Short title: Stomatal conductance under fluctuating light

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The impact of slow stomatal kinetics on photosynthesis and water use efficiency under fluctuating light

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One sentence summary

Whole-plant transpiration rapidity corroborated leaf-level stomatal kinetics in banana, but impacts of stomatal dynamics under fluctuating light depended on other factors like time of day.

Author Contribution

S.C. and T.L. supervised the experiments. D.E. performed the leaf gas exchange experiments. J.v.W. performed the whole-plant transpiration experiment. D.E., J.v.W., and S.C. analyzed the data. D.E., T.L. and S.C. wrote the manuscript. All authors reviewed and approved the final manuscript.

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Abstract

Dynamic light conditions require continuous adjustments of stomatal aperture. The kinetics of stomatal conductance (g_s) are hypothesized to be key to plant productivity and water use efficiency. Using step-changes in light intensity, we studied the diversity of light-induced g_s kinetics in relation to stomatal anatomy in five banana genotypes (*Musa* spp.) and modelled the impact of both diffusional and biochemical limitations on photosynthesis (A). The dominant photosynthesis limiting factor was the diffusional limitation associated with g_s kinetics. All genotypes exhibited a strong limitation of A by g_s, indicating a priority for water saving. Moreover, significant genotypic differences in g_s kinetics and g_s limitations of A were observed. For two contrasting genotypes the impact of differential g_s kinetics was further investigated under realistic diurnally fluctuating light conditions and at whole-plant level. Genotype-specific stomatal kinetics observed at the leaf level were corroborated at whole-plant level by transpiration dynamics, validating that genotype-specific responses are still maintained despite differences in g_s control at different locations in the leaf and across leaves. However, under diurnally fluctuating light conditions the impact of g_s speediness on A and intrinsic water use efficiency ($_i$WUE) depended on time of day. During the afternoon there was a setback in kinetics: absolute g_s and g_s responses to light were damped, strongly limiting A and impacting diurnal $_i$WUE. We conclude the impact of differential g_s kinetics depended on target light intensity, magnitude of change, g_s prior to the change in light intensity and particularly time of day.

Introduction

In order to survive, plants need to balance CO_2 uptake for photosynthesis with water loss via transpiration. By adjusting their aperture, stomata control gaseous exchange between the leaf interior and the external atmosphere. Stomatal aperture is adjusted by moving solutes into or out of the guard cells. These changes in osmotic potential elicit water movement in or out of the guard cells, altering turgor pressure and subsequently aperture. In general, stomatal opening in well-watered C3 and C4 species is triggered by high light intensity, low vapour pressure deficit (VPD) and low CO_2 concentrations. Opposite environmental conditions (low light, high VPD and high [CO_2]) stimulate stomatal closure (Assmann and Shimazaki, 1999; Outlaw, 2003; Lawson and Morison, 2004). Therefore, in a dynamic field environment, stomata are continuously adjusting aperture to achieve an appropriate balance between carbon gain and water loss (Pearcy, 1990; Lawson and Blatt, 2014). Most research has studied stomatal conductance (g_s) and photosynthesis (A) under steady-state conditions. A high g_s under steady-state conditions is associated with high A and consequently improved growth (Fischer et al., 1998; Franks, 2006). However, as g_s kinetics are typically a magnitude slower than those of A, the speed at which these steady-state values are reached in a fluctuating environment have a great influence on the growth and water use efficiency (Lawson and Blatt, 2014; Kaiser et al., 2016; McAusland et al., 2016; Taylor and Long, 2017; De Souza et al., 2020; Yamori et al., 2020). In a fluctuating field environment, light intensity is one of the most variable environmental conditions as it changes continuously by moving cloud covers and shading from adjacent plants (Pearcy, 1990; Slattery et al., 2018; Morales and Kaiser, 2020). In this way, stomata frequently experience alternating light intensities, inducing stomatal responses that change A, g_s and the ratio of these, the intrinsic water use efficiency ($_i$WUE). The balance between CO_2 gain and H_2O loss under changing light intensities is disturbed by delayed g_s responses (Vialet-Chabrand et al., 2017; Slattery et al., 2018). Limitations of A after an increase in light intensity are the combination of diffusional and biochemical limitations. Biochemical activation has been shown to majorly limit A during short lightflecks (Soleh et al., 2017; Taylor and Long, 2017; Acevedo-Siaca et al., 2020). Under longer light periods, limitations have been mainly attributed to stomatal limitations, with biochemical activation only limiting for a short time (< 10 min) because of rapid activation of RuBP regeneration and Rubisco (Mott and Woodrow, 2000; Kaiser et al., 2016; Deans et al., 2019a; De Souza et al., 2020). The slower g_s increase to increased light intensity limits the CO_2 uptake for

