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Responses of photosynthesis and stomatal conductance to atmospheric humidity in some mediterranean *Abies* species

J.M. Guehl[1], J. Bouachrine[1], R. Zimmermann[2] and E. Dreyer[1]

[1]*Laboratoire de Bioclimatologie-Ecophysiologie Forestière, Station de Sylviculture et Production, INRA, Centre de Nancy, F-54280 Seichamps, France, and*
[2]*Lehrstuhl für Pfanzenökologie, Universität Bayreuth, Postfach 3008, D-8580 Bayreuth, F.R.G.*

Introduction

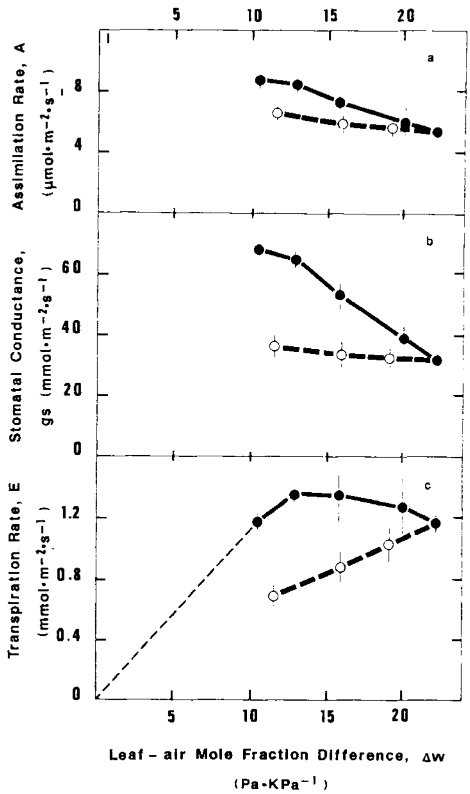
Leaf gas-exchange has long been shown to be sensitive to changes in the water vapor mole fraction difference between the leaf and the air (Δw) (Sandford and Jarvis, 1986; Schulze, 1986). It has been proposed (Guehl and Aussenac, 1987; Grieu *et al.*, 1988) that decreasing CO_2 assimilation in response to increasing Δw is not only due to stomatal closure, but could be, at least partially, a consequence of altered mesophyll photosynthetic capacity. However, that interpretation is not consensual (Terashima *et al.*, 1988). We report herein results providing further evidence for the existence of a mesophyll effect in response to increasing Δw in some mediterranean *Abies* species. The study was also aimed at determining whether the different species examined exhibit differences in their water use efficiencies.

Materials and Methods

Responses of CO_2 assimilation rate *(A)* and transpiration rate *(E)* to varying Δw were assessed under controlled environmental conditions with an open gas-exchange measurement system on intact or excised shoots of different mediterranean coniferous species. Stomatal conductance (g_s) and intercellular CO_2 concentration (C_i) were calculated from the gas-exchange data using classical equations (see Guehl and Aussenac, 1987). Prior to Δw being increased, the short-term response of gas-exchange to increasing ambient CO_2 concentration (C_a) was assessed, and the corresponding $A(C_i)$ functions were determined, thus allowing the analysis of CO_2 assimilation in terms of mesophyll photosynthetic capacity (demand function, see Fig. 1) and diffusional limitation of CO_2 supply to the chloroplasts (supply function). The $A(C_i)$ functions were also used to determine the marginal water cost of CO_2 assimilation ($\partial E/\partial A$) (Guehl and Aussenac, 1987) and to examine the gas-exchange regulation with respect to the optimization theory of Cowan and Farquhar (1977).

Results and Discussion

Increasing Δw resulted in markedly lowered A (Fig. 1a) and g_s (Fig. 1b) in seedlings of *Abies nordmanniana*. Stomatal closure was efficient enough for the *E* (Δw) response to exhibit a maximum at



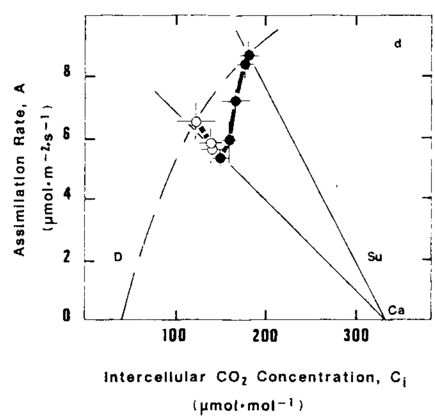


Fig. 1. Gas-exchange response (**a**, **b**, **c**) and CO_2 assimilation rate *vs* calculated intercellular CO_2 concentration (**d**) as leaf-to-air water vapor mole fraction difference was increased stepwise (closed symbols) and then returned (open symbols) near its initial level in 3 yr old *A. nordmanniana* seedlings. Bars are ± 1 SEM, $n = 4$. *D*: demand function; *Su*: supply function; C_a, ambient CO_2 concentration. Air temperature, 22.0 ± 0.5°C, incident photosynthetic photon flux density, 500 μmol·m^{-2}·s^{-1}.

