

## Photosynthetic light-use by three bromeliads originating from shaded sites (*Ananas ananassoides*, *Ananas comosus* cv. Panare) and exposed sites (*Pitcairnia pruinosa*) in the medium Orinoco basin, Venezuela

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### Abstract

Three *Bromeliaceae* species of the medium Orinoco basin, Venezuela, were compared in their light-use characteristics. The bromeliads studied were two species of pineapple, *i.e.* the wild species *Ananas ananassoides* originating from the floor of covered moist forest, and the primitive cultivar Panare of *Ananas comosus* mostly cultivated in semi-shaded palm swamps, and *Pitcairnia pruinosa*, a species abundant in highly sun exposed sites on rock outcrops. *Ananas* species are Crassulacean acid metabolism (CAM) plants, *P. pruinosa* is a C<sub>3</sub> plant. Plants were grown at low daily irradiance (LL = 1.3 mol m<sup>-2</sup> d<sup>-1</sup> corresponding to an incident irradiance of 30 μmol m<sup>-2</sup> s<sup>-1</sup>) and at high irradiance (HL = 14.7 mol m<sup>-2</sup> d<sup>-1</sup> or 340 μmol m<sup>-2</sup> s<sup>-1</sup>), and CO<sub>2</sub> and H<sub>2</sub>O-vapour gas exchange and photochemical (q<sub>p</sub>) and non-photochemical quenching (q<sub>NP</sub>) of chlorophyll *a* fluorescence of photosystem 2 (PS2) were measured after transfer to LL, medium irradiance (ML = 4.1 mol m<sup>-2</sup> d<sup>-1</sup> or 95 μmol m<sup>-2</sup> s<sup>-1</sup>) and HL. All plants showed flexible light-use, and q<sub>p</sub> was kept high under all conditions. LL-grown plants of *Ananas* showed particularly high rates of CAM-photosynthesis when transferred to HL and were not photoinhibited.

*Additional key words:* chlorophyll fluorescence, Crassulacean acid metabolism, gas exchange.

### Introduction

The centre of radiation and diversification of the genus *Ananas* of the *Bromeliaceae* is thought to be northern South America possibly somewhere in the medium Orinoco-region, western Venezuela (Leal and Antoni 1981a,b,c). There are several wild species of *Ananas*, among them *A. ananassoides*, which are typical plants of the floor of closed humid forests, *i.e.* of shaded habitats. World-wide the dominant cultivated pineapple variety is *A. comosus* cv. Spanish Red. *A. comosus* has been well characterized in terms of growth (Bartholomew and Kadzimin 1977, Nose *et al.* 1977, 1981), CO<sub>2</sub> fixation (Joshi *et al.* 1965, Neales *et al.* 1980, Nose *et al.* 1986, Medina *et al.* 1991a, 1993, 1994), O<sub>2</sub> evolution (Coté *et al.* 1989) and apparent quantum yield (Borland and

Griffiths 1989). Along the medium Orinoco basin a number of primitive cultivars are traditionally cultivated on a commercial basis for local consumption, including *A. comosus* cv. Panare. They grow well under partial shade of trees, particularly as cultivated in the "morichales", *i.e.* swampy areas within savannas, under the shade of the "moriche" palm *Mauritia flexuosa* (Aristeguieta 1968), whereas *A. comosus* cv. Spanish Red is normally cultivated in open fields under full sun exposure.

Thus, it appeared interesting to compare light-use characteristics of *A. ananassoides* and *A. comosus* cv. Panare under different light regimes, *i.e.* when grown under low and high irradiance, respectively, and

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*Abbreviations:* CAM - Crassulacean acid metabolism; F - fluorescence of light adapted leaf; F<sub>o</sub> - minimal fluorescence of dark adapted leaf; F' - minimal fluorescence of light adapted leaf; F<sub>m</sub> - maximum fluorescence of dark adapted leaf; F' - maximum fluorescence of light adapted leaf; g - leaf conductance for water vapour; HL - high light; LL - low light; ML - medium light; P<sub>N</sub> - net photosynthetic rate (CO<sub>2</sub>-uptake); PS2 - photosystem 2; q<sub>NP</sub> - non-photochemical quenching coefficient; q<sub>p</sub> - photochemical quenching.