A, while the slower g_s decrease to decreased light intensity results in unnecessary water loss. The limitation of *A* by the slower kinetics of g_s has been shown to be significant in well-watered C3 species (Farquhar and Sharkey, 1982; Jones, 1998; Lawson and Blatt, 2014; McAusland et al., 2016; Deans et al., 2019a). Rapid g_s kinetics therefore have been hypothesized to maximize *A* and $_i$WUE, as steady-state values under the new conditions can be rapidly achieved (Lawson and Blatt, 2014; Papanatsiou et al., 2019; Kimura et al., 2020; De Souza et al., 2020). The g_s kinetics are, together with the final steady-state g_s the plant reaches, crucial to determine the plant performance (Franks and Farquhar, 2007; Vico et al., 2011; McAusland et al., 2016; Qu et al., 2016; Faralli et al., 2019b; Yamori et al., 2020). The importance of diversity in g_s kinetics was highlighted by De Souza et al. (2020), who showed a three-fold higher variability in carbon assimilation between cassava genotypes under fluctuating light than under steady-state conditions, mainly caused by differences in stomatal limitation. However, to our knowledge, the diversity of g_s kinetics across varieties has never been investigated at whole-plant level nor under diurnally fluctuating light conditions.

Here our research aimed to explore biodiversity in light-induced stomatal dynamics across genotypes and evaluate for the first time the impact on whole-plant level. We studied the diversity of light-induced g_s kinetics in relation to stomatal anatomy in five banana genotypes (*Musa* spp.) with distinct transpiration phenotypes (van Wesemael et al., 2019). We modelled the impact of diffusional and biochemical kinetics on *A* under single step-changes in light intensity and modelled the impact of differential g_s kinetics on *A* and $_i$WUE under realistic diurnal fluctuating light conditions. By comparing the g_s kinetics in response to step-changes with the g_s responses under fluctuating light conditions, we gain insight into the importance of stomatal kinetics on diurnal carbon gain and water use efficiency.

Results

A and g_s response to step-changes

Increasing light intensity from 100 to 1000 µmol m^{-2} s^{-1} induced a strong stomatal opening response (Fig. 1). The g_s response followed a sigmoidal pattern. A similar sigmoidal limiting pattern was observed for *A* in all genotypes, indicating a strong limitation of *A* by g_s in banana (Fig. 1). Between genotypes there were significant differences in the speed of g_s increase. Steady-state *A* and g_s under high light intensity were reached in three out of five genotypes. In contrast, the genotypes Cachaco and Leite continued to increase g_s and *A* slowly after 90 min of 1000 µmol m^{-2} s^{-1}. The subsequent decrease in light intensity from 1000 to 100 µmol m^{-2} s^{-1}resulted in a rapid g_s decrease, which also followed a sigmoidal pattern (Fig. 1). Photosynthesis, on the other hand, as expected decreased instantly because light became the limiting factor (Fig. 1).

Modelling steady-state & light-induced responses of g_s

The steady-state stomatal conductance at 100 µmol m^{-2} s^{-1} ($g_{s,100}$) and 1000 µmol m^{-2} s^{-1} ($g_{s,1000}$) did not differ significantly between genotypes (Fig. 2a, Supplemental Table S1). $g_{s,100}$ ranged from 0.023 to 0.040 mol $m^{-2}s^{-1}$, while $g_{s,1000}$ ranged between 0.14 and 0.16 mol $m^{-2}s^{-1}$ (Fig. 2a, Supplemental Table S1).

The speed of g_s increase varied strongly between the banana genotypes and the modelled variables differed significantly (Fig. 2b-c, Supplemental Table S1). The genotype with the slowest g_s increase, Cachaco, had an average time constant K_i of 17 min, while the fastest genotype, Mbwazirume, had a K_i of 6.4 min (Fig. 2b, Supplemental Table S1). The speed of the decrease in g_s (K_d) was also genotype-dependent (Fig. 2c, Supplemental Table S1). K_d was about 2 fold higher in Cachaco (9.5 min) than in Mbwazirume (4.4 min). Across all genotypes, K_i was significantly correlated with K_d (R^2 = 0.41, P < 0.001; Fig. 2d & Supplemental Fig. S1). However, the decrease in g_s was significantly faster than the increase (P < 0.001). K_i was significantly correlated with the time to reach 95, 90 and 50% of steady-state g_s under the high light intensity (R^2 = 0.27 – 0.57, P < 0.001; Supplemental Fig. S1). Also the maximal slope of g_s

