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Comparison of gas exchanges between *in situ* and abscised leaves of high arbor trees: a case study of *Cylobalanopsis glauca* under three habitats

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Abstract It has been difficult to monitor the gas exchanges of tall arbor trees using portable equipment, e.g. Li-6400, as it is hard to reach to the leaf samples *in situ*. Due to the tree heights, we aimed to compare the gas exchange between *in situ* and abscised leaves of *Cylobalanopsis glauca* under three habitats, with the purpose of identifying a possible methodology with which we might be able to use abscised rather than *in situ* leaves. The results showed that after the samples were abscised, the leaf stomatal conductance (g_s) immediately increased before dropping gradually later. The extent of this change was found to be temperature-dependent. The linear relationships either between g_s and transpiration (E), or between g_s and net photosynthesis (P_n) were significant but the former had a higher correlation, indicating that the opening of the stomata has a more intensive effect on E than on P_n . Temperature is a key factor affecting the variation of gas exchanges of the abscised leaves, with higher temperature in the karst area resulting in a rapid E loss and leading to the fact that water stress occurs earlier to the part stomatal closure, which in turn decreases P_n . A reliable duration for measuring the gas exchanges from the abscised leaves is determined by leaf temperature. In the karst area where the leaf temperature is frequently over 32°C in the summer, the reliable duration can last only 3–6 min after abscission, while in the Guilin Botanical

Garden (non-karst area) with leaf temperatures of about 32°C, the reliable duration can last 10 min; in the green house, it is at around 20°C, and the reliable duration will possibly last 20 min.

Keywords *in situ*, abscised leaves, gas exchange, *Cylobalanopsis glauca*, habitat, reliable duration

1 Introduction

Plant ecophysiology developed greatly in the recent twenty years due to eco-environmental problems and the invention of modern portable measurement equipments (PME). With the fast and accurate advantage of PME, gas exchange, energy exchange, chlorophyll fluorescence, water potential, water flow in the plant, and canopy and root growth can be measured under field conditions, promoting the development of both individual ecophysiology and community ecophysiology (Jiang, 2004).

The photosynthetic rate, stomatal conductance and transpiration rate are main gas exchange parameters. Photosynthesis and transpiration proceed simultaneously as gas exchange. Stomata, the gateway of gas exchange, regulate and control photosynthesis and transpiration. Plants may have a variety of strategies to adapt to drought environments in the aspect of water physiology. Transpiration and stomatal conductance are very sensitive to many environmental factors (Roberts, 2000; Deng et al., 2002). Plants balance the water by transpiration, and may improve water use efficiency to adapt the drought environment by means of stomatal regulation (Whitehead, 1998; Sparks and Black, 1999; Zhang, 2003). Portable equipments can be used to measure the photosynthesis, fluorescence, stomatal conductance and transpiration *in situ*, which can be used to interpret the eco-physiological association between the plant and the environment. However, it is very difficult to position the equipment so as to reach to the leaves high on top of the tall canopy of arbor trees. When studying the arbor species, researchers usually measure the

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leaves and branches below the canopy or seedlings and saplings instead of *in situ* big trees, but very few studies went directly to tall arbor trees (Zheng and Zhao, 1997; Feng et al., 2002; Zhang et al., 2005). Some researchers measured the gas exchange of abscised branches preserved in bottled water (Ke et al., 2002), but did not analyze how each gas exchange parameter data changed after abscission. Photosynthesis does not cease immediately while the leaf is cut, but still proceeds in a time bucket. Therefore, studying the change in gas exchange characteristics of abscised leaves of arbor trees is ecophysiologicaly important and significant, with which we can determinate the optimal period for measuring gas exchange, thereby predicting the ecophysiological dynamic of the individual and the community. *Cylobalanopsis glauca* mainly distributes in subtropical terrain of eastern China, in both the non-karst and karst areas. This paper aims to study the stomatal conductance, photosynthesis and transpiration of *in situ* and abscised leaves of *C. glauca*, hence to determine the optimal measurement period of the abscised leaves, thereafter providing a reference and method for studies when sampling tall trees.