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transferred to different irradiance for measurements of photosynthesis. For further comparison we used another terrestrial bromeliad which normally grows under full sun exposure, *e.g.* on the surface of granitic rock outcrops or inselbergs in savannas, *Pitcairnia pruinosa*. *P. pruinosa* is a C<sub>3</sub>-plant, species of *Ananas* are Crassulacean acid metabolism (CAM) plants and *A. comosus* is the most

## Materials and methods

The plants of *Ananas* were brought from Venezuela to Darmstadt in February 1989 as slips of mature plants and were cultivated in a greenhouse. The site of collection of *A. ananassoides* was near the Parguaza river between Caicara and Pto. Ayacucho. The plants of *A. comosus* cv. Panare came from a farm in the medium Orinoco basin near Caicara. Seeds of *Pitcairnia pruinosa* were collected on the Galipero inselberg near Pto. Ayacucho in March 1991 (see Fig. 1 in Medina *et al.* 1991b for locations). Four to five months old seedlings were used for the experiments. Conditions during growth and measurements were: day/night temperatures of 26/16 °C and relative humidities of 60/80 %. This corresponds to water vapour pressure deficits of the atmosphere of  $6.7/7.3 \times 10^{-3}$ . CO<sub>2</sub> concentrations were at the level of the local ambient atmosphere. Light period was 12 h. High light (HL) grown plants received daily doses of irradiance of 14.7 mol(photons) m<sup>-2</sup> d<sup>-1</sup> and low light (LL) grown plants 1.3 mol(photons) m<sup>-2</sup> d<sup>-1</sup>. In some measurements medium light (ML) was used at a daily dose of 4.1 mol(photons) m<sup>-2</sup> d<sup>-1</sup>. These daily light doses correspond to average instant irradiances of HL 340, ML 95 and LL 30 μmol m<sup>-2</sup> s<sup>-1</sup>. Irradiances (photosynthetically active radiation at 400 - 700 nm) were determined with a LI-COR 190 quantum sensor (LI-COR Inc., Lincoln, NE, USA).

Gas exchange was measured in a climate controlled chamber of the phytotron in Darmstadt using a CO<sub>2</sub>/H<sub>2</sub>O porometer (*H. Walz GmbH*, Effeltrich, Germany) as it is described in Keller and Lüttge (1991). A part of the youngest fully developed leaf was clamped into a small cuvette and tightened with the aid of a sealant (*Terostat*,

important crop plant with CAM. We measured photosynthetic gas exchange (CO<sub>2</sub>, H<sub>2</sub>O-vapour) and photochemical (q<sub>P</sub>) and non-photochemical (q<sub>NP</sub>) quenching of chlorophyll fluorescence and found high flexibility of light-use irrespective of species, mode of photosynthesis and irradiance, respectively.

*Teroson*, Heidelberg, Germany). Net gas fluxes for CO<sub>2</sub> and H<sub>2</sub>O-vapour and derived parameters were calculated using the equations given by Cowan (1977), Hall (1982) and Farquhar and Sharkey (1982).

The PAM 101 fluorometer of *H. Walz GmbH* was used to measure the chlorophyll *a* fluorescence of photosystem 2 (PS2). The photochemical (q<sub>P</sub>) and non-photochemical (q<sub>NP</sub>) quenching coefficients were calculated according to Schreiber and Bilger (1993) as:  $q_P = (F'_m - F)/(F'_m - F'_o)$ , and  $q_{NP} = 1 - (F'_m - F'_o)/(F_m - F_o)$ , where values of *F* give fluorescence of chlorophyll *a* of PS2 and *F*<sub>o</sub> is minimal fluorescence yield of the dark adapted sample in weak measuring light, *F*'<sub>o</sub> is the minimal fluorescence yield of the light adapted sample in weak measuring light, *F* is the fluorescence of the light adapted sample, *F*<sub>m</sub> is the maximum fluorescence yield of the dark adapted sample under a saturating light pulse and *F*'<sub>m</sub> is the maximum fluorescence of the light adapted sample under a saturating light pulse.