increase and decrease ($Sl_{max,i}$ and $Sl_{max,d}$) were significantly correlated with the time constant K as the magnitude of g_s change was similar across genotypes (R^2 = 0.52 & 0.49 for g_s increase and decrease respectively, $P < 0.001$; Supplemental Fig. S1). During light-induced stomatal opening comparable differences across genotypes were present in $Sl_{max,i}$ as in K_i. The lowest $Sl_{max,i}$ values were observed for the genotype Cachaco and the highest values for Mbwazirume (Supplemental Fig. S2, Supplemental Table S1). $Sl_{max,d}$ was highest for the genotype Kluai Tiparot, while Leite showed the lowest $Sl_{max,d}$ (Supplemental Fig. S2, Supplemental Table S1). Analogous to the opening and closing time constant, the absolute slope of closing was significantly higher than the opening slope ($P < 0.001$).

Impact of stomatal opening speed on *A*

The speed of the increase in g_s following a step-change in light intensity from 100 to 1000 µmol m^{-2} s^{-1} strongly determined CO_2 uptake during this period. The speed of changes in stomatal conductance in all genotypes accounted for more than 89 % of *A* limitation (Supplemental Fig. S3a). The time to reach 95% of steady-state *A* at 1000 µmol m^{-2} s^{-1} (A_{1000}) was greater than 30 min for almost all genotypes and differed significantly between Cachaco (51.9 min) and the genotypes Mbwazirume (30.3 min) and Banksii (29.5 min) (Fig. 3a, Supplemental Fig. S4, Supplemental Table S2). This timing of *A* limitation was significantly correlated with the time to reach 95 % , 90 % and 50 % of steady-state g_s ($P < 0.001$, R^2 = 0.42-0.48), while there was no significant relation with the time to reach 95% or 90% of the maximum carboxylation rate of Rubisco (V_{cmax} , Supplemental Fig. S1, Supplemental Fig. S3). The timing to reach 95% of steady-state V_{cmax} was less than 20 minutes in all genotypes, while the timing to reach 95% of steady-state g_s was much longer and ranged between 41 and 69 minutes (Supplemental Fig. S3, Supplemental Table S2). The durations of *A* limitation was also significantly correlated with the modelled time constant for g_s increase (K_i) ($P < 0.001$, R^2 =0.67, Supplemental Fig. S1). The percentage limitation of *A* was significantly higher in Cachaco (20.6 %) compared to the genotypes Mbwazirume (10.2 %), Leite (10.2 %) and Banksii (8.5 %) (Fig. 3b) and was significantly related to both K_i and the time to reach 90 % and 50 % of steady-state g_s, confirming the impact of stomatal limitation on *A* (Supplemental Fig. S1).

¡WUE response to step-changes in light intensity

The step increase in light intensity induced an initial increase in *A* that was relatively larger than the increase in g_s. These responsiveness differences increased ¡WUE, reaching the maximum ¡WUE during the light period in all cases within 7.5 min (Supplemental Fig. S5). After reaching a maximal value, ¡WUE decreased as both g_s and *A* gradually increased (Supplemental Fig. S5). ¡WUE only stabilized when both *A* and g_s reached steady-state. The genotype Cachaco had a significantly higher mean ¡WUE during the high light period compared to Mbwazirume (Supplemental Fig. S6). The mean ¡WUE during the high light period was significantly correlated with the time constant K_i and $Sl_{max,i}$ with slower g_s responses resulting in higher ¡WUE (R^2 = 0.12 & 0.42, $P < 0.05$, Supplemental Fig. S1). The reduction in light intensity from 1000 to 100 µmol m^{-2} s^{-1} instantaneously lowered ¡WUE as *A* immediately declined because of light limitation (Supplemental Fig. S5). The mean ¡WUE during this low light period was significantly higher in Kluai Tiparot, than in Leite (Supplemental Fig. S6). The mean ¡WUE was significantly correlated to the stomatal closing variables K_d and $Sl_{max,d}$ with faster g_s responses resulting in higher ¡WUE (R^2 = 0.36 & 0.26, $P < 0.001$, Supplemental Fig. S1).

Stomatal anatomy

Banana has elliptical-shaped guard cells surrounded by four to six subsidiary cells (Rudall et al., 2017). Abaxial stomatal density, stomatal length, guard cell size and subsidiary cell size were quantified from the leaf part enclosed in the gas exchange cuvette and significant differences between genotypes were observed (Supplemental Fig. S7). Stomatal density and stomatal length were not correlated with any of the modelled light-induced g_s kinetics (Fig. 4, Supplemental Fig. S1). However, these correlations between anatomy and g_s kinetics were significant if the genotype Cachaco with lowest g_s rapidity was not considered (Fig. 4). In this case, stomatal density was significantly correlated with the time constant *K* as well as the maximum slope of g_s response Sl_{max} during both stomatal opening and closing ($P < 0.01$; R^2 = 0.25 – 0.46).

