Effects of temperature at constant air dew point on leaf carboxylation efficiency and CO_2 compensation point of different leaf types

J.A. Weber[1]*, J.D. Tenhunen[2] and O.L. Lange[3]

[1] Biological Station, University of Michigan, Ann Arbor, Michigan 48109-1048, USA,
[2] Systems Ecology Research Group, San Diego State University, San Diego, California 92182, USA, and
[3] Lehrstuhl für Botanik II der Universität Würzburg, Mittlerer Dallenbergweg 64, D-8700 Würzburg, Federal Republic of Germany

Abstract. The effect of temperature on photosynthesis at constant water-vapor pressure in the air was investigated using two sclerophyll species, *Arbutus unedo* and *Quercus suber,* and one mesophytic species, *Spinacia oleracea.* Photosynthesis and transpiration were measured over a range of temperatures, 20–39° C. The external concentration of CO_2 was varied from 340 µbar to near CO_2 compensation. The initial slope (carboxylation efficiency, CE) of the photosynthetic response to intercellular CO_2 concentration, the CO_2 compensation point (Γ), and the extrapolated rate of CO_2 released into CO_2-free air (R_l) were calculated. At an external CO_2 concentration of 320–340 µbar CO_2, photosynthesis decreased with temperature in all species. The effect of temperature on Γ was similar in all species. While CE in *S. oleracea* changed little with temperature, CE decreased by 50% in *Q. suber* as temperature increased from 25 to 34° C. *Arbutus unedo* also exhibited a decrease in CE at higher temperatures but not as marked as *Q. suber.* The absolute value of R_l increased with temperature in *S. oleracea,* while changing little or decreasing in the sclerophylls. Variations in Γ and R_l of the sclerophyll species are not consistent with greater increase of respiration with temperature in the light in these species compared with *S. oleracea.*

Key words: Carboxylation efficiency – Compensation point (CO_2) – Photosynthesis (temperature, humidity) – Sclerophyll – Transpiration.

* To whom correspondence should be addressed

Introduction

Midday stomatal closure is characteristic of many species growing in arid and semi-arid environments (Schulze et al. 1974, 1975 a, b; Lange and Meyer 1979; Tenhunen et al. 1984). Decreased stomatal conductance during midday, which is often dependent on the humidity of the air (Lange et al. 1971; Lösch and Tenhunen 1981), can result in reduced transpirational water loss. Simultaneously, CO_2 uptake through photosynthesis also decreases. However, Schulze et al. (1975a) found that the internal CO_2 concentration (C_i) in leaves of *Prunus armeniaca* growing in the Negev Desert did not decrease during midday stomatal closure. More recently, Tenhunen et al. (1984) found that leaves of *Quercus suber* exhibited a strong midday depression of photosynthesis and transpiration rates during the summer dry season in the evergreen scrub near Lisbon, Portugal. Even though leaf conductance decreased by a factor of four, C_i of the leaves remained essentially constant throughout the day. Diurnal variation of the initial slope of photosynthetic response to CO_2 ($A:C_i$ response) was determined by exposing leaves to different CO_2 concentrations over a series of days which had similar variation in light, temperature, and humidity. This slope, or carboxylation efficiency (CE; Forrester et al. 1966), declined strongly with increasing leaf temperatures above 30° C, accompanied by increasing vapor-pressure difference between leaf and air (VPD). Similar behaviour was found with *Arbutus unedo* (see Beyschlag 1984).

The present research had three goals: i) to determine whether the variation in CE measured in the field could be reproduced under similar conditions in the laboratory by exposing the leaves to stepwise changes in CO_2 concentration, ii) to see if other species behaved in a similar manner, and

iii) to examine more closely the relationship between photosynthesis and transpiration as CE varies. *Arbutus unedo* and *Quercus suber,* sclerophyllous trees found in the evergreen scrub of Portugal (Tenhunen et al. 1981), were chosen because they exhibit strong midday stomatal closure. These species are distributed along the coast of the Iberian Peninsula and along the northern shore of the Mediterranean Sea in more maritime areas (Walter and Straka 1970, p. 309). As with many evergreen sclerophylls, these species are apparently well adapted to survive the prolonged summer drought that is typical of their normal habitat. As a comparison, *Spinacia oleracea* (spinach) was chosen because it has a mesophytic leaf type and is commonly studied in the laboratory. Although there are no previous data describing the effect of leaf temperature on CE in *S. oleracea,* we might expect that it should behave in a manner similar to other mesophytic species, such as *Triticum aestivum* (Jolliffe and Tregunna 1968; Ku and Edwards 1977).