2 Materials and methods

2.1 Sites and materials

The study site was located in Yanshan Town, Guilin, China (25°15'N, 150 m elevation), with an annual average temperature of 19°C and rainfall of 1900 mm. *C. glauca* was studied in three different habitats: potted seedlings in the greenhouse, tall adult trees (about 16 m) on haplic acrisol at non-karst area in the Guilin Botanical Garden; tall adult trees (about 8 m) on *Perudic cambisols* soil at karst areas in Yanshan Park. In the Guilin Botanical Garden, *C. glauca* grows at the subdued mountainside, where the soil is thick and acid red, covered by a layer of litter, while in Yanshan Park, *C. glauca* grows at the rocky slope, where the soil is alkaline brown and 80% of the surface is occupied by bare rock with disconnected topsoil.

2.2 Methods

We employed a Li-6400 portable photosynthesis system (Li-cor, USA) to measure the gas parameters (net photosynthesis P_n , temperature T_a , stomatal conductance

g_s , transpiration rate E , photosynthetically active radiation PAR etc.) of mature and healthy leaves of *C. glauca* in three sites from Aug–Sept, 2006 and Jan, 2007. The potted seedlings had been grown in a plastic greenhouse until we started to do the measurements. Considering that the seedlings might become dormant because of low temperature during winter, we moved them to a 20°C room with air-conditioning for a week on 2nd Jan, 2007 before measuring. We used the solar light source from windows and complemented by a fluorescent lamp (40 W) from the top ceiling to recover photosynthetic activity from dormancy. The measurement conditions are listed in Table 1. Potted seedlings were exposed to mixed solar and fluorescent lamp radiation for an hour before measuring, then the sample leaf was set on the Li-cor 6400-02B chamber displayed under 500 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ artificial light for half an hour. Measurements under field conditions were carried out from 8:00–14:00 on sunny days. We sampled the abscised leaves (together with sticks) from the low and middle heights of the side canopy where it must be exposed to sunshine (the sticks of the top canopy were too high to reach) in the field area. We inserted the abscised stick into wet soil in a plastic bag immediately, and then measured it at once using natural solar radiation. We set the record frequency at 1 min intervals for each abscised leaf sample. The temperature slightly varied during the measuring period in field conditions, which could be changed more intensively in the karst area than in the non-karst area, hence we summed up the temperature range for 32°C (31–33°C), 34°C (33–35°C), 36°C (35–37°C) and 38°C (37–39°C) in the karst area, and for 32°C in non-karst area where the temperature slightly varied between 31 and 32°C.

2.3 Data statistics

We employed Excel software to analyze the correlations and to draft the graph; setting gas exchange as an independent factor, we used one-way ANOVA on SPSS to compare the significance between treatments. 1) For the abscised leaves of potted seedlings, the data of each continuous 5 min period after abscission from the leaf sample were put together in a dataset; hence, we had four datasets for abscised leaves. Meanwhile, for the *in situ* leaves, all the data were put into one dataset. We then compared the P_n and E of the significant differences between each dataset for abscised leaves and the dataset for

Table 1 The source of the plant material and measurement condition

material source	no. of leaves	individuals	<i>in situ</i> measurement duration/min	abscised measurement duration/min	temperature/°C	photosynthetically active radiation $/(\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1})$	day of measurement
potted seedling	4	4	6	60	20	500	Jan 9, 2007
non-karst site	3	2	6	14	32	external light*	Sept 1, 2006
karst site	9	3	6	6	≥ 32	external light*	Aug 22, 2006

Solar radiation ranged from 350–600 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ in field. All the *in situ* leaf samples were abscised and measured, but a part of the abscised samples were measured *in situ*.

in situ leaves. 2) For the abscised leaves in field conditions, the data of each 1 min period after abscission from different leaves were considered a dataset; hence we had 6 datasets for abscised leaves in the karst area (we measured 6 min for each leaf) and 14 datasets in the non-karst area (we measured 14 min). Meanwhile, for those *in situ* leaves, all the data were put into one dataset. We then compared the P_n and E of the significant differences between each dataset for abscised leaves and for *in situ* leaves. It was hypothesized that if there are no significant differences between the data of the after- N^{th} min of abscised leaves and the *in situ* leaves, it could be deduced that it is reliable to measure the parameter in N min after leaf abscission.

3 Results and discussion

3.1 Stomatal conductance dynamic of *C. glauca* leaf from *in situ* and abscised leaves

The leaf tissue's physiological and biochemical processes will alter after the leaf is cut from the live plant due to a change in the supply system of water and nutrients. Figure 1 shows the stomatal conductance g_s dynamic of the potted seedlings leaves after abscission in 1 h of monitoring. Given a light intensity of $500 \mu\text{mol}/(\text{m}^2 \cdot \text{s})$, comparing to the *in situ* sample, g_s of the four abscised leaf samples was slightly higher and increased gradually in the first few minutes, and in 3 samples, this increase lasted for 12–25 min. Then g_s decreased straight down until becoming steady at $0.2\text{--}0.4 \mu\text{mol}/(\text{m}^2 \cdot \text{s})$ after 30–40 min.

