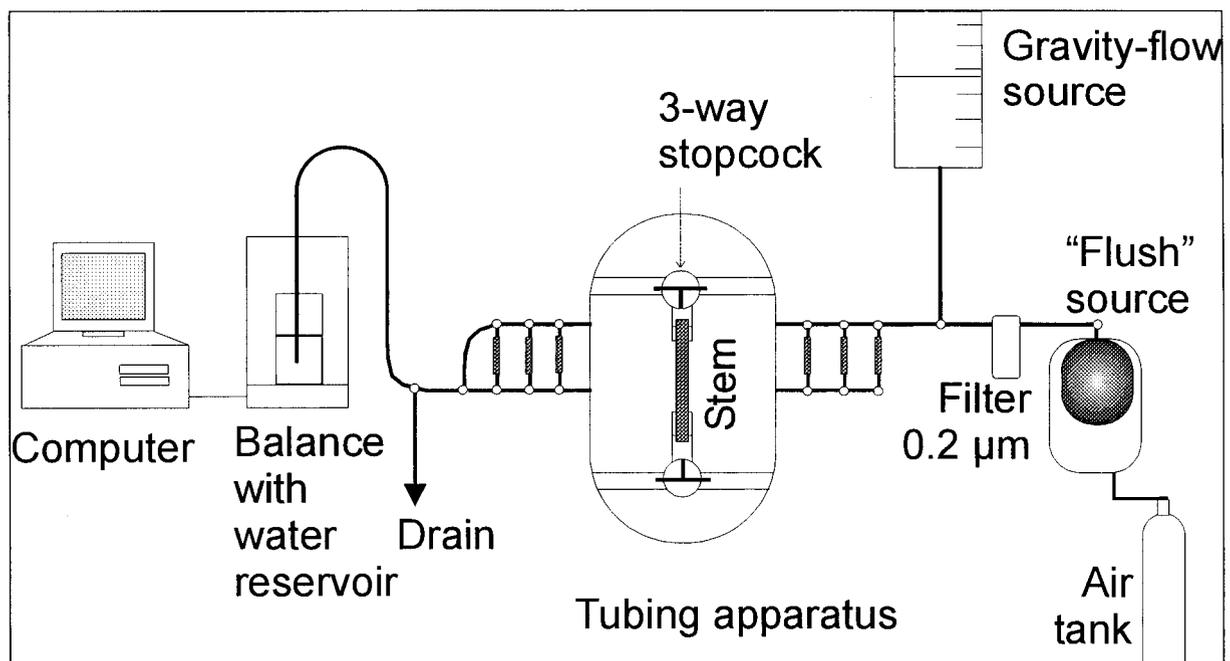


Fig. 1. Apparatus for measuring hydraulic conductivity and embolism (modified according to Sperry, 1993).

Germany) measured the flow rate through the stem segments under the known pressure gradient. A computer interfaced with the balance automated the measurements and calculations (Fig. 1). The program 'Xylemcon' was designed to facilitate the measurements. The following parameters were entered for each stem segment: title (species name and segment number), mean water potential as estimated before, segment diameter (included for reference), segment length (used to calculate conductivity and therefore essential), pressure in cm of water (also used to calculate conductivity; the height of the water surface on the balance was subtracted from the height of the water surface of the elevated reservoir), water evaporation from the water reservoir on the balance and water temperature as estimated before. The measurement was started by opening the appropriate stopcocks and routing efflux from a stem segment to a reservoir on the balance. The weight increase on the balance was recorded every 30 s giving the mass flow rate of solution through the studied stem segment. The mass flow rate was corrected for water evaporation from the reservoir on the balance. The mass flow rate divided by the pressure gradient along the segment resulted in a hydraulic conductivity. A temperature term corrected the reading to 20 °C. Usually after 4–5 conductivity measurements, the values achieved stability. The process was manually stopped after 8–10 measurements, and the mean of the last 5 readings was stored. After determination of the initial conductivity on all stem segments, flow was routed through all stems at once under a pressure of 0.08–0.1 MPa (Sperry, 1993) from a pressurized tank of solution for about 1 h. The purpose of this 'flush' was to promote the dissolving of air in embolized vessels. The conductivity of each segment was measured again, and the process repeated (usually 3–8 flushes) until the conductivity remained nearly stable with successive flushes, or declined at least 10%. The percentage by which the initial conductivity of each segment was below its maximum conductivity was referred to as percentage loss in conductivity or percentage embolism and was plotted against the mean water potential. Some of the flushed segments were stained with 0.1% aqueous safranin to confirm that flushing removes embolism. The large pith cells of *Sambucus nigra* remained unstained by the dye indicating that no solution passed the pith during conductivity measurements.

