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Gas exchange of two CAM species of the genus *Cissus* (vitaceae) differing in morphological features

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Abstract. Pattern and magnitude of stem gas exchange were studied under controlled conditions on two CAM species of the genus *Cissus* differing in morphological features. In the cactus-like liana *Cissus quadrangularis*, at water vapour deficit of the air (VPD) lower than 400 mPa Pa^{-1} during daytime, under 24/16 °C and 27/16 °C temperature regime, CO_2 uptake occurred during daytime and nighttime but night fixation was responsible for 74 and 77% respectively of the CO_2 fixed during the whole diurnal cycle; the contribution of night fixation increased up to 84% at VPD of 590 mPa Pa^{-1} under 27/15 °C. In *Cissus* sp., a slightly succulent xerophytic liana with mesophytic deciduous leaves, at 27 °C day temperature and VPD of 520–540 mPa Pa^{-1}, under both 12 and 16 °C night temperature, CO_2 uptake occurred exclusively during the night; however at lower day temperatures (18–20 °C) and lower VPD (169–269 mPa Pa^{-1}) substantial CO_2 uptake was observed in the light. Transpiration was higher in *Cissus* sp. than in *Cissus quadrangularis* under all of the conditions applied; moreover night transpiration in *Cissus* sp. contributed more to total day transpiration as compared with *Cissus quadrangularis*. The results support the opinion that the nocturnal gas exchange has a preeminent role in *Cissus* sp. as compared with *Cissus quadrangularis*. Indeed under conditions which enhance evaporative demand even well-watered plants of *Cissus* sp. resort totally to night fixation. In contrast *Cissus quadrangularis* which shows a larger resistance to water loss and possesses an abundant water storing parenchyma as compared with *Cissus* sp. resorts totally to night CO_2 fixation only under drought stress.

Introduction

The genus *Cissus* is found throughout both the moist and arid tropics of the world and includes about 300 species, most of which are lianas. Rain forest lianas and arid environment lianas show remarkably diverse vegetative structures. Thus *Cissus gongylodes* Burk., a liana of the tropical rain forests of South America, is characterized by large thin leaves. *Cissus* lianas of arid environments have adopted one or more xeromorphic features. *Cissus trifoliata* L. a liana climbing on columnar cacti of the semiarid region near Coro (Venezuela) has a lignified stem incapable of photosynthesis and succulent leaves which are shed under drought. *Cissus quinquangularis* Chiov. and *C. rotundifolia* Blume have green stems and long-living succulent leaves. *Cissus quadrangularis* L. and *C. cactiformis* Gilg show cactus-like green stems and short-lived, small and fleshy leaves which are shed under drought. Among *Cissus* lianas of semiarid environments, one undescribed species from Kenya possesses slightly succulent green stems and deciduous mesophytic leaves. Specimens of this plant can be seen growing in a number of Botanic Gardens and succulent plant collections in Europe.

Cissus species have been found to be capable of CAM [7, 8, 10, 14, 17, 18, 19, 20]. It is most interesting that leaves of the rain forest liana *C. gongylodes* show CAM-like diurnal fluctuations of malic acid [19] but perform daytime CO_2 uptake and have no nighttime CO_2 net exchange (unpublished experiments), a phenomenon termed CAM-cycling [15]. CAM-cycling has been reported for some epiphytic bromeliads and orchids as well as for the more primitive species of the Crassulaceae. In *C. trifoliata*, CAM is operative in a facultative manner [10]. The mesophytic leaves of the above mentioned *Cissus* sp. exhibit high overnight malate accumulation; the stem also shows overnight malate accumulation, but in amounts several times lower than that in the leaves [19]. Leaves and stems of *C. quadrangularis* show overnight malate accumulation; stem behaviour is that of a CAM obligate that shifts to CAM-idling under drought-stress [18, 19, 20].