This indicates that the stomata were getting slightly larger after abscission, which might have resulted from the phenomena that when the stick is cut, it leads to xylem vessel opening and the water column withdrawing, hence, in this study, the water flow reversed and the leaf water potential ascended briefly. Leaf shrink resulted in the stomata opening passively and temporarily, and after that closing gradually (Malone, 1994; Lou, 2004). This shows that the stomata of the abscised plant would close gradually in response to micro-environmental changes that would meanwhile influence CO_2 absorption and water transpiration.

Under non-karst field conditions, compared to potted seedlings, we could observe that the g_s dynamic progressed differently during the measuring period 6–16 min after abscission (Fig. 2). In three leaf samples, g_s did not show evident changes in the first few minutes, but after that decreased dramatically. As the leaf temperature is much higher under field conditions than that in an air-conditioned room, leaf respiration rate and other tissue metabolism in the studied field plants must be more active than those in the potted seedlings, thus the water loss from the tissue organ through the stomata was also higher in field plants than that in potted seedlings in our study. Therefore, the stomata closure rate caused by water deficiency could be faster in field plant abscised leaves. We can speculate from Fig. 2 that g_s of *C. glauca* at the non-karst field did not change obviously in the 6 min after abscission.

Meanwhile, under karst field conditions, g_s declined after leaf abscission, being very obvious at $T = 34^\circ\text{C}$,

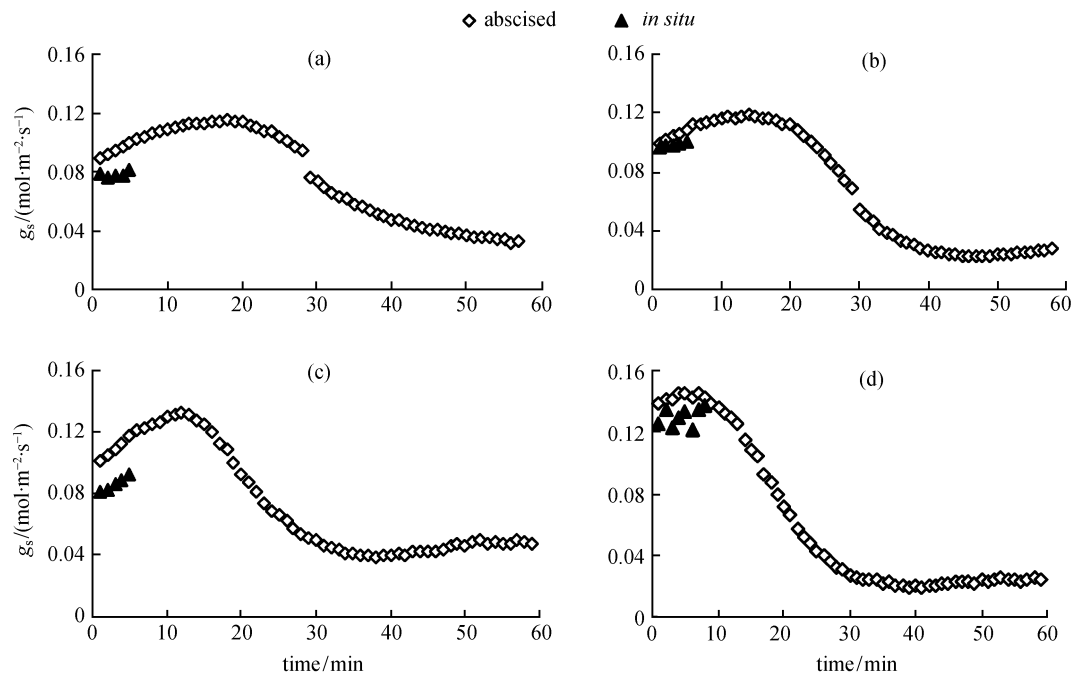


Fig. 1 The change of leaf stomatal conductance of potted *C. glauca* seedling after the stem was abscised

