Photosynthesis Decrease and Stomatal Control of Gas Exchange in *Abies alba* Mill. in Response to Vapor Pressure Difference

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ABSTRACT

The responses of steady state CO$_2$ assimilation rate ($A$), transpiration rate ($E$), and stomatal conductance ($g_s$) to changes in leaf-to-air vapor pressure difference ($\Delta W$) were examined on different dates in shoots from *Abies alba* trees growing outside. In Ecouves, a provenance representative of wet oceanic conditions in Northern France, both $A$ and $g_s$ decreased when $\Delta W$ was increased from 4.6 to 14.5 Pa KPa$^{-1}$. In Nebias, which represented the dry end of the natural range of *A. alba* in southern France, $A$ and $g_s$ decreased only after reaching peak levels at 9.0 and 7.0 Pa KPa$^{-1}$, respectively. The representation of the data in assimilation rate ($A$) versus intercellular CO$_2$ partial pressure ($C_i$) graphs allowed us to determine how stomata and mesophyll photosynthesis interacted when $\Delta W$ was increased. Changes in $A$ were primarily due to alterations in mesophyll photosynthesis. At high $\Delta W$, and especially in Ecouves when soil water deficit prevailed, $A$ declined, while $C_i$ remained approximately constant, which may be interpreted as an adjustment of $g_s$ to changes in mesophyll photosynthesis. Such a stomatal control of gas exchange appeared as an alternative to the classical feedforward interpretation of $E$ versus $\Delta W$ responses with a peak rate of $E$. The gas exchange response to $\Delta W$ was also characterized by considerable deviations from the optimization theory of IR Cowan and GD Farquhar (1977 Symp Soc Exp Biol 31: 471–505).

Stomata of many species have been shown to be sensitive to changes in the water vapor pressure difference between the leaf and the air ($\Delta W$), even in well-watered plants (17,19). In most species increasing $\Delta W$ around a leaf or the plant results in the closure of the stomata, but the mechanisms by which $\Delta W$ influences the stomatal conductance ($g_s$) remain unclear. If an increase of $\Delta W$ is accompanied by increasing transpiration rates ($E$), the water potential of the bulk leaf may decrease, thereby influencing $g_s$ by a feedback reaction (6,11). In fact, the response of $E$ to $\Delta W$ often exhibits a peak rate of $E$ (11, 14, 19) which has been interpreted as a direct influence of $\Delta W$ on $g_s$ (feedforward response). The mechanism of feedforward could involve gradients of water potential in the epidermis that are due to direct evaporation from peristomatal and guard cells and are independent of leaf water potential.

Simultaneous measurements of $g_s$ and CO$_2$ assimilation rates ($A$) in response to $\Delta W$ have been made in many studies. Both $A$ and $g_s$ decrease as $\Delta W$ is increased and it has commonly been assumed that the decrease in $A$ is entirely due to stomatal closure. Furthermore, several authors (7, 10, 13, 14, 18) have noticed that variations of gas exchange rates in response to $\Delta W$ were consistent with the optimization theory proposed by Cowan and Farquhar (5). Optimal stomatal functioning is that which minimizes water loss over a short time period (1 d) for a given quantity of CO$_2$ assimilation. Optimal functioning would be achieved if $g_s$ varied in such a manner as to keep the partial derivative

$$\frac{\partial E}{\partial g_s} = \frac{\partial E}{\partial A} \frac{\partial A}{\partial g_s},$$

constant with time. $\frac{\partial E}{\partial A}$ is largely dependent on the species and on the plant water status. Direct determination of $\frac{\partial E}{\partial A}$ is usually made (13, 14, 18) by altering $\Delta W$ to change $g_s$ and measuring $E$ and $A$. This method is appropriate only if the obtained changes in $A$ are entirely due to the stomata.

It has been shown recently (2, 16, 20) that in some herbaceous and woody species increasing $\Delta W$ and $E$ decreased the $A$ versus intercellular CO$_2$ partial pressure ($C_i$) response curve, thus indicating a decrease in the mesophyll photosynthesis. In a previous study (9) we found a mesophyll photosynthesis decline in response to $\Delta W$ in the temperate coniferous species used in the present study, *Abies alba*. No data have been published showing the precise roles of stomata and mesophyll in the decline in leaf CO$_2$ assimilation. Methods proposed recently (12, 15), which are designed to assess quantitatively the extent to which variations in $A$ are due to stomatal or nonstomatal effects, might provide answers to these points.