Native embolism and refilling

The accumulation of embolism under natural conditions was estimated in November and December of 1995, in 1996 from May to November at approximately 4-week intervals, and in February 1997 in each species. This native embolism was measured by harvesting branches which were wrapped in plastic bags before sampling, cutting segments from them under water, and measuring the native percentage loss of hydraulic conductivity using the flushing technique described above. The results were added to the hydraulic vulnerability curves and also plotted as seasonal variations in native xylem embolism (PLC-n). As described above, hydraulic vulnerability curves give the relationship between water potential and percentage loss of conductivity. Therefore, knowing a seasonal course of minimal stem water potential and the hydraulic vulnerability curve equation of a plant species, a theoretical seasonal course of native percentage loss of conductivity can be calculated that corresponds to the seasonal variation of minimal stem water potential. This was done for each shrub species based upon the stem water potential measurements in 1996 and referred to as PLC- Ψ . From these PLC- Ψ curves additional courses of PLC were derived assuming that xylem embolism is accumulated

during the growing season without refilling of embolized xylem (PLC+).

Results

Microclimate and stem water potential

In 1994, a drought period lasted from the middle of June to the middle of August. No daily rainfall above 1 mm was observed, except on three thunderstorm days in July 1994. The drought period was even longer in the growing season of 1995, lasting from the middle of June to the end of August. For 3 weeks in August 1995, no precipitation was recorded. On the contrary, 1996 had a rainy growing season with an even distribution of precipitation (Fig. 2, columns; Fig. 3). Table 1 shows that the growing season of 1996 was distinctly wetter than the growing seasons of 1994 and, above all, 1995. However, the precipitation in May to September 1996 fitted best the long-standing mean of precipitation. Accordingly, the summers of 1994 and 1995 were warmer, and the summer of 1996 colder than the long standing mean (Table 1).

These microclimatic conditions affected the water potential courses of both shrub species. Predawn as well as minimal stem water potentials of *Sorbus aucuparia* (Fig. 3A) became increasingly more negative during the dry months in 1994, but recovered on the three rainy days in July 94. The most negative value was -4.2 MPa. At the end of the drought period, the stem water potential of *Sorbus* recovered quickly. In spite of the drought, *Sambucus nigra* (Fig. 3B) experienced very consistent stem water potentials and showed no values deeper than -1.7 MPa. The similar microclimatic conditions in 1994 and 1995 resulted in similar stem water potential patterns in these years. In 1995, *Sorbus aucuparia* also showed large variations of its water potential, and *Sambucus nigra* the same small fluctuation of the seasonal courses of the stem water potential extremes as in 1994. In 1996, because of the rainy growing season, less variations of water potential were found in both species than in 1994 and 1995 (Fig. 3).

Predawn shoot and stem water potentials were in good agreement. The midday leaf water potential was, in accordance with the segmentation hypothesis (Zimmermann, 1978), usually 0.1–0.5 MPa (*Sambucus*)

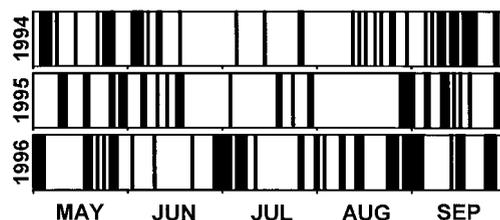


Fig. 2. Distribution of precipitation in the growing seasons of 1994, 1995 and 1996. Days with a sum of precipitation ≥ 1 mm are shown as black bars.