Materials and methods

The plants of *A. unedo* were collected at the Research Station Quinta São Pedro, Sobreda, Portugal near Lisbon. Plants of *Q. suber* were obtained from the Department of Forestry, Technical University of Lisbon. During the autumn and winter the potted plants were kept in a greenhouse of the Botanical Garden in Würzburg, FRG; during spring and summer they were placed outside. The plants of *S. oleracea* (cv. Yates) were grown from seed in greenhouses at Würzburg. In one experiment, a plant of *S. oleracea* was not watered for 3 d before measurements were made. Pre-dawn water potential, measured with a Scholander pressure chamber, was −14 bar for desiccated plants compared with −5 bar for well-watered plants.

The measurement apparatus was a portable mini-cuvette system (Lange et al. 1984) built by Heinz Walz Mess- und Regeltechnik, Effeltrich, FRG. Absolute CO_2 concentration was measured with an infrared gas analyzer (Binos 1; Leybold-Heraeus, Hanau, FRG). Relative humidity in the leaf chamber was measured with a capacitance-type sensor (Coreci, Lyon, France). Differential CO_2 and water-vapor concentrations across the mini-cuvette were measured with a dual-channel gas analyzer (Binos 1). For a more complete description of the mini-cuvette, control and analyzing systems see Lange and Tenhunen (1984). Photosynthetic photon flux density was 1190 μmol m^{-2} s^{-1} which was saturating for all species at the CO_2 concentrations used. Various CO_2 concentrations were produced by mixing CO_2-free air with pure CO_2 using mass-flow controllers (Walz, Effeltrich, FRG). Three to four external CO_2 concentrations between 75 and 340 μbar were used to determine the initial slope of the $A:C_i$ response curve. Vapor pressure of gas entering the leaf chamber was set by first saturating the gas with water vapor in a sparging bottle then passing the water-saturated gas through a cold trap at the desired dewpoint temperature. In order to simulate the natural variation in relative humidity with temperature, the absolute humidity entering the chamber was held constant, producing an increase in the vapor-pressure difference between leaf mesophyll and air (VPD) with increasing temperature (Table 1).

Leaf temperature (t_l) was changed in 3–5° C steps starting at 20–25° C depending on the species. At least once with each species, T_l was adjusted to the starting temperature at the end of the experiment. The data for each replicate were taken from a single leaf within a few hours. Calculation of slopes (carboxylation efficiency, CE), x-intercepts (CO_2 compensation points, Γ), and y-intercepts (an estimate of CO_2 release into CO_2-free air, R_l, Ludlow and Jarvis, 1971) were made using lest-squares linear regression of all the points shown in Fig. 1. Each experiment was replicated. Calculation of the intercellular CO_2 concentration (C_i) was according to the equations of Leuning (1983). Boundary-layer conductance in the cuvette was assumed to be 0.05 m s^{-1} (Lange and Tenhunen 1984).

Results

Responses of net photosynthetic rate (A) to intercellular CO_2 concentration (C_i) at constant irradiance and different combinations of leaf temperature (T_l) and air-to-leaf vapor-pressure difference (VPD) are shown for all three species in Fig. 1. Note that the scale of the ordinant axes is different for each of the three species. Variation of VPD with leaf temperature is shown in Table 1. We will use the designation T_l:VPD to indicate that both factors changed in parallel when temperature was changed. The lesser increase in VPD with T_l for well-watered *S. oleracea* resulted primarily from a much higher transpiration rate than the other species (Fig. 3A). Net photosynthetic rate measured at 320–340 μbar external CO_2 concentration (C_a) and 21% O_2 declined with increasing T_l:VPD in all three species (Fig. 2A). The rate of decline in A with T_l above 30° C was quite similar for well-watered *S. oleracea* and *A. unedo,* and for water-stressed *S. oleracea* and *Q. suber.* The percent reduction was greater in *Q. suber* and water-stressed *S. oleracea* than in *A. unedo* and well-watered *S. oleracea.* Returning the temperature to 25° C caused the photosynthetic rate to increase to somewhat less than the original values. In both *S. oleracea* and *A. unedo,* A was not strongly affected by T_l:VPD at lower temperatures, 20–25° C and 25–30° C, respectively, whereas at higher T_l:VPD, A declined more rapidly. Above 25° C, *Q. suber* exhibited a strong and continual decrease in A with increasing T_l:VPD.

