

Drought relations of shrub species: assessment of the mechanisms of drought resistance*

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Summary. Relatively static factors such as depth of rooting and cuticular conductance and relatively dynamic factors such as stomatal control and changes in the components of water potential were used to assess the drought resistance characteristics of six deciduous shrub species. Predawn water potential during a prolonged drought averaged -2.13 and -3.51 MPa in species known to have deep and shallow patterns of rooting, respectively. It is thus surprising that the osmotic potential at the turgor loss point averaged only -3.01 MPa in the shallow rooted group. The water potential at which irreversible cell damage occurred was the same in both groups (-4.9 MPa), and minimum values observed in the field never dropped below -4.0 MPa. There was, however, a pronounced difference between the two groups with regard to stomatal behavior. This allowed us to characterize the deep-rooted species as avoiders of stress which would cause prolonged stomatal closure whereas the shallow-rooted species had to tolerate prolonged periods of closed stomata.

The purpose of this paper is to describe and compare some of the mechanisms of drought resistance in these six hardwood species using both data collected in the field and data obtained under laboratory conditions. The field studies included frequent measures of predawn water potential and periodic diurnal measures of water potential and leaf conductance. A series of laboratory studies, including controlled dehydration-rehydration experiments and the construction of pressure-volume curves, were used to provide information on the components of the water potential equation and on critical values for stomatal closure, survival time and irreversible tissue injury. Classically, both field and laboratory approaches have been extensively utilized to classify the drought relations of species, but they have been rarely used in parallel. We sought to couple these two approaches and in so doing, to evaluate the relative importance of several parameters in drought resistance.

Introduction

Plants resist the possible damaging effects of drought by either avoiding or tolerating the stress exposure (Levitt 1972) but a mixture of both strategies is more often represented.

A year long study of the water relations of shrub sized specimens of *Cornus mas*, *C. sanguinea*, *Crataegus monogyna*, *Quercus pubescens*, *Sorbus aria* and *Viburnum lantana* was conducted on a periodically watered site in a garden and on a field site. In the east of Austria, our six species are commonly found on dry sites, with only *Cornus sanguinea* and *Crataegus monogyna* extending to more humid soils. These two species occupy a wider "European" range, the other four are classified as submediterranean species. All six are found on moderately acidic to moderately alkaline soils of average nutrient content and have average to high light and temperature requirements (cf. Ehrendorfer et al. 1972).

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Methods and materials

The six study shrub species were investigated in parallel at two sites. One site was in the garden of the Universität für Bodenkultur (University of Agriculture) Vienna, Austria, while the other site was located on the outskirts of Vienna in a protected landscape zone on a south-southeast exposed slope of Leopoldsberg at the Wienerwald border of the Vienna basin. The soils in the garden were at least 70 cm deep and were periodically irrigated. The site on Leopoldsberg is classified as a *Quercetum pubescentis* shrub community containing many sub-Mediterranean and Pannonic species at their northern or western limit, respectively. This site frequently experiences drought because of the steep slope, exposure and thin (< 10 to 30 cm) rocky soils (Pararendsina on calcareous sandstone). The sandstone parent material is sufficiently fractured to allow some deep rooting. A large-scale excavation of the root systems of our study specimens was not feasible at this protected site. However, the general rooting pattern of our six species is well known from the older European literature (Hempel and Wilhelm 1893; Oberdorfer 1979): *Cornus mas*, *C. sanguinea* and *Viburnum lantana* are shallow-rooted; *Crataegus monogyna*, *Quercus pubescens* and *Sorbus aria* are deep-rooted species.

In the garden, one shrub of each species was chosen while duplicate shrubs were used at Leopoldsberg. Studies were initiated in June 1978 and were terminated one year later. The study was divided into three parts: (1) the seasonal progression of the components of water status, (2)

the diurnal patterns of water status, and (3) the drought resistance characteristics of the species during the peak of the drought which occurred during the summer of 1978.