Titrateable protons were determined by titration against 0.01 M NaOH to pH 8.4 (Lüttge 1988).

All measurements of gas exchange and chlorophyll fluorescence were performed in parallel, first under the irradiance the plants had experienced during growth. For HL grown plants irradiance was then reduced to ML and then further to LL. For the LL grown plants the procedure was reverse with transfer to ML and then HL. Leaf gas exchange was recorded continuously but analyses were performed for the measurements on the third day under any irradiance when chlorophyll fluorescence was measured in parallel.

## Results

For depicting daily courses of the performance of the three species grown under LL or HL and transferred before measurements to LL, ML or HL notations are used in Figs. 1 - 3, where the first entry gives the irradiance during growth, *i.e.* LL or HL, and the second entry the irradiance during measurements, *i.e.* LL, ML or HL, as detailed in materials and methods.

The two CAM species *A. ananassoides* and *A. comosus* cv. Panare showed CO<sub>2</sub> uptake (P<sub>N</sub>) almost

exclusively during the dark period (phase I of CAM *sensu* Osmond 1978). Stomata were largely closed during the light period as shown by the curves of leaf conductance for water vapour (g). An early morning (phase II) CO<sub>2</sub>-uptake was observed in both species under all conditions except HL/LL, and there was only a small indication of late-afternoon CO<sub>2</sub>-uptake in some cases, *e.g.* in LL/LL and LL/ML for *A. ananassoides* and in LL/LL for *A. comosus* cv. Panare (Figs. 1 and 2). On

average 98 % of the total amount of  $\text{CO}_2$  was taken up during the dark period.

The light dose received by CAM-plants during the day is known to determine the degree of dark-fixation of  $\text{CO}_2$  during the subsequent night (Nobel and Hartsock

1983). This is also borne out by the present results, where in both species and for both LL and HL grown plants the maximum rates of nocturnal  $\text{CO}_2$ -uptake and total integrated  $\text{CO}_2$ -uptake (Table 1) increased when measured under increasing irradiance, *i.e.* from LL to ML