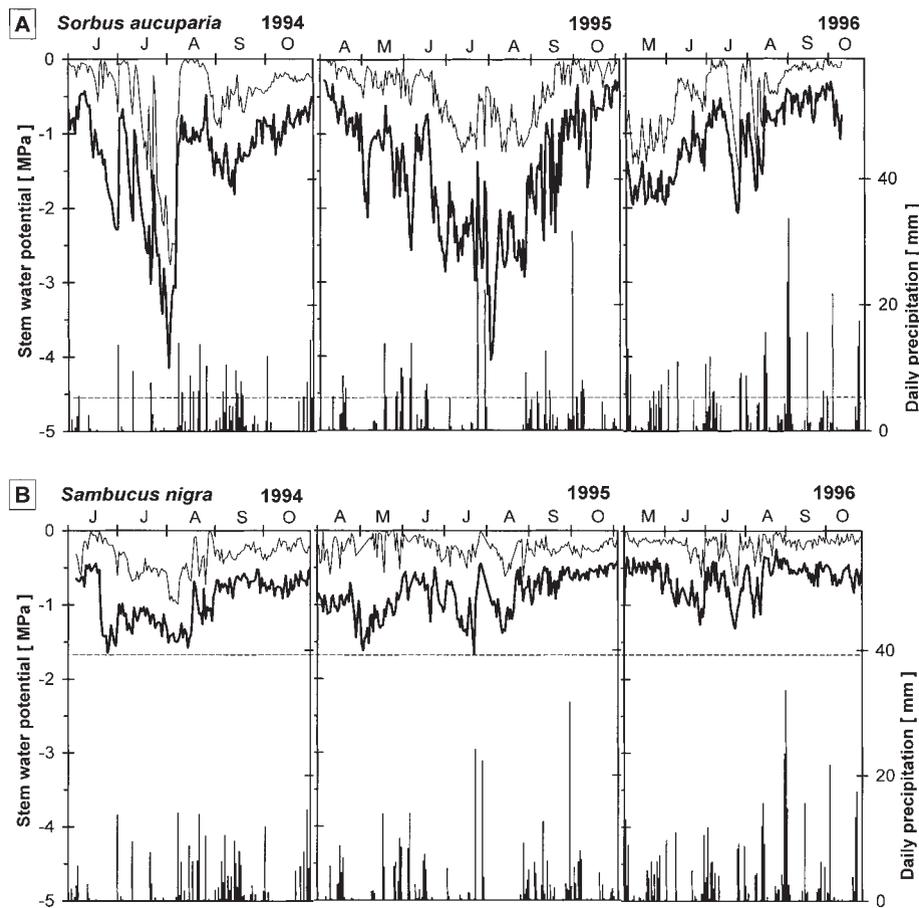


Fig. 3. Seasonal changes of predawn (thin lines) and most negative (thick lines) daily stem water potentials of *Sorbus aucuparia* (A) and *Sambucus nigra* (B) as well as the daily sums of precipitation (columns) in the 1994, 1995 and 1996 growing seasons. The dashed horizontal lines indicate the water potentials causing 80% embolism as calculated from the hydraulic vulnerability curve equations (Fig. 4). The predawn and minimal daily stem water potentials are means of two stem psychrometer measurements. Every year, the measurements were carried out on other shrub individuals.

Table 1. Precipitation, number of days with precipitation ≥ 1 mm and the means of the daily means of temperature in the growing seasons of 1994, 1995 and 1996, compared with the long-standing mean (1951–1980) measured at the German Meteorological Service weather stations in Leverkusen (precipitation) and Düsseldorf (temperature)

	Precipitation in May to September (mm)	Number of days with precipitation ≥ 1 mm in May to September	Mean of the daily temperature means in May to September ($^{\circ}\text{C}$)
1994	305.4	47	18.4
1995	267.0	42	17.9
1996	354.8	58	15.9
Long-standing mean 1951–1980	365.0	53.9	16–17

or 0.1–1 MPa (*Sorbus*) lower than the minimal stem water potential.