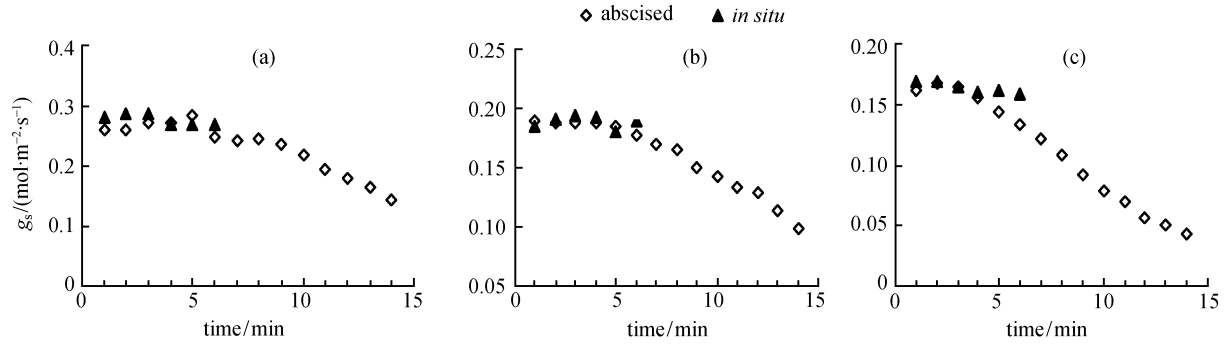


Fig. 2 The change of leaf stomatal conductance of *C. glauca* tree in Guilin Botanical Garden (non-karst area) after the stem was abscised

though the descending absolute value was small (Fig. 3). The flat curve of $T=38^{\circ}\text{C}$ indicated the slowest closure rate of stomata after leaf abscission, illustrating that temperature is not the critical factor influencing stomata closure rate of the abscised leaf during the first 6 min in this study. As stomata movement is usually the quickest evidence of the response to plant photosynthetic adaptation to environmental changes (Zhao et al., 2003), g_s may change rapidly with the alteration of water supply due to leaf abscission. Under high temperature conditions in the karst area, although temperature might affect the leaf physiological process rate, it could at the same time affect water loss rate. However, the slight stomata change could be ignored in a short time under certain permissible errors at either individual or community level.

3.2 Correlation of P_n and g_s between *in situ* and abscised leaves under different habitats

The stomata play an important role in optimizing photosynthesis and transpiration (Cai et al., 2004). The photosynthetic capacity of an abscised leaf could change with changes in the stomatal openness. Under two field conditions, we obtained lesser datasets due to a short measuring period compared to the potted condition. We analyzed the P_n process after leaf abscission and compared them to the *in situ* dataset under potted and non-karst conditions, and also analyzed the P_n process after leaf abscission under karst conditions (Fig. 4). The trend pattern of P_n and g_s from the potted leaf was coherent, in which P_n *in situ* was slightly lower than that after