Seasonal progression

The seasonal evaluation of the components of water status consisted of biweekly measurements of predawn xylem pressure potential (hereafter referred to as predawn water potential) at each site and the development of pressure-volume curves on leaves collected once per week. At each sampling time, a foliated branch from each species was collected, stored in a plastic sack and brought as rapidly as possible to the laboratory. The branch was recut under water, covered with plastic and left overnight to resaturate. On the next day, a fully resaturated leaf was removed from the branch and weighed, the water potential was determined with a pressure chamber and the leaf was reweighed. Then repeated fresh weights before and after each determination of water potential were made on the leaf. For each water potential determination, the chamber was pressurized and depressurized very slowly (i.e., at less than $0.01 \text{ MPa} \cdot \text{s}^{-1}$). Between readings, the leaf was allowed to transpire freely outside the pressure chamber. By using three pressure chambers simultaneously, it was possible to determine between 15 and 20 pressure-volume curves in a single day (i.e., 2–4 leaves per species). Typically, there were between 7 and 12 pressure chamber measurements and between 14 and 24 fresh weight measurements per leaf. Leaves were oven-dried at 100°C for 24 h and weighed to determine dry weight. The theoretical considerations involved with pressure-volume curves and their graphical display have been extensively discussed (Roberts and Knoerr 1977; Tyree et al. 1978; Richter 1978; Hinckley et al. 1980; Tyree and Richter 1981, 1982).

Diurnal patterns

Diurnal patterns of water status and stomatal activity were measured six times during the summer of 1978 and once during the spring of 1979 at each site. Xylem pressure potential or total leaf water potential (ψ_t) and leaf conductance to water vapor transfer (g_{wv}) were measured hourly and environmental variables (e.g., solar radiation, wet and dry bulb temperatures) were measured every 30 min from before sunrise to after sunset. Four leaves were taken from each species, each from approximately the same location with respect to exposure and stage of leaf development: two were used to estimate ψ_t with a pressure chamber and the other two were used to measure g_{wv} with a ventilated diffusion porometer (Körner and Cernusca 1976).

Drought resistance

The drought resistance characteristics of the six species from Leopoldsberg were assessed in the last week of August 1978 when predawn ψ_t ranged from -1.39 (*Q. pubescens*) to -3.16 MPa (*V. lantana*). The methods employed were adapted from those described for such laboratory studies in the literature (e.g., Oppenheimer 1932, Pisek and Berger 1938, Rouschal 1938, Pisek and Winkler 1953, Larcher 1960). The same foliated branch used to provide leaves for the development of pressure-volume curves was allowed to dry under a light bank after resaturation. Light levels were

near $350 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, air temperature was $23 \pm 2^\circ \text{C}$ and relative humidity was $40 \pm 10\%$. Periodically, leaves were removed, pressure chamber and fresh weight readings were taken and these leaves were placed in a container of sand filled with water to the top of the sand. The petiole of each leaf was placed in the sand, the container was covered with plastic and stored for 24 h in the dark. On the next day, the petioles of these leaves were blotted dry and then the leaves were weighed, oven-dried for 24 h at 100°C and reweighed. From another branch which had not been allowed to dehydrate, 5 to 8 fully saturated leaves were weighed and then oven-dried and reweighed. The ratio of saturated to oven dried weight was used to calculate saturated weights for leaves on which we had only oven-dried weights. We used the leaves from the pressure-volume part of the study to test this method for obtaining saturated weights for all species; our estimate was always within 1% or better of the measured value.

For any leaf, the following readings were available: (1) the time since the start of the experiment and from the fully saturated condition, (2) water potential (ψ_t), (3) relative water content (R), (4) the resaturation water deficit (D) (Oppenheimer 1963) and (5) any observations on the condition of the foliage following 24 h of resaturation. The resaturation water deficit (D) is defined by the following equation:

$$D = \frac{\text{Original saturated wgt.} - \text{Resaturated wgt.}}{\text{Original saturated wgt.} - \text{Oven-dry wgt.}} \times 100 (\%)$$

According to Oppenheimer (1963) irreversible injury is indicated by a D value of 10% or more. From parallel pressure-volume curves, it was possible to know the turgor pressure or the osmotic potential for any time, ψ_t or R .

