



Green barks of trees from drought deciduous forests (“bosque seco”) in northern Peru/southern Ecuador do not perform CAM

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With 14 figures

Abstract: Trees from drought deciduous forests (“bosque seco”) in northern Peru and southern Ecuador regularly shed their leaves at the onset of seven months-long periods without rain. This way they very effectively reduce the bulk water consumption by leaf transpiration, still losing small amounts of water through their bark, but at the risk of too little or no carbon gain when leaf-less. Seven species studied here have good developed green cortex tissue on stems and axes, as especially evident for the “bottle tree” *Ceiba trischistandra* (A. Gray) Bakhuisen (Bombacaceae). In several leaf-less tree species at the end of summer drought, when xylem sap flows are very low, indications of higher xylem flows at night as compared to day-time were found, which led to the question of whether the trees are capable of performing CAM in their axes. However, although quite low in some cases, the pH of the cortex tissues did not fluctuate diurnally. In addition, no night-time carbon uptake could be observed. Although no net carbon gain was measured in *C. trischistandra* and *Erythrina smithiana* Krukoff (Fabaceae) photosynthetic activity of the green cortex was sufficient to re-assimilate between 50% to 60% of the carbon released by mitochondrial respiration. In contrast, the obligate CAM plant *Cereus diffusus* (Britton & Rose) Werdermann (Cactaceae), which was studied as a reference in the same environment, showed both diurnal pH-fluctuations in its green tissue with lowest values before sun rise, and net carbon fixation at night.

Keywords: Green stem cortex tissue, CAM, *Cereus diffusus*, C3-photosynthesis, *Ceiba trischistandra*, summer deciduous trees, seasonal dry forest

Introduction

Drought deciduous forests (so-called “bosque seco”) are found in southern Ecuador and northern Peru approximately between 4° and 5° S (Walter & Breckle 2004, Lauerer et al. 2008). They are the evolutionary result of the long-lasting effects of the cold Humboldt current at the Pacific coast nearby, but sheltered off by a low coastal range in the west, and the strong lee-side effect of the Andes shielding off the normally predominant moist air flows from the Amazon Basin in the east. As a consequence of this situation, summers with air temperatures up to 40°C last regularly seven months without any rain, followed by about 3 months of little and 2 months of sufficient rain, in total allowing for the

very slow growth of an open forest up to 25 m in height. Trees regularly shed their leaves in summer giving the forest a physiognomic impression of being dead – for the dominating brown and black colours – if it were not for some flowering trees. When rainfall increases, the forest completely turns into green, but for no longer than 2–3 months. Trees appear to permanently face the dilemma of either dying from water stress – when maintaining leaves too long in their canopies during the dry period – or dying from too little carbon gain when in the leaf-less mode, for not being able to support the permanently respiring, non-green plant parts with assimilates from photosynthesis.

However, photosynthesis in tissues other than leaves is well known (e.g. Horna & Zimmermann 2002, Küppers 1989,

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Abstract

Trees from drought deciduous forests (“Bosque Seco”) in northern Peru and southern Ecuador regularly shed their leaves at the onset of seven months-long periods without rain. This way they very effectively reduce the bulk water consumption by leaf transpiration, still losing small amounts of water through their bark, but at the risk of too little or no carbon gain when leaf-less. Seven species studied here have good developed green cortex tissue on stems and axes, as especially evident for the “bottle tree” *Ceiba trischistandra* (A. Gray) Bakhuisen (Bombacaceae). In several leaf-less tree species at the end of summer drought, when xylem sap flows are very low, indications of higher xylem flows at night as compared to day-time were found, which led to the question of whether the trees are capable of performing CAM in their axes. However, although quite low in some cases, the pH of the cortex tissues did not fluctuate diurnally. In addition, no night-time carbon uptake could be observed. Although no net carbon gain was measured in *C. trischistandra* and *Erythrina smithiana* Krukoff (Fabaceae) photosynthetic activity of the green cortex was sufficient to re-assimilate between 50% to 60% of the carbon released by mitochondrial respiration. In contrast, the obligate CAM plant *Cereus diffusus* (Britton & Rose) Werdermann (Cactaceae), which was studied as a reference in the same environment, showed both diurnal pH-fluctuations in its green tissue with lowest values before sun rise, and net carbon fixation at night.

Keywords

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44 Introduction

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46 Drought deciduous forests (so-called “bosque seco”) are found in southern Ecuador
47 and northern Peru approximately between 4° and 5° S (WALTER & BRECKLE 2004,
48 LAUERER et al. 2008). They are the evolutionary result of the long-lasting effects of
49 the cold Humboldt current at the Pacific coast nearby, but sheltered off by a low
50 coastal range in the west, and the strong lee-side effect of the Andes shielding off the
51 normally predominant moist air flows from the Amazon Basin in the east. As a
52 consequence of this situation, summers with air temperatures up to 40°C last
53 regularly seven months without any rain, followed by about 3 months of little and 2
54 months of sufficient rain, in total allowing for the very slow growth of an open forest
55 up to 25 m in height. Trees regularly shed their leaves in summer giving the forest a
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59 face the dilemma of either dying from water stress - when maintaining leaves too
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61 in the leaf-less mode, for not being able to support the permanently respiring, non-
62 green plant parts with assimilates from photosynthesis.

63
64 However, photosynthesis in tissues other than leaves is well known (e.g. HORNA &
65 ZIMMERMANN 2002, KÜPPERS 1989, LINDER & TROENG 1981, PFANZ &
66 ASCHAN 2001, SPRUGEL & BENECKE 1991), and especially for succulent CAM
67 plants they have been intensely studied (e.g. VON WILLERT et al. 1992, NOBEL &
68 HARTSOCK 1986). Therefore, the idea is intriguing that trees living in an extremely
69 seasonal dry forest might perform CAM or CAM-cycling in the cortex of their axes
70 when leaf-less.

71
72 As it is well known from the literature (e.g. KLUGE & TING 1978) CAM allows for net
73 carbon gain at night, while stomata are closed during daytime. This adaptation is
74 evident for many leaf-less stem succulent representatives of e.g. Cactaceae and
75 Euphorbiaceae (e.g. NOBEL & HARTSOCK 1986, VON WILLERT et al. 1992). CAM
76 can be expressed in various ways: It may range from a C3-type pattern of
77 photosynthesis at daytime to nearly exclusive night-time CO₂ uptake. For example, a
78 highly variable CAM with a shift from CAM-cycling to “full-CAM” and to CAM-idling
79 depending on plant water supply was observed in *Delosperma tradescantioides*
80 (Aizoaceae; HERPPICH et al. 1996), *Aptenia cordifolia* (Aizoaceae; HERPPICH &
81 PECKMANN 1997) and *Ceraria fruticulosa* (Portulacaceae; VESTE et al. 2001). This
82 CAM plasticity is assumed to be of particular adaptive value, as it may be found
83 within the same individual during progression of development and as a response to
84 severe but predictable environmental changes (HERPPICH et al. 1996, VESTE &
85 THIEDE 2004). On the other hand, in the CAM-cycling mode, neither nocturnal CO₂
86 uptake nor release could be observed, but a pronounced accumulation of malate and
87 citrate [e.g. in *Monilaria moniliformis* (Aizoaceae; VESTE et al. 2001), *Othonna opima*
88 (Asteraceae; VESTE 2005), *Talinum* (Talinaceae, formerly Portulacaceae; HARRIS
89 & MARTIN 1991), *Sedum* (Crassulaceae; GRAVATT & MARTIN 1992), *Pelargonium*
90 (Geraniaceae; JONES et al. 2003) and Cactaceae (MARTIN & WALLACE 2000)].
91 Even for the non-succulent conifer *Welwitschia mirabilis* in the Namib desert a small
92 CAM-related CO₂ uptake or CAM-cycling has been discussed (VESTE 2004, VON
93 WILLERT et al. 2005). In this context, it has been assumed that the nocturnal re-
94 fixation of respiratory CO₂ in the CAM-cycling mode may be ecologically relevant to

95 help maintain a positive carbon balance or to reduce CO₂ losses (MARTIN 1996,
 96 HERPPICH 2004, HERRERA 2009) and that it may provide the ability to rapidly
 97 switch between unrestricted C3 photosynthesis - when well-watered - and reduced
 98 water loss due to CAM idling - when drought-stressed (HERPPICH et al. 1996,
 99 VESTE & THIEDE 2004).

100
 101 For leaf-less trees of the drought-deciduous forest studied here, slightly higher xylem
 102 flows at night as compared to daytime have been recorded at the end of the dry
 103 summer period (REINER ZIMMERMANN, personal communication; KÜPPERS B.I.L.
 104 et al. 2008). This reversed night/day flow situation could indicate slightly increased
 105 water vapour conductances at night, probably comparable to those found in leaves of
 106 CAM plants, when they open their stomata at night. This observation furthermore
 107 implemented the question of whether the cortices of the drought-deciduous trees are
 108 capable of performing CAM, especially because irregularly spaced stomata have
 109 been recorded along rib surfaces of the succulent, always leaf-less stems of the
 110 cactus *Stenocereus gummosus* (GIBSON & NOBEL 1986).

111
 112 In order to address this question a reference plant – the cactus *Cereus diffusus* - was
 113 chosen, for which it could be assumed that it is obligatorily performing CAM, as
 114 shown in studies with the closely related species *Cereus validus* (LÜTTGE & NOBEL
 115 1984). Individuals of *Cereus diffusus* investigated here grew in the immediate
 116 neighbourhood of the studied trees. A comparison of the daily patterns of cortex gas
 117 exchange and tissue pH-values of trees with that of the cactus should clearly indicate
 118 whether the trees follow the physiological CAM trait of the cactus or not.