Vessel length and hydraulic vulnerability curve

The vessel lengths of *Sorbus aucuparia* and *Sambucus nigra* were estimated from preliminary experiments: 80% of the studied branches had no vessels longer than 0.5 m. Therefore, the stem segments used for the hydraulic

vulnerability curves were located 0.5–0.6 m from the original cut end of the branch.

The hydraulic vulnerability curves of *Sorbus aucuparia* and *Sambucus nigra* clearly differed in shape (Fig. 4). A flat curve was measured for *Sorbus aucuparia*. A water potential of -5.3 MPa gave 90 PLC and -6 MPa 99 PLC. A zero offset of about 40 PLC resulted from the use of not-recent xylem. The native embolism from previous stress events (freezing or drought) prevented

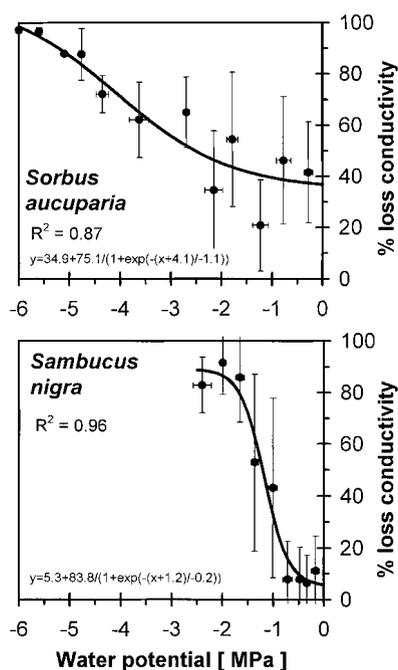


Fig. 4. Hydraulic vulnerability curves on 5–8 mm diameter stem segments of *Sorbus aucuparia* and *Sambucus nigra*. Percentage loss of hydraulic conductivity (PLC) is plotted versus the water potential causing the measured PLC-values. Each point is the mean of the water potential and PLC measurements done in 0.5 MPa (*Sorbus aucuparia*) and 0.3 MPa (*Sambucus nigra*) intervals on 10–25 stem segments. Error bars are standard deviations. The solid lines resulted from sigmoidal regression and are described by the given equations.

a measure of a zero PLC. The curve of *Sambucus nigra* was steep, mostly increasing between -1 and -2 MPa. A water potential of -2.2 MPa gave 90 PLC. Because most of the studied stem segments of *Sambucus* were 1-year-old, only a small zero offset of 5–10 PLC was estimated.

Native embolism and refilling

In 1996, *Sorbus aucuparia* showed native embolism rates (PLC-n) around 40%, and *Sambucus nigra* around 10% throughout the year (Fig. 5). These values corresponded to each zero offset in the hydraulic vulnerability curves. The steady courses of PLC-n at the level of the zero offset values indicate that in 1996 no embolism occurred in both species. From the courses of PLC-n, PLC- Ψ , and PLC-+ (Fig. 5) the refilling features of the studied species were derived: On the one hand, *Sorbus* showed PLC- Ψ as well as PLC-+ values in the range of the standard deviation of PLC-n. This indicates that really no embolism occurred in this shrub species in 1996. On the other hand, PLC- Ψ rose from the level of PLC-n (10 PLC) to about 60 PLC in *Sambucus*, exceeding the positive standard deviation of PLC-n by far. PLC- Ψ increased with decreasing water potentials and decreased again to 10 PLC with increasing minimal stem water