Results

Predawn water potentials

Predawn water potential (predawn ψ_t) values from both sites showed comparable effects of the prolonged drought of 1978 since the garden site dried almost as severely as the Leopoldsberg site before being watered (Table 1). Minimum predawn ψ_t ranged from -1.78 MPa in *Sorbus aria* to -3.55 MPa in *Cornus sanguinea*. *Sorbus aria*, *Crataegus monogyna* and *Quercus pubescens* had less negative predawn ψ_t than *Cornus mas*, *C. sanguinea* and *Viburnum lantana* at both sites. A relatively high predawn ψ_t is thus characteristic for species with deeper and more extensive root sys-

Table 1. Minimum predawn water potentials (predawn ψ_t) and minimum ψ_t s observed in 1978 for the six shrub species from the garden site and from Leopoldsberg. All values in – MPa

Species	Garden Site		Leopoldsberg Site	
	Predawn ψ_t	Min. ψ_t	Predawn ψ_t	Min. ψ_t
<i>Sorbus aria</i>	0.76	2.91	1.78	3.19
<i>Crataegus monogyna</i>	0.92	2.51	2.28	3.31
<i>Quercus pubescens</i>	1.03	2.53	2.35	3.12
<i>Viburnum lantana</i>	2.58	3.36	3.35	3.92
<i>C. sanguinea</i>	2.91	3.80	3.55	3.79
<i>Cornus mas</i>	3.08	3.95	3.54	3.86

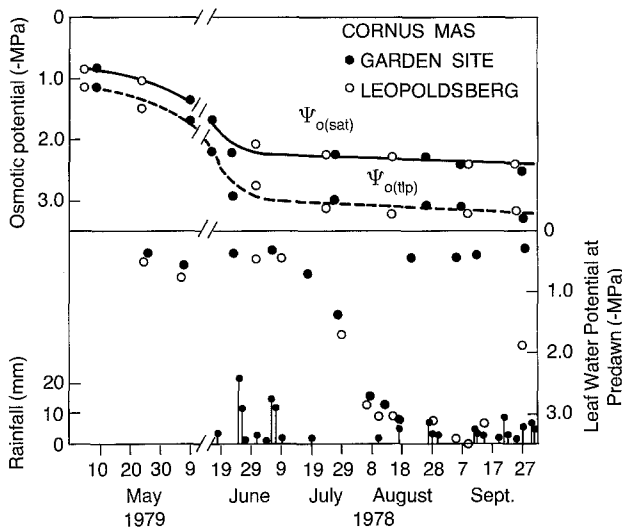


Fig. 1. The seasonal course of the osmotic potential at full saturation ($\psi_{o(sat)}$), the osmotic potential at the turgor loss point ($\psi_{o(tlp)}$), and predawn leaf water potential for leaves from *Cornus mas* shrubs located in the garden of the Universität für Bodenkultur (●) and on Leopoldsberg (○). Shrubs were watered heavily from 19 to 24 August in the garden

tems. Such roots are presumably in contact with moist soil layers and can establish a water potential equilibrium with them during the night. Some authors have, therefore, used predawn ψ_t to infer the rooting behavior of plants (Ritchie and Hinckley 1975, Eliás 1978, Huzulák 1980, Hinckley et al. 1981, Lucier and Hinckley 1982), and our results on species with independently characterized rooting behavior support this reasoning. Following light rains on August 27, 28 and 30 where the top 4 to 8 cm of soil was wetted, only predawn ψ_t in *Viburnum lantana* recovered (from -3.35 to -2.08 MPa, Hinckley et al. 1980). In contrast, very heavy watering in the garden on August 19 through 24 resulted in the recovery of all species. In addition, the difference in average predawn ψ_t between the deep and shallow rooted species was greater at the garden site (1.96 MPa) than on the Leopoldsberg site (1.34 MPa). The deeper soil of the garden site was compared to the Leopoldsberg site may have resulted in a greater expression of rooting behavior in the deep rooted species.

Seasonal progression of the components of water potential

The osmotic potential at full saturation ($\psi_{o(sat)}$) and at the turgor loss point ($\psi_{o(tlp)}$) were estimated from the pressure volume curves and are presented for *Cornus mas* (Fig. 1). As we discussed in an earlier paper (Hinckley et al. 1980), these components do not fluctuate widely except during periods of leaf development or leaf senescence. Bud burst occurred around April 10 in both the garden and on Leopoldsberg. The first pair of leaves of *Cornus mas* was distinguishable on April 16 in the garden and on April 19 on Leopoldsberg. By mid-June, leaf and shoot expansion was completed. Visible leaf senescence was first noted during the last week of September on Leopoldsberg and during the first week of October in the garden.