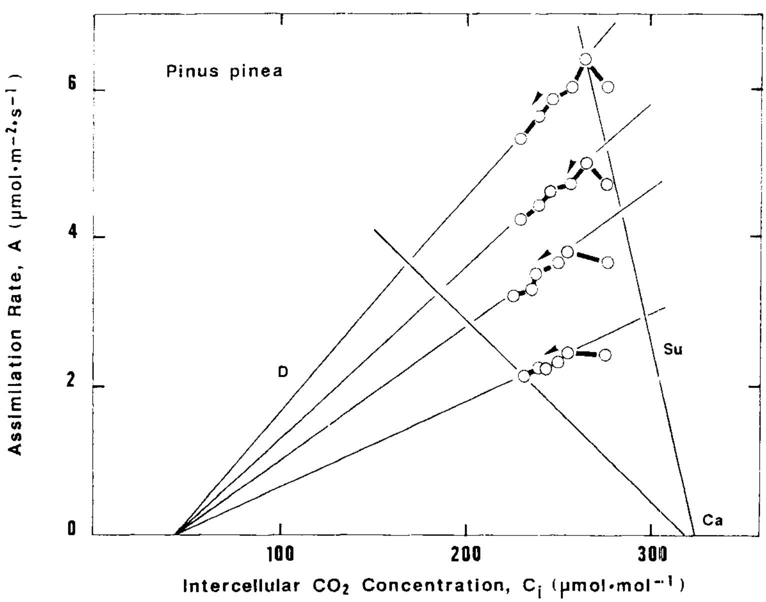


Fig. 2. Carbon dioxide assimilation rate *versus* intercellular CO_2 concentration as leaf-to-air water vapor mole fraction difference was increased stepwise from 7.0 to 22.0 Pa·kPa^{-1} in 4, 1 yr old *P. pinea* seedlings. Arrowheads indicate increasing Δw. *D*: demand function; *Su*: supply function; C_a, ambient CO_2 concentration. Air temperature, 22.0 ± 0.5°C, incident photosynthetic photon flux density, 500 μmol·m^{-2}·s^{-1}.

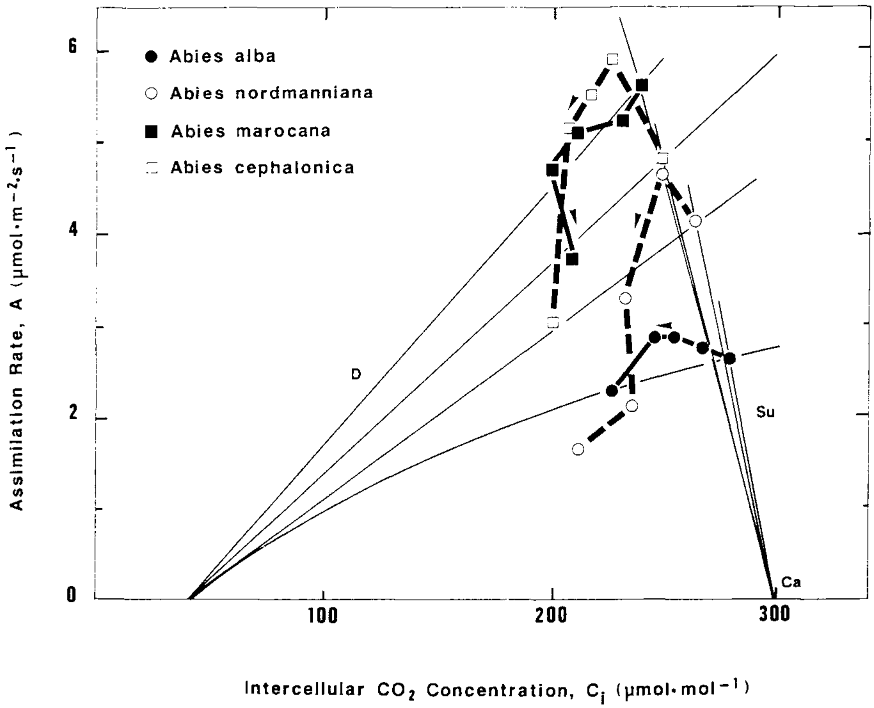


Fig. 3. Carbon dioxide assimilation rate *versus* calculated intercellular CO_2 concentration as leaf-to-air vapor mole fraction difference was increased stepwise from 5.0 to 15.0 Pa·kPa^{-1} in excised water-supplied shoots (3 shoots from different trees for each species) harvested from 25 yr old stands of 4 *Abies* species. Arrowheads indicate increasing Δw. For each species, demand *(D)* and supply *(Su)* functions are represented for the point of lowest Δw. C_a: ambient CO_2 concentration. Air temperature, 22.0 ± 0.5°C, incident photosynthetic photon flux density, 460 μmol·m^{-2}·s^{-1}.