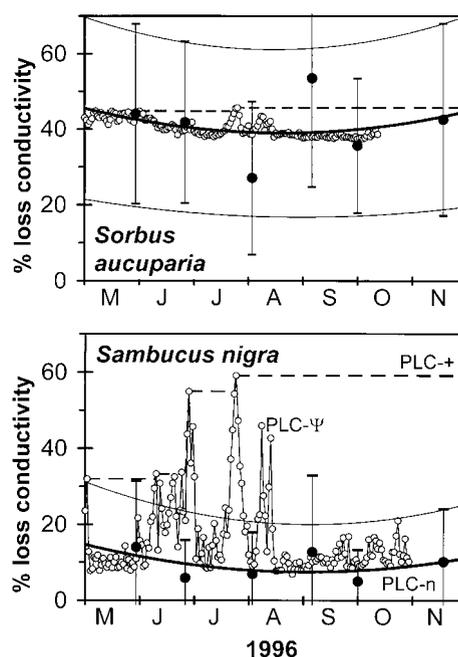


Fig. 5. Seasonal development of native embolism rates in *Sorbus aucuparia* and *Sambucus nigra* in 1996, expressed as percentage loss of hydraulic conductivity (PLC). Results are shown as filled circles and thick solid lines which are the best-fit second-order polynomial regressions. These courses are referred to as PLC-n in the text. Error bars are standard deviations ($n = 10$ – 30) and the thin lines are the best-fit second-order polynomial regressions of the standard deviations. The thin curves with open-circles, referred to as PLC- Ψ in the text, are calculated from the seasonal courses of minimal stem water potential in the growing season of 1996 (Fig. 3). The calculations are based upon the relationship between water potential and loss of hydraulic conductivity given in the hydraulic vulnerability curve equations (Fig. 4). From these PLC- Ψ curves, courses of PLC were derived assuming that loss conductivity is accumulated during the year without refilling of embolized xylem (PLC-+). These curves are shown as dashed lines.

potentials. PLC-+, as a cumulative PLC- Ψ , showed high values around 60 PLC at the end of the growing season 96. The fact that PLC- Ψ decreased three times from a high to the PLC-n level, and that a difference of 50% existed between PLC-n and PLC-+, shows that *Sambucus* did suffer from embolism in 1996, but refilled its embolized xylem vessels on the rainy days of this growing season.

Figure 6 confirms these results. It shows the courses of native embolism (PLC-n) of both shrub species in 1996 again (see Fig. 5), but also the PLC-n values measured at the end of 1995, and at the beginning of 1997. At the end of 1995, the measured native state of embolism reached $60 \pm 15\%$ (November) and $71 \pm 6\%$ (December) in *Sorbus aucuparia* (Fig. 6). This was as expected because the minimal stem water potential of *Sorbus* (Fig. 3A) reached -4.1 MPa in the drought period of 1995, equivalent to a conductivity loss of approximately 75% (Fig. 4). These high native embolism rates indicate that *Sorbus* did not refill its embolized vessels in autumn 1995.

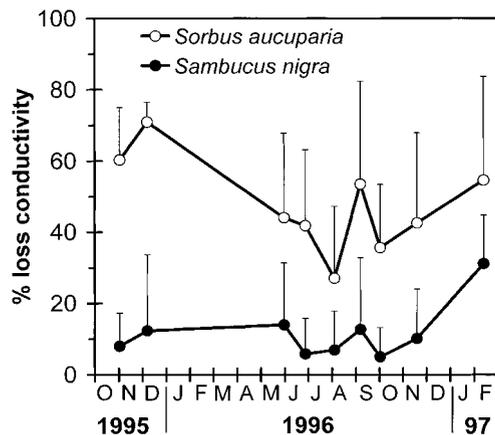


Fig. 6. Seasonal development of native embolism rates of *Sorbus aucuparia* and *Sambucus nigra* in 1996 (see Fig. 5) as well as at the end of 1995 and at the beginning of 1997, expressed as percentage loss of conductivity (PLC). Error bars are standard deviations ($n = 5-30$).