119 120 121 **Materials and methods**

122 123 **Study site**

124 The type of drought deciduous forest studied here is an extremely seasonal dry
 125 forest and located approximately 175 km WSW of Loja in southern Ecuador and 60
 126 km north of Sullana in northern Peru. These forests extend ca. 40 km in N-S- and ca.
 127 60 km in E-W-direction. Located in the west of the Andean ridges they are almost
 128 completely sheltered off from the rain delivering Amazon Basin. In the west they are
 129 sheltered off from the Pacific Ocean by the shallow mountain ridges of the “Cerros de
 130 Amotape”. Measurements were performed at W 80°44.357' and S 4°21.890' at the
 131 foresters' station named “Sauce Grande” north of the settlement of “El Angolo” in an
 132 area completely fenced off from the surrounding landscape (for details see
 133 LAUERER et al. 2008).

134 135 136 **Climate and vegetation**

137 The particular topography results in a period free of rain lasting from 6 months (June
 138 to November) to sometimes 10 months (Fig. 1A). Air humidity is high from the impact
 139 of the nearby cold Pacific Ocean, as indicated by succulent epiphytes visible in the
 140 leafless canopies. Mean annual temperature at 700 m above sea level (= a.s.l.) is
 141 about 21.7°C with little annual variation (Figs. 1A and B). Fog is formed frequently at
 142 night, but it is not available to shrubs and trees. Rain falls mainly from January to
 143 April (Fig. 1) with large variation from year to year (VASQUEZ et al. 2007), and it is
 144 strongly affected by altitude.

At 200-300 m above sea level precipitation allows for an open scrub with a high portion of succulent species (e.g. *Armatocereus cartwrightianus* (Britton & Rose) Backeb. Ex A. W. Hill (Cactaceae) see Fig. 2A and B). At 700-1000 m a.s.l. a typical “bosque seco” of up to 25 m high trees with stems of up to 70 cm diameter at breast height (= dbh) reaches a coverage of estimated 90% (Figs. 2C and D). In Fig. 3 the physiognomies of the vegetation during the dry period in the leaf-less stage and after rain in the leafy stage are compared.

Species analyzed

All species analyzed concerning bark performance are natives of the “bosque seco” (VASQUEZ et al. 2007, LAUERER et al. 2008); they are briefly described here following the naming of “The Plant List” (<http://www.theplantlist.org/>) in December 2014.

Ceiba trischistandra (A. Gray) Bakhuisen (Malvaceae, formerly Bombacaceae), which is a typical “bottle tree” of up to 20 m height (PATZELT 2002) and dbh of up to 1.5 m (VASQUEZ et al. 2007), grows with a huge pith in the stem. Its bark is shiny green and remains smooth even along old stems (Fig. 4). Analysis of bark gas exchange focused on this particular species.

Caesalpinia paipai Ruiz & Pav. (Caesalpinaceae) grows as a small sized tree of dbh up to 25 cm (VASQUEZ et al. 2007), the bark of which remains smooth even along the stem (Fig. 5A).

Eriotheca ruizii (K. Schumann) A. Robyns (Malvaceae, formerly Bombacaceae) is an intermediate sized tree of dbh up to 60 cm (VASQUEZ et al. 2007), the scale bark of which is covered by semi-circular areoles. Since the bark is thin - despite being of the scale type – green cortex is found all along axes and stem (Fig. 5B).

Erythrina smithiana Krukoff (Caesalpinaceae) is an intermediate to tall sized tree of 15 m (VASQUEZ et al. 2007) and more. Its stem is covered by a rough, red-brownish scale bark bearing thorns. Beneath bark “depressions” the cortex is green even along the stem (Fig. 5C). In Fig. 2D trees in flower (red canopies) are clearly visible.

Loxopterygium huasango Spruce ex Engl. (Anacardiaceae) grows as an intermediate to tall tree of up to 23 m height and a dbh of up to 40 cm (VASQUEZ et al. 2007). Its greyish scale bark is of fine fissures covering green cortex tissue (Fig. 5D).

Capparis eucalyptifolia Haught. (Capparaceae) grows as a small sized tree of up to ca. 7 m height with a dbh of up to 30 cm (DINTER & ZIMMERMANN 2008). Only underneath the bottom of cracks - where the bark is thin so that light can penetrate the outer cortex – green tissue can be found in small spots (Fig. 5E, red arrow).

Cochlospermum vitifolium (Willdenow) Spreng. (Bixaceae, formerly Cochlospermaceae) is an intermediate sized tree of bhd up to 60 cm (VASQUEZ et al. 2007) with a fine fissured, grey scale bark along the stem (Fig. 5F), covering green cortex tissue (not shown).

195 In order to compare photosynthetic performance of tree barks with that of a reference
196 species known to obligatorily perform CAM a *Cereus diffusus* (Britton & Rose)
197 Werdermann (Cactaceae) was chosen growing in the immediate neighbourhood of
198 *Ceiba trischistandra*. *Cereus* reaches a height of ca. 2 m only, and it does not grow
199 leaves. It is a so-called stem succulent and performs CAM in the cortex of its axes.

202 **Cortex pH-value**

203 In situ measurements of pH-values were made in the outer cortex tissues using pH
204 indicator strips (Figs. 6A). For this, the bark was carefully scratched off with a knife
205 and/or razor blade so that the green cortex became exposed. On this freshly
206 prepared area the sensitive part of the indicator strip was lightly pressed for about 1-
207 2 minutes. This was a fully sufficient time to change the colour of the strip.

210 **Analysis of CO₂- and H₂O- gas exchange of bark**

211 Gas exchange of the barks was analyzed with a LiCor 6400 CO₂- H₂O- porometer
212 (Li-Cor, Nebraska, USA) in an open system mode (FIELD et al. 1991, VON WILLERT
213 et al. 1995, KÜPPERS & HÄDER 1999) combined with its so-called “conifer
214 chamber”. The latter was attached to the bark under investigation and sealed off
215 against surrounding air with mastic (Fig. 6). Several technical problems had to be
216 faced: First, it was rarely possible to control temperature of the enclosed bark in full
217 daylight since the cooling efficiency of this system is rather limited. However, since
218 the stems and axes were upright the radiation load was moderate. Secondly, the
219 conifer chamber with its mastic sealing left a reduced section open for light
220 penetration. These limitations could not be avoided. Despite this, a qualitative
221 analysis of CAM or normal C₃-photosynthesis was clearly possible, only conclusions
222 based on quantifications of gas exchange have to be made with special care.

224 In some cases stem sections were completely covered by aluminium foil (partly
225 together with the gas exchange chamber; not shown) in order to study the responses
226 in complete darkness.

230 **Results**

232 **Gas exchange and cortex pH of the reference CAM plant *Cereus diffusus***

233 Fig. 7 shows the diurnal course of CO₂ exchange and water loss of the stem of
234 *Cereus diffusus*. During the night from September 4th to 5th, a very low net CO₂
235 uptake was observed at almost no transpiration, while net CO₂ release at very low
236 transpiration was measured during the day. At the night from September 5th to 6th,
237 CO₂ exchange was for hours close to zero. Evidence for an underlying CAM pattern
238 is given by the independent pH measurements of the sub-epidermal tissue (Fig. 8):
239 Over 4 days the pH fell from about 5.3 at dawn to about 4.2 in the morning before
240 dusk, irrespective of the plant growing in half-shade or fully exposed. When
241 completely sheltering off a normally sun exposed stem from light (not shown) its pH
242 value remained constantly low (around 4.3, Fig. 8, black dots and line)) indicating
243 that (organic) acids accumulated in the dark could not be used by C₃ photosynthesis.
244 When removing the cover the stem's pH in the light immediately rose to the level
245 observed before in daylight.

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Bark gas exchange and cortex pH of drought-deciduous trees

All trees, without exception, exhibit green cortex tissues beneath their barks in those sections, where the bark is thin (e.g. underneath cracks) and, obviously, sufficient light is transmitted to induce chlorophyll formation in chloroplasts of the outer cortex cells (e.g. Fig. 5E). It is, therefore, assumed, that all are capable of performing photosynthesis along their axes.

As a representative tree species, diurnal courses of bark gas exchange of *Ceiba trischistandra* were studied (Fig. 9): Water loss from its bark is similar to that of *Cereus diffusus* both in magnitude and in diurnal pattern (Fig. 7), which indicates a very low bark conductance for water vapour (g_{bark}). When plotting bark transpiration as a function of simultaneously measured vapour pressure deficit (vpd; Fig. 10) a highly linear relationship becomes evident over the whole vpd range, indicating that bark transpiration is only controlled by air humidity. The slope of this relationship results a $g_{\text{bark}} = 2.3 \text{ mmol m}^{-2} \text{ s}^{-1}$ typical for many trees (NOBEL 1991).

Irrespective of this similarity between cactus and tree concerning water loss from bark, their CO_2 exchange differs. In *Ceiba* it is only half the rate of that of *Cereus*, and it is always negative, even during daylight (Fig. 9). Although the low signal was always noisy clear effects of light can be detected on Sept. 3rd: After the low light phase in the morning, carbon loss is reduced in response to a light-fleck in the morning ("peak 1"). A more pronounced reduction in carbon release occurs in response to a light-fleck in the afternoon ("peak 2", red arrows in Fig. 9C). Furthermore, before noon of Sept. 4th, a bark section together with the gas exchange chamber was completely darkened ("light off" in Fig. 9A), which resulted in higher net CO_2 release. After removing the coverage, photosynthetic activity again reduced carbon losses ("light on" in Fig. 9A and red arrows in Fig. 9C). Spot-like measurements of bark gas exchange in *Erythrina smithii* (not shown) resulted the same pattern.

Taking the CO_2 exchange rates of Fig. 9 close to the indicated light peaks and from the "light-off-on" experiment and plotting them against the simultaneously measured photosynthetic active radiation (PPFD) shows typical (but noisy) light response curves of C3 photosynthesis (Fig. 11). However, none of them reaches a light compensation point.