Ten to fourteen day old leaves were about the youngest material that could be used in the pressure chamber and, typically, $\psi_{o(sat)}$ for these leaves was greater than -1.0 MPa in all species. In fully mature leaves, $\psi_{o(sat)}$ fluctuated only slightly and ranged from -1.60 MPa in *Viburnum lantana* to -2.89 MPa in *Crataegus monogyna* (Table 2). *Quercus pubescens* was an exception to the common behavior of the five other species as both $\psi_{o(sat)}$ and $\psi_{o(tlp)}$ decreased in mature leaves as the summer progressed. The decrease on Leopoldsberg appeared to follow the progression of the drought; for example, as the drought progressed, $\psi_{o(tlp)}$ decreased from -2.65 to -3.76 MPa. In contrast, these values continued to decrease in the garden even following irrigation. The osmotic potential at the turgor loss point averaged 1.0 MPa more negative than $\psi_{o(sat)}$ in mature leaves but ranged from a difference of 0.83 MPa in *Cornus sanguinea* to 1.09 MPa in *Sorbus aria*. In immature leaves, the difference between $\psi_{o(sat)}$ and $\psi_{o(tlp)}$ was less (Fig. 1).

Diurnal patterns

Figure 2 illustrates the diurnal patterns of leaf conductance (g_{wv}), turgor pressure (pressure potential) and ψ_t for *Sorbus aria* and *Cornus mas* for three different days. All days were clear (between 1,750 and 1,920 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ radiation at solar noon) and warm (between 24.2 and 27.8°C). Turgor pressure was calculated from associated pressure-volume curves.

The first day, 24 May 1979, represented a day of adequate soil moisture when leaves were still expanding (Fig. 2). In both species, predawn ψ_t was greater than

Table 2. Comparison of the various tissue parameters estimated from a pressure-volume curve in the six species at the end of August from the Leopoldsberg site. $\psi_{o(sat)}$ = osmotic potential at full saturation, $\psi_{o(tlp)}$ = osmotic potential at the turgor loss point, R_{tlp} = relative water content of the leaf tissue at the turgor loss point, $\Delta\psi_{o(sat,tlp)}$ = the passive change in osmotic potential between full saturation and the turgor loss point, and $\Delta\psi_{o(100-90)}$ = the passive change in osmotic potential as relative water content decreases from 100 to 90%

Species	$\psi_{o(sat)}$ (-MPa)	$\psi_{o(tlp)}$ (-MPa)	R_{tlp} (%)	$\Delta\psi_o$ (MPa)		Predawn ψ_t (-MPa)
				(sat.-tlp)	(100-90)	
<i>Sorbus aria</i>	2.37	3.46	80.0	1.09	0.45	1.76
<i>Crataegus monogyna</i>	2.89	3.94	74.9	1.05	0.33	1.87
<i>Quercus pubescens</i>	2.45	3.51	76.2	1.06	0.34	1.39
<i>Viburnum lantana</i>	1.60	2.56	73.0	0.96	0.28	3.16
<i>Cornus sanguinea</i>	2.36	3.19	75.8	0.83	0.27	2.86
<i>Cornus mas</i>	2.27	3.23	70.9	0.96	0.28	3.10

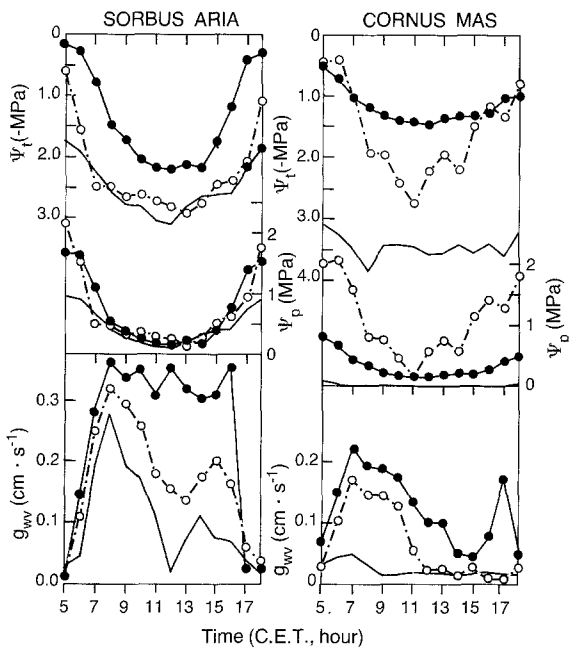


Fig. 2. Diurnal trends of leaf conductance (g_{wv}), turgor pressure (ψ_p) and leaf water potential (ψ_t) for *Cornus mas* and *Sorbus aria* for May 24, 1979 (solid dot, solid line, garden site), September 5, 1978 (open dot, dashed line, garden site) and August 28, 1978 (solid line, Leopoldsberg)