Sambucus nigra showed a measure of around 10% native loss conductivity at the end of 1995 (Fig. 6), although the minimal stem water potential of this shrub species decreased to -1.7 MPa in the hot and dry summer of 1995 (Fig. 3B). As estimated from the vulnerability curve of *Sambucus nigra* (Fig. 4), -1.7 MPa corresponded to approximately 80 PLC. As outlined above, this difference of about 70% between measured and calculated PLC in *Sambucus* might be explained by refilling of embolized xylem during wet periods. In winter 1995/1996 the first hard frost occurred at the end of December (data not shown). Therefore, the high native PLC in *Sorbus aucuparia* in November and December 1995 was not caused by frost embolism. On the contrary, the winter of 1996/1997 was very cold from the beginning (data not shown), and the increased February PLC-values of both species were probably due to frost embolism. Frost-induced embolism formation is caused by another mechanism than drought-induced embolism (Sperry and Sullivan, 1992; Sperry, 1993, 1995; Hacke and Sauter, 1996). This mechanism will not be discussed in this paper.

Discussion

In 1965, Scholander *et al.* already gave a good survey of the water potential ranges of species from different habitats. They found no values below -2.5 MPa for forest trees (Scholander *et al.*, 1965). Richter also listed the minimal water potentials of species from contrasting environments (Richter, 1976): for woody species from mesic sites he gave a range between -1.5 and -2.5 MPa. On the one hand, with a minimal stem water potential of -1.7 MPa *Sambucus* fitted well in this range. On the other hand, *Sorbus* showed lower values than -2.5 MPa. Its stem water potentials below -4 MPa were

comparable with the minima found on Chaparral shrubs (-3 to -4 MPa, Bowman and Roberts, 1985), and other species from sites with pronounced drought periods (Richter, 1976). Moreover, the stem water potential, as dealt with in the present paper, is generally less negative than the leaf water potential because of the high path resistances stem-branch and branch-leaf (Zimmermann, 1978, 1983). Richter states that 90% of the field water potentials given in the recent literature are derived from pressure chamber measurements on leaves or small twigs (Richter, 1997). This has to be taken into account when comparing stem water potential values with literature data. Dixon *et al.* determined on *Thuja occidentalis* about 0.1–0.4 MPa lower leaf than stem water potentials (Dixon *et al.*, 1984). In *Sambucus*, the daily minimal leaf water potential was usually 0.1–0.5 MPa, and in *Sorbus* 0.1 to, under extreme conditions, 1 MPa lower than the daily minimal stem water potential (Vogt, 1999). That means, the leaf water potential of *Sorbus* might drop to -5 MPa. Obviously, *Sorbus aucuparia* experienced extremely negative water potentials and high daily and seasonal fluctuations of water potential. So, *Sorbus* was classified as an anisohydric species. *Sambucus nigra*, categorized as an isohydric species, experienced small daily and seasonal variations of stem water potential. These findings agree with the results of discontinuous water and osmotic potential measurements (Linnenbrink *et al.*, 1992). Gas exchange measurements (Vogt and Lösch, 1999) confirm the classification of the studied species to different hydroecological types.

Loss of hydraulic conductivity is a direct measure of cavitation and embolism formation in the xylem vessels (Tyree and Sperry, 1989). The hydraulic vulnerability curves related each hydroecological type of *Sorbus* and *Sambucus* with their different vulnerability to drought-induced xylem cavitation. *Sorbus* was less vulnerable to embolism of the two species, losing nearly 100% of its hydraulic conductivity around -6 MPa. This wide 'safe' water potential range made *Sorbus* rather invulnerable to cavitation, but it is still exceeded by some other species: *Acer saccharum* (Sperry and Tyree, 1988) shows nearly the same vulnerability curve as *Sorbus*, but Chaparral shrubs like *Heteromeles arbutifolia* (incipient loss of conductivity at -4.0 MPa, nearly total loss of conductivity at -8.0 MPa, Jarbeau *et al.*, 1995), mangrove species like *Rhizophora mangle* (-3.0 – -7.0 MPa, Sperry *et al.*, 1988b) and species of the highly invulnerable genus *Juniperus* (-4.0 – -9.0 MPa, Sperry and Tyree, 1990; Sperry and Sullivan, 1992) are even less vulnerable to xylem cavitation than *Sorbus*. The hydraulic vulnerability curve of *Sambucus nigra* was steep, mostly increasing between -1 and -2 MPa, and 90 PLC was already reached at -2.2 MPa. Thus, *Sambucus* belongs to the most vulnerable species yet studied. Similar curves are found for *Populus* species (Tyree *et al.*, 1994b), for