To check for an underlying temperature effect, net carbon exchange rates from the entire diurnal courses in Fig. 9 have been plotted as a function of chamber temperature (Fig. 12), Data were classified for rates measured in "darkness" and in light assumed to nearly saturate photosynthesis (PPFD $\geq 300 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$; time span between blue arrows in Fig. 9C, all intermediate values omitted). The difference between CO_2 exchange rates measured in darkness (black squares) and those determined in light (green circles) amounts from 0.2 to 0.5 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, and it even infers a temperature optimum of photosynthesis around 25-30°C. This indicates that photosynthesis was always lower than mitochondrial respiration, which resulted in net carbon losses from the bark. In saturating light, however, between 50 to 60 % of respired carbon are re-fixed by photosynthesis.

296 For the tree *Ceiba* pH values of cortex tissue have also been monitored (Fig. 13).
 297 Irrespective of whether the bark was grown in sun, on a small or a giant stem or in
 298 the shade, or whether it was artificially darkened, pH values showed no diurnal
 299 fluctuations. They remained between 5.8 and 6.9 and were highest on the darkened
 300 cortex (Fig. 13). Obviously, no diurnal variation of organic acids pattern is detectable
 301 and therefore, no CAM and CAM-cycling could be detected.

302
 303 Similarly, the other tree species showed no diurnal pH patterns in the cortex (Fig.
 304 14), but their values differed much, with highest pH in *Erythrina* and lowest in
 305 *Loxopterygium huassango*. The significance of these differences is not understood.

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310 Discussion

311
 312 The type of drought-deciduous forest in southern Ecuador and northern Peru
 313 investigated here is extremely seasonal with up to ten months without rain and only
 314 two months of leafy canopies. One would assume that in such a harsh environment
 315 particular plant adaptations have evolved. For the cacti living here, knowledge from
 316 the literature predicts a CAM-type photosynthesis very effectively saving water at
 317 very slow growth (e.g. LARCHER 2003, LÜTTGE & NOBEL 1984), while trees
 318 regularly shedding their leaves may completely lack carbon gain when leaf-less but
 319 still have to maintain respiration at high summer temperatures over months. This led
 320 to the question of whether such trees might be able to perform photosynthesis in their
 321 cortices of axes. Photosynthesis in tissues other than leaves is well known (e.g.
 322 HORNA & ZIMMERMANN 2002, KÜPPERS 1989, LINDER & TROENG 1981,
 323 PFANZ & ASCHAN 2001, SPRUGEL & BENECKE 1991), and especially for
 324 succulent CAM plants it has been intensely studied (e.g. VON WILLERT et al. 1992,
 325 NOBEL & HARTSOCK 1986). Therefore it is of interest to know whether these trees
 326 are even able to perform CAM in the cortex of their axes. This question was
 327 addressed at the end of the dry season, when many succulent plants were visibly
 328 shrunken due to the depleted water storage, clearly indicating that all plants were
 329 seriously suffering from drought stress.

330
 331 Although the stem succulent, leaf-less cacti *Cereus* spec. are obligatory CAM plants
 332 (LÜTTGE & NOBEL 1984), net CO₂ exchange at night in the investigated *Cereus*
 333 *diffusus* was around compensation at almost no transpiration. This is in agreement
 334 with observations of VON WILLERT et al. (1992) in the Succulent Karoo. For a
 335 severely drought stressed *Psilocaulon subnodosum* (A.Berger) N.E.Br. these authors
 336 reported a maximum CO₂ uptake rate of 0.3 μmol m⁻² s⁻¹ lasting for 1 hour only, while
 337 for the rest of the day the carbon loss rate amounted up to - 2 μmol m⁻² s⁻¹. Also
 338 *Othonna opima*, formerly described as a C₃-succulent (VON WILLERT et al. 1992),
 339 is able to re-cycle respiratory CO₂ (CAM-cycling mode, VESTE 2005).

340
 341 Despite the missing net carbon gain at night, this gas exchange pattern together with
 342 the typical pH oscillation – being lowest before dawn and highest in the afternoon -
 343 clearly show that *Cereus diffusus* is a CAM plant with the possibility of full-CAM,
 344 CAM-idling or CAM-cycling, respectively, like in many other cacti (RAYDER & TING
 345 1981, PATEL & TING 1987, GIBSON & NOBEL 1986, NOBEL 1988). Even though
 346 the nocturnal CO₂ uptake was low, changes in cortex pH were considerable. This

347 pattern emphasizes the ecophysiological importance of CAM-cycling in many desert
348 plants.

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350 When comparing both the diurnal gas exchange patterns and cortex pH patterns of
351 the trees with those of the cactus (which, in sensu stricto, is not a tree (see e.g.
352 KÜPPERS (1985) for definition), it is clearly evident that none of the trees performs
353 CAM, especially because in no case cortex pH oscillated diurnally.

354

355 However, the CO₂ gas exchange responses of tree barks observed here are very
356 similar to those known from other C3 plants (e.g. KÜPPERS 1989, SPRUGEL &
357 BENECKE 1991), from green, developing cones of *Pinus sylvestris* (LINDER &
358 TROENG 1981, KOPPEL et al. 1987) and green, non-ripe fruits (e.g. KÜPPERS
359 1989, PFANZ & ASCHAN 2001). Similarly, up to 50-60% of the carbon released from
360 respiration in *Ceiba* was refixed by photosynthesis (Figs. 11 and 12). Furthermore,
361 the linear relationship between bark transpiration and vpd over a wide vpd range
362 (Fig. 10) indicates that, as to be expected, no stomatal control is exerted, most likely
363 because stomata are no longer present after the onset of secondary thickening of
364 axes. However, this appears to be different in cacti for which stomata have been
365 found along ribs of stems (GIBSON & NOBEL 1986).

366

367 PFANZ & ASCHAN (2001) reviewed the literature on light penetration into cortex
368 tissues covered by light absorbing bark. Wherever there are cracks in such barks,
369 light might penetrate into the cortex at the base of the cracks, because here the bark
370 layer is thin; the cortex becomes green by light-induced chlorophyll formation. This
371 situation should be similar in *Erythrina* and *Capparis* studied here (Figs. 5C and E).

372

373 Obviously, the drought deciduous trees from the “bosque seco” studied here have to
374 gain sufficient assimilates during a short, 2- to 3-months’ period of green canopies,
375 from which they have to cover all carbon costs of the rest of the year. The restricted
376 annual carbon gain results in limited annual growth so that trees in this forest grow
377 much slower as compared to other forests.

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575 **Figure legends**

576

577 Fig. 1.

578 Course of precipitation and air temperature at the foresters' station "Sauce Grande"
 579 ca. 5km north of El Angolo.

580 **A:** Records of monthly precipitation (redrawn from VASQUEZ et al. 2007, not
 581 available after spring 2007) and air temperature (own data) over time. Long periods
 582 without rain are clearly visible. In 1998 the “El Nino”-event resulted high amounts of
 583 rainfall. Since 2003 annual precipitation is much reduced. Annual courses of air
 584 temperature and monthly observed extreme values clearly indicate the tropical
 585 situation with little seasonal but large short-term – here monthly – variation.

586 **B:** Climate diagram after H. Walter (see BRECKLE 2002 for detailed definition)
 587 constructed from the data in **A**. A mean daily temperature amplitude of 14.8°C was
 588 determined at 21.7°C mean annual temperature. Absolute observed minimum and
 589 maximum were +6.0°C and +41.2°C, respectively. Mean annual precipitation of 698
 590 mm includes the “El Nino”-event of 1998 but may not reflect the long-term situation.

591
 592

593 Fig. 2.

594 **A, B:** Open scrub at 200-300m above sea level (= a.s.l.) with trees of *Loxopterygium*
 595 *huasango* Spruce ex Engl., *Browningia microsperma* (Werdermann & Backeberg) Marshall
 596 and *Armatocereus cartwrightianus* (Britton & Rose) & Backeb. ex A.W.Hill during the dry
 597 season. Coverage is less than 40 %. This area is not fenced off and browsing
 598 animals (cattle, goats etc.) likely enforce their effects on species composition and
 599 coverage.

600 **C, D:** „Bosque seco“ (estimated coverage 90%) at 700-1000m a.s.l. during the dry
 601 season with *Erithrina smithii* Krukoff in flower (red). This area is fenced off from
 602 browsing animals except for a controlled population of deer. **C:** The arrow indicates
 603 position of lodges at the foresters´ station, close to which this study was performed.

604
 605

606 Fig. 3.

607 Vegetation of the extremely seasonal dry forest near „El Angolo“ in the leaf-less
 608 stage in August 2005 (**A, C**) and in the leafy stage after rain in March 2006 (**B, D**).

609 **A, B:** View from Cerro Callana (ca. 800m a.s.l.) towards SW and Pacific coast
 610 desert. Background left: El Tablon; background center: Angelito Mts.. Note the
 611 coastal desert inversion layer (**A**) indicating relatively high air humidity. The greenish
 612 section is coloured from evergreen, epiphytic bromeliads rather than tree leaves. **C,**
 613 **D:** View to open (left) and fenced sections (right) with trans-sectionally running roots
 614 of *Ceiba trischistandra*. Elevation 650 m a.s.l., view towards N.

615
 616

617 Fig. 4.

618 **A:** Forest section dominated by the bottle tree *Ceiba trischistandra* (A. Gray) Bakhuisen,
 619 the green bark is evident. **B:** A singular, huge individual of *C. trischistandra*. For
 620 comparison of size note the person to the right of the stem base. **C:** The green bark
 621 of *C. trischistandra* was marked in 2006 by an unknown person, a year before this
 622 photograph was taken. In the glyphs (e.g. in the number “6”) the green bark was
 623 already completely regenerated.