–0.55 MPa in *Cornus mas* and minimum ψ_t was –1.42 MPa in *Cornus mas* and –2.22 MPa in *Sorbus aria* (Table 2). Leaf conductance increased and then leveled off near $0.34 \text{ cm} \cdot \text{s}^{-1}$ in *Sorbus aria* while it decreased in the late morning in *Cornus mas*. Late afternoon recovery was noted in g_{wv} in *Cornus mas*. Turgor pressures started at 1.66 and 0.81 MPa in *Sorbus aria* and *Cornus mas*, respectively, and reached minima below 0.2 MPa associated with minima in ψ_t in both species. Turgor pressure in *Cornus mas* was not high, neither when compared to *Sorbus aria* nor to itself on 5 September. This is an example of how readily a young leaf can come under stress (Karlic and Richter 1983).

On 5 September, soil moisture was again adequate following irrigation of the garden site and leaves were fully mature and assumed to be drought hardened. The large drop in ψ_t during the day with turgor pressures remaining the same or higher than those noted on 24 May was the major change associated with leaf maturation and drought hardening in both species. Mid afternoon stomatal closure was apparent in both species, but was greater in *Cornus mas* than in *Sorbus aria*. Vapor pressure deficits were substantially greater on 24 May than on 5 September. For example, maximum vapor pressure deficits exceeded 3.5 kPa on 24 May while they never exceeded 2.5 kPa on 5 September. Thus, it is surprising that stomata were more closed here than at the first date despite good turgor in both species. This could be the effect of increased stomatal sensitivity to vapor pressure deficits, perhaps enhanced by the accumulation of abscisic acid during the previous drought period.

The last day course shown in Fig. 2 is for 28 August during the peak of the drought on Leopoldsberg. Predawn ψ_t was –3.10 MPa in *Cornus mas* and –1.76 MPa in *Sorbus*

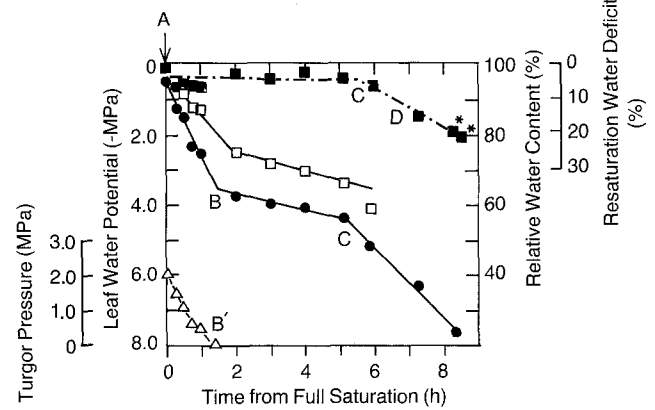


Fig. 3. Controlled dehydration study with foliated branches of *Sorbus aria* (see Table 3 for data from other five species). ■ resaturation water deficit, □ relative water content, ● leaf water potential, △ turgor pressure. A point of full saturation, B point of change from stomatal to cuticular water loss, B' point where turgor pressure equals zero (turgor loss point), C point of irreversible tissue damage, D Oppenheimer's (1963) point of irreversible turgor loss, * visual injury to the leaf appears

Table 3. Results of controlled dehydration study on foliated branches of six shrub species (see Fig. 3 for an example). The water potential (ψ_t) and the relative water content (R) at which damage occurred and the time necessary to go from point A (full saturation) to point B (transition between stomatal and cuticular water loss) and the time from point B' (turgor loss point) to C (estimated damage point) are given

Species	Damage		Time from	
	ψ_t (-MPa)	R (%)	A to B (h)	B' to C (h)
<i>Sorbus aria</i>	4.75	62.7	1.4	3.8
<i>Crataegus monogyna</i>	5.25	57.1	1.9	2.1
<i>Quercus pubescens</i>	4.55	62.5	4.8	4.3
<i>Viburnum lantana</i>	4.50	46.9	3.8	7.9
<i>Cornus sanguinea</i>	5.15	48.1	5.1	11.8
<i>Cornus mas</i>	5.08	45.7	6.5	11.6

bus aria. Minimum ψ_t for *Sorbus aria* was only 0.2 MPa less than on 4 September while in *Cornus mas* it was 1.11 MPa less. Turgor pressure was about 0.08 MPa less on 28 August than on 5 September in *Sorbus aria* and as a consequence, values of g_{wv} were only slightly less than on 5 September. In contrast, turgor pressures were either near or equal to zero the entire day in *Cornus mas*. Stomata were mostly closed the entire day.