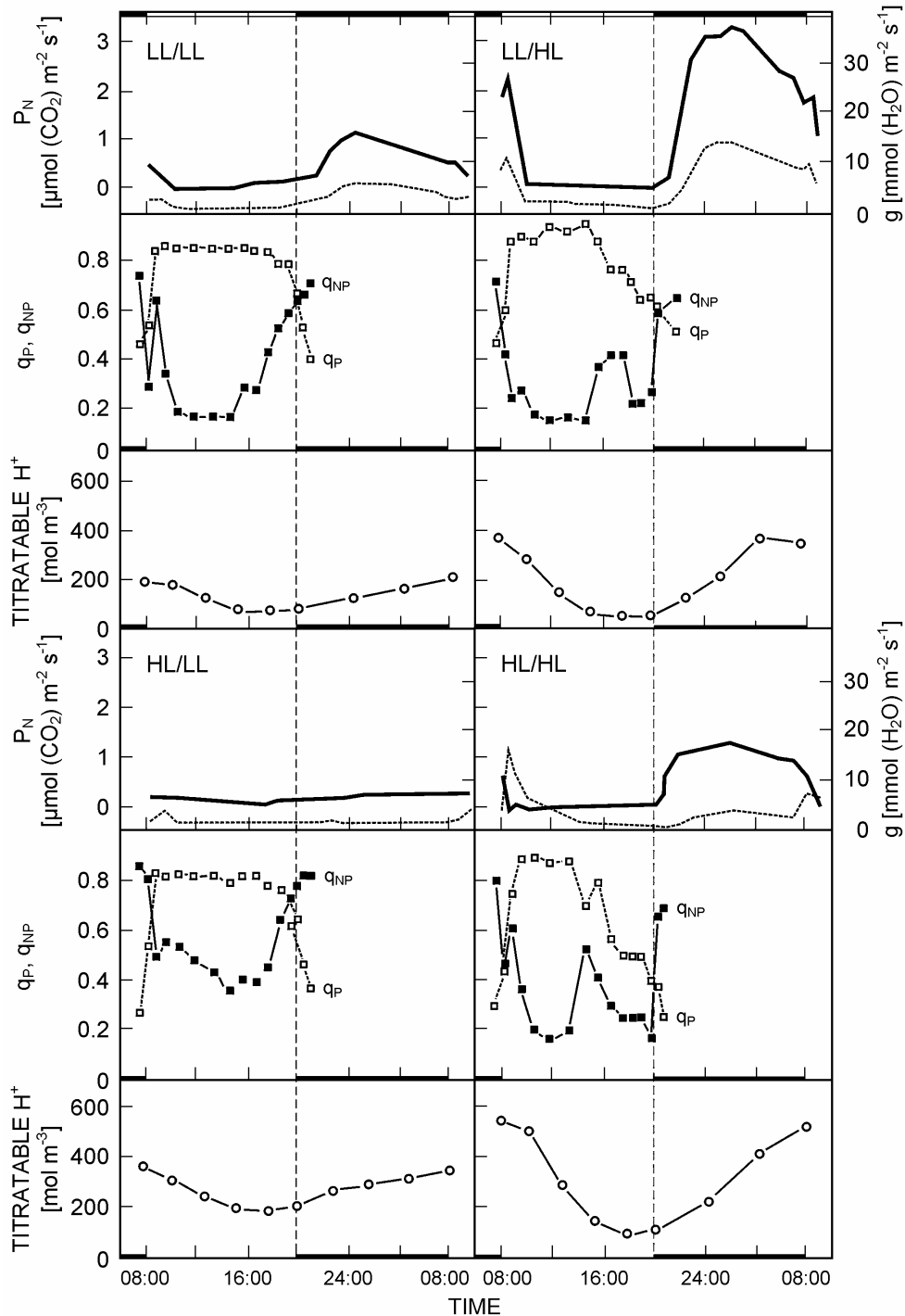


Fig. 1. Recordings of  $\text{CO}_2$ -uptake ( $P_N$ , solid lines) and leaf conductance for water vapour ( $g$ , dotted lines), photochemical quenching ( $q_P$ , open squares) and non-photochemical quenching ( $q_{NP}$ , closed squares), and titratable acidity (open circles) for LL and HL grown plants of *A. ananassoides* measured at LL and HL, respectively. (For explanation of notations see text.) Measurements except for titratable acidity were also performed under ML but only the integrated data of  $P_N$  are reported for this treatment in Table 1.