Previously published data [7, 8, 10, 14, 17, 18, 19, 20] and comparative research on a number of *Cissus* species in progress in our laboratory suggest that CAM is a widespread feature in the genus *Cissus*; moreover among the adaptive mechanisms to aridity displayed in this genus, the role of CAM is thought to be fundamental while succulence could be a more recent adaptation which has facilitated the spread of the genus from the wet into the arid tropics [19].

In this work we examine stem gas exchange of *C. quadrangularis* and *Cissus* sp.. The comparison between two species that differ dramatically in morphological features can be very useful to assess the role of CAM in their ecology. Since day and night temperatures greatly influence carbon assimilation of CAM plants [5, 22] the relationship between gas exchange and day/night temperature regime has been taken into consideration. In several CAM species stomata have been known to respond directly to changes in ambient air humidity [6, 12]. Since air humidity and thus water-vapour pressure deficit of the air (VPD) at an unchanged dew-point temperature is determined by air temperature, the effects of temperature on gas exchange might in reality reflect the effects of VPD on stomatal opening. Therefore attention has been paid also to the relationship between CO_2 exchange and VPD of the air; besides transpiration has been measured under different day/night temperature regimes at variable as well as at constant VPD of the air.

Materials and methods

Cissus quadrangularis is a cactus-like liana native to the tropical and subtropical xeric woods of Africa, Arabia, Madagascar, East India and Moluccas [4]. *Cissus* sp. is a xerophytic liana not yet taxonomically described. Herbarium specimens of *Cissus* sp. are preserved at the herbarium of the Dipartimento di Biologia Vegetale, University of Naples. Live plants are to be found in the collections at the Botanical Garden of the University of Naples and also at the Botanical Garden of the University of Heidelberg (collected by Prof. Rauh in Kenya, coll. n° Ke 850).

Characteristics of *C. quadrangularis* stems include thick cuticle, bilayered epidermis of small cells with about 50 stomata per mm^2, cortex showing several layers of photosynthetic parenchyma, and pith consisting of abundant water-storing parenchyma with scanty chloroplasts. The stem of *Cissus* sp. has four whitish, longitudinal ridges covered with a multilayered cork tissue bearing short, unbranched dead hairs on the outermost layer; the four green longitudinal bands separating the ridges are covered with a threelayered epidermis of small cells bearing a thick cuticle; stomata are slightly sunken below the surface at a frequency of about 25 per mm^2. Due to the characteristics of the outermost cell layers of the stem only the surface of the green longitudinal bands (66% of the total) is active in gas exchange. During drought stress the green longitudinal bands curl and the cork ridges draw together effectively avoiding further water loss. Vascular bundles under the cork ridges are characterized by very large vessels as compared with vascular bundles under the green longitudinal bands. Both cortex and pith parenchyma of *Cissus* sp. contribute to photosynthesis and water storage; however, chloroplasts are more numerous in the thin cortex parenchyma than in the thicker larger-celled parenchyma. As previously reported [19], succulence is higher in *C. quadrangularis* than in *Cissus* sp. (13.31 and 8.86 g $H_2O\,dm^{-2}$ respectively) while mesophyll succulence is higher in *Cissus* sp. than in *C. quadrangularis* (3.60 and 2.22 g $H_2O\,mg^{-1}$ chlorophyll respectively; the value for the latter species refers exclusively to the chlorenchyma, since the water tissue had been removed).

For the experiments clonal plants of *Cissus quadrangularis* L. and *Cissus* sp. were grown in the greenhouse. For each species clonal plants were obtained by stem cuttings from individuals cultivated for many years in the greenhouse of the Botanical Garden of the Faculty of Sciences, University of Naples.

