The Control by Atmospheric Factors and Water Stress of Midday Stomatal Closure in *Arbutus unedo* Growing in a Natural Macchia

J.D. Tenhunen, O.L. Lange, and D. Jahner
Lehrstuhl für Botanik II, Universität Würzburg, Mittlerer Dallenbergweg 64, D-8700 Würzburg, Federal Republic of Germany and Research Station Quinta São Pedro, Sobreda, Portugal

**Summary.** Midday closure of stomata of well-watered (Ψ between −10 and −25 bar) or moderately stressed (Ψ between −25 and −35 bar) *Arbutus unedo* plants occurs when midday leaf temperatures increase above 30 °C and vapor pressure difference between leaf air spaces and the external air increases above approximately 30 mbar/bar. Moderate water stress decreases maximum conductance and may result in greater sensitivity to high leaf temperature and vapor pressure deficit, which results in earlier closure and later reopening of stomata. Severe water stress (Ψ of −50 bar) changes the form of the daily pattern observed for leaf conductance. A single morning peak in conductance occurs followed by decrease in conductance over the remainder of the day. Morning fog in Portugal during the dry season may facilitate stomatal opening and may allow improvement of carbon balances of the leaves for short periods, but contributes little to improvement of plant water balances over the longer term.

**Introduction**

Long-term water stress, in the case of the desert plants *Hammada scoparia*, *Zygophyllum dumosum*, and *Artemisia herba-alba*, has been observed to increase the tendency of plants to limit water use by midday closure of stomata (Schulze et al. 1980). At any particular water potential, prevailing leaf temperature and leaf to air vapor pressure deficit appear to determine stomatal conductance (Schulze et al. 1972). Similar results were obtained by Lange and Meyer (1979), when leaf gas exchange of potted grapevines was monitored while plants were subjected to soil drying treatments. Investigations of stomatal behavior and water relations of plants growing in an evergreen macchia near Lisbon, Portugal (Tenhunen et al. 1981a; Lösch et al. 1982) demonstrated that midday stomatal closure occurs in leaves of many of these sclerophyllous plant species during the hot and dry summer season.

Of those sclerophylls studied, *Arbutus unedo* was among the species which responded most sensitively to high leaf temperature and low humidity at midday by closing stomata. With *Arbutus unedo* and other sclerophylls it was possible to reproduce the midday closure phenomenon under simulated habitat conditions in an environmental chamber (Tenhunen et al. 1980, 1981b; Lange et al. 1982). Studies under controlled conditions will allow progress in analysis of the complex interactions of atmospheric and internal factors affecting midday stomatal closure. Nevertheless, further information can be obtained under field conditions which allow us to better define situations in which midday closure occurs and to understand the significance of midday closure in seasonal or annual regulation of leaf gas exchange.

Extremely dry weather during 1981 at the Research Station Quinto São Pedro near Lisbon, made it possible to expose individual plants of *Arbutus unedo* by differential watering to specified ranges of water potential over a two month period. It was then possible to examine in more detail than in other previous studies, the effect of water stress on stomatal response to atmospheric environmental conditions by observing the diurnal course in stomatal conductance for leaves of plants with different water potentials on the same day. Observations were made both on days when leaf temperatures and vapor pressure deficits remained low and days when temperatures and vapor pressure deficits increased to levels normally causing midday stomatal closure and depression of gas exchange. In addition, the influence of morning fog on stomatal conductance and plant water balance during the dry season was studied.

**Methods**

Field experiments were conducted with *Arbutus unedo* during the summer dry period of 1981 in a natural evergreen macchia at the Research Station Quinto São Pedro, Sobreda, Portugal. The macchia is of a type related to the order of the Quercetalia ilex as described by Braun-Blanquet (1952) and is dominated by sclerophyllous species such as *Quercus coccifera*, *Pistacia lentiscus*, *Phillyrea angustifolia*, *Arbutus unedo*, *Myrtus communis*. The Atlantic character of this Mediterranean scrub as well as the low soil pH of the habitat is reflected by the presence of scattered *Quercus suber* trees and numerous *Ulex parviceps* shrubs. The weather was exceedingly dry during both winter 1980/81 and spring and summer 1981. Early morning water potentials of *Arbutus unedo* experiencing the natural course of summer drought were measured with a pressure chamber of the Scholander type (Scholander et al. 1965). Water potential decreased rapidly during July and reached approximately −50 bar by the beginning of August. (Fig. 1) Measurements were done with terminal shoots because petioles of individual leaves severed under high pressure. Little change in early morning water potential occurred during August and September. A strong thunderstorm on September 25 replenished soil water content and plant water potentials increased continuously day and night over a two day period until plant water potential was approximately −10 bar.
During the first week of August, individual plants of *Arbutus unedo* were supplied with different amounts of water such that well-watered plants maintained a pre-dawn water potential of approximately ~10 bar during the next two months. These plants were scattered within the macchia stand, and the height of the trees was 2 to 2.50 m. Moderately-watered *Arbutus* trees were maintained with a pre-dawn water potential of approximately ~25 bar which was similar to the pre-dawn water potential which occurred naturally during the summer 1980 (Tenhunen et al. 1981a). Daily time course of total leaf conductance (including boundary layer), incident light intensity above the canopy (PAR), vapor pressure deficit between leaf air spaces and the external air (ALVPD), leaf temperature (TL), transpiration rate into the porometer cuvette, and plant xylem water potential (ψ) were determined for unwatered, moderately-watered, and well-watered plants. Data are plotted as a function of daylight savings time in Portugal as was used by Tenhunen et al. (1981a) and Löscher et al. (1982). During the dry season, only present year leaves were found on the *Arbutus* shrubs. The average leaf responses shown are in each case for leaves equally spaced along a single twig of the present year growth. Thus, each sample consists of a relatively young leaf, two or three leaves of intermediate age, and an older leaf of the same branch. All leaves under consideration were fully differentiated. Except for water potential (pressure chamber), data were obtained with a LI-1600 steady-state porometer (LiCor Inc., Lincoln, Neb.). Boundary layer conductance of the leaf in the porometer cuvette was constant and approximately equal to 2,000 mmole m^-2 s^-1. Leaf to air vapor pressure deficit was calculated from measured air temperature, leaf temperature, and relative humidity. Conductance was determined from calculated ALVPD and measured transpiration rate. During the initial measurement periods of high external humidity on each day (2 measurements on August 8, 3 on August 14, 3 on August 23, and 2 on September 2) cuvette relative humidity was set at 70% in order to obtain a reliable estimate of conductance. Assuming this conductance to be valid as well for ambient humidity, transpiration rates were corrected for the AVLPD which would have occurred at ambient humidity and included in the figures. Further details of methods were reported previously (Tenhunen et al. 1980, 1981a).

**Results**

Diurnal time courses of atmospheric environmental factors, total leaf conductance for water vapor, and xylem water potential in well-watered and unwatered plants of *Arbutus unedo* on a warm summer day are shown in Fig. 2. Leaf temperatures remained below 30°C and vapor pressure deficits between leaf air spaces and the external air remained below 25 mbar/bar. Even though experiencing extreme water stress, unwatered plants maintained relatively high rates of transpiration. Under these moderate atmospheric conditions and as expected from previous observations (Tenhunen et al. 1981a, 1981b; Löscher et al. 1982), no closure of stomata occurred at midday. Rather, conductance decreased gradually throughout the day until stomatal closure occurred at sundown. Water stress was seen to decrease the maximum conductance. Since leaf conductance decreases only slightly during the midday period, the diurnal course of transpiration rate into the porometer cuvette is strongly influenced by change in ALVPD and peaks at midday.