With respect to the optimization theory, further questions arise from the existence of a mesophyll photosynthesis effect of $\Delta W$. How can one determine $\frac{\partial E}{\partial A}$ and how far do $A$ and $E$ variations remain consistent with optimization?

The aim of the present study was to try to elucidate these issues. It was conducted on two provenances of *A. alba*, a coniferous species of western Europe which is of particular economic interest in France. Increasing dieback of *A. alba* in western Europe might be partly a consequence of its high sensitivity to humidity and water stress.

MATERIALS AND METHODS

Plant Materials. The two provenances of *Abies alba* were Nebias—a southern provenance from the piedmont of the eastern Pyrenees—representative of the dry end of the natural range of *A. alba* in southern France (42°51’N, 2°08’E, 600 m elevation) and Ecouves—a more northern low elevation (300 m) prove-

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1 Abbreviations: $\Delta W$, water vapor difference between the leaf and the air (Pa KPa$^{-1}$); $E_a$, ambient partial vapor pressure (Pa KPa$^{-1}$); $W_a$, partial vapor pressure of leaf internal air (Pa KPa$^{-1}$); $g_s$, stomatal conductance for CO$_2$ diffusion (mmol m$^{-2}$ s$^{-1}$); $E$, transpiration rate (mmol m$^{-2}$ s$^{-1}$); $A$, CO$_2$ assimilation rate (mol m$^{-2}$ s$^{-1}$); $C_i$, intercellular CO$_2$ partial pressure (Pa KPa$^{-1}$); $C_a$, ambient CO$_2$ partial pressure (Pa KPa$^{-1}$); $S$, stomatal component of changes in $A$; $M$, mesophyll component of changes in $A$; $\Psi_m$, predawn xylem water potential (MPa).
nance from the Basse-Normandie (48°31'N, 0°04'E)—which has a maritime climate characterized by frequent drizzle and overcast sky conditions, but summer water deficits are not infrequent. The experiment was carried out near Nancy in northeastern France on 20 year old trees (two trees of Écouves, three of Nebias). Stand density was 5000 trees ha⁻¹. At the end of the 1983 growing season the height of the trees was about 5 m and the average basal diameter was 5.6 cm in both provenances.

**Experimental Methods.** The measurements were performed on different days in August 1983 and in August, September, and October 1984. On a given day, the distal parts of three full-sunlight-exposed branches were harvested from the sample trees. The cut ends were plunged into water immediately. In the laboratory, the apical current-year shoots of the branches were cut under water and their bases were sealed into water-filled tubes so that the water supply of the shoots was not interrupted. The tubes containing the shoots were then placed in a Siemens assimilation chamber in which air temperature, ambient CO₂ partial pressure (C₀), photosynthetic photon flux density, and water vapor pressure (Wᵥ) could be controlled. CO₂ and H₂O exchange measurements were begun immediately, each measurement was an average value representative of three shoots. It had been found previously that in constant experimental conditions the shoots could remain in the chamber for at least 8 h without altering their gas exchange rates. The measurements were all completed within this time interval.

By means of a regulation system, which constantly adjusted the CO₂ partial pressure of the air entering the assimilation chamber, C₀ was held constant. C₀ and the difference in CO₂ partial pressure of air streams (60 L h⁻¹) entering and leaving the chamber were measured with Hartman and Braun Uras 2 IR gas analyzers after drying the air through sodium chloride filled tubes. An amount of water vapor equivalent to the transpirational flux was continuously eliminated by condensation in a vapor trap through which a bypass air circuit (300 L h⁻¹) was passed. Vapor pressure of the air entering and leaving the chamber and of the air in the bypass circuit after the vapor trap was measured with lithium chloride sensors.