The experiments were performed on stems without leaves. For measurements of CO_2 exchange, three weeks before the experiments the plants were transferred to a growth cabinet under a 12-hour light/dark cycle and an irradiance of $180\,\mu E\,m^{-2}\,s^{-1}$ PAR at the level of the gas exchange chamber; illumination was provided by a combination of 65 W fluorescent tubes and 60 W incandescent lamps. Air humidity in the growth cabinet was not controlled. The plants were adequately watered. CO_2 exchange was measured in an open system with a differential infrared gas analyzer (URAS Hartmann and Braun) using the climatized gas exchange chamber (Siemens) described by Schulze [13]. Parts of stems remaining in connection with their mother plants were enclosed in the gas exchange chamber which was kept in the growth cabinet. An airstream from outdoors (Botanical Gardens) was sucked through the gas exchange chamber. Temperature and humidity in the gas exchange chamber were regulated to track growth cabinet conditions. Plants were kept under each experimental temperature regime for at least two full day/night cycles before readings were taken. Calculations of water-vapour pressure deficit (VPD) of the air streaming in the gas exchange chamber were made from recordings of dew-point temperature and air temperature.

Measurements of transpiration were made in the growth cabinet simultaneously on both species. For each species two cuttings, each consisting of two fully-developed internodes, were collected from watered plants. After sealing the cut surfaces with paraffin, the cuttings were weighed at the beginning and at the end of both the light and dark period by means of a precision balance. The cuttings were exposed exactly with the same orientation in relation to the incident light ($105\,\mu E\,m^{-2}\,s^{-1}$ PAR). Plants were kept under each experimental regime for a full day/night cycle before measurements were taken.

For malate determinations segments 1 cm in length were taken from the middle of the fifth internode below the apex. Two segments from two branches formed one sample. The samples were collected in duplicate at the end and at the beginning of the light period. The malate content was measured enzymatically after Hohorst [3] in aqueous extract obtained as previously described [2].

Results

In plants of *C. quadrangularis* under day/night temperature regimes of 24/16 and 27/16 °C (Fig. 1a and b) the greater part of CO_2 uptake occurs during the night but a considerable quantity of CO_2 is also fixed during the day. Maximal rates of CO_2 uptake occur early in the dark period; afterwards CO_2 uptake decreases slowly to relatively low values at the end of the dark period. Immediately following illumination, a burst of CO_2 uptake occurs; subsequently CO_2 fixation declines rapidly to near the compensation point; thereafter CO_2 uptake increases steadily to reach relatively high values at the end of the light period. At 'light off' a drop in CO_2 uptake is followed by a sharp increase towards the maximal values.

The increase in day temperature from 24 to 27 °C and in daytime VPD of the air from 250 to 389 and 590 m Pa Pa^{-1} results in a decrease in daytime CO_2 uptake, whereas the contribution of night CO_2 fixation progressively increases (Table 1).

After three days without watering at day/night temperature of 24/15 °C and VPD of 500/173 m Pa Pa^{-1} night fixation accounts for 88% of total daily carbon fixation (Table 2).

After one month without watering, plants of *C. quadrangularis* under 24/16 °C temperature regime and daytime VPD of 341 m Pa Pa^{-1}, as well as plants under 27/16 °C temperature regime and daytime VPD of 407 m Pa Pa^{-1} fix CO_2 almost exclusively during the night (Table 2); total daily carbon uptake is reduced to 40% under 24/16 °C and to 37% under 27/16 °C as compared with well watered plants.

Under 27/16 °C temperature regime *C. quadrangularis* accumulates 53.77 m mol malic acid per m^2 of stem surface area during the night. The values of accumulation calculated from nocturnal CO_2 uptake, on the basis of one mole