Controlled experiments

This section will deal with controlled experiments designed to determine the time necessary to reach the point of stomatal closure (a measure of tissue capacitance or buffering), the time between full stomatal closure and the point of irreversible tissue damage (a further measure of tissue buffering plus an estimate of the effectiveness of cuticular conductance in controlling water loss), and the water potential and the relative water content at the points of (1) stomatal closure and (2) tissue injury (Fig. 3, Table 3). Thus, our

approach adds to the results of "classical" dehydration studies (e.g., Pisek and Berger 1938) the dimensions of leaf water potential and turgor pressure (cf. Duhme 1974).

Initially, the foliated branch was fully saturated (point A in Fig. 3). With removal from a source of water, there was a rapid decrease in water potential and then a transition to a slower rate of decrease in water potential. This transition point (B) coincided with the turgor loss point (B') in all six species. Stomata were probably fully closed at this point. The time to go from point A (fully saturated state) to point B (complete stomatal closure) ranged from 1.4 h in *Sorbus aria* to 6.5 h in *Cornus mas*. The time required from point B' to C (turgor loss to irreversible tissue damage) is probably more critical and ranged from 2.1 h in *Crataegus monogyna* to 11.8 h in *Cornus sanguinea*. The total time from full saturation to potential cellular damage was the shortest in *Crataegus monogyna* (4.0 h) and was the longest in *Cornus mas* (18.1 h).

Discussion

We have now amassed some information on plant parameters related to drought resistance. It seems appropriate to use these data in an attempt to divide our six species into groups according to the tolerance – avoidance concept of Levitt (e.g. 1972) and to discuss the pertinent mechanisms involved in our division.

A comparison of the ψ_t minimums reached in the field (Table 1) with ψ_t values inducing tissue injury (Table 3) shows that even during the peak of the drought there remained between 0.58 and 1.94 MPa of leeway for the six species, so that the danger of direct dehydration injury never arose; it was avoided even during the rather extreme drought of 1978. Therefore, we shall have to deal only with "indirect drought resistance"; that is, avoidance or tolerance of drought induced metabolic strain. Such metabolic strain would not lead to immediate injury but would affect the overall performance of the plant, probably with negative consequences for growth and competition. Metabolic strain, as has been shown repeatedly (e.g. Hsiao 1973), is induced at different water potential levels for different fundamental processes. We must therefore find a process indicative of plant performance in the field and which is documented in our data. Indeed we find such a process: a plant may either keep the stomata open during a drought period and avoid the carbohydrate starvation induced by prolonged closing; or it may tolerate such closing for a variable length of time. The effects of drought on photosynthesis and the subsequent impacts on the long-term survival of plants on dry sites has been stressed previously (Zelniker 1968). It results in a convenient criterion for ranking species on a gliding scale from full avoidance to pronounced tolerance.

It helps in our task that the point of stomatal closing under the influence of water stress is for all our species closely connected with the turgor loss point (Fig. 3). A given value for total water potential at the turgor loss point may be reached by contributions from three different factors (Table 2). *Crataegus monogyna* has the lowest $\psi_{o(tlp)}$ (-3.94 MPa). A very low osmotic potential at full saturation (factor 1) in *Crataegus monogyna* is further reduced by a moderate passive drop in the osmotic potential (factor 2); that is, as relative water content decreases from 100 to 90%, ψ_o decreases another 0.33 MPa from the saturation