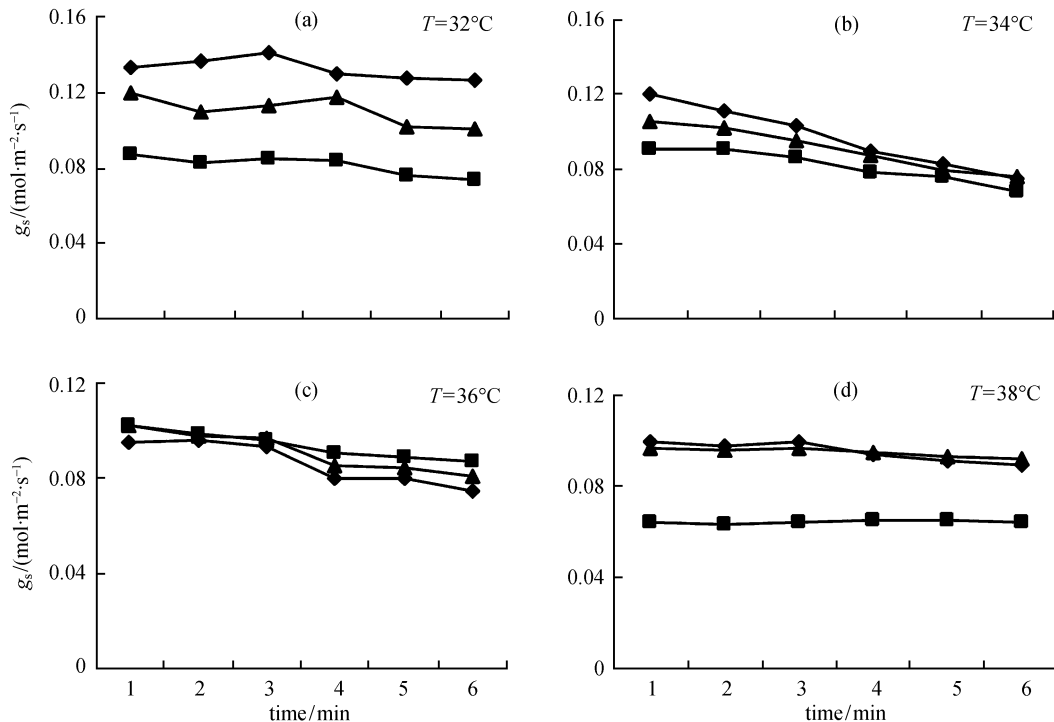


Fig. 3 The change of leaf stomatal conductance of karst *C. glauca* tree after the stem was abscised under different temperature conditions. (a) $T=32^{\circ}\text{C}$; (b) $T=34^{\circ}\text{C}$; (c) $T=36^{\circ}\text{C}$; (d) $T=38^{\circ}\text{C}$.

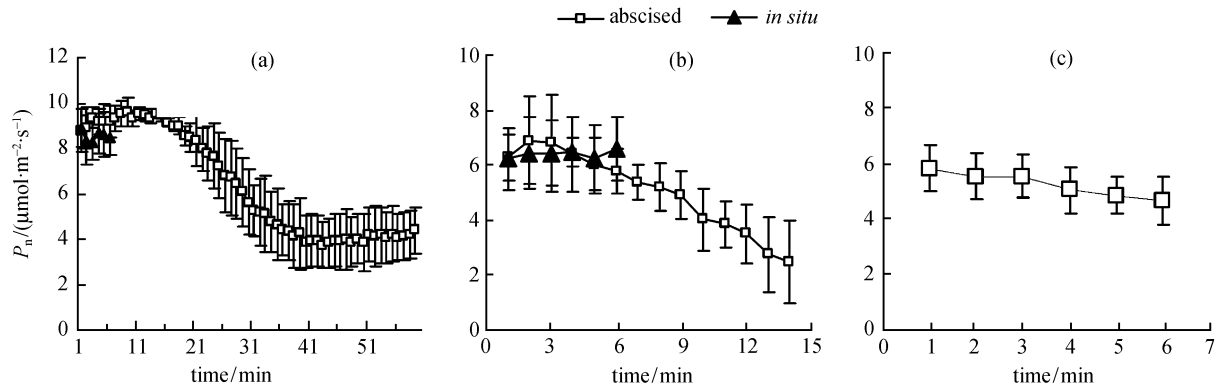


Fig. 4 The change of leaf net photosynthesis of *C. glauca* *in situ* and abscised under three habitats. (a) potted; (b) non-karst site; (c) karst site.

abscission in a short time. During the one-hour measuring period, P_n of abscised leaves ascended slightly in a few minutes and maintained a high point at the beginning, then inflexed at 12–25 min and dropped to 2.6–5.6 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ at 30–40 min, becoming relatively stable. P_n of the short term after abscission was lower under two field conditions than that under potted conditions. Under the non-karst condition, P_n of the abscised leaves ascended slightly in the first 3 min, which was a little higher than that of the *in situ* leaves; it then started to descend at the 5th min. Meanwhile, under the karst condition, P_n of abscised leaves remained steady in the first 3 min, then slightly descended from 3–6 min.

Graphing the coordinates with leaf P_n and g_s , and using Excell binomial for simulation, we obtained the fitting equation for the abscised leaves under three habitats (Fig. 5). The correlation coefficient R of P_n-g_s under the potted condition with the control temperature and radiation reached 0.98, indicating a close relationship wherein the decrease of P_n must be affected closely by gradual closing of the stomata. Meanwhile, the R of P_n-g_s under a non-karst condition was still fairly high at 0.73, though it was the smallest among the three; and the fact that R under the karst condition was 0.90 implied that g_s has a stronger

influence on P_n compared to that under the non-karst condition.