The results of the regression analysis of the data in Fig. 1 are plotted as functions of T_l and VPD in Fig. 2C–H. While the evergreen species had generally higher values of Γ than spinach (Fig. 2C) at a given $T_l,$ there was essentially no difference when Γ was plotted as a function of VPD (Fig. 2D). The variation of CE with T_l:VPD was quite different among the species (Fig. 2E–F). In *S. oleracea* there was a small increase in CE to 33° C, followed by a decline. For *Q. suber* there was a decline in CE with increasing temperature.
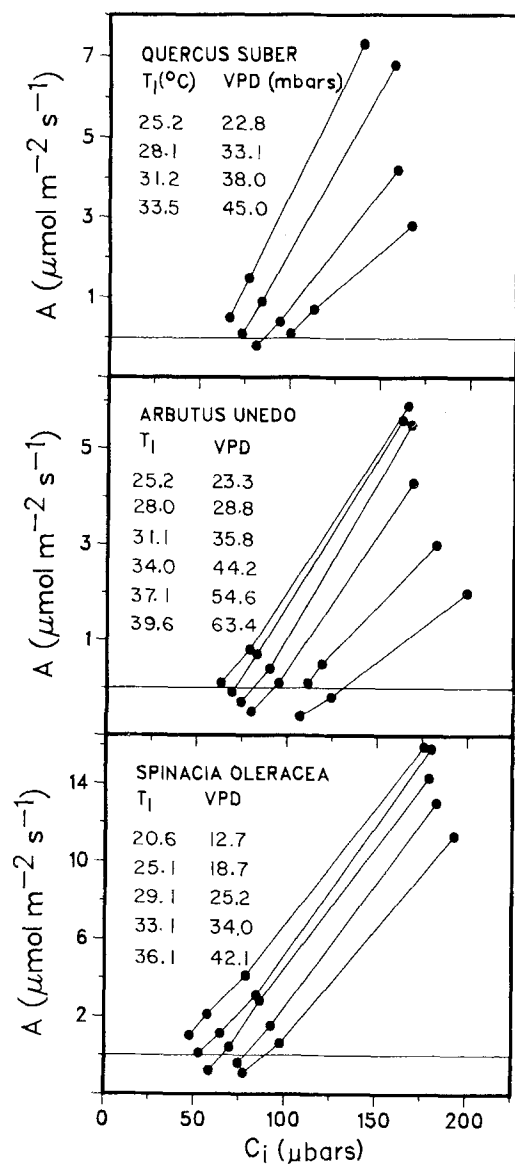
Fig. 1. Photosynthetic rates (A) of *Quercus suber*, *Arbutus unedo*, and *Spinacia oleracea* as functions of calculated internal CO_2 concentration and leaf temperature (T_l). T_l (° C) and VPD (mbar) are indicated next to each of the curves

Table 1. Variation of leaf temperature (T_l), air-to-leaf vapor-pressure difference (VPD), vapor pressure in the air surrounding the leaf (VPA), and vapor pressure of the gas entering the leaf chamber (VPin). Mean and SD for T_l, VPA, and VPD