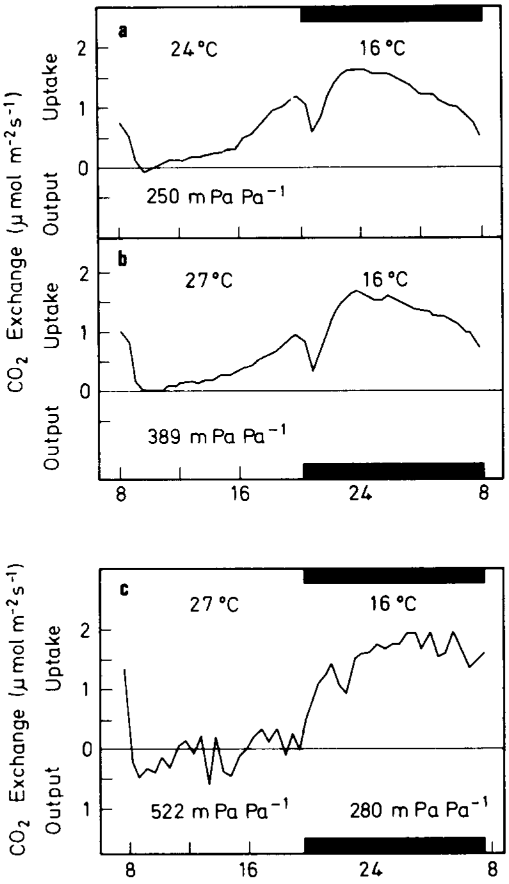

Fig. 1. Diurnal pattern of net CO_2 exchange in watered plants of *Cissus quadrangularis* (a and b) and *Cissus* sp. (c). PAR was 180 µE $m^{-2}s^{-1}$. Water vapour deficit of the air during the night was 0 for a and b. Day/night values of CO_2 concentration in the airstream sucked from outdoors through the gas exchange chamber were 342/423 ppm for a and b, and 354/431 ppm for c.

of malic acid produced per mole of CO_2 fixed is 53.34 m mol m^{-2} and closely corresponds to the value measured. Accumulation of malic acid by plants under 27/16 °C temperature regime after one month without watering is 30.96 m mol m^{-2}, while the value calculated from CO_2 fixation at night is 24.70 m mol m^{-2}. The difference is due to recycling of endogenously produced CO_2.

In *Cissus* sp, under 27/16 °C day night temperature regime at day/night VPD of 522/280 m Pa Pa^{-1}, CO_2 is fixed predominantly in the dark (Fig. 1c) while daytime CO_2 exchange is rather slight.

In *Cissus* sp. under 18/12 °C day/night temperature regime at daytime VPD of 169 m Pa Pa^{-1} and under 20/12 °C day/night temperature regime at daytime VPD of 269 m Pa Pa^{-1} net CO_2 uptake occurs throughout the whole light period

Table 1. CO$_2$ exchange of *Cissus quadrangularis* and *Cissus* sp. as a function of day/night temperature regime and water vapour pressure deficit (VPD) of the air. Experimental conditions as in Figs 1 and 2.

Temperature regime day/night	Air VPD m Pa Pa^{-1} day/night	CO$_2$ uptake			Nighttime/total CO$_2$ uptake %
		daytime	nighttime	total m mol m^{-2} 24 h^{-1}	
		m mol m^{-2} 12 h^{-1}			
C. quadrangularis					
24/16	250/0	18.91	53.43	72.34	74
27/16	389/0	15.75	53.34	69.09	77
27/15	590/157	10.91	57.23	68.14	84
Cissus sp.					
27/16	522.280	0.52	65.09	65.61	99
18/12	169/0	26.43	54.48	80.91	67
20/12	269/0	27.27	63.95	91.23	70
25/12	441/0	16.84	70.77	87.61	81
27/12	541/105	− 7.34*	69.57	62.23	112

*Minus indicates release of CO$_2$.

(Fig. 2a and b); however under 20/12 °C nighttime CO$_2$ uptake is higher than under 18/12 °C (Table 1). Under 25/12 °C temperature regime at daytime VPD of 441 m Pa Pa^{-1} (Fig. 2c) nighttime CO$_2$ uptake further increases but a large CO$_2$ output takes place during phase III of the diurnal CAM cycle [11]; although CO$_2$ uptake at the end of the light period becomes significant the total daily CO$_2$ fixation results slightly lower as compared with the plants under 20/12 °C (Table 1). At 27/12 °C temperature regime and day/night VPD of 541/105 mPa Pa^{-1} (Fig. 2d) during the light period the initial burst of CO$_2$ uptake is followed by significant CO$_2$ releases during about two hours, thereafter CO$_2$ exchange becomes rather slight; during the night CO$_2$ uptake is as high as in plants under 25/12 °C (Table 2).