The following conditions prevailed in the assimilation chamber during the measurements: air temperature, 20°C; incident photosynthetic photon flux density, 460 μmol m⁻² s⁻¹ provided by a high pressure sodium lamp; ambient partial CO₂ pressure 300 ± 5 Pa MPa⁻¹; ΔW was increased stepwise from 4.6 (sometimes 5.6) to 6.7, 8.9, 11.2, 14.5, and in one instance to 16.7 Pa KPa⁻¹. When ΔW was increased in the assimilation chamber, after steady state gas exchange measurements in given conditions, it took about 15 min before ΔW reached its new value. Partial vapor pressure of leaf internal air (Wᵢ) was taken to be equal to saturating vapor pressure at leaf temperature. Needle temperature was measured in some cases with a Chromel-Constantan thermocouple and never exceeded the air temperature by more than 0.2°C. For the calculation of ΔW, leaf temperature was thus considered to be equal to air temperature. Measurements of gas exchange rates were taken as the steady state values after a period of 1 to 2 h adjustment by the shoots to the assimilation chamber conditions. Because the system lag for A and E measurements was not the same, it was possible to determine transient rates only in situations for which the time evolution of gas exchange was slow. For the calculation of E and A, the sample leaf area was determined as the sum of the projected needle areas measured with a photoelectric surface integrator.

The equations used to calculate gₑ and Cₛ were those given by Caemmerer and Farquhar (3) (see "Appendix"). The diffusion of CO₂ in the stomatal pore was treated by taking into account the simultaneous flux of water vapor. We did not take into account the boundary layer conductance which was of an order of magnitude greater than the stomatal conductance. Also the cuticular transpiration flux was neglected as compared with the stomatal flux.

Stomatal (S) and nonstomatal (M = 1 - S) components of change in A were assessed quantitatively by using a method proposed recently (15) (see "Appendix" for details of the calculation). S and M can be evaluated by considering the displacement of the demand function and of the supply function on the same (A, Cₛ) graph. The demand function is the A versus Cₛ response curve, it defines the mesophyll photosynthetic capacity. The supply function is a line with an x-axis intercept equal to Cₛ (1 - E/[E + E/2]) and a negative slope equal to -(gₑ + E/2).

A more precise definition of the demand and supply functions is given in the "Appendix." Since the supply function defines the diffusional limitation to CO₂ assimilation, the intersection of the demand function with the supply function will give the actual values of A and Cₛ (Fig. 1). In most cases it was not possible to determine the pathway of the experimental points on the (A, Cₛ) graph for the transient gas exchange. Quantification of S, for a given displacement of steady state demand and supply functions, was thus made by considering, respectively, that only stomata (Sₛ) or mesophyll photosynthesis (Sₘ) are affected by changes in a first phase (Fig. 2). The effective and unknown value S will be intermediate between Sₛ and Sₘ. For the calculations made in the present study, Sₛ and Sₘ were not fundamentally different.

![Fig. 1](image1.png)

Fig. 1. Supply (Su) and demand (D) functions in the case of a simultaneous CO₂ and H₂O diffusion system. The intersection of D and Su will define the actual A and Cₛ values.

![Fig. 2](image2.png)

Fig. 2. Calculation of the relative stomatal contribution to the variation in CO₂ assimilation rate from 0 to 1. D₀ and Dₛ, Su₀ and Suₛ, A₀ and Aₛ, and A₁ are, respectively, the demand and supply functions and CO₂ assimilation rates before (0) and after (1) the variation. A₀ and Aₛ are the theoretical values of A assuming, respectively, that the demand and supply functions remain constant at first during the variation. a and b are the two extreme pathways for the variation from 0 to 1.
and \((S_1 + S_2)/2\) was taken as an estimate of \(S\).

Since in *A. alba* changes in \(A\) in response to \(\Delta W\) cannot entirely be attributed to a stomatal effect (9), \(\partial A/\partial g\), could not be determined as a local slope of the \(A(g)\) curve (7, 13, 14, 18). An alternative method was used here by considering the partial derivative \(\partial A/\partial g\), on a given demand function (see "Appendix").

**RESULTS**

For a given \(\Delta W\) value, both provenances showed a wide range of \(A, E,\) and \(g\) values for the different dates (Fig. 3). Such variations were unexpected and no measurements have been made of the physiological parameters which could explain them. Particularly, no water potential measurements were made on the trees before shoot harvesting. However, afterward it was possible to relate the curves of Figure 3 to predawn xylem water potential \(\Psi_p\) values obtained from trees of a 20 year old Douglas fir stand near our experimental trees. These values (Table I) are to be considered here only as an index of water stress.