Species	T_l (° C)	VPA (mbar)	VPD (mbar)	VPin (mbar)
Quercus	25.2 ± 0.1	10.2 ± 0.3	22.8 ± 0.4	7.0
suber	28.1 ± 0.1	9.2 ± 0.1	30.1 ± 0.2	
	31.2 ± 0.1	8.8 ± 0.4	38.0 ± 0.5	
	33.5 ± 0.1	8.4 ± 0.2	45.0 ± 0.3	
Arbutus	25.2 ± 0.1	9.4 ± 0.1	23.3 ± 0.1	7.1
unedo	28.0 ± 0.1	9.8 ± 0.2	28.8 ± 0.2	
	31.1 ± 0.1	10.4 ± 0.2	35.8 ± 0.2	
	34.0 ± 0.1	10.3 ± 0.2	44.2 ± 0.2	
	37.1 ± 0.1	10.2 ± 0.2	54.6 ± 0.2	
	39.6 ± 0.1	10.6 ± 0.3	63.4 ± 0.3	
Spinacia	20.6 ± 0.1	11.8 ± 0.4	12.7 ± 0.5	9.9
oleracea	25.1 ± 0.1	14.0 ± 0.2	18.7 ± 1.0	
	29.1 ± 0.2	15.5 ± 0.7	25.2 ± 1.0	
	33.1 ± 0.1	17.1 ± 1.0	34.0 ± 1.1	
	36.1 ± 0.1	18.5 ± 0.8	42.1 ± 1.0	
Spinacia	25.7 ± 0.1	9.0 ± 0.4	24.4 ± 0.1	6.2
oleracea	28.1 ± 0.1	8.3 ± 0.7	30.4 ± 0.9	
(water-	30.6 ± 0.5	7.9 ± 0.4	37.0 ± 1.6	
stressed)	33.0 ± 0.1	7.0 ± 0.4	43.7 ± 0.4	

crease; and in *A. unedo*, a decrease followed by an increase.

Spinacia oleracea which had not been water stressed had a much higher stomatal conductance to water vapor (G) than the other species (Fig. 3 C–D); however, after water stress G was reduced and more sensitive to changes in T_l:VPD. The stomatal response of the evergreen species to increasing T_l:VPD was greater than that of the unstressed *S. oleracea*, but similar to the stressed *S. oleracea*. Changes in G could also affect photosynthetic rate through changes in C_i. For our studies, C_i (Fig. 3 E–F) changed little (*S. oleracea* and *A. unedo*) or varied in a manner inconsistent with limitation by G (i.e., C_i increased with decreasing G in *Q. suber* and water-stressed *S. oleracea* at T_l above 29° C). Only with the increase in temperature from 26° to 29° C in the water-stressed *S. oleracea* did C_i decline. Lower C_i in water-stressed compared with non-water-stressed *S. oleracea* may indicate a greater limitation by G, although water stress has been shown to reduce photosynthetic capacity as well as leaf conductance (Bunce 1977; Collatz et al. 1976; Collatz 1977; Kaiser 1984; Matthews and Boyer 1984).

The fact that G had different sensitivities to increasing T_l:VPD in the different species could reflect a difference in the relationship of photosyn-