Whole-plant transpiration response at dawn

The significant differences in g_s speed at leaf level observed between the two extreme genotypes Cachaco and Mbwazirume were confirmed at the whole-plant level under a step increase in light intensity from darkness (Fig. 5) and under a gradually increasing light intensity (Supplemental

Fig. S8). After the onset of light in the morning, transpiration rate increased significantly faster in Mbwazirume compared to Cachaco (Fig. 5a-b, Supplemental Fig. S8a). After a step increase in light intensity, a significant increase in transpiration rate was observed after *c.* 15 min in Mbwazirume, while in Cachaco this was only after 25 min (Fig. 5a-b). Similar faster increases in transpiration rate of Mbwazirume were observed under a gradually increasing light intensity (Supplemental Fig. S8a). The temporal response of whole-plant transpiration rate to a step increase in light intensity was also modelled following the sigmoidal model (Eqn. 1) and the time constants *K*i differed significantly between genotypes (Supplemental Fig. S9). Similar to the response at leaf level, Cachaco, had an average time constant K_i of 20 min, while Mbwazirume, had a K_i of 8.5 min (Supplemental Fig. S9). The difference in transpiration responses was also reflected in the transpiration rate before and after dawn. The whole plant transpiration rate did not differ significantly between both genotypes pre-dawn, but after the step change in light intensity, the transpiration rate was significantly higher in Mbwazirume for 90 minutes, whereafter both genotypes reached similar steady-state transpiration rates (Fig 5b). Likewise, the transpiration rate under gradually increasing light intensity did not differ pre-dawn, but was significantly higher in Mbwazirume after the onset of light (Supplemental Fig. S8b).

Impact of diurnal light fluctuations on g_s, A and $_i$WUE

To evaluate the impact of g_s kinetics on diurnal A and $_i$WUE, plants were subjected to fluctuating light intensities and phenotyped over an entire diurnal period. Similar to the transpiration rate measured at the whole-plant level, the morning increase in g_s at leaf-level under gradually increasing light intensity was faster in Mbwazirume compared to Cachaco (Fig. 6a). The time constant for the g_s increase (K_i) was significantly higher in Cachaco ($P < 0.005$, Fig. 6b). However, the faster increase of g_s in Mbwazirume, did not result in increased A (Fig. 6c). Maximum potential A values at specific light intensities were determined from light response curves and compared to those measured under the diurnal conditions. Under the gradual increasing light intensities experienced in the morning, maximum A values were achieved, indicating there was no g_s limitation under these light-limiting conditions (Fig. 7). A similar A with lower g_s during the morning, led to a significantly higher mean $_i$WUE in Cachaco ($P < 0.05$, Fig. 6d).

Throughout the day, g_s kinetics were in most cases significantly faster for the genotype Mbwazirume compared to Cachaco (Fig. 8a), again confirming the previously observed kinetics (Fig. 2, Fig. 5). However, under fluctuating light conditions g_s kinetics were dependent on the magnitude of light intensity change, g_s values prior to the light intensity change and the time of the day (Fig. 8a). During the afternoon there was a setback in kinetics: the absolute g_s and the g_s responses to light were damped (Fig.7, Fig. 8). Simultaneously A decreased greatly in the afternoon, which could be mainly attributed to a reduction in g_s. The limitation of A in the afternoon was three times higher in Cachaco (52.6 %) compared to Mbwazirume (17.5 %) (Fig. 7, Fig. 9d). The reduction of g_s in the afternoon resulted in a significantly lower average diurnal g_s (Fig. 9a) which translated into a greater diurnal $_i$WUE in Cachaco compared to Mbwazirume (Fig.8c, Fig. 9c).

Discussion

Stomatal behaviour greatly limits photosynthesis in banana

Step-changes in light intensity have shown to induce an uncoupling of A and g_s in many species (Barradas and Jones, 1996; Lawson and Blatt, 2014; McAusland et al., 2016; Faralli et al., 2019a). However, all banana genotypes maintain a tight coupling between A and g_s following a step increase in light intensity (Fig. 1). This indicates a strong stomatal control of photosynthesis, which is demonstrated by diffusional limitations accounting for over 89 % of A limitation (Supplemental Fig. S3a). This high stomatal limitation of A is explained by the slow g_s response (Fig. 1, Fig. 2) relative to the faster biochemical activation. The time required for biochemical activation was much lower and not correlated with the time for steady-state A and g_s (Supplemental Fig. S3). Similar to Deans et al. (2019a) and De Souza et al. (2020), the speed of changes in g_s was the predominant limitation of A. This behaviour shows that banana strongly controls stomatal aperture, resulting in water conservation at the expense of potential carbon gain, which supports the early work of Aubert and Catsky (1970). This prioritizing of water conservation in banana can be explained by its intrinsic need to maintain a high leaf water potential (Turner and Thomas, 1998).