Cissus sp. is able to perform high CAM activity in the greenhouse also under 36/20 and 31/19 °C maximum/minimum day temperature. In table 3 nocturnal malic acid accumulation of greenhouse plants is compared with nocturnal malic acid accumulation of plants in the growth cabinet under 26/16 °C temperature regime. The data indicate that malic acid accumulation increases with increasing temperature and increasing diurnal temperature fluctuation as well as with increasing daytime VPD.

Table 2. CO$_2$ exchange of *Cissus quadrangularis* as a function of day/night temperature regime, water vapour pressure deficit (VPD) of the air and watering. Experimental conditions as in Fig. 1.

Temperature regime day/night	Air VPD m Pa Pa^{-1} day/night	CO$_2$ uptake			Nighttime/ total CO$_2$ uptake %	Days without watering
		daytime	nighttime	total m mol m^{-2} 24 h^{-1}		
		m mol m^{-2} 12 h^{-1}				
24/15	500/173	7.80	57.14	64.94	88	3
24/16	341/0	1.09	27.50	28.59	96	30
27/16	407/0	0.82	24.70	25.52	97	30

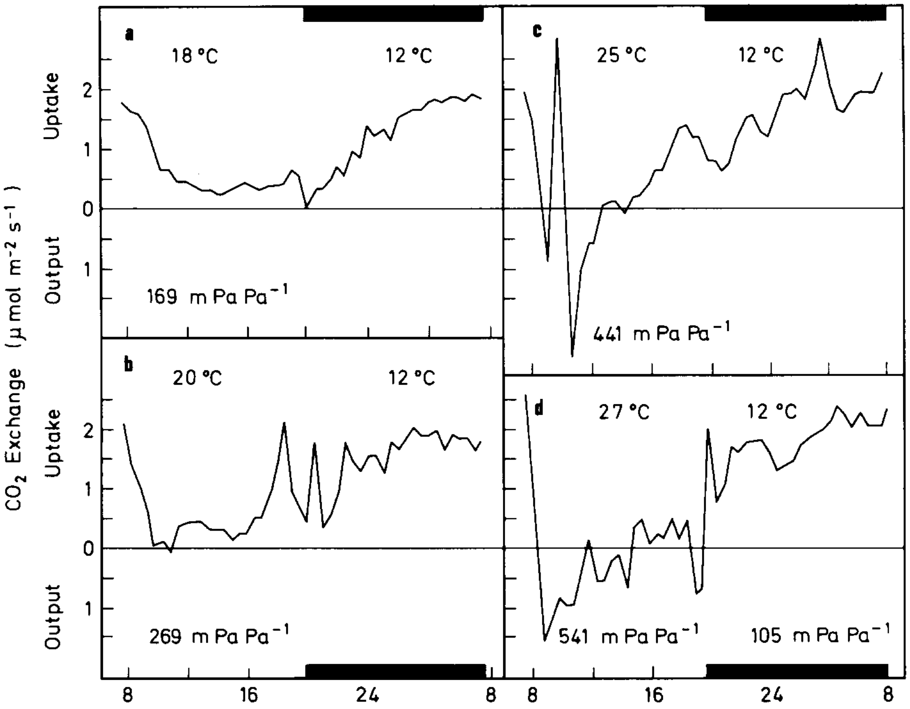

Fig. 2. Diurnal pattern of net CO_2 exchange of watered plants of *Cissus* sp. under constant night temperature and varying day temperature. Water vapour deficit of the air during the night was 0 for a, b and c. Day/night values of CO_2 concentration in the airstream sucked from outdoors through the gas exchange chamber were 354/431 ppm. Other experimental conditions as in Fig. 1.