In Ecouves, the lowest values of \(A\) were reached on August 27 as \(\Psi_p\) was about \(-1.10\) MPa, thus indicating a considerable soil water deficit. On August 8 higher values of \(A\) were noticed in spite of similar \(\Psi_p\) values. This might be due to the fact that on August 27 the shoots had, for the same \(\Psi_p\) value, experienced pronounced water stress for a longer period than on August 8.

In Nebias, maximum assimilation rates were the same on August 9 and 30 and \(A\) was even highest on August 30 when \(\Delta W\) was greater than \(8.9\) Pa KPa\(^{-1}\). Assimilation rates were highest during October in both provenances. On September 28 in Ecouves, \(A\) was lower than on October 15 in spite of optimum water supply conditions (\(\Psi_p = -0.24\) MPa).

\(A, E,\) and \(g\) were generally higher in Ecouves than in nebias on comparable dates. At high \(\Delta W\), the values for Nebias were, however, greater than those for Ecouves for the responses obtained during late August, when \(\Psi_p\) was lowest. Surprisingly high \(E\) and \(g\) values were found in both provenances at the beginning of August. With the exception of the measurements made during that period, the responses of \(E\) and \(g\) were less variable with time than the response of \(A\), but the curves had the same relative positions.

The \(\Delta W\) response curves of the two provenances differed in shape (Fig. 3). In Ecouves \(A\) and \(g\), decreased continuously when \(\Delta W\) was increased from 4.6 to 14.5 Pa KPa\(^{-1}\). In Nebias \(A\) and \(g\), were greatest at about 9.0 and 7.0 Pa KPa\(^{-1}\), respectively. In Nebias the \(E\) versus \(\Delta W\) response always exhibited a peak rate of \(E\). This means that above a given \(\Delta W\) value, which was not constant with time, stomatal closure was efficient enough to offset increasing \(\Delta W\). In Ecouves such responses were only observed on August 27 and September 28.

In Figure 4 the data from Figure 3 are shown as intersections of demand and supply functions, and relative stomatal components of changes in \(A\) are given for some intervals of increasing \(\Delta W\). The demand functions of Figure 4 were extrapolated from experiments not reported here in which responses of \(A\) to \(C_a\) were established on different dates and \(\Delta W\) values. The resulting \(A(C_c)\) curves (demand functions) were constant in shape and two different demand functions \(D_1\) and \(D_2\) could be obtained one from the other by a transformation which maintained the ratio \(D_1(C_c)/D_2(C_c)\) constant with \(C_c\). It was thus possible to define the demand function for each experimental point of Figure 4. Displacements of the demand function—i.e., changes in the mesophyll photosynthesis—explained primarily the variations of \(A\) when \(\Delta W\) was changed.

In Ecouves, sensitivity of \(A\) and of mesophyll photosynthesis to \(\Delta W\) was highest on August 27. On that date, as \(\Delta W\) was increased from 4.6 to 8.9 and then to 14.5 Pa KPa\(^{-1}\), \(S\) accounted for 16 and 22% of the decline in \(A\), respectively. Mesophyll photosynthesis decrease and stomatal closure operated in such a manner as to maintain \(C_c\) const. In the responses of August 8 and September 28 a constant \(C_c\), response took place only as \(\Delta W\) was increased above 8.9 and 11.2 Pa KPa\(^{-1}\), respectively. Below

![Figure 3](https://www.plantphysiol.org/)

**Fig. 3.** Relationship between leaf-to-air vapor pressure difference (\(\Delta W\)) and rate of CO\(_2\) assimilation (\(A\)), rate of transpiration (\(E\)) and stomatal conductance (\(g\)) on different dates for the provenances Nebias and Ecouves of *A. alba.*
these values, stomata explained about 50% of the decrease in A. On October 15, when the general level of A was highest, the mesophyll contributed to the slight decrease of A by only 25% as \( \Delta W \) was increased from 4.5 to 14.5 Pa KPa\(^{-1}\).