about Δw = 12 Pa·kPa^{-1} (Fig. 1c), thus supporting the postulate (Schulze, 1986) that alterations of leaf water status are not involved in the responses of A and g_s to Δw. Analyzing the data in an A *vs* C_i graph (Fig. 1d, closed symbols) showed, as had already been found for other coniferous species (Guehl and Aussenac, 1987; Grieu *et al.*, 1988), that the experimental points did not remain on the initial demand function. That such a reponse pattern actually denotes an effect of Δw on the mesophyll photosynthetic capacity, and is not an artifact due to improper C_i calculation (Terashima *et al.*, 1988), was shown in the second phase of the experiment in which Δw was returned near its initial low level. During that phase, A recovered partially, with the data points remaining approximately on the same supply function (Fig. 1d, open symbols), thus indicating that the recovery of A was almost fully accounted for by a recovery of mesophyll photosynthesis. Fig. 2 gives a further example of uncoupling between diffusional and mesophyll photosynthetic processes in response to increasing Δw: *Pinus pinea* seedlings, having a leaf diffusional struc-

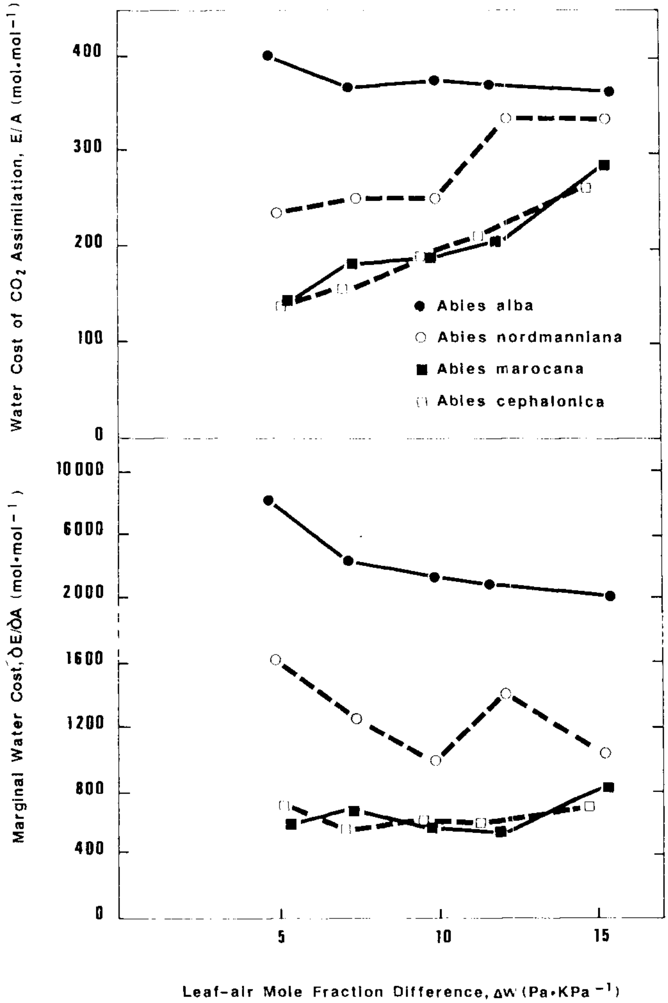


Fig. 4. The effect of increasing leaf-to-air water vapor mole fraction difference on water cost and marginal water cost CO_2 assimilation in 4 *Abies* species. Same data as in Fig. 3.

ture not fundamentally different from that of the *Abies* exhibited a pure stomatal response (constant *D* function) of *A* to Δw between 10.0 and 22.0 Pa·kPa^{-1}.

Significant differences in the gas-exchange response to Δw (Fig. 3) were found in a comparative study on 4 *Abies* species originating from different high elevation regions of the Mediterranean area. *A. cephalonica* and *A. marocana* had the highest *A* values for a given Δw. These 2 species had also the lowest *E/A* and $\partial E/\partial A$ ratios (Fig. 4) and, furthermore, $\partial E/\partial A$ was constant with Δw, which indicates optimization between CO_2 assimilation and transpirational water losses

(Cowan and Farquhar, 1977). In *A. nordmanniana* and *A. alba, E/A* and $\partial E/\partial A$ were higher and optimization was not achieved. These results are in good agreement with the growth performances of the studied species in southern France.

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