value of -2.89 . Cell walls are elastic (factor 3), so that the turgor loss point is only reached at the rather low relative water content of 74.9%. *Sorbus aria* uses a different strategy: its $\psi_{o(sat)}$ of -2.37 MPa is intermediate for the six species and its cell walls appear more rigid ($R_{tlp} = 80.0$) than the other species; these poorly expressed mechanisms for avoidance of stomatal closure in *Sorbus aria* are compensated for by a rapid decrease in the osmotic potential whenever water is lost ($\psi_{o(100-90)} = 0.45$). This is enough to give this species second rank. *Quercus pubescens* relies on both elastic cell walls and a moderate decrease in osmotic potential when water is lost to reach a $\psi_{o(tlp)}$ of -3.51 MPa. Dehydration of *Cornus sanguinea* starts at virtually the same level of $\psi_{o(sat)}$ as in *Sorbus aria*; however, it has a $\psi_{o(tlp)}$ of only -3.19 (fifth place). This is caused by the very gradual passive decrease in the osmotic potential ($\psi_{o(100-90)} = 0.27$). The influence of rather elastic cell walls in *Cornus sanguinea* does not help in this case. The most important disadvantage for *Viburnum lantana* is obviously its very high $\psi_{o(sat)}$ which confines this species to last place. In this way, we obtain a ranking for one of the components of avoidance behavior, namely the value of the water potential at the turgor loss point. There are, however, other components involved in avoidance which result in a more or less different ranking.

The second means of avoidance comes from the rooting behavior. Deep roots and the exploitation of moister soil layers during a drought are certainly avoidance features. It is interesting that the three species with lowest turgor loss points are also the first three in respect to their predawn ψ_t (Table 1). However, the ranking changes slightly: now *Sorbus* is ranked first, with *Crataegus* and *Quercus* approximately the same and in second place. These three species are separated by a wide gap from *Viburnum lantana* and the *Cornus* species. The difference between species with avoidance features and those without is here far more pronounced than in the first line of evidence.

A third mechanism of avoidance is illustrated by the controlled dehydration of branches (Table 3, Fig. 3). It may be assumed that a long time interval between full saturation and the turgor loss point indicates cautious stomatal behavior; this would mean that some loss in the capacity to synthesize carbon substances is tolerated in exchange for better water economy. *Quercus pubescens* changes its role here and joins the tolerant group. Larcher (1960) also observed a gradual reduction in transpiration in this species beginning at high R values. *Sorbus* and *Crataegus* keep their stomata wide open until complete turgor loss enforces rapid closure.

We do not think that our data demonstrate all of the features relevant for positioning a plant on a tolerance-avoidance scale. An integration of the effects of all factors (both known and unknown to us) is possibly given by the behavior of stomata in the field (Fig. 2).

As has been discussed previously (Stocker 1956, Hinckley et al. 1978), diurnal behavior of stomatal activity can be broadly classed into three general patterns; a schematic overview, based on results from numerous field studies, is given in Fig. 4. The first pattern, stomata open all day, results from conditions where soil water potential, frictional potential losses and the vapor pressure gradient between the leaf and the atmosphere are not limiting. Patterns 2a and b are found on days when either frictional potential losses or vapor pressure gradients reduce stomatal opening.

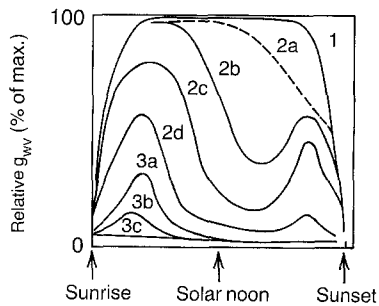


Fig. 4. Hypothetical patterns 1, 2, 3 of leaf conductance (g_{wv}). Pattern 1: g_{wv} not limited by predawn or diurnal water potential or vapor pressure gradient. Pattern 2: One or more factors limiting; however, water potential is always above the turgor loss point. Pattern 3: Water potential at or below the turgor loss point for part or the entire day

Table 4. The conductance patterns (see Fig. 4 for definitions and Fig. 2 for examples) found in the six species for three conditions: (1) early (24 May 1979) in growing season, moist soil, (2) late (4 September 1978), following drought recovery, moist soil and (3) late (29 August 1978), dry soil. All three days were clear with maximum air temperatures between 24.2 and 27.8° C. Water relations parameters are also given for these days. Predawn ψ_t = predawn water potential, ψ_t min = minimum ψ_t observed during a day course, $\psi_{o(tlp)}$ = osmotic potential (equal to ψ_t) at the turgor less point