Clusia uvitana (incipient loss of conductivity at -0.5 MPa/nearly total loss of conductivity at -2.5 MPa, Zotz *et al.*, 1994), *Populus balsamifera* ($-0.7/-2.5$ MPa, Hacke and Sauter, 1995), *Ochroma pyramidale* ($-0.9/-1.7$ MPa, Machado and Tyree, 1994), *Pseudobombax septenatum* ($-0.9/-1.7$ MPa, Machado and Tyree, 1994), *Schefflera morototoni* ($-1.0/-2.0$ MPa, Tyree *et al.*, 1991), *Betula occidentalis* ($-1.2/-2.1$ MPa, Sperry and Sullivan, 1992), *Salix gooddingii* ($-1.4/-1.7$ MPa, Pockman *et al.*, 1995), and *Populus fremontii* ($-1.5/-1.7$ MPa, Pockman *et al.*, 1995).

The small vulnerability to drought-induced xylem cavitation made it possible for *Sorbus aucuparia* to experience a wide seasonal variation in stem water potential. The hydraulic conductivity was maintained even as the field water potentials fell below -4 MPa during drought in 1994 and 1995. The deep water potential of -6 MPa which might cause total loss of hydraulic conductivity was never reached in the field. The consistent field stem water potentials of *Sambucus nigra* paralleled its considerable vulnerability to embolism formation. Nearly total blockage of sap flow might already occur at -2.2 MPa. Therefore, only small fluctuations of field water potential are tolerable for this shrub species to maintain vitality. Thus, the different cavitation resistances of *Sorbus* and *Sambucus* adjusted the ranges of field stem water potential these species experienced.

Furthermore, the results show indirectly that *Sambucus* refilled embolized vessels, but *Sorbus* did not reverse embolism. Refilling in *Sambucus* was most probably due to predawn water potentials rising to near zero in autumn 95 and during the rainy growing season of 1996. Refilling of embolized vessels at near zero, but slightly negative water potentials was observed before. As pointed out by Yang and Tyree, positive pressures are not required for refilling to occur (Yang and Tyree, 1992). But if refilling is simply explainable by xylem pressures rising to $-2\sigma/r$ (where σ is the surface tension of water at the largest air/water meniscus and r the radius of the conduit lumen containing the emboli (Yang and Tyree, 1992)), it is not obvious why vessels did not refill in *Sorbus* in autumn 1995. During this time of the year, both shrub species experienced near zero water potentials. Further, no remarkable difference in conduit diameter exists between *Sorbus* and *Sambucus* (Vogt, 1999) that would explain differences in embolism removal (Yang and Tyree, 1992; Edwards *et al.*, 1994). Species-specific differences in wood structure such as the interaction of xylem parenchyma, vessel wall chemistry and the geometry of intervessel pits as considered earlier (Holbrook and Zwieniecki, 1999), or a metabolic control of refilling (Salleo *et al.*, 1996) may explain species-specific differences in refilling. Most recently, an increased concentration of macromolecules in the small amount

of water remaining in embolized vessels of *Rhizophora mangle* was considered to be involved in embolism repair (Melcher *et al.*, 2001).

It might be that refilling is a species-specific ability and is related to the hydroecological type and cavitation resistance of a species. Perhaps, anisohydric species like *Sorbus* are able to risk the loss of functional xylem because of their wider 'embolism-safe' water potential range. Isohydric species like *Sambucus* undergo small fluctuations of water potential so that a total blockage of sap flow is prevented. The water potential of *Sambucus* is kept high by a quite sensitive stomatal control of transpiration (Vogt and Lösch, 1999). But beside this avoidance strategy, refilling of embolized vessels may additionally contribute to drought survival.

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