Diversity in light-induced stomatal responses

Stomatal responses to changes in light intensity have been shown to vary at an inter- and intra-specific level (Vico et al., 2011; Drake et al., 2012; McAusland et al., 2016; Qu et al., 2016; Durand et al., 2020; De Souza et al., 2020). A higher steady-state g_s has been linked with faster light-induced g_s responses (Drake et al., 2012; Kaiser et al., 2016; McAusland et al., 2016; Wachendorf and Küppers, 2017; Sakoda et al., 2020). Although the differences observed in steady-state g_s values between banana genotypes were not significant, their g_s kinetics differed strongly (Fig. 2). These results suggest that other factors such as stomatal anatomy, hydraulic conductance and membrane transporters are involved in determining the rapidity of changes in g_s.

The banana B genome is often related to drought tolerance because of its center of origin and its natural occurrence in drier habitats under full sunlight (Perrier et al., 2011; Janssens et al., 2016; Eyland et al., 2021). Within the investigated banana genotypes we observed significant differences in the speed of increase and decrease in g_s (Fig. 2b,c). However, differences across

genotypes were not explained by their genomic constitution (see Materials & Methods), which is in agreement with the wide diversity of transpiration phenotypes observed irrespective of genomic constitution (van Wesemael et al., 2019).

Consistent with previous works in other species (Vico et al., 2011; McAusland et al., 2016; Faralli et al., 2019a), the speed of g_s increase and decrease were significantly correlated (Fig. 2d). Decreases in g_s were faster than opening in all banana genotypes (Fig. 2d), which is not the case for all crops (McAusland et al., 2016; Qu et al., 2016). The faster g_s closure again indicates that banana prioritises water conservation over maximization of carbon uptake.

The two most extreme genotypes Cachaco and Mbwazirume, with the slowest and fastest g_s responses respectively, also showed at the whole-plant level differences in the light-induced speed of transpiration rate increase (Fig. 5, Supplemental Fig. S8, Supplemental Fig. S9). This finding suggests that despite possible differences in g_s control of water loss at different locations of the leaf (Matthews et al., 2017) and across leaves of different age (Urban et al., 2008) genotype-specific responses are still maintained. Leaf level measurements of light-induced g_s kinetics are thus in line with whole-plant responses. To our knowledge, this is the first report confirming stomatal kinetics at the whole-plant level. The genotype-specific difference in whole-plant transpiration responses at dawn was validated at the leaf level with g_s increasing faster in Mbwazirume under gradually increasing light intensity (Fig. 6a). This faster g_s increase in Mbwazirume did not result in higher *A*, indicating that at dawn, under gradually increasing low light intensities, g_s was not limiting *A* and was higher than necessary for maximal *A* (Fig. 6 & Fig. 7). These results demonstrate that the impact of g_s kinetics on *A* and $_i$WUE depend on the time of the day and the light conditions. The uncoupling of g_s and *A* under increasing light conditions at dawn was not beneficial for carbon uptake. Gosa et al. (2019) called this period after dawn in tomato the golden hour because in dry climates it is the time of the day with the highest g_s. Later in the day, VPDs become too high, restricting g_s (Gosa et al., 2019). Breeding for an even higher g_s during this golden hour was suggested to improve plant productivity. However, care must be taken to breed for an improved morning CO_2 uptake, rather than for a high g_s with associated uncoupling of *A* and g_s. Although the absolute water loss resulting from excessive morning g_s might be relatively low because of low evaporative demands at dawn (Chaves et al., 2016), it may lead to a crucial decrease in overall plant water status.

Despite the confirmed genotypic differences in stomatal kinetics, the impact of g_s kinetics on A and $_i$WUE before noon hardly differed between the genotypes Cachaco and Mbwazirume under field-mimicking light conditions (Fig. 7, Fig. 8). This could be explained by lower amplitudes of light switches compared to a single step-change in light intensity and/or g_s values not being at steady-state prior to changing light intensity. The genotype-specific speed of the g_s response observed under a single step-change in light intensity did not explain the diurnal $_i$WUE, indicating that g_s kinetics only partially affect diurnal water use efficiency and carbon gain (Fig. 9b,c). The absolute g_s and the g_s responses to light decreased strongly in the afternoon, and this effect was more pronounced in the genotype Cachaco (Fig. 7, Fig. 8a). The three times higher afternoon limitation of A in the genotype Cachaco compared to Mbwazirume, resulted in a significant higher diurnal $_i$WUE (Fig. 9c,d). The genotype Cachaco with the slowest g_s kinetics thus achieved the highest $_i$WUE, showing that not only g_s speed but also the g_s diurnal pattern determines the overall water use efficiency and carbon gain. Although the mechanism behind the afternoon g_s reduction remains largely unknown, it is commonly hypothesized to be related to circadian regulation of ABA sensitivity and associated endogenous signals regulating the clock, such as feedback loops from photosynthate accumulation (Mencuccini et al., 2000; Haydon et al., 2013; Delorge et al., 2014; Resco de Dios and Gessler, 2018). We show that under fluctuating light conditions this intrinsic diurnal pattern of absolute g_s decrease and g_s light responsivity reduction is decisive for diurnal $_i$WUE (Fig. 9c).