A plot of night CO_2 uptake, as a percentage of total daily CO_2 uptake, versus daytime VPD irrespective of temperature (Fig. 3), clearly shows that both *C. quadrangularis* and *Cissus* sp. by increasing VPD increasingly resort to night CO_2 fixation.

Transpiration measurements under day/night temperature 26/15 °C and VPD 752/500 mPa Pa^{-1} show that water loss is higher in *Cissus* sp. as compared with *C. quadrangularis* during the dark period (Table 4) while during the light period

Table 3. Night accumulation of malic acid in the stem of *Cissus* sp. Figures are the means of two replicates. The reported values of temperature and air water vapour pressure deficit (VPD) for the greenhouse are the maximum and minimum of the day. VPD was calculated on the basis of RH values.

	Temperature regime day/night	Air VPD m Pa Pa^{-1} day/night	Photoperiod hours day/night	Malic acid m mol m^{-2}
Greenhouse	36/20	602/0	15/9	70.21
Greenhouse	31/19	500/0	12/12	64.67
Growth cabinet	26/16	240/0	12/12	42.94

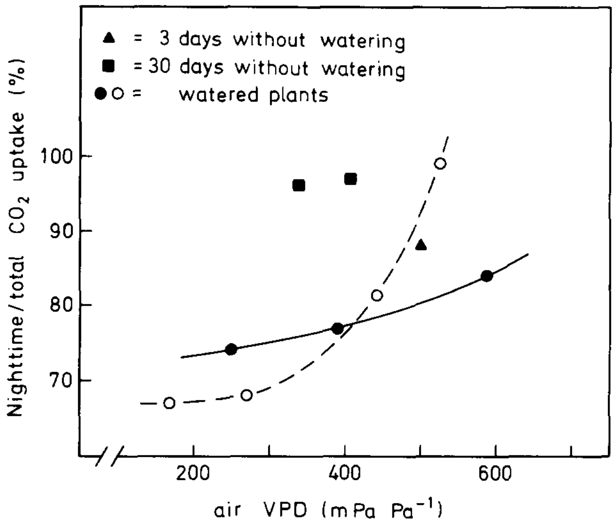

Fig. 3. Relationship between night CO$_2$ uptake as a percentage of total daily CO$_2$ uptake and water vapour deficit (VPD) of the air during daytime for *Cissus quadrangularis* (●, ▲,■) and *Cissus* sp. (○).

it is lower in *Cissus* sp.; transpiration values referred to the whole diurnal cycle are quite similar in the two species. After seven days the same cuttings used in the above measurements, kept in the growth cabinet throughout that period under the same temperature regime, show a marked reduction of the daytime transpiration which is more pronounced in *C. quadrangularis* than in *Cissus* sp.; in contrast nighttime transpiration is only slightly reduced in *C. quadrangularis*,

Table 4. Transpiration of *Cissus quadrangularis* and *Cissus* sp. as a function of day/night temperature regime and water vapour pressure deficit (VPD) of the air. Measurements were taken in the growth cabinet simultaneously on both species under 105 μE m^{-2} s^{-1} PAR. Figures are the means of two replicates. For *Cissus* sp. the values in parentheses refer to unit surface area actually active in gas exchange (green longitudinal band).

Temperature regime day/night	Air VPD mPa Pa^{-1} day/night	Water loss			Nighttime/total water loss %
		daytime	nighttime	Total mol m^{-2} 24 h^{-1}	
		mol m^{-2} 12 h^{-1}			
C. quadrangularis					
26/15	752/500	2.22	0.68	2.90	23
26/15	600/300	0.29*	0.52*	0.81*	64*
15/15	250/250	0.35	0.95	1.30	73
Cissus sp.					
26/15	752/500	1.97 (2.98)	0.92 (1.39)	2.89 (4.37)	32
26/15	600/300	0.48 (0.73)*	1.15 (1.74)*	1.63 (2.47)*	71*
15/15	250/250	0.49 (0.74)	2.13 (3.23)	2.62 (3.97)	81

*The figures refer to measurements made after seven days on the same cuttings used for the above measurements. The cuttings were kept in the growth cabinet.

while it is even increased in *Cissus* sp.; moreover in both species nighttime transpiration largely exceeds daytime transpiration.