Over the same temperature range (25–34° C) CE declined by about 50% in *Q. suber* compared with no change in *S. oleracea*. In *A. unedo*, CE increased with T_l up to about 32° C; above this temperature CE declined, reaching 50% of the maximum at 39° C. The values for CE were greater in *S. oleracea* than in the two evergreens, reflecting the higher photosynthetic capacity in *S. oleracea*. The extrapolated CO_2 release into CO_2-free air, R_l, varied differently with T_l:VPD among the three species (Fig. 2 G–H). *Spinacia oleracea* had the lowest R_l at any given temperature. In *S. oleracea*, the overall trend is a decrease in R_l; in *Q. suber*, an in-
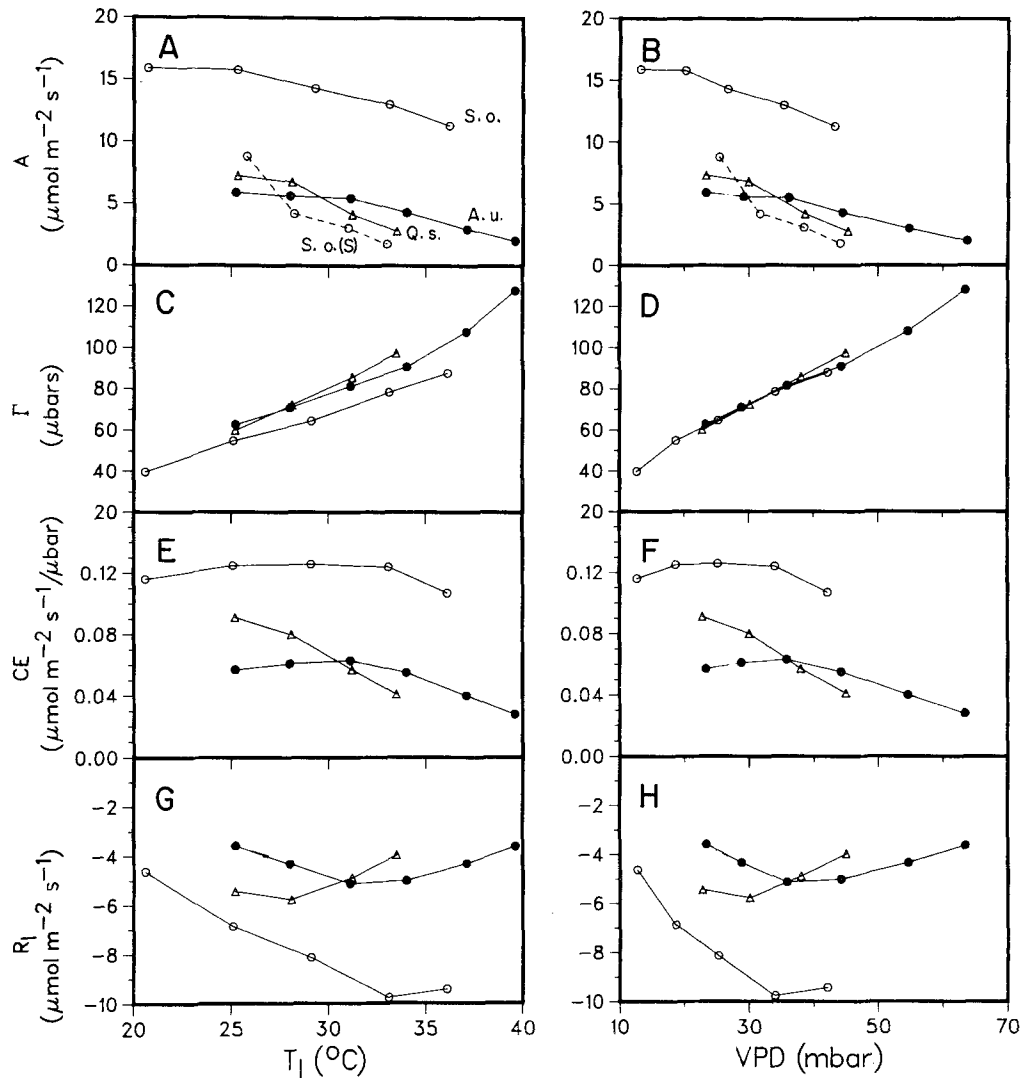
Fig. 2A–H. Variation with leaf temperature (T_l) and air-to-leaf vapor-pressure difference (VPD) of: photosynthesis (A) at 320–340 µbar CO_2 external to the leaves, CO_2 compensation point $(\varGamma)$, initial slope of the $A:C_i$ response (CE), and the extrapolated release of CO_2 into CO_2-free air (R_l). The values of CE, $\varGamma$, and R_l were derived from linear regressions on the data in Fig. 1. (△) *Quercus suber*, *Q.s.*, (●) *Arbutus unedo*, *A.u.*, (○) *Spinacia oleracea*, *S.o.*; dashed line refers to data from water-stressed plant (S)

thesis (A) to transpiration (E). In well-watered *S. oleracea*, E increased by more than three fold over the temperature range (Fig. 3A); however, in water-stressed *S. oleracea*, E declined with increasing T_l:VPD. For both *Q. suber* and *A. unedo*, E initially increased then decreased with increasing T_l. In Fig. 4, A measured at C_a of 320–340 µbar CO_2 but different T_l:VPD is plotted as a function of E. The arrows indicate increasing T_l:VPD. Also shown in Fig. 4 are lines representing a constant $A:E$ ratio. For *S. oleracea*, increasing E was correlated with a decrease in A; however, when the plant was water-stressed the response was reversed so that E and A declined together with increasing T_l:VPD. In *A. unedo* and *Q. suber*, E and A were

initially inversely related, but became almost directly proportional at higher T_l. One result of the responses of E and A to T_l was that the A:E ratio for the sclerophylls and for water-stressed *S. oleracea* decreased less with increasing T_l:VPD than for the unstressed *S. oleracea*.