In Nebias two phases could be distinguished in response to \( \Delta W \). When \( \Delta W \) was increased from 4.6 to 11.2 Pa KPa\(^{-1}\) or to 8.9 Pa KPa\(^{-1}\) (August 9) mesophyll photosynthesis was enhanced. This effect was particularly pronounced on August 30. With the exception of August 9, stomatal closure started before the mesophyll photosynthesis reached its maximum. In a second phase, when \( \Delta W \) was increased above 11.2 or 8.9 (August 9) Pa KPa\(^{-1}\), stomata and mesophyll were both responsible for the decline in A but M was superior to S. With the exception of October 16, above 11.2 Pa KPa\(^{-1}\) the response was also of a constant C type in Nebias.

For some increases of \( \Delta W \), particularly at high \( \Delta W \), it was possible to measure the transient gas exchange before the steady state was reached. The results given in Figure 5 show that at first stomata did not respond to the increase in \( \Delta W \). Mesophyll photosynthesis was affected first, probably as a consequence of the transient enhancement of water losses by transpiration. Stomata responded only 15 to 20 min later than the mesophyll photosynthesis (Fig. 5) and in a final phase, prior to the attainment of a steady state by A and E, g, alone was responsible for the further decrease of A.

Marginal water costs of CO\(_2\) uptake, calculated by Eq. 7 (“Appendix”), are shown in Figure 6. \( \partial E/\partial A \) values were highest and were extremely unstable as \( \Delta W \) was varied in both provenances at the beginning of August, thus indicating absence of optimization. In Nebias \( \partial E/\partial A \) was stable versus \( \Delta W \)—i.e. a better optimization level was achieved on and after August 30. In Ecouves \( \partial E/\partial A \) could be considered as stable only after September 28, though the values were still higher than in Nebias. In mid October both provenances exhibited equivalent and stable \( \partial E/\partial A \) values.

**DISCUSSION**

In *A. alba* mesophyll photosynthetic capacity alterations explained most of the changes in A in response to increasing \( \Delta W \). Mesophyll photosynthesis decline in response to \( \Delta W \) has been found in other species such as the herbaceous *Helianthus annuus* (2, 20), *Chenopodium album* (2), *Xanthium strumarium* (16), or the woody *Eucalyptus microcarpa* (16). Compared with the results of these studies, the declines found here were extremely pronounced and started at low \( \Delta W \) levels.

The response of mesophyll photosynthesis to \( \Delta W \) seems to be linked to a species sensitivity since in *Glycine max* (2) and in the sclerophyllous woody species *Nerium oleander* (8) the decrease in A in response to \( \Delta W \) has been shown to be induced by a decrease in the CO\(_2\) supply to the leaf due to reduced leaf conductance.

Considering steady state situations, Sharkey (16) has established that in some species mesophyll photosynthesis decline was related to the intensity of transpirational water losses. He found that decreasing E after a maximum in the E versus \( \Delta W \) response was accompanied by a recovery in A due to an improvement of the leaf water status. In *A. alba* we have found declines of E...
immediate decline in mesophyll photosynthesis. The subsequent stomatal closure reduced $E$ to the steady state level of point 5 (Fig. 3) which was inferior to that of point 4, but $A$ did not recover, thus indicating a short-term irreversibility of the mesophyll effect. Therefore the mesophyll effect of $\Delta W$ might not be a consequence of the spatial variations in the leaf water status, but the consequence of transient high water losses and low water potentials due to the important time lag (15–20 min) in the response of stomata to an increase in $\Delta W$. Within such a determination the rate at which $\Delta W$ is increased should constitute an important factor of variations which has not been tested here.

The abrupt $\Delta W$ increases which were used in our study could partly be responsible for the high sensitivity of mesophyll photosynthesis that we have found in A. alba.

Considering the results through the displacements of demand and supply functions (Fig. 4) allowed us to determine how stomata and mesophyll photosynthesis interacted when $\Delta W$ was increased. That stomatal and mesophyll responses to $\Delta W$ are at least partly independent finds experimental evidence in the first stages of increasing $\Delta W$ in Figure 4. In Nebias the negative values of $S$ noticed on August 30 and October 5 below 11.2 Pa KPa$^{-1}$ indicate that the stomata closed while mesophyll photosynthesis increased. In Ecouves, with the exception of August 27, stomata closed during the first stages, while mesophyll photosynthesis was affected only a little.