Under the experimental conditions with constant air VPD of 250 mPa Pa^{-1} and constant temperature of 15 °C during the diurnal cycle (Table 4) both daytime and nighttime transpiration are higher in *Cissus* sp. than in *C. quadrangularis*; besides, nighttime transpiration in both species is higher than daytime transpiration. Taking into account that in *Cissus* sp. the surface area which is actually active in gas exchange, (the longitudinal green bands) corresponds to 66% of the total surface area, transpiration values are really much higher than those of *C. quadrangularis* (Table 4). Transpiration rates on a stem fresh weight basis are also higher in *Cissus* sp. as compared with *C. quadrangularis* (Table 5).

Nighttime transpiration as a percentage of total water loss during the diurnal cycle is higher in *Cissus* sp. than in *C. quadrangularis* under all the experimental conditions.

Discussion

Patterns of dark CO_2 fixation in watered plants of *C. quadrangularis* and *Cissus* sp. differ primarily in that the maximal rate of CO_2 fixation is reached early in the dark period in *C. quadrangularis*, whereas this occurs towards the end of the dark period in *Cissus* sp. (Figs 1 and 2).

In both the *Cissus* species studied CO_2 exchange occurs throughout the whole light period, suggesting that stomata, under the experimental conditions are open to some degree during the entire light period.

In *C. quadrangularis* CO_2 gas exchange appears to be effectively controlled by water (Tables 1 and 2). Under high water availability gas exchange occurs during both day and night. Under drought CO_2 fixation in the light is suppressed while night CO_2 uptake persists. Moreover, as previously reported [18] malic

Table 5. Daytime and nighttime transpiration rates of *Cissus quadrangularis* and *Cissus* sp. on a stem fresh weight basis.

Temperature regime day/night	Air VPD mPa Pa^{-1} day/night	Water loss daytime	nighttime	total
		m mol g^{-1} 12 h^{-1}		m mol g^{-1} 24 h^{-1}
C. quadrangularis				
26/15	752/500	1.15	0.35	1.50
26/15	600/300	0.15*	0.27*	0.42*
15/15	250/250	0.18	0.49	0.67
Cissus sp.				
26/15	752/500	1.41	0.66	2.07
26/15	600/300	0.34*	0.82*	1.16*
15/15	250/250	0.35	1.52	1.87

*The figures refer to measurements made after seven days on the same cuttings used for the above measurements. The cuttings were kept in the growth cabinet.

acid accumulation in the dark and deacidification in the light are less pronounced in well watered plants as compared with scarcely watered and droughted plants. The data presented suggest that temperature at least within the range considered, is not a major factor which influences the diurnal pattern of gas exchange in *C. quadrangularis*. In spite of that in both watered and stressed plants (Tables 1 and 2) CO_2 uptake in the light is higher at 24 °C than at 27 °C daytime temperature suggesting that stomatal conductance is lower at 27 °C; the reason for this could be a high internal concentration of CO_2 [1] depending on the increase of malic acid decarboxylation and mitochondrial respiration with increasing temperature [5].

In *Cissus* sp. CO_2 uptake occurs throughout the whole light period at 18 and 20 °C daytime temperature, whereas net CO_2 output takes place during phase III of the CAM cycle at 25 and 27 °C daytime temperature. The release of CO_2 in the light at high temperature suggests that the rate of photosynthesis in *Cissus* sp. is lower than the rate of CO_2 production by malate decarboxylation and respiration probably because under the experimental conditions irradiance is limiting; on the other hand it is likely that stomata are not completely closed during the phase III.