Discussion

Recent data on *Quercus suber* (Tenhunen et al. 1984) and *Arbutus unedo* (Beyschlag 1984) show that midday depression in photosynthesis under natural conditions is not necessarily linked through reduction in C_i caused by stomatal closure. In these species, and others (Schulze et al. 1975a), C_i re-
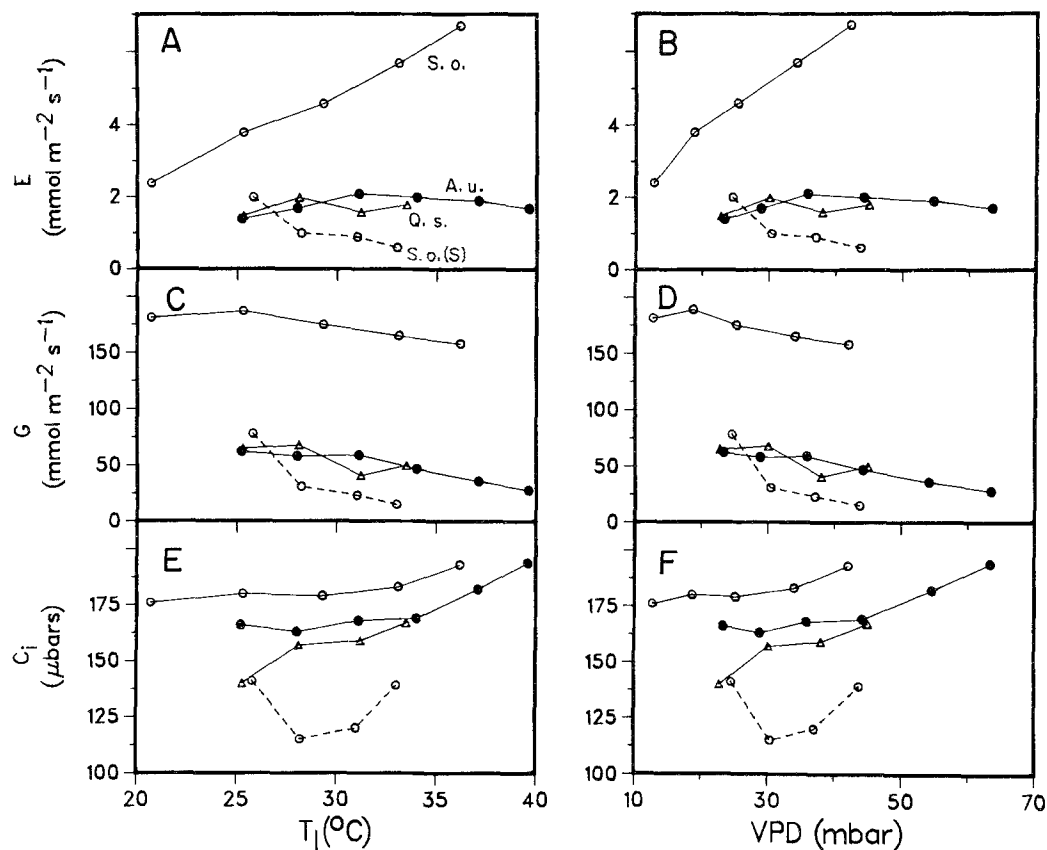
Fig. 3A–F. Variation of transpiration rate (E), leaf conductance (G), and intercellular CO_2 concentration (C_i) with leaf temperature (T_l) and air-to-leaf vapor-pressure difference (VPD) at external CO_2 concentration of 320–340 µbar and saturating photosynthetic photon flux density. (△) *Quercus suber, Q.s.*, (●) *Arbutus unedo, A.u.*, (o) *Spinacia oleracea, S.o.*; dashed line refers to data from water-stressed plant (S)