Impact of stomatal anatomy on responses

Stomatal density as well as the size have been reported to affect g_s kinetics (Hetherington and Woodward, 2003; Drake et al., 2012; Raven, 2014; Sakoda et al., 2020). However, McAusland et al. (2016) and Faralli et al. (2019a) reported no or only a weak inter- and intra-specific correlation between stomatal anatomy and light-induced g_s kinetics. We confirmed that stomatal density and size were not correlated with the g_s kinetics (Fig. 4, Supplemental Fig. S1). Remarkably, the genotype with the slowest increase in g_s, Cachaco had the second highest density and the smallest stomata. Without this genotype a significant correlation between density and the speed of g_s increase and decrease was observed (Fig. 4). This exception suggests that the surface-to-volumes ratios are not always directly related to stomatal speed as this assumes uniform ion transport activity per surface area (Lawson and Blatt, 2014).

Conclusion

Our findings show that there is diversity in g_s rapidity to light within closely related banana genotypes and that slow stomatal responses and not biochemical activation greatly limit *A*. The priority of banana for water saving is shown by strong stomatal control of *A* and faster decrease in g_s than increase. The observed diversity in g_s rapidity was not related to stomatal anatomy and therefore suggests that variation is rather driven by functional components. We show here for the first time that the g_s rapidity observed at the leaf level can also be found at the whole-plant level. However, under fluctuating light conditions, g_s rapidity is only one of the many physiological factors determining overall plant water use efficiency and carbon gain.

Materials & methods

Experiment 1: Leaf gas exchange response to a step-change in light intensity

Plant material and growth conditions

Banana plants (*Musa* spp.) were obtained through the International Musa Transit Center (ITC, Bioversity International), hosted at KU Leuven, Belgium. Plants of five genotypes from different subgroups were selected: Banksii (subgroup Banksii, AA genome, ITC0623), Cachaco (Bluggoe, ABB genome, ITC0643), Kluai Tiparot (Kluai Tiparot, ABB genome, ITC0652), Leite (Rio, AAA genome, ITC0277) and Mbwazirume (Mutika-Lujugira, AAA genome, ITC1356). Plants were grown in 800 ml containers filled with peat-based compost (Levingtons F2S, UK) under 350 µmol m^{-2} s^{-1} Photosynthetic Photon Flux Density (PPFD) in a 12 h : 12 h light : dark cycle with temperature and relative humidity at 26 ± 1 °C and 70 ± 10 %, respectively. Plants were well-watered and starting from week three a Hoagland nutrient solution was added. Measurements were performed when plants were fully acclimated and seven weeks old.

Leaf gas exchange measurements

Photosynthetic rate (A) and stomatal conductance to water (g_s) were measured every 30 s on the middle of the second youngest fully developed leaf using a LI-6400XT infrared gas analysis and dew-point generator model LI-610 (LI-COR, USA). Light was applied by an integrated LED light source. The leaf cuvette maintained a CO_2 concentration of 400 µmol mol^{-1}, a leaf temperature of 25°C and a VPD of 1 kPa. All measurements were performed before 14:00 h to avoid circadian influences.

Stomatal response to a step-change in light intensity

The light intensity was kept at 100 µmol m^{-2} s^{-1} until A and g_s were stable for 10 min. Once steady-state was reached, light intensity was increased to 1000 µmol m^{-2} s^{-1} for 90 min. Then, light intensity was lowered back to 100 µmol m^{-2} s^{-1} for 30 min.