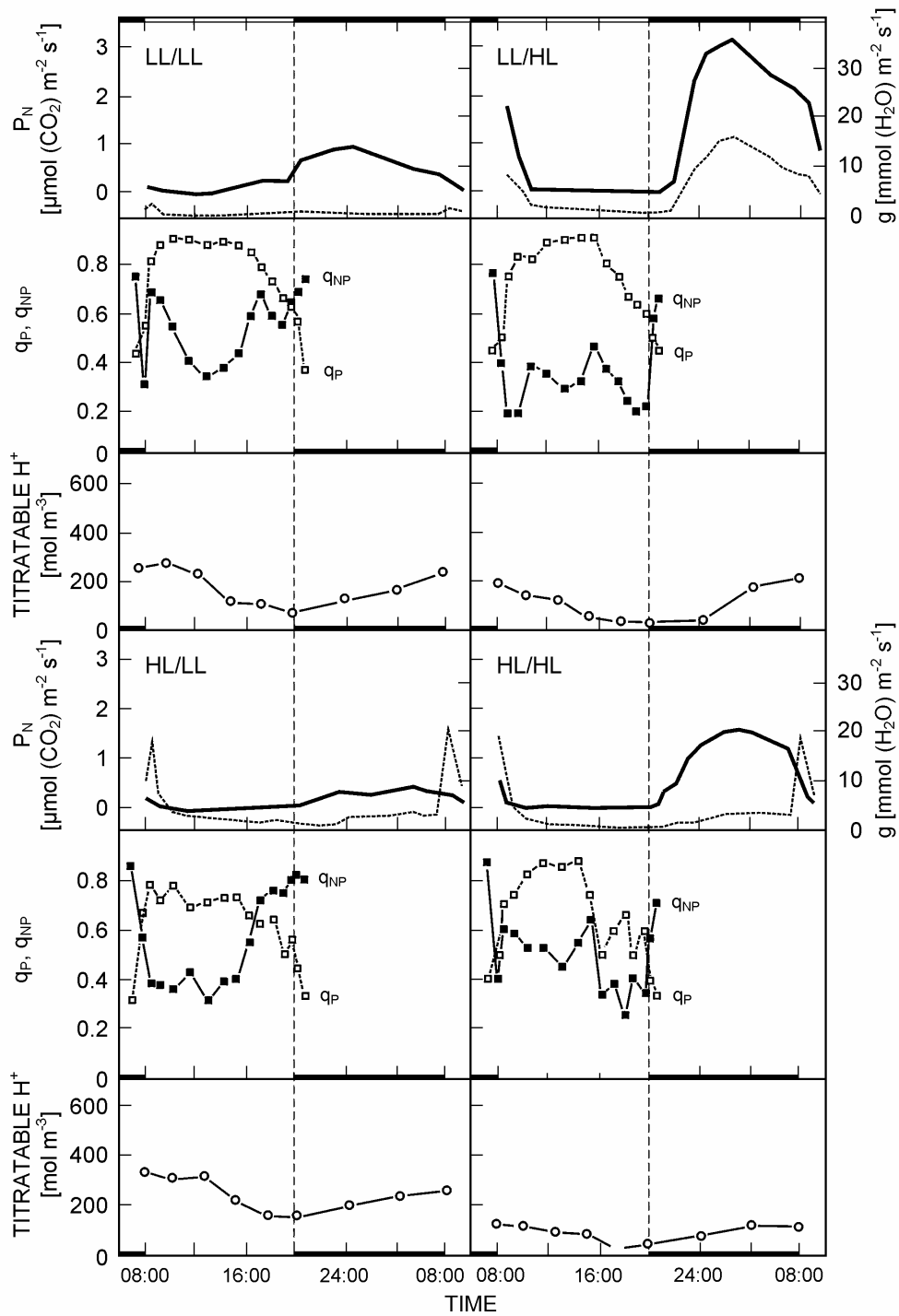


Fig. 2. Measurements of *A. comosus* cv. Panare, all further details as in Fig. 1.

and HL. Interestingly, the highest integrated  $\text{CO}_2$ -uptake rates were obtained for LL/HL plants, *i.e.* about twice as large as for HL/HL plants. Apparently growth at HL has led to development of a lower  $\text{CO}_2$ -fixation capacity than growth at LL and transfer from LL to HL does not subject the plants to photoinhibition so that they can utilize the

increased irradiance for CAM-photosynthesis. This is supported by the quenching coefficients of chlorophyll fluorescence. Photochemical quenching,  $q_P$ , is always high during the day as long as nocturnally stored organic acid is remobilized (phase III of CAM). It drops when organic acid remobilization is completed and internal

Table 1. Integrated rates of CO<sub>2</sub>-uptake [ $\mu\text{mol m}^{-2} \text{d}^{-1}$ ] determined for 24 h of the day for the two CAM species of *Ananas* and for the 12 h of the light period for the C<sub>3</sub>-species *P. pruinosa* grown under HL and LL and transferred for measurements to HL, ML and LL, respectively.