624
 625

626 Fig. 5.

627 All species studied here have green cortex tissue irrespective of whether it is covered
 628 by smooth, stringy or rough scale bark. **A:** When carefully scratching off the smooth
 629 bark of *Caesalpinia paipai* Ruiz & Pav. green cortex tissue becomes clearly visible
 630 (red arrow). In this species green tissue is found all along stem, branches and twigs.

631 **B:** Underneath the lightly rough scale bark of *Eriotheca ruizii* (K. Schumann) Robyns
 632 intense green cortex tissue is found along all axes. **C:** *Erythrina smithii* Krukoff exhibits
 633 a very rough, red-brownish bark. Beneath bark “depressions” green tissue can be
 634 found even all along the stem (red arrow). **D:** Underneath the slightly rough scale
 635 bark of *Loxopterygium huasango* Spruce ex Engl. only a very thin layer of green tissue
 636 is found (red arrow) easily erased when scratching off the bark. **E:** Only underneath
 637 the bottom of cracks - where the bark of *Capparis eucalyptifolia* Haught is so thin that
 638 light can penetrate the outer cortex – green tissue can be found in small spots (red
 639 arrow). **F:** Axes and especially the stem of *Cochlospermum vitifolium* (Willdenow)
 640 Spreng. (Cochlospermaceae) grow a fine fissured, grey scale bark, covering green
 641 cortex tissue (not shown).

642
 643
 644

645 Fig. 6.

646 **A:** For measurement of the cortex tissue pH the bark of *Ceiba trischistandra* was
 647 carefully scratched off using a sharp knife, thereafter the pH was obtained using pH
 648 stripes. **B:** Set-up of the CO₂-/H₂O-porometer for analysis of bark gas exchange in
 649 *Ceiba trischistandra*. Porometer head attached to the stem and connected to its
 650 console. The system is powered by a car battery continuously re-loaded by a solar
 651 panel during daylight. **C:** Porometer head with the so-called „conifer chamber“
 652 attached to the stem and carefully sealed off by mastic. The light sensor is attached
 653 to the bark in the exposition of the chamber. Further explanation in the text.

654
 655

656 Fig. 7.

657 Diurnal course of light (PPFD) measured outside the chamber (see Fig. 6B),
 658 transpiration and CO₂ exchange of the bark in *Cereus diffusus*. Gas exchange
 659 exhibits small rates only. Temperature of chamber air ranged from (minimum 15.1°C)
 660 17-25°C at night to 30-38°C (maximum 40.1°C) during the day at light >600 μmol
 661 quanta m⁻² s⁻¹, driving the vapour-pressure deficit from 3hPa at night to 25-45hPa
 662 (maximum 57,5hPa) during the day (not shown).

663
 664
 665

666 Fig. 8.

667 In branches of *Cereus diffusus* exposed to normal diurnal changes in radiation the
 668 pH value oscillates between 4 in the morning and 5.3 at dusk, independently of
 669 whether the branch grows in the open (red dots) or shade of a tree (blue squares). In
 670 a covered branch organic acids accumulate in the vacuoles of cortex cells (not
 671 shown but see e.g. LÜTTGE & KLUGE 2012) pulling the pH to low levels and
 672 maintaining it there until photosynthesis is reactivated by removing the aluminium
 673 cap (“opened”, black diamonds).

674
 675

676 Fig. 9.

677 Diurnal courses of bark gas exchange in *Ceiba trischistandra*. Shown are PPFD
 678 (red), transpiration (blue) and net CO₂ exchange (green). Although the signal-to-
 679 noise ratio is very poor the effects of light are fully evident: A light-fleck in the
 680 morning (peak 1) and another in the afternoon (peak 2) initiated the rise (less
 681 negative) exchange in carbon dioxide (red arrows in **C**). This was further tested

682 around noon on Sept. 4th by artificially covering the chamber (“light off” in **A**) and re-
 683 opening it (“light on” in **A**). In darkness net CO₂ release increased, in light it
 684 decreased. Temperature effects on bark CO₂ exchange are also evident: Falling
 685 temperatures all night long (from 25 to 15°C) result in a gradually declining dark
 686 respiration (time-spans between two blue arrows (in **C**), respectively. Transpiration
 687 (in **B**) was always very low (< 0.05 mmol m⁻² s⁻¹ at night and < 0.2 mmol m⁻² s⁻¹
 688 during the day).

689

690

691 Fig. 10.

692 Plotting bark transpiration against vapour pressure deficit (= vpd) from the diurnal
 693 courses in Fig. 9 shows a highly linear relationship (except for a tiny curvature at low
 694 vpd). This clearly shows that stomatal regulation does not occur. The slope of the line
 695 gives the “bark conductivity”, the magnitude of which (ca. 2.3 mmol m⁻² s⁻¹, slope of
 696 line times air pressure of ca. 1000 hPa) is comparable to cuticular conductance of
 697 many leaf epidermis.

698

699

700 Fig. 11.

701 Light response of net CO₂-exchange of the bark indicating “normal” photosynthetic
 702 activity. Since mitochondrial respiration in light is larger than bark photosynthesis, net
 703 CO₂-exchange is always negative. Data are from Fig. 9. Because of the poor signal-
 704 to-noise relation only data points close to a light dependent signal (morning peak 1:
 705 red open diamonds; afternoon peak 2: red triangles; on-off-experiment: black dots)
 706 have been chosen.

707

708

709 Fig. 12.

710 Temperature response of net carbon exchange (= net respiration) of *Ceiba*
 711 *trischistandra* [data from Fig. 9, selected for darkness (black squares) and PPFD >
 712 300 μmol m⁻² s⁻¹ (green circles). Respiration increases strongly with temperature, but
 713 at light levels almost saturating photosynthesis net CO₂ release is clearly reduced.

714

715

716 Fig. 13.

717 Irrespective of exposition of bark (sun, shade, artificially darkened) or stem size, pH
 718 values showed no diurnal oscillations. pH remained comparatively high (compare to
 719 other species in Fig. 14).

720

721

722 Fig. 14.

723 In none of the tree species investigated did cortex pH oscillate. However, different
 724 species exhibit different levels of cortex pH, ranging from 4.3 up to 6.8.

725

Fig. 1A

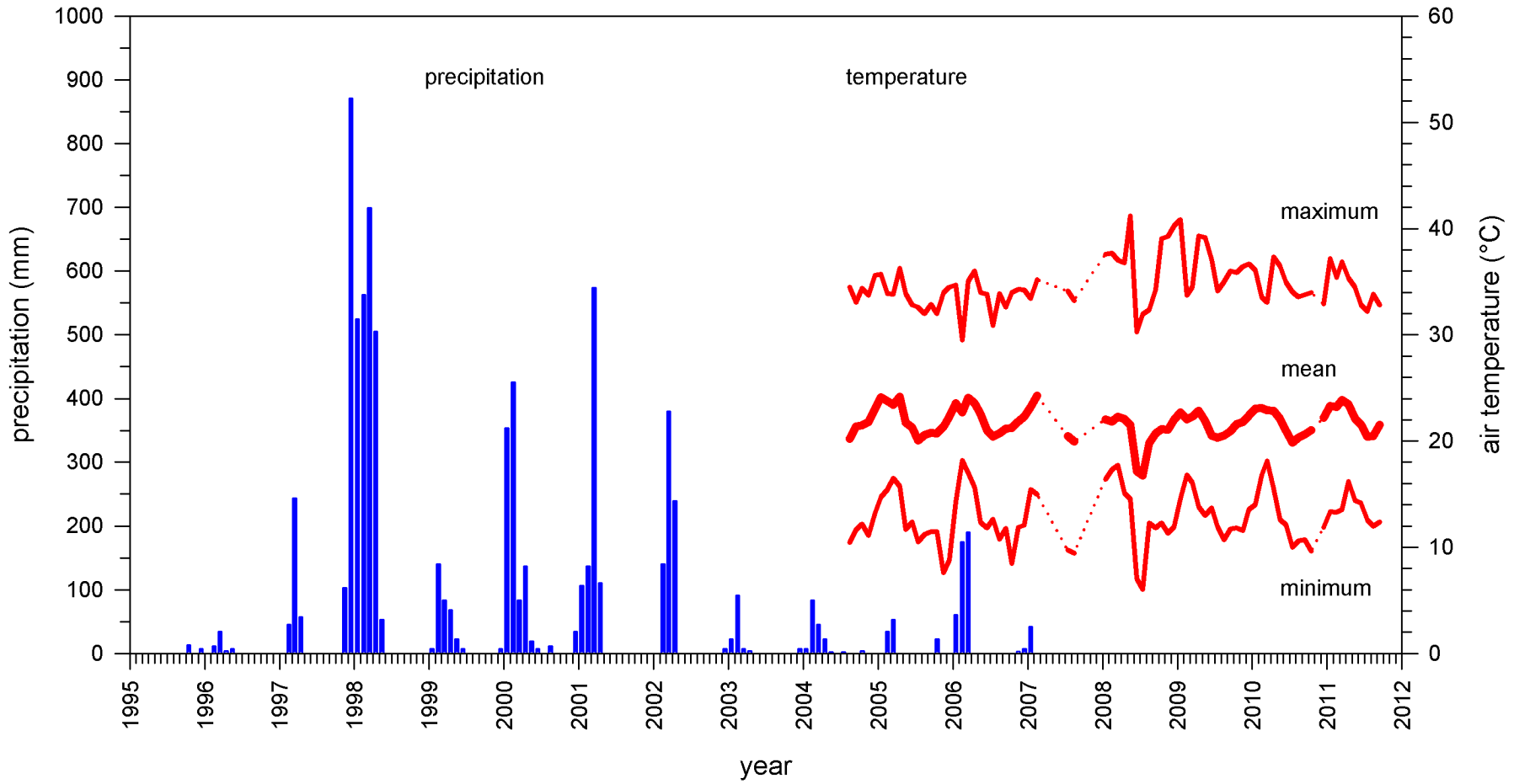


Fig. 1B

Sauce Grande (708 m)