The presence in the two provenances of critical $\Delta W$ values above which the decline in $g$, was sufficient to reduce $E$ (Fig. 3) might be interpreted by a feedforward stomatal response to humidity (6) in terms of water relations. Our results suggest a different type of interpretation of the maximum shaped $E$ versus $\Delta W$ curves, based on a relationship between $g$, and $A$ (22, 23). Experimental support for such an interpretation exists in the constant $C$, phase which was often observed (Fig. 2). During the constant $C$, phase, the mesophyll contributions were predominant in the changes of $A$ (Fig. 4), and stomatal closure occurred after the mesophyll photosynthesis decline (Fig. 5). These observations do not constitute a demonstration of absence of feedforward, since they could simply indicate a difference in response time of mesophyll photosynthesis versus stomata. Two further observations can nevertheless be put forward for ascribing the existence of peak rates in the response of $E$ to $\Delta W$ to an adjustment of $g$, to events occurring in the mesophyll tissues (21–23). First, constant $C$, expresses approximate proportionality between $A$ and $g$, (Eq. 1, “Appendix”). Second, with the exception of the data obtained on August 8 and 9, the maximum of $E$ versus $\Delta W$ occurred at lower $\Delta W$ values when the constant $C$, phase started at lower $\Delta W$. Such a stomatal control, which has never been reported relative to effect of $\Delta W$ on gas exchange, may thus be proposed here as an alternative to the classical feedforward interpretation of the optimum shaped $E$ versus $\Delta W$ curves.

Stomatal control of gas exchange was approximately consistent with the optimization theory—i.e. $\Delta E/\Delta A$ was stable versus $\Delta W$ in Figure 6—only in the situations of optimum $\Psi$, (Table 1) for which the mesophyll photosynthesis decline at high $\Delta W$ was lowest (Fig. 4), in Nebias after August 30 and in Ecouves after September 28. These results bear out those of other authors (18) who found optimization to be realized for the gas exchange response to $\Delta W$ in species for which no mesophyll effect of $\Delta W$ was noticed.

Nevertheless, optimization cannot be given as a general rule for the gas exchange response to $\Delta W$, since in the two provenances of A. alba used here considerable deviations from optimization were noticed (Fig. 6) for the situations where the mesophyll effects of $\Delta W$ prevailed and the constant $C$, phase of stomatal control was greatest.

Long-term optimization of gas exchange should imply a de-

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**Fig. 5.** Rate of CO$_2$ assimilation ($A$) against intercellular CO$_2$ partial pressure ($C_I$) during the $\Delta W$ transition between 11.2 (4) and 14.5 (5) Pa KPa$^{-1}$ in the provenance Ecouves on September 28. $a$ and $b$ are the two extreme theoretical pathways for the variation from 11.2 to 14.5 Pa KPa$^{-1}$ considering respectively 'stomata first' and 'mesophyll first' hypotheses. $c$ is the effective pathway along which transient gas exchange rates are reported. After steady state gas exchange measurement at 11.2 Pa KPa$^{-1}$, $\Delta W$ was increased and it took 15 min for $\Delta W$ to reach 14.5 Pa KPa$^{-1}$. The first transient experimental point was assessed 15 min later and the following points were taken at 10 min intervals. $D$, demand function, $Su$, supply function.

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**Fig. 6.** Marginal unit water cost of CO$_2$ assimilation ($\delta E/\delta A$) as a function of leaf-to-air vapor pressure difference ($\Delta W$). Data from Figure 1. (●) Ecouves; (O) Nebias.

when $\Delta W$ was increased, but never a recovery in $A$. Bunce (2) has studied the response of $A$ and $E$ to $\Delta W$ in different wind speed conditions. He found that the $E$ response curve was markedly affected by the wind speed, but the $A$ response remained unchanged. His conclusion was that the mesophyll photosynthesis decline he observed was independent of the transpiration and of the water potential of the bulk leaf, and was the consequence of a direct effect of $\Delta W$ on mesophyll photosynthesis through mechanisms which could include localized leaf water deficit.