Plants	Growth irradiance	Irradiance during measurements		
		HL	ML	LL
<i>A. ananassoides</i>	HL	45	32	5
	LL	115	29	30
<i>A. comosus</i>	HL	45	45	11
	LL	103	53	30
<i>P. pruinosa</i>	HL	277	149	61
	LL	277	141	47

CO<sub>2</sub> concentrations, which are very high and saturating Rubisco with its substrate during organic acid decarboxylation in phase III (Lüttge 2002), decrease

drastically. The  $q_{NP}$ , mirrors  $q_P$ , it drops during phase III and shows an increase when organic acid remobilization is completed, although the latter may be only transient in some cases (Figs. 1 and 2).

Much higher maximum rates of CO<sub>2</sub>-uptake were attained by the C<sub>3</sub>-species *P. pruinosa* in the light period than by the two CAM species in the dark period, and hence also higher integrated daily rates (Table 1, Fig. 3). Photochemical quenching,  $q_P$ , was high and non-photochemical quenching,  $q_{NP}$ , low throughout the day except in the HL/LL plants, where both quenching coefficients decreased continuously. In the LL/HL plants  $q_{NP}$ , increased somewhat after the first hours of light. Overall these data show, however, that irrespective of whether the plants of *P. pruinosa* were grown at LL or HL they made similar use of increasing irradiance from LL to ML and HL for increasing photosynthesis during the measurements.