[8 - 11]

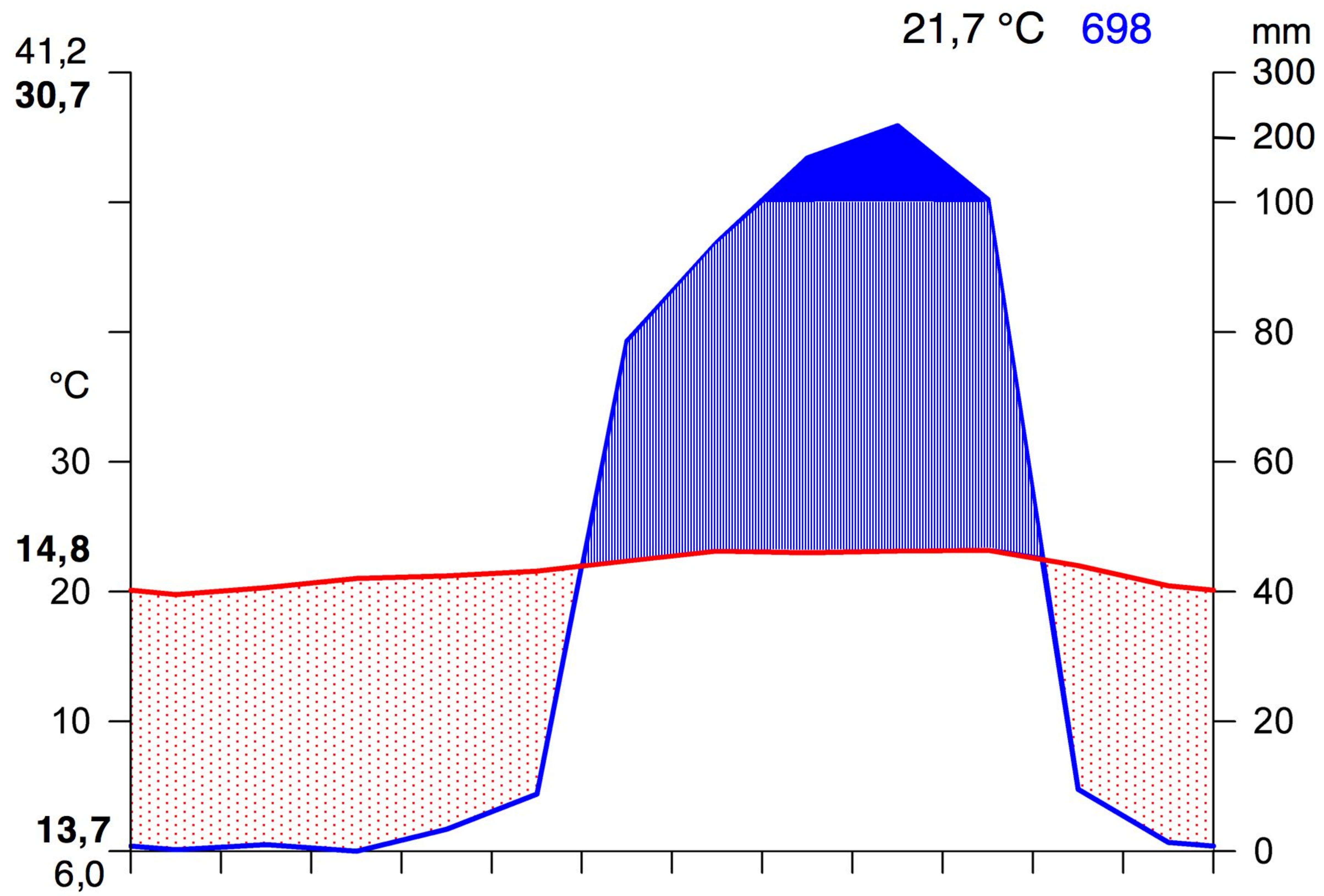


Fig. 2A



Fig. 2B



Fig. 2C



Fig. 2D



Fig. 3A



Fig. 3B





Fig. 3C



Fig. 3D



Fig. 4A

Fig. 4B



Fig. 4C



Fig. 5A