mained remarkably constant throughout the period of depressed gas exchange during the hottest and driest part of the day. More detailed examination of the data of Tenhunen et al. (1984) and Beyschlag (1984) showed that photosynthetic characteristics change with temperature at constant external water vapor pressure, in particular the initial slope of the $A:C_i$ response (CE) declines with increasing T_l:VPD. While T_l is an obvious factor that can affect photosynthetic response, there are reports that VPD either through transpiration rate (e.g., Sharkey 1984) or directly (Reseman and Raschke 1984) can affect photosynthetic response. Under natural conditions, T_l and VPD change in parallel (e.g. Schulze et al. 1974; Tenhunen et al. 1984), so that separating effects of these two factors using data from the field is difficult. Since we simulated the temperature and humidity conditions in the field, our data do not allow for unequivocal separation of these two factors.

Most published reports indicate little effect of T_l on CE over a broad range of T_l, for instance, in *Tritium aestivum* (Jolliffe and Tregunna 1968;

Ku and Edwards 1977), *Phaseolus vulgaris* (Peisker et al. 1979), *Gossypium hirsutum* (Troughton and Slatyer 1969), and *Eucalyptus pauciflora* (Kirschbaum and Farquhar 1984). However, Doley and Yates (1976) found a large effect of temperature on mesophyll resistance (calculated according to Ludlow and Jarvis (1971) assuming $\Gamma = 0$) in the C_4 grass, *Astrebla lappacea*. If CE in C_3 plants is controlled by the characteristics of ribulose-1,5-bisphosphate carboxylase/oxygenase as proposed by Farquhar et al. (1980) and von Caemmerer and Farquhar (1981), interpretation of our data as a temperature effect would require a temperature effect on the enzyme such that its activity would decline with increasing T_l within the temperature range studied.

As noted above, other possibile explainations of the variation we found are direct effects of transpiration rate or VPD on photosynthetic metabolism. Thompson et al. (1965), who investigated the effect of humidity on the photosynthetic response to temperature in *Citrus jambhiri*, found a definite depression in photosynthesis at high temperature
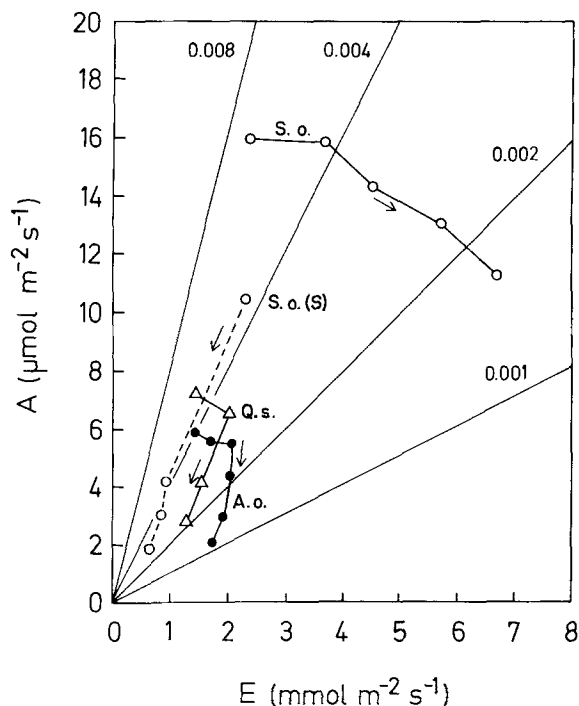
Fig. 4. Relationship between transpiration (E) and photosynthesis (A) at 320–340 µbar CO_2 external. *Lines* marked 0.001 to 0.008 indicate constant A/E in mol CO_2/mol H_2O. Increasing leaf temperature and VPD is indicated by *arrows* next to each curve. ($\triangle$) *Quercus suber, Q.s.*, ($\bullet$) *Arbutus unedo, A.u.*, ($\circ$) *Spinacia oleracea, S.o.*, *dashed line* refers to data from water-stressed plant (S)