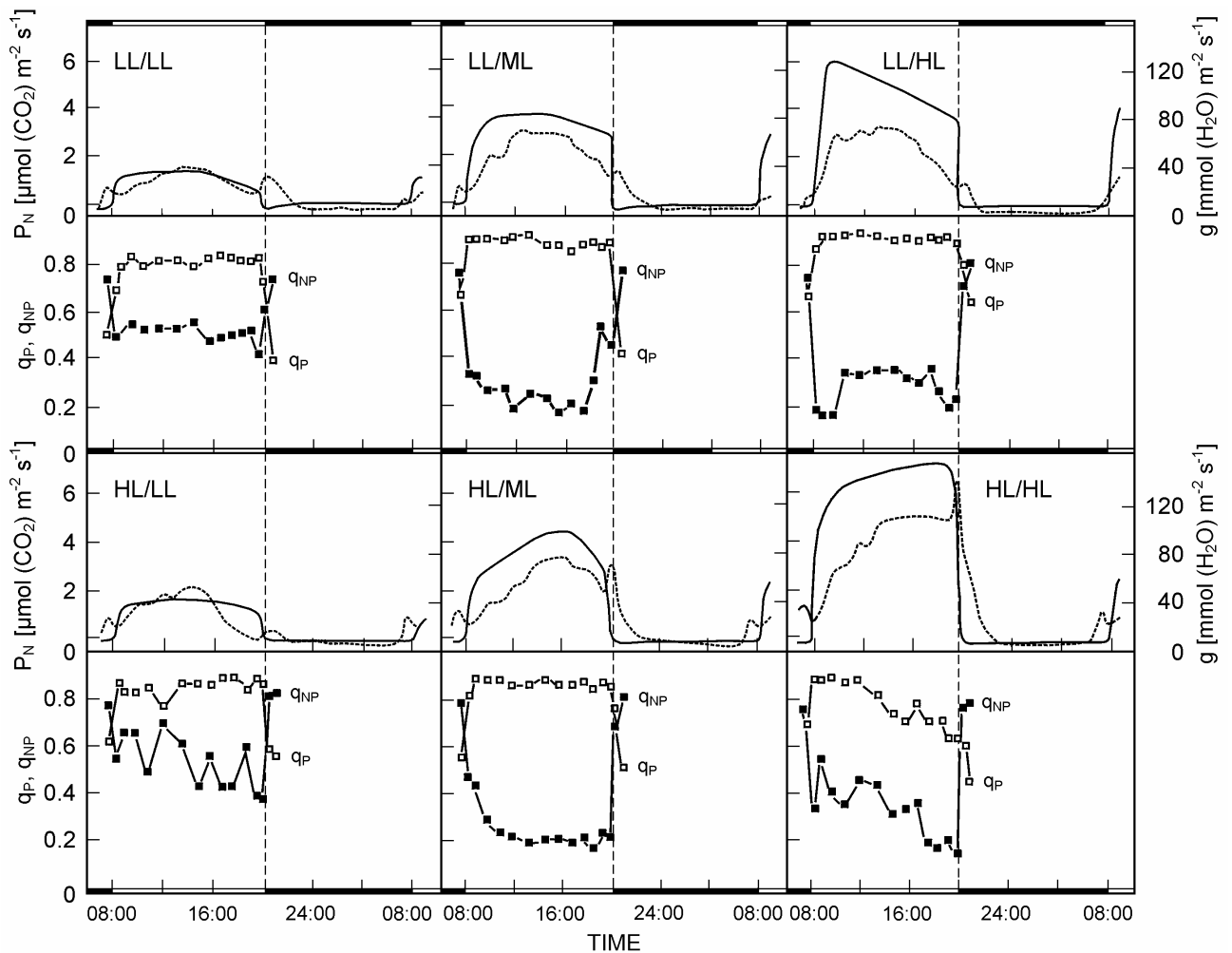


Fig. 3. Recordings of CO<sub>2</sub>-uptake ( $P_N$ , solid lines) and leaf conductance for water vapour ( $g$ , dotted lines), photochemical quenching ( $q_P$ , open squares) and non-photochemical quenching ( $q_{NP}$ , closed squares) for LL and HL grown plants of *P. pruinosa* measured at LL, ML and HL. (For explanation of notations see text.)

## Discussion

In previous studies all four phases of CAM were found in *Ananas* (Nose *et al.* 1977, 1986, Neales 1980). In the present study net CO<sub>2</sub>-uptake of *A. comosus* and *A. ananassoides* occurred predominantly during the night (phase I). During the day stomata were mainly closed with no net gas exchange. It is reported that water stress could be the main reason for the lack of CO<sub>2</sub>-uptake in phases II and IV (Osmond 1978, Nose *et al.* 1981).

Although plants were watered twice a week it is possible that water stress occurred in the present study because the plants were relatively large (*ca.* 70 cm high and *ca.* 100 cm in diameter) and planted in pots (17 cm in diameter).

The three species studied appeared to be remarkably flexible in light-use. Shade grown plants did not show any indication of photoinhibition when transferred to high light as  $q_P$  always remained high. Interestingly, the shade grown plants of the wild species *A. ananassoides* originating from shaded humid forest floor sites and the cultivar *A. comosus* cv. Panare cultivated in semi-shaded moist palm swamps showed even better performance when transferred to high light than the high light grown

plants. In their natural habitats they may experience dynamically changing irradiance (Medina *et al.* 1994), temporarily also including rather high irradiances, *e.g.* during sun flecks, and thus, they may have evolved the competence of using high irradiances where they occur even if they are mainly subjected to shade during growth. The C<sub>3</sub>-species *Pitcairnia pruinosa* originating from highly sun exposed sites of granitic inselbergs as expected showed high rates of photosynthesis, which somewhat surprisingly was not altered when the plants were grown at low light.

A high flexibility of light use as shown by the present data was also observed for high light and low light grown plants of the CAM species *Kalanchoë pinnata* (*Crassulaceae*) where shade grown plants also did not suffer photoinhibition when transferred to high light as long as they were well watered and supplied with nitrogen (Lüttge *et al.* 1991a,b). This flexibility is interesting for explaining habitat occupation and niche width of wild species and for cultivation of pineapple cultivars under various light regimes.

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