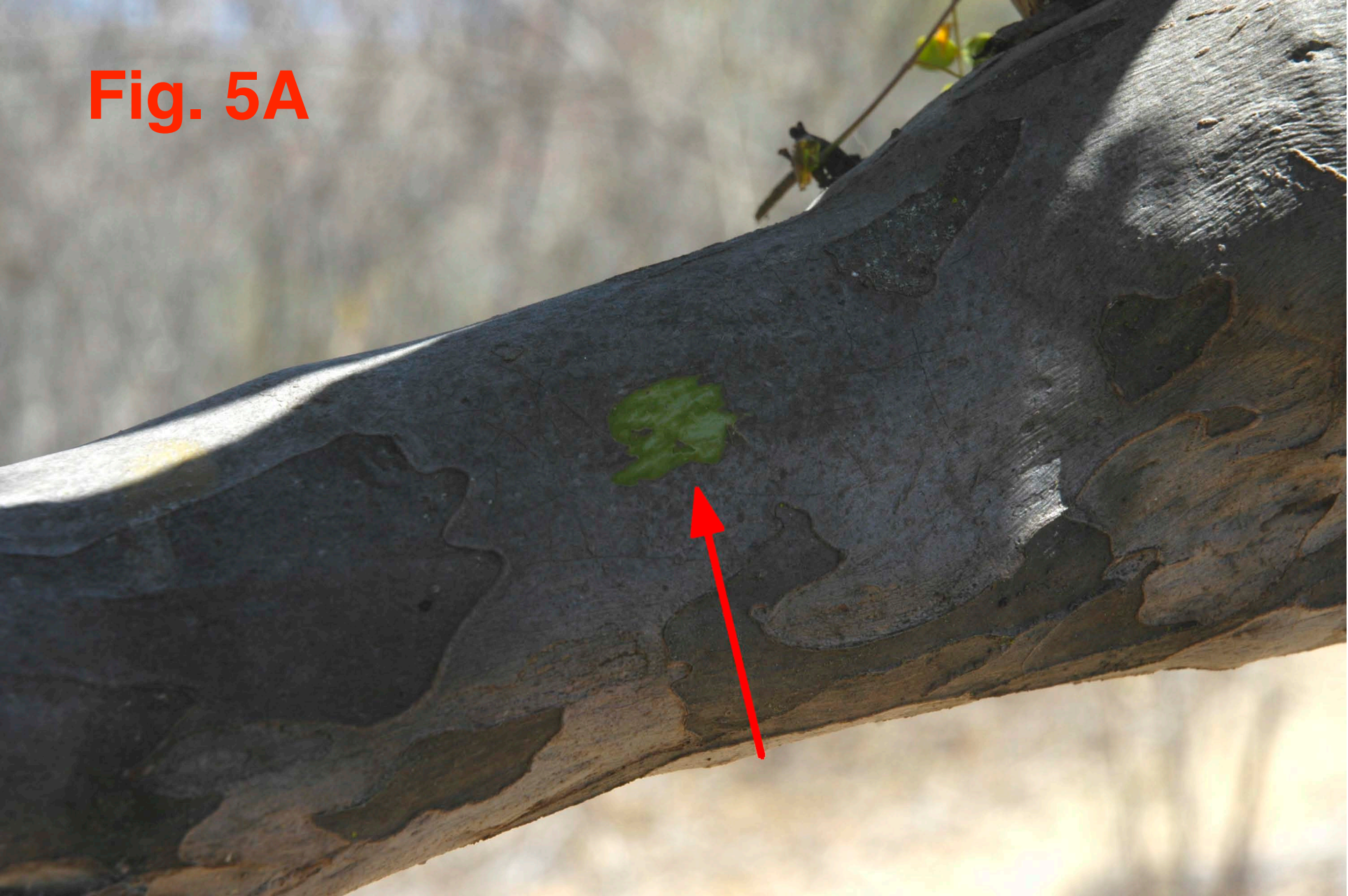


Fig. 5B



Fig. 5C

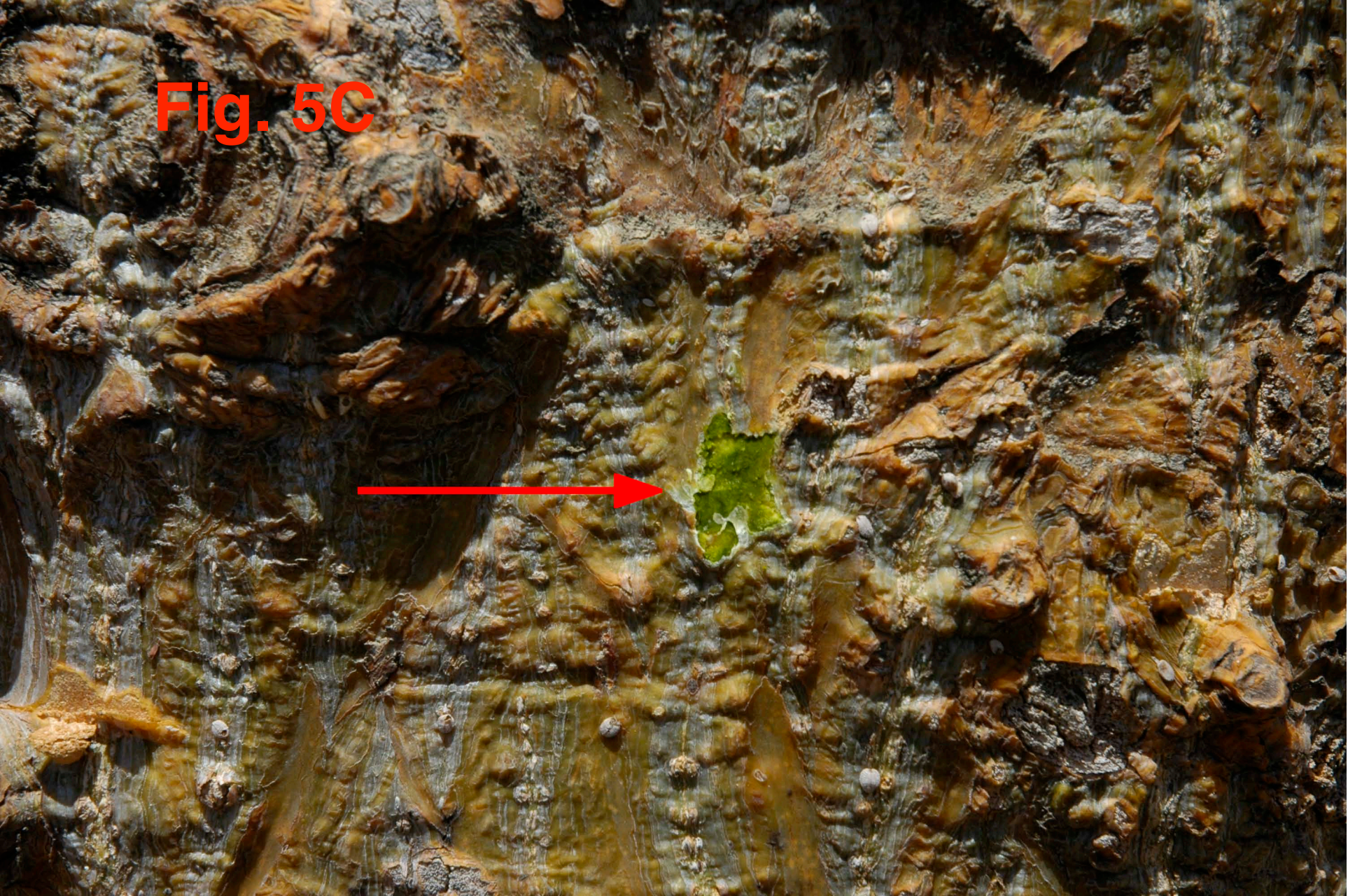


Fig. 5D



Fig. 5E

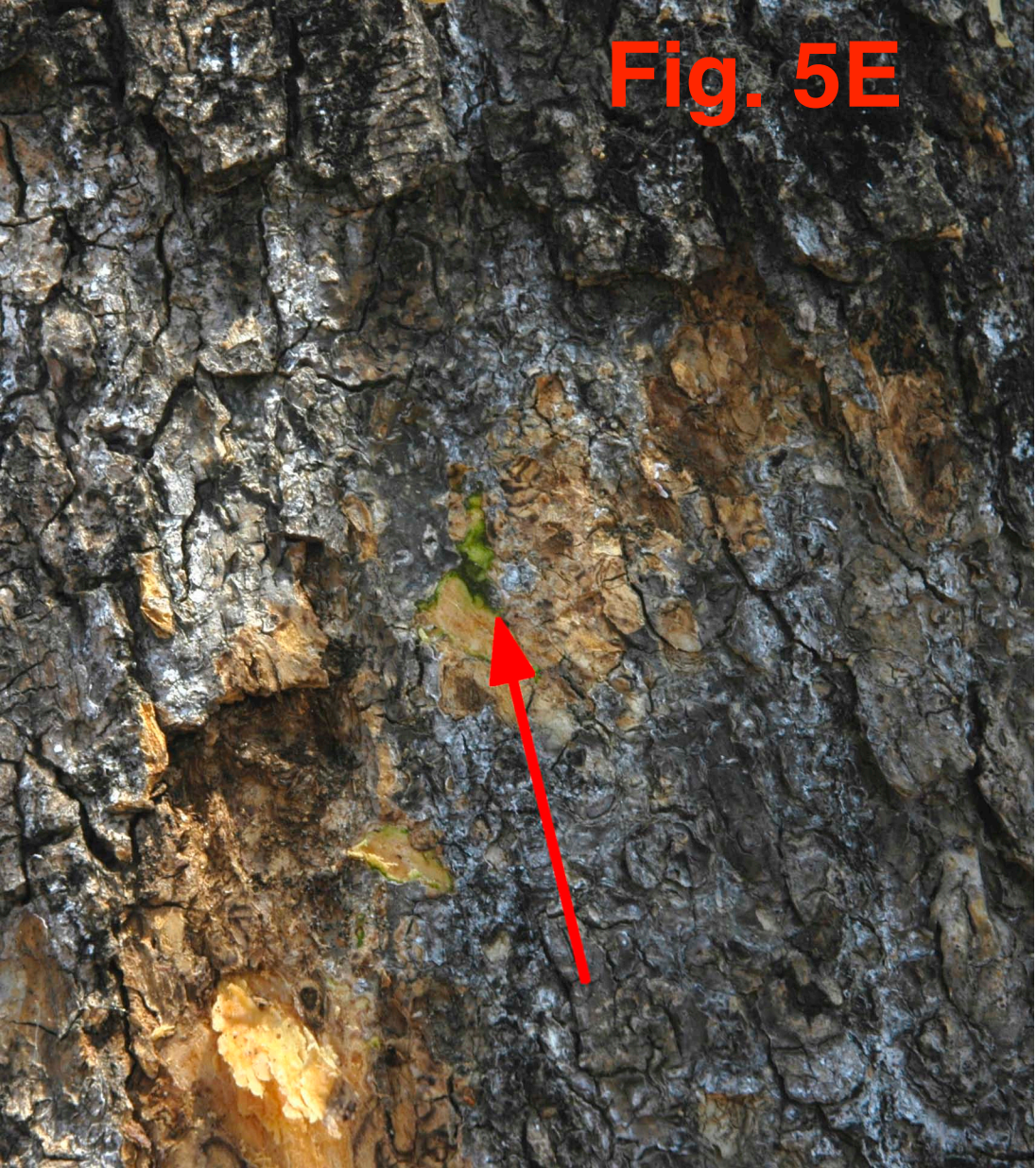


Fig. 5F