3.3 Correlation of E and g_s between *in situ* and abscised leaves under different habitats

Soil water is the key factor for stomatal opening and closure. The soil water supply ceased after the stick was abscised, however, the leaf still used water from vessels and other tissues by motivation of the transpiration; therefore transpiration would continue and could last for some time. Figure 6 shows the process of E under different conditions. Under potted conditions, E increased slightly in the few minutes after abscission and kept on increasing for 12–25 min, then began to drop down, after 30–40 min to 0.4–0.6 $\text{mmol}/(\text{m}^2 \cdot \text{s})$, then remaining stable. This indicates that when the stick was abscised, the signal of negative water pressure caused by the vessel water column broken would have passed quickly to the leaves, resulting in a quick water stipulation change in leaf cells that leads to the stomata opening wider, hence the water vapor inside the leaves could spread through the stomata at a quick rate, with an evidence that transpiration increased in a short time (Guo et al, 1997). During the one-hour measuring period

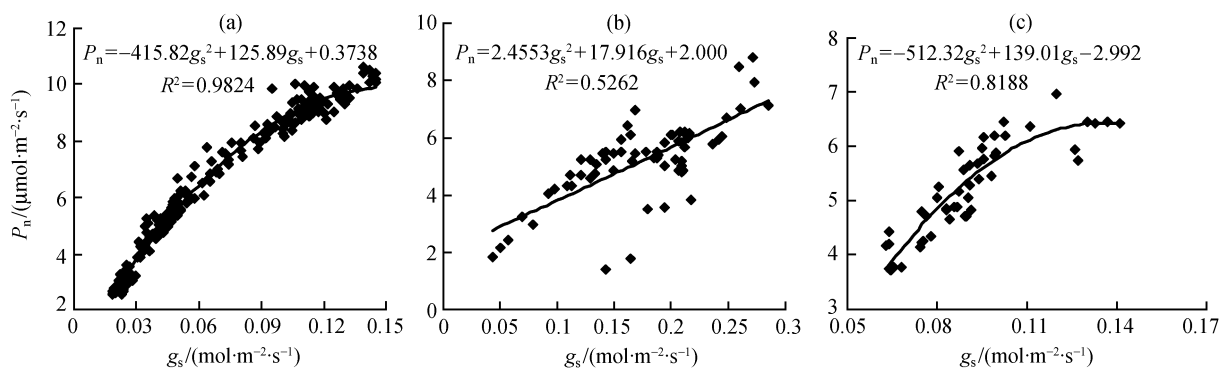


Fig. 5 The correlation between net photosynthesis and stomatal conductance of the abscised leaves under three habitats. (a) potted; (b) non-karst site; (c) karst site.

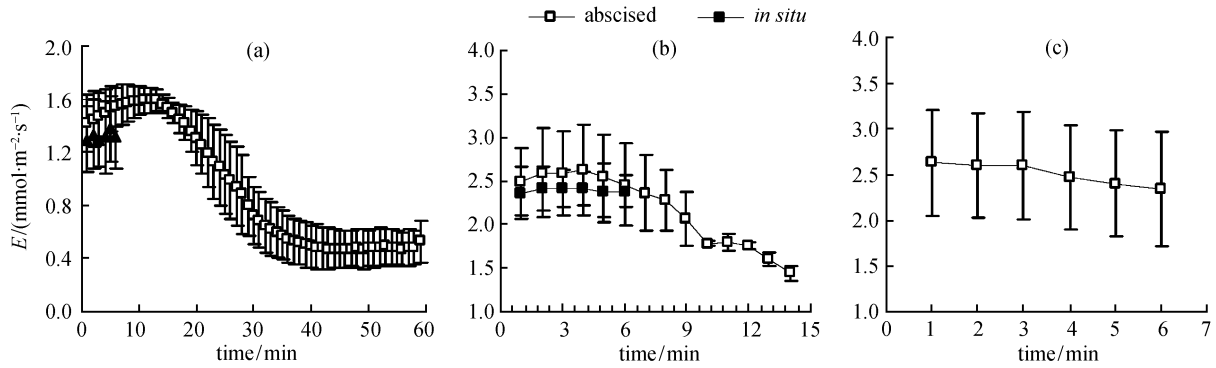


Fig. 6 The change of leaf transpiration of *C. glauca* *in situ* and abscised under three habitats. (a) potted; (b) non-karst site; (c) karst site.