The increase in g_s after the increase in light intensity and the decrease in g_s after the decrease in light intensity followed a sigmoidal pattern and was modelled using the non-linear sigmoidal model described in Vialet-Chabrand et al. (2017):

$$g_s = \left(g_{s,1000} - g_{s,100}\right) e^{-e^{\left(\frac{\lambda - t}{K} + 1\right)}} + g_{s,100} \qquad \text{(Eqn. 1)}$$

With g_s the stomatal conductance at time t, K the time constant for rapidity of g_s response (min), λ the lag time of the sigmoidal curve (min), $g_{s,100}$ and $g_{s,1000}$ (mol m^{-2} s^{-1}) the steady-state g_s at 100 and 1000 µmol m^{-2} s^{-1} respectively. Parameter values were estimated for each individual plant using non-linear model optimization in R (V 3.4.3). K_i indicates the g_s increase time constant, K_d the g_s decrease time constant. The maximum slope of g_s during opening and closing was calculated and defined as Sl_{max}. Intrinsic water use efficiency ($_i$WUE) was calculated as $_i$WUE = A/g_s. Outlying values (0.5 % quantile; $_i$WUE < 0 or > 400 µmol mol^{-1}) caused by low g_s were discarded for plotting.

Stomatal and biochemical limitation analysis

Photosynthesis was considered to be limited until 95 % of steady-state A at 1000 µmol m^{-2} s^{-1} was reached (McAusland et al., 2016). The percentage of limitation of A was calculated by comparing the measured A with the maximal steady-state A under 1000 µmol m^{-2} s^{-1} according to McAusland et al., (2016):

$$Limitation\ of\ A\ (\%) = \frac{\int_0^t \sum (A_{max} - A_{measured})}{\int_0^{90} \sum A_{measured}} \quad \text{(Eqn. 2)}$$

With A_{max} the value reached at 95 % of steady-state A under 1000 µmol m^{-2} s^{-1}, $A_{measured}$ the measured A and t the time where 95 % of steady-state A is reached.

The delay in obtaining maximum potential A under 1000 µmol m^{-2} s^{-1} is determined by the stomatal opening speed as well as the rate of biochemical activation. The activation rate of Rubisco is the main biochemical limiting component during step changes in light exceeding several minutes (Mott and Woodrow, 2000; Way and Pearcy, 2012). To quantify the relative contributions of biochemical and stomatal limitations a differential method was applied (Jones, 1985; Wilson et al., 2000; Grassi and Magnani, 2005; Deans et al., 2019b). As explained by Deans et al. (2019b), the forgone A because of biochemical and stomatal limitation was calculated as:

$$\mathrm{d}A_{biochem} = \frac{\partial A}{\partial V_{cmax}} \mathrm{d}V_{cmax} \quad \text{(Eqn. 3)}$$

and

$$\mathrm{d}A_{stom} = \frac{\partial A}{\partial g_{sc}} \mathrm{d}g_{sc} \quad \text{(Eqn. 4)}$$

Where V_{cmax} is the maximum velocity of Rubisco for carboxylation and g_{sc} the stomatal conductance to CO_2. V_{cmax} at every time point was calculated by solving the Rubisco-limited photosynthesis as described by Farquhar et al., (1980) for V_{cmax}:

$$V_{cmax} = \frac{(A+R_d)(C_i+K_m)}{(C_i-\Gamma^*)} \quad \text{(Eqn. 5)}$$

Where C_i is the CO_2 concentration in the intercellular airspaces of the leaf. R_d represents the mitochondrial respiration for which average dark respiration rates were used. Γ* is the photorespiratory compensation point and K_m is the effective the Rubisco Michaelis-Menten constant for CO_2 under 21% O_2. Values for Γ* and K_m were taken as the average for C3 species at 25°C as described by Hermida-Carrera et al. (2016), 41.2 and 529.4 µmol mol^{-1} respectively. Mesophyll conductance to CO_2 was assumed to be infinite. g_{sc} at every time point was calculated as:

$$g_{sc} = \frac{g_s}{1.6} \quad \text{(Eqn. 6)}$$

The relative stomatal limitation (σ_{stom}) was then calculated as:

$$\sigma_{stom} = \frac{\int_0^t \mathrm{d}A_{stom}dt}{\int_0^t \mathrm{d}A_{biochem}\mathrm{d}t+\int_0^t \mathrm{d}A_{stom}\mathrm{d}t} \quad \text{(Eqn. 7)}$$

Where *t* represents the time where 95 % of steady-state *A* under 1000 µmol m^{-2} s^{-1} was reached. Timings representing the g_s and *A* increase were calculated at 95, 90 and 50% of steady-state values under 1000 µmol m^{-2} s^{-1}. Timings for V_{cmax} were calculated at 95 and 90% of steady-state values.