Species	Condition	Conductance pattern	Water relations parameters (-MPa)		
			Predawn ψ_t	ψ_t min	$\psi_{o(tlp)}$
<i>Sorbus aria</i>	(1) early	1	0.14	2.22	2.42
	(2)	2b	0.59	2.91	3.12
	late, moist				
(3) late, dry	2c	1.76	3.12	3.46	
<i>Crataegus monogyna</i>	(1)	2a	0.71	2.70	3.16
	(2)	2c	0.51	2.51	3.64
	(3)	2d	1.87	3.20	3.94
<i>Quercus pubescens</i>	(1)	2b	0.35	2.24	2.42
	(2)	2b	0.32	2.53	3.08
	(3)	2c	1.39	2.84	3.51
<i>Viburnum lantana</i>	(1)	2b	0.89	1.99	2.26
	(2)	2b	0.15	1.74	2.52
	(3)	3b	3.16	3.71	2.56
<i>C. sanguinea</i>	(1)	2b	0.46	1.67	1.74
	(2)	2c	0.05	2.55	2.88
	(3)	3a	2.86	3.60	3.19
<i>Cornus mas</i>	(1)	2b	0.52	1.42	1.52
	(2)	2d	0.41	2.75	3.08
	(3)	3b	3.10	3.86	3.23

When soil water potential begins to limit, patterns 2c and d are found. Pattern three is noted when predawn ψ_t is either near $\psi_{o(tlp)}$ (Patterns 3a and b) or more negative than $\psi_{o(tlp)}$ (Pattern 3c).

The six species studied fall within this classification scheme (Fig. 2, Table 4). Interestingly, pattern one was found only in *Sorbus aria* possibly indicating the rarity of finding non-limiting conditions in field environments at all times throughout a day course. Some form of Pattern 2

prevailed on most occasions while pattern 3 was found only during the driest period in the species with low predawn ψ_t values, *Cornus sanguinea*, *C. mas* and *Viburnum lantana*.

When leaves were just mature and the soil was moist, the following ranking of the pattern of leaf conductance of a species (from most to least open during the day) was possible: *Sorbus aria* > *Crataegus monogyna* > *Quercus pubescens* = *C. sanguinea* = *Cornus mas* = *Viburnum lantana* (Table 4). As shown in the laboratory, *Quercus pubescens* had conservative stomatal behavior. In fully mature leaves which had undergone a period of dryness and subsequent recovery, the following ranking was noted: *Sorbus aria* = *Quercus pubescens* = *Viburnum lantana* > *Cornus sanguinea* = *Crataegus monogyna* > *Cornus mas*. A comparison of these two rankings illustrates the effect of leaf aging on the maintenance of a favorable ψ_p which permits stomatal opening. In addition, the exposure to a drought resulted in more cautious stomatal behavior in all species except *Quercus pubescens* and *Viburnum lantana*. Whether the initial ranking would be maintained with no drought exposure is not known. Even the mildest drought appears to alter the sensitivity of stomata to vapor pressure deficit (Pezeshki and Hinckley 1982). The combination of leaf aging and species specific exploitation of a layered soil column with non-uniform moisture characteristics during a drought period can be best assessed by comparing the first ranking with the next. In fully mature leaves under conditions of dry soil, the following ranking of leaf conductance patterns was made: *Sorbus aria* = *Quercus pubescens* > *Crataegus monogyna* > *Cornus sanguinea* > *Viburnum lantana* = *Cornus mas*.

Species that maintained high values of predawn ψ_t had more open stomata under drought conditions than species that had low values. In addition, the group of species with high values of predawn ψ_t had relatively low values of $\psi_{o(tlp)}$ (-3.62 MPa) as compared to the other group (-3.01 MPa) (Table 2). Although all species tried to maintain ψ_t levels above $\psi_{o(tlp)}$ during the day (Fig. 2), the group of species with the low values of predawn ψ_t had both predawn and midday ψ_t values that were more negative than $\psi_{o(tlp)}$ during a one to two week period in late August and early September (Fig. 1). This group of species underwent an appreciable stress even at the garden site (Fig. 1, Table 1). Therefore, it might be expected that the two *Cornus* species and *Viburnum lantana* would do poorly on drought sites. However, the abundance of these species on the dry, south slope of Leopoldsberg suggested otherwise. Their competitive advantage must therefore depend on successful tolerance, not on avoidance of a drought-induced reduction in photosynthesis. We can only speculate upon the mechanisms involved in this tolerance. One factor might be found in the lower carbohydrate requirements for the development and metabolic maintenance of the restricted root system of these species.

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