Fig. 6A

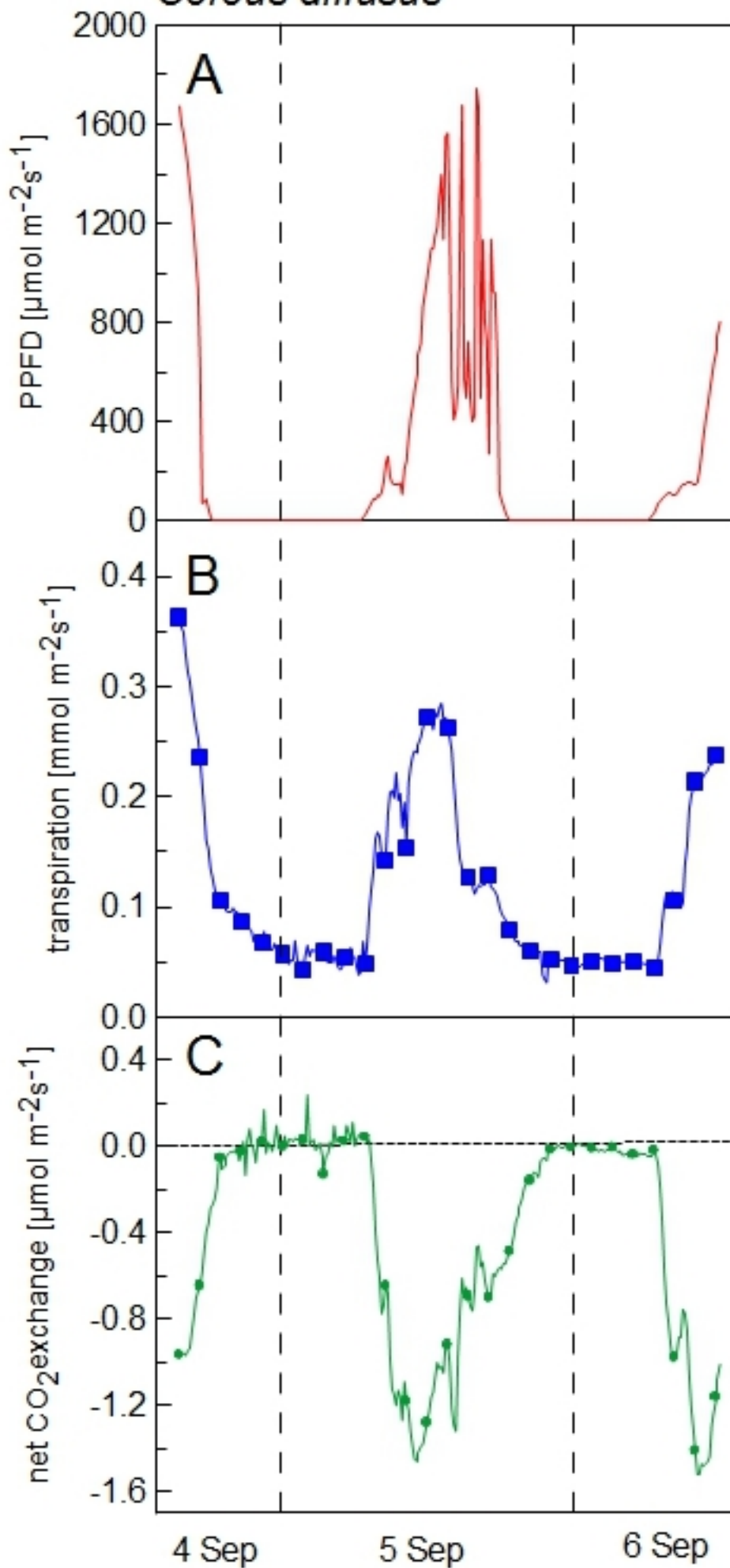




Fig.
6B

Fig. 6C





Cereus diffusus

Fig. 8

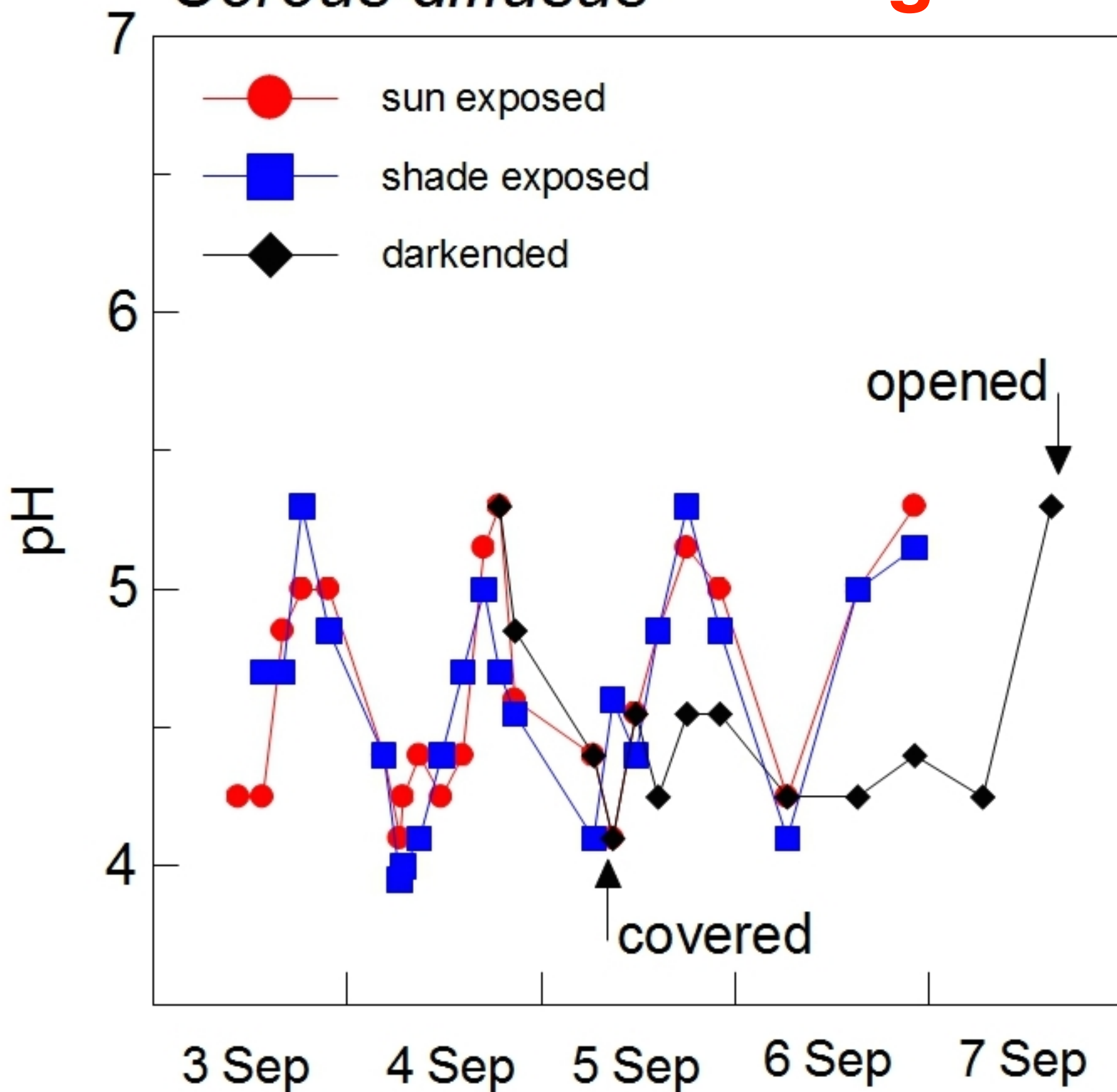
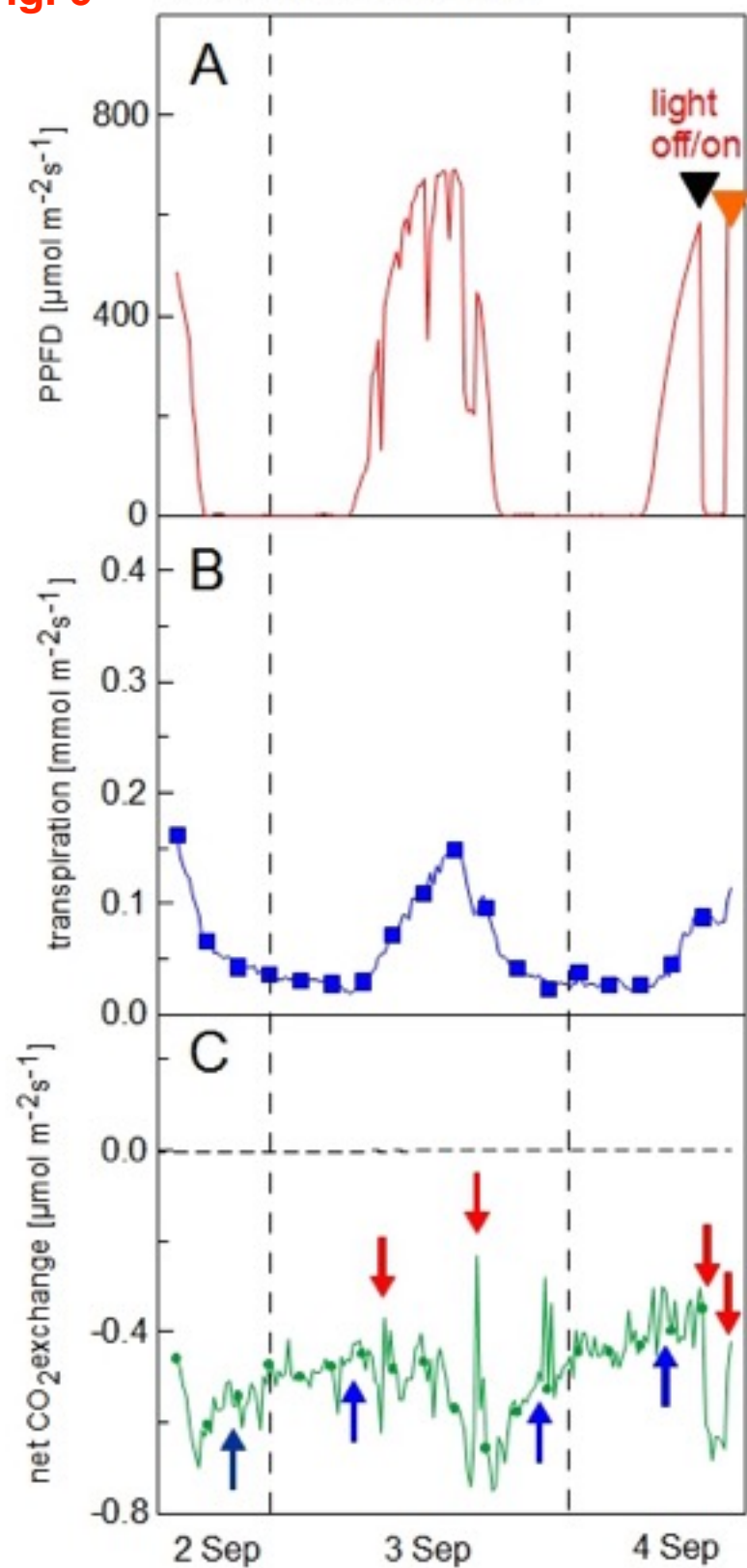