consisting of g_s variation, E increased slightly and then dropped down to a relatively stable value. Under the non-karst condition, E also increased slightly after abscission in the first 4 min, and then dropped down. E was higher in abscised leaves during the first 6 min than that of *in situ* leaves, and was much lower after the 8th min in abscised leaves. Under the karst condition, the E of the abscised leaves seemed not to change in the first 3 min, and dropped down slightly from 4–6 min. Graphing the coordinates with leaf P_n and g_s , and using Excell linear simulation, we obtained the $E-g_s$ fitting equation for the abscised leaves under three habitats (Fig. 7). The correlation coefficient R of $E-g_s$ reached 0.998 under the potted condition and 0.834 under the non-karst condition, but was a fairly small 0.386 under the karst condition. This shows that E was correlated strongly to stomata closure under the abscised potted condition with temperature and radiation control. However, E was correlated weakly to stomata closure under field conditions with high environmental temperatures but without any control in our treatments, implying that the factors that influence E could be very complicated.

3.4 Comparison of gas exchange of *in situ* and abscised leaves under potted condition

Analyzing the mean difference and standard error of P_n and E *in situ* and abscised in different time buckets of the

same leaf samples, we found that P_n and g_s were positive at the 1–5 min, 5–10 min and 10–15 min periods but negative at 15–20 min (Table 2). With reference to the *in situ* dataset, P_n errors of abscised leaves in the four time buckets were 6%, 9%, 6% and –10%, respectively. The variance analysis shows that for both P_n and E , the difference between groups was not significant (significance level $p=0.05$) neither in the first 20 min, nor the first 21 min, nor the first 22 min, but became significant while adding the dataset of the 23rd min (Table 3). That is to say, gas exchange parameters were not significantly different among the datasets for abscised leaves within 23 min and *in situ*; therefore, abscised leaves can represent the *in situ* leaves if we measure the gas exchange in a 23 min period.

3.5 The declining dynamic of P_n and E of abscised leaves at different temperatures under field condition

The result of variance analysis shows that neither P_n nor E was significantly different among data derived in 6 min under the karst condition at temperatures of 32 and 38°C, but P_n was significantly different at temperatures of 34 and 36°C (Table 2). Further results of multiple comparisons showed that P_n was significantly different between data of the 4th, 5th, 6th minute and those of the 1st, 2nd, 3rd minute at 38°C under the karst condition, which implies

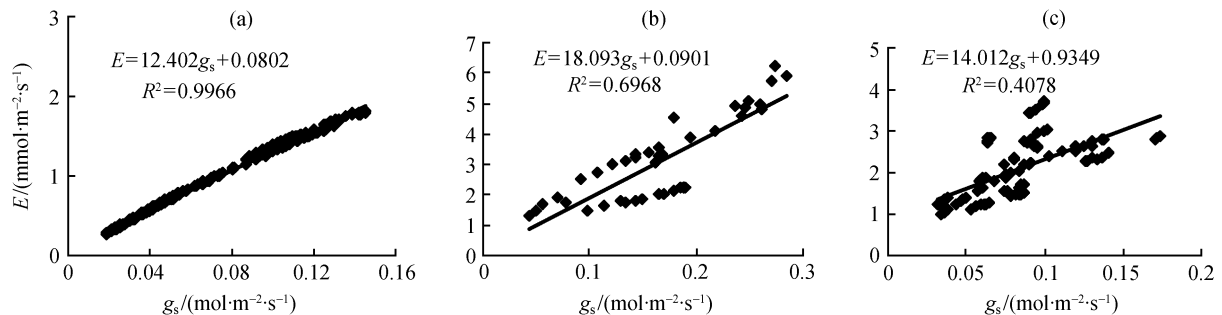


Fig. 7 The correlation between transpiration and stomata conductance of abscised leaves under three habitats. (a) potted; (b) non-karst site; (c) karst site.

Table 2 Comparison of gas exchange of abscised leaves at different periods and their difference from *in situ* stage

duration after abscission.		0–5 min			5–10 min			10–15 min			15–20 min		
		mean	std. error	MD	mean	std. error	MD	mean	std. error	MD	mean	std. error	MD
$P_n/(\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1})$	I	8.89	0.26	0.57	8.89	0.26	0.83	8.89	0.26	0.56	8.89	0.26	-0.94
	A	9.34	0.19		9.45	0.14		9.46	0.06		7.96	0.33	
$g_s/(\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1})$	I	0.11	0.01	0.01	0.11	0.01	0.02	0.11	0.01	0.01	0.11	0.01	-0.02
	A	0.12	0.01		0.12	0.00		0.12	0.00		0.09	0.01	
$E/(\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1})$	I	1.42	0.06	0.14	1.42	0.06	0.21	1.42	0.06	0.15	1.42	0.06	-0.24
	A	1.52	0.05		1.57	0.03		1.57	0.02		1.18	0.07	

Number of leaves is 4, data in 20 min was used for analysis; I = *in situ*, A: abscised; MD: mean difference.