when vapor pressure in the air surrounding the leaf (VPA) was low, but not when VPA was high. However, they did not present data on C_i for their experiments. Jenson (1975) in salt-stressed *Phaseolus vulgaris* and Leach (1979) in *Triticum aestivum* found a decrease in CE with increasing VPD. Neither Jolliffe and Tregunna (1968), who maintained a constant water-vapor pressure entering the leaf chamber, nor Ku and Edwards (1977), who maintained a constant VPD of 11–15 mbar, found a major change in CE with T_l in *Triticum aestivum*. More recently, Forseth and Ehleringer (1983), Ball and Farquhar (1984), and Sharkey (1984) found that increasing VPD caused a decline in the CO_2-saturated rate of photosynthesis, but no change in CE. Preliminary data on *Q. suber* indicated that increasing VPD at constant T_l caused a reduction in A at 340 µbar CO_2. Sharkey (1984) proposed that localized water stress produced by increased transpiration leads to reduced photosynthetic capacity. However, Bunce (1984) presented data on *Chenopodium album* and *Helianthus annuus* in which A declined with increasing VPD (19–30 mbar) but was not always related to increased E. Reseman and Raschke (1984) showed

that above 30 mbar VPD, CE declined in *Arbutus unedo*. Raschke (1982) has reported that application of abscisic acid to leaves can reduce CE and the CO_2-saturated rate of photosynthesis. He has proposed that increased VPD may in some way induce the production and-or redistribution of abscisic acid inside the mesophyll cells.

Considering the data in Fig. 4, a simple increase in E cannot explain the change in A observed. Only in *A. unedo* and *Q. suber* at low T_l and VPD, and in unstressed *Spinacia oleracea* was decreased A associated with increased E. In all other cases E and A changed almost proportionally. A change in the proportion between photosynthetic and respiratory activity could produce a change in the shape of the $A:C_i$ response. However, if respiratory rate increased more rapidly with T_l and-or VPD in *A. unedo* and *Q. suber* compared with *S. oleracea*, then a relatively greater increase in Γ should be expected. Our data do not support this possibility, since the variation in Γ with T_l:VPD was not appreciably different among the three species (Fig. 2). Bauer and Martha (1981) and Bauer et al. (1983) have shown that for a wide range of species, Γ is essentially the same at a given T_l and varies similarly with T_l. The generally higher Γ at a given T_l for the evergreen species could be the result of a relatively higher mitochondrial respiratory rate in the light. A more direct means of estimating respiratory activity in the light is determining the y-intercept of the $A:C_i$ response (Ludlow and Jarvis 1971). The fact that the y-intercept, an estimate of CO_2 released into CO_2-free air (R_l), increased or changed little with T_l and-or VPD in *Q. suber* and *A. unedo* leads to the conclusion that respiratory rate did not increase markedly, and may have even declined. On the other hand, R_l declined in *S. oleraceae* with increasing T_l:VPD up to 33° C. Thus, we can conclude that for *Q. suber* and *A. unedo* the variation in R_l and Γ with increasing temperature is not consistent with an increase in respiratory activity.

Whatever the mechanism, change in T_l:VPD from 25 to 35° C can have a major effect on the initial slope of the $A:C_i$ response of some species. This response is especially evident in *Quercus suber* and confirms the response measured in the field (Tenhunen et al. 1984). The combined responses of Γ and R_l in the sclerophylls strongly indicates that there is a reversible inactivation of the photosynthetic system by increasing T_l:VPD, resulting in a reduction of CE. The combined effect of decreasing CE and increasing Γ in the sclerophylls is a larger reduction in A with increasing T_l:VPD and maintenance of a greater C_i at a given stomatal

conductance to water vapor than if only Γ increased, as in *S. oleracea*. The relevance of this response may be in the avoidance of low C_i values which at high irradiance, VPD, and T_l might lead to photoinhibition (Powles and Critchley 1980) when stomates close during the midday depression. Further studies are needed to separate clearly the effects of temperature from those of VPD on photosynthetic response.

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