Fig. 9*Ceiba trischistandra*

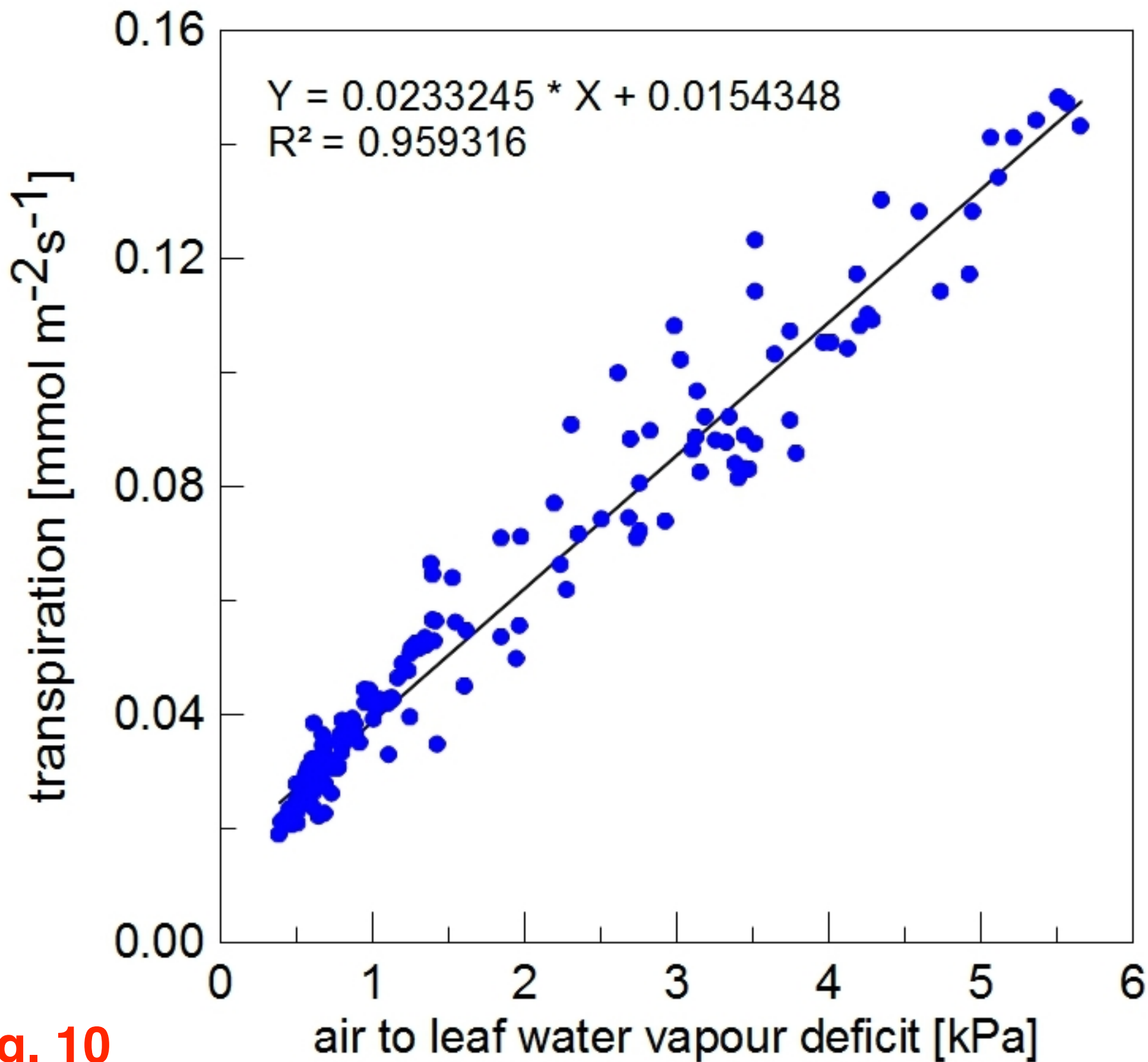


Fig. 10

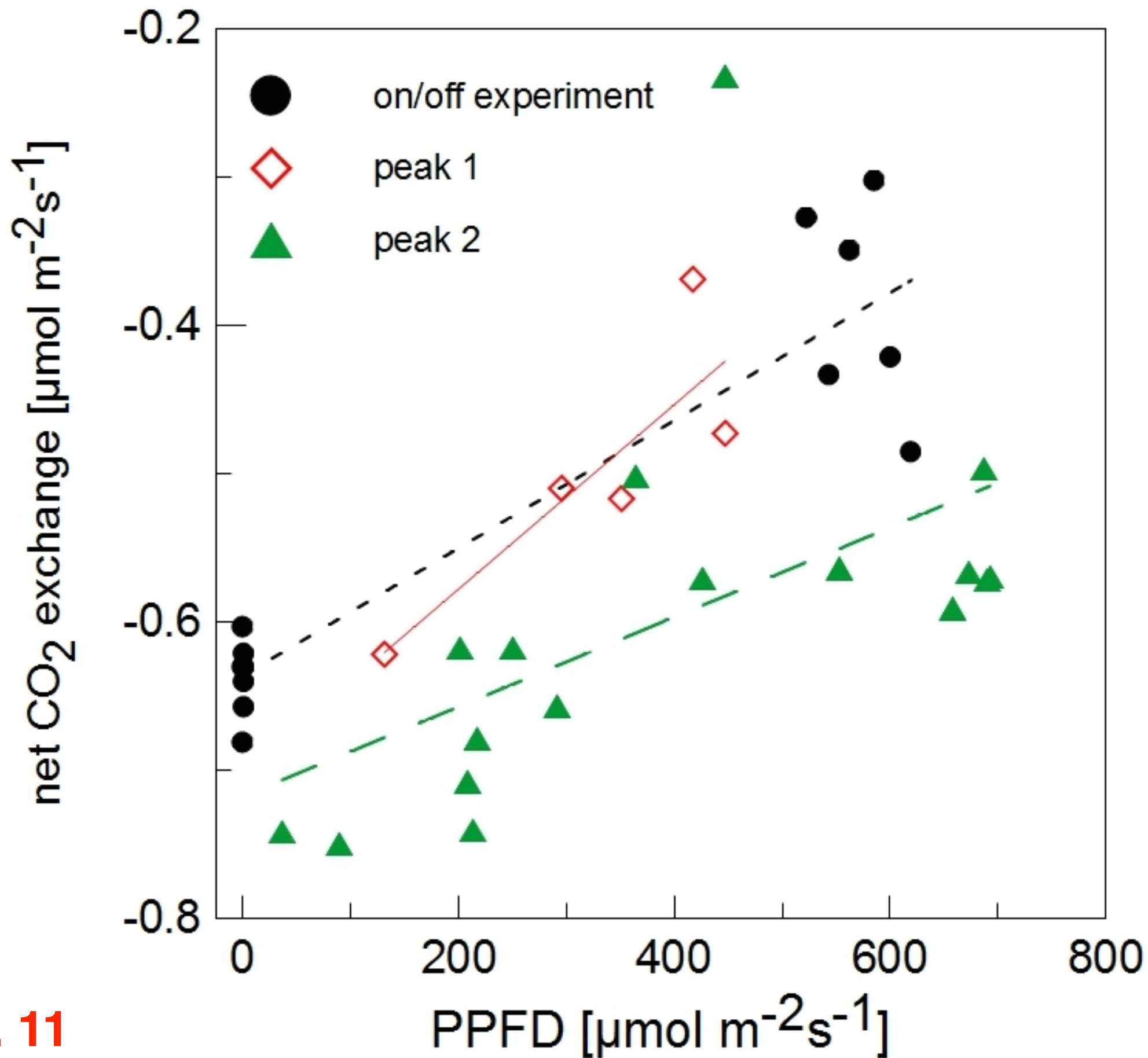


Fig. 11

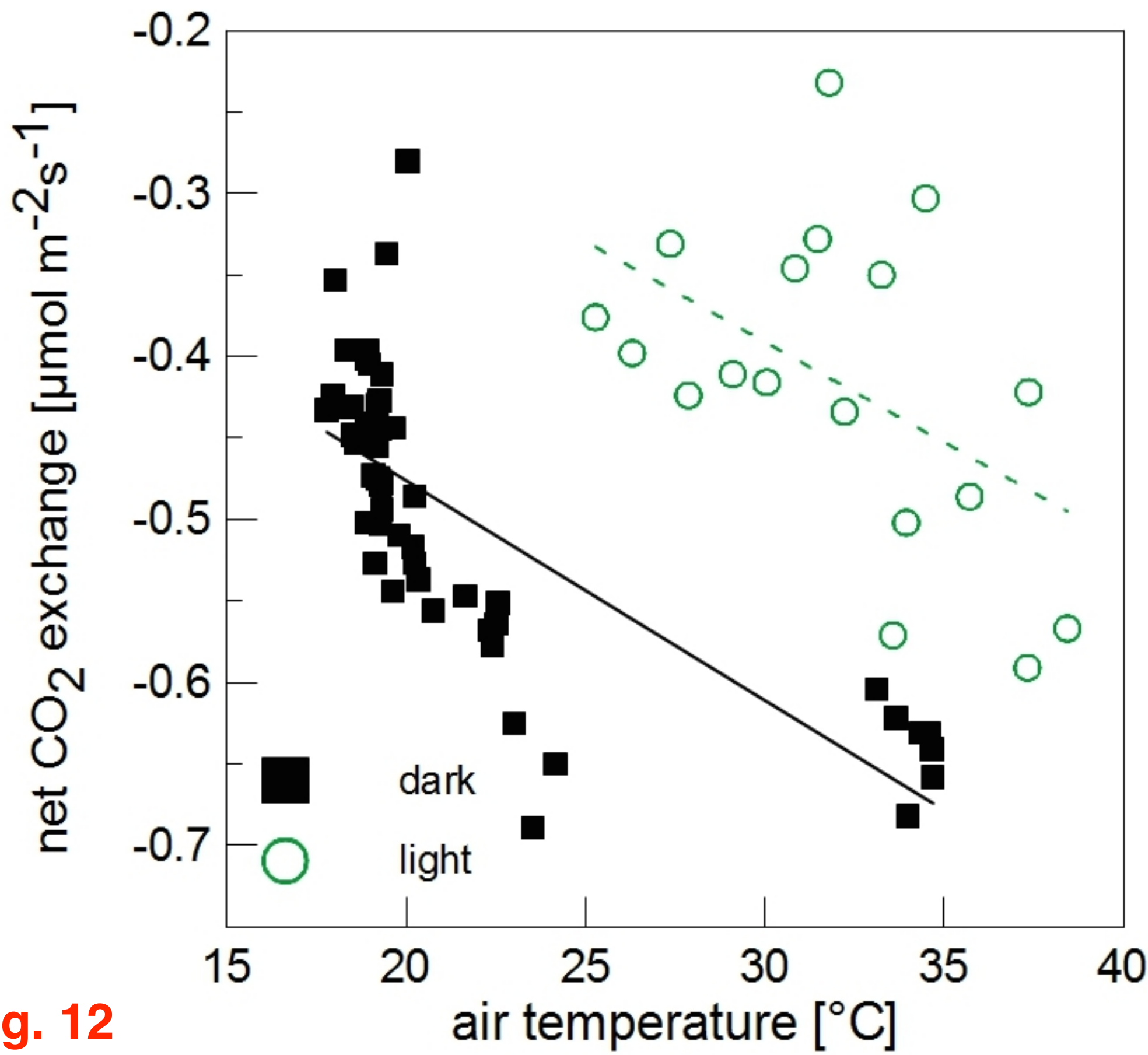


Fig. 12

Fig. 13

Ceiba trischistandra