Table 3 One-way ANOVA of P_n and E of abscised leaf samples from potted seedlings

parameter		no. of duration measurement after stem was abscised				
		20	21	22	23	24
P_n	F	1.20	1.22	1.57	1.84	1.99
	sig.	0.285	0.262	0.082	0.027*	0.013*
E	F	1.12	1.35	1.62	1.97	2.31
	sig.	0.351	0.179	0.066	0.015*	0.003*

*The mean difference is significant at the 0.05 level.

that the data for abscised leaves would be unreliable after 3 min if we used abscised leaves to replace *in situ* leaves. Consequently, the data on gas exchange measured using abscised leaves are generally reliable within 3 min, even when the temperature is high in the karst area. Under the non-karst condition, P_n and E of abscised samples at 32°C did not decline obviously at the beginning. However, the result of variance analysis showed that neither P_n nor E inter-group were significantly different among the dataset in 11 min, but P_n was significantly different among the datasets at 12 min and E was significant at 14 min with sig. < 0.05. Therefore, we can conclude that it must be reliable to measure the abscised leaves within 10 min at the given temperature under a non-karst condition.

4 Conclusions

The photosynthetic function is still active after leaf abscission from the live plant, which usually progresses through a long period from normal activity (like *in situ* leaves) to finally subsiding and ceasing. In this paper, we studied the gas exchange declining dynamic of abscised leaves under different habitats and compared them with those of *in situ* leaves. The main conclusions of the abscised leaves are as follows:

1) The initial response of stomata to abscission was to enlarge in the first 3 min to the first 12 min (due to water potential increasing temperately), then to close gradually. The time and degree of this stomatal change varied greatly according to temperature variation. The mechanism of this stomatal change may be due to physiological and biochemical processes in histiocytes which surely require further study.

2) E was significantly and linearly correlated to g_s , indicating that E was intensively affected by stomatal closure. Karst environment is very different from non-karst area, and it usually has higher temperature. E of the abscised leaf is consistent with leaf temperature. Higher leaf temperature may result in higher transpiration, and cause more water loss in leaf tissue, resulting in earlier water stress and faster stomatal closure.

Table 4 One-way ANOVA of P_n and E among leaf samples in abscised duration from field trees

parameter	karst				non-karst			
	$T/^\circ\text{C}$	no. of duration measurement	F	sig.	$T/^\circ\text{C}$	no. of duration measurement	F	sig.
P_n	32	6	0.43	0.819	32	6	0.36	0.869
	34	6	7.19	0.003*	32	11	2.12	0.060
	36	6	4.41	0.016*	32	12	2.71	0.016*
	38	6	0.94	0.491	32	13	3.53	0.003*
E	32	6	0.09	0.993	32	6	0.09	0.997
	34	6	11.77	0.000*	32	13	1.60	0.144
	36	6	1.78	0.192	32	14	2.08	0.045*
	38	6	0.03	0.999	–	–	–	–

* The mean difference is significant at the 0.05 level.

3) P_n was also significantly correlated to g_s , however, the correlation coefficient of P_n-g_s was smaller than that of $E-g_s$. Thus, though P_n was obviously affected by stomatal closure, those influences on P_n were very complicated, and P_n might be affected by other factors besides stomatal closure.

4) For the abscised leaves, gas exchange characteristics may vary along with temperature differences. High temperature accelerates the leaf transpiration rate and reduces the free water content of leaf tissue, advancing the water stress; the lower the temperature is, the slower photosynthetic inclining process of abscised leaves is.

Consequently, we conclude that the reliable duration for measuring gas exchanges from the abscised leaf is determined by leaf temperature. The reliable duration could be more than 20 min when the temperature is low (e.g. 20°C), or could be 6–10 min when the temperature is high (e.g. 32°C), but could be limited to 3 min when the temperature is very high (e.g. $\geq 34^\circ\text{C}$). Thus, when studying the leaf gas exchange of tall arbor trees with portable equipments, it is reasonable to measure the abscised leaf as replacement for the *in situ* one in a certain time according to plant characteristics and temperature.

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