The data shown in Figure 5 suggest a different interpretation of the mesophyll effect. In response to the abrupt increase in $\Delta W$, stomata did not close at first, thus causing a transient enhancement of water losses which could be responsible for the
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crease in \( \delta E/\delta A \) with increasing soil water depletion or decreasing water potential (4). From the results in Figure 6 and the data in Table I it becomes evident that the inverse was true in the provenances studied here. The highest values of \( \delta E/\delta A \) were observed at the beginning of August 1983 when \( g_* \) was particularly high. The physiological significance of these high \( g_* \) values remains unclear (role in the mineral nutrition?). It has been found elsewhere (1) that the daily transpiration of A. alba, Abies nordmanniana, and Abies numidica seedlings reaches a marked maximum around August 10 near Nancy and declines abruptly afterward. Is such a time-evolution pattern representative only for the current-year foliage, or can it be extrapolated to older needles? These observations show that nonadaptation of stomatal control in A. alba in terms of water economy characterizes not only the short-term response of \( A \) and \( E \) to \( \Delta W \) but also the longer-term variations of gas exchange in response to water stress or in relation to seasonal physiological changes.

Within this general framework, there were considerable differences between Ecouves and Nebias. Ecouves had higher CO\(_2\) assimilation and transpiration rates than Nebias in favorable water availability and humidity conditions. This situation was reversed when both soil water and humidity deficit prevailed. That latter characteristic plus the better maintenance of a constant \( \delta E/\delta A \) by Nebias may at least partially explain its greater production level in drier sites as compared with the provenance Ecouves.

APPENDIX

Definition of the Supply Function in the Case of Combined CO\(_2\) and H\(_2\)O Fluxes. By considering simultaneous CO\(_2\) and H\(_2\)O fluxes through the stomatal pore, CO\(_2\) diffusion is described (3) by

\[
A = g_* (C_u - C_i) - E \left( \frac{C_o + C_i}{2} \right)
\]

or, rearranging,

\[
C_o - C_i = \frac{A + EC_o}{g_* + E/2}.
\]

From Eq. 2 it becomes evident that the supply function (constant \( g_* \) and \( E \)) is defined by a line with an \( x \)-axis intercept equal to \( C_o (1 - E/[g_* + E/2]) \) and a negative slope equal to \(- (g_* + E/2) \) on a \((A, C_o)\) graph (Fig. 1). Differences with a single \( CO_2 \) diffusion system (single \( C_o \) equal to \( C_u \)) and slope equal to \(- g_* \) may amount in A. alba to more than 5% in high transpiration conditions.

Partitioning of Changes in \( A \) in Stomatal and Mesophyll Components. In the transition between state 0 and state 1 in Figure 2, two extreme pathways can be considered.

(a) Stomatal conductance varies initially without the alteration of mesophyll photosynthesis which only changes in a second phase at constant \( g_* \); the relative stomatal component in the total variation \((A_0 - A_1)\) is given by \( S_t = \frac{(A_0 - A_1)}{(A_0 - A_1)} \).

(b) Mesophyll photosynthesis varies first and \( g_* \) only changes afterward; the stomatal component is then equal to \( S_m = \frac{(A_m - A_0)}{(A_0 - A_1)} \).

Relative mesophyll components are \( S_m = 1 - S_t \) and \( M_m = 1 - S_m \), respectively.

The effective pathway, which is between these two extremes, is characterized by a stomatal component \( S \) intermediate between \( S_t \) and \( S_m \).

Calculation of \( \delta E/\delta g_* (\delta A/\delta g_*)\). Differentiation of Eq. 1 gives

\[
dA = d g_*(C_u - C_i) - dC_i g_* - \frac{(C_o + C_i)}{2} dE - \frac{E}{2} dC_i.
\]

Vapor diffusion through the stomata may be written as

\[
E = \frac{1.6(W_v - W_o)g_*}{1 - (W_v + W_o)/2} = 1.6 \Delta W g_*.
\]

Where 1.6 is the ratio of CO\(_2\) and water vapor diffusivities in air. Assuming that needle temperature is not affected by changes in \( g_* \), differentiation of Eq. 4 provides

\[
dE = \frac{1.6 \Delta W}{1 - (W_v + W_o)/2} dg_*.
\]

Combining the partial differential forms of Eqs. 3, 4, and 5 for vapor pressure difference in air, assuming that needle temperature is not affected by changes in \( g_* \), differentiation of Eq. 4 provides

\[
\frac{\partial A}{\partial g_*} = \frac{1.6 \Delta W}{1 - (W_v + W_o)/2} \frac{E}{g_*} + \frac{g_* + g_m + E/2}{g_*}.
\]

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