The data in Table 1 indicate that *Cissus* sp. demands relatively low day/night temperature (20/12 °C) to perform high CO_2 fixation throughout the diurnal cycle.

Dark fixation is maximal under 25/12 °C temperature regime (Table 1). Nevertheless in the greenhouse at 36/20 °C and daytime VPD of 602 m Pa Pa^{-1} and at 31/19 °C and daytime VPD of 499 m Pa Pa^{-1} accumulation of malic acid was even higher than in the growth cabinet at 26/16 °C and daytime VPD of 240 m Pa Pa^{-1} (Table 3) indicating higher nocturnal CO_2 fixation in the greenhouse plants of *Cissus* sp. under higher degree of air dryness during daytime. However it cannot be excluded that the greater day length a/o the higher irradiance may be responsible for the higher CAM activity in the greenhouse plants, probably owing to more abundant carbohydrate reserves available under those conditions for acid synthesis. Nevertheless at 12 °C night temperature nocturnal CO_2 uptake as a percentage of total CO_2 uptake (Table 1) increases with increasing day temperature and water-vapour deficit of the air (Fig. 3). Increased contribution of nighttime fixation to total daily CO_2 fixation with increasing day temperature has been reported for *Ananas comosus* [9]; however in this species at 15 °C daytime temperature CO_2 uptake occurs predominantly by day. In contrast, in *Cissus* sp., the principal contribution to total carbon gain results from night CO_2 fixation under any temperature regime.

At 27 °C day temperature under high VPD total daily CO_2 uptake is similar in magnitude in *Cissus* sp. and *C. quadrangularis*; however, in *Cissus* sp. carbon gain depends exclusively on night CO_2 uptake, while in *C. quadrangularis* only 84% of the total CO_2 uptake in the diurnal cycle is fixed during the night (Table 1). Nevertheless, after prolonged water shortage in *C. quadrangularis* night fixation is entirely responsible for carbon gain, which is markedly reduced as compared with watered plants (Table 2).

Under abundant soil water availability at low VPD of the air the ratio of nighttime CO_2 fixation to total daily CO_2 fixation (Fig. 3) is higher in *C. quadrangularis* than in *Cissus* sp.; however at high VPD of the air it increases more sharply and becomes higher in *Cissus* sp. as compared with *C. quadrangularis* suggesting that the stomata of *Cissus* sp. respond effectively to daytime air VPD (Fig. 3).

The results of transpiration measurements under the constant temperature of 15 °C and constant VPD of 250 $mPa\,Pa^{-1}$ highlight the importance of night transpiration and thus of night gas exchange in the two species. It is interesting to note that under any of the experimental conditions all transpiration values — day, night and total for the whole diurnal cycle — are higher in *Cissus* sp. as compared with *C. quadrangularis* (Tables 4 and 5). Moreover night transpiration in *Cissus* sp. contributes more to total day transpiration as compared with *C. quadrangularis* (Table 4). Water shortage determines an increase of night transpiration in *Cissus* sp. while daytime transpiration decreases strikingly; in contrast in *C. quadrangularis* both night and day transpiration decreases but night transpiration is higher than day transpiration.

The bulk of data relative to CO_2 exchange and transpiration clearly indicate a preeminent role of nocturnal gas exchange in *Cissus* sp. as compared with *C. quadrangularis*. Under conditions enhancing evaporative demand and promoting short term drought — such as high temperature and high water vapour deficit of the air — watered plants of *Cissus* sp. resort almost exclusively to the CAM mode of photosynthesis whereas watered plants of *C. quadrangularis* still show some daytime CO_2 uptake.

Thus the data lead to the conclusion that under short term drought the role of CAM as an adaptive mechanism is more important in *Cissus* sp than in *C. quadrangularis* which shows a relatively higher resistance to water loss, as indicated by the lower transpiration rates, and possesses an abundant water tissue which prevents rapid changes in plant water content.

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