Stomatal anatomy measurements

Stomatal impressions of the abaxial surface of the leaf were made when stomata were completely closed using impression material. Impression were made by applying dental polymer according to the protocol of Weyers & Johansen (1985), followed by covering the polymer with nail varnish and placement on a microscope slide. Impressions were only taken from the abaxial side, because stomatal densities are generally 75 % higher compared to the adaxial side in banana, therefore majorly determining gas exchange as shown by Brun (1961). Stomatal anatomy was quantified using an EVOS digital inverted microscope. Stomatal density was determined in three microscopic field of views of 1.12 mm^2 captured with a 10 x objective lens (54 to 117 stomata

per field of view). Guard cell length (µm), guard cell size (mm²) and lateral subsidiary cell size (mm²) were determined in three microscopic field of views of 0.07 mm² captured with a 40 x magnification respectively (four to seven stomata per field of view). Measurements were performed in ImageJ software (http://rsb.info.nih.gov/ij).

Experiment 2: Whole-plant transpiration response at dawn

Plant material and growth conditions greenhouse experiment

For the genotypes Cachaco and Mbwazirume, 12 plants were grown for seven weeks in a greenhouse prior to the experiment. Plants were grown in 10 l containers filled with peat-based compost. At the start of the experiments, the six most homogenous plants per genotype were selected based on leaf area. Weight of each plant was followed by a multi-lysimeter setup of high precision balances, registering the weight every 60 seconds (1 g accuracy, Phenospex, Heerlen, NL). The soil was covered by plastic to avoid evaporation and ensure only waterloss through transpiration. The transpiration rate was calculated by differentiating the raw weight data over time. The soil water content was determined by subtracting the plastic pot weight, the dry soil weight and the plant weight from the total weight measurement. Dry soil weight was calculated as a function of the soil volume (bulk density = 0.2267 g cm^{-3}). Leaf area was calculated by weekly top view imaging and modelled over time by a power law function (Paine et al., 2012):

$$leaf\ area\ = k\ +\ a * days^{b} \quad \text{(Eqn. 8)}$$

The daily plant weight was estimated from the projected leaf area using genotype-specific correlations ($n > 50$; $R^2 >= 0.94$). Plants were watered with a nutrient solution during the night and kept at well-watered conditions. Radiation was collected every 5 min via a sensor (Skye instruments, UK) inside the greenhouse. Supplemental lighting of 14 W m^{-2} at plant level was provided when solar radiation was below 250 W m^{-2} during the daytime. Temperature and relative humidity data were collected using six data loggers (Trotec, DE) registering data every 5 min. The onset of light was defined as the moment when intensity increased above 2 W m^{-2}.

Plant material and growth conditions controlled environment experiment

For the genotypes Cachaco and Mbwazirume, three plants were grown in a growth chamber with relative humidity of 70 % and temperature of 24 °C. Plants were grown hydroponically in containers with 350 ml medium (see van Wesemael et al. (2019) for specific nutrient composition) and placed under adjustable LED panels (LuminiGrow 600R1, Lumini technology

Co. Ltd., China) providing 120 µmol m^{-2} s^{-1} in a 12 h/12 h light/dark cycle. Plants were 5 weeks old at the start of the experiment and weighted prior to the experiment to normalize for plant mass. Biomass was again measured after 8 days, at the end of the experiment. Water loss of each plant was followed by a multi-lysimeter setup of high precision balances (0.01 g accuracy, Kern, Germany). Balances were connected to a computer registering the weight every 10 seconds.

Experiment 3: Impact of diurnal light fluctuations on g_s, A and ¡WUE

Plant material and growth conditions

Four plants of the genotypes Cachaco and Mbwazirume were grown in a greenhouse. Plants were grown in 4 l containers filled with peat-based compost and maintained under well-watered conditions. After 8 weeks plants were moved to a growth chamber with relative humidity 70 ± 15 % and temperature 28 ± 2 °C.

Leaf gas exchange measurements

A and g_s were measured every minute on the middle of the second youngest fully developed leaf using a LI-6800 infrared gas analyser (LI-COR, USA). The leaf cuvette maintained a CO_2 concentration of 400 µmol mol^{-1}, a leaf temperature of 28 °C and a VPD of 1 kPa. The light intensity was programmed to fluctuate throughout the day. Plants were placed under adjustable LED panels (LuminiGrow 600R1, Lumini technology Co. Ltd., China) that mimicked light fluctuations inside the LI-6800 leaf cuvette. The g_s response was described using the non-linear sigmoidal model of Vialet-Chabrand et al. (2013) where light or dark steps were sufficiently long for model optimization (Eqn. 1). A light response curve with A in function of photosynthetic photon flux density (PPFD) was modelled for each individual based on A values recorded during the first six hours of the day that were not limited by g_s. The nonrectangular hyperbola-based model of Prioul & Chartier (1977) was optimized as described by Lobo et al. (2013):

$$A = \frac{PPFD*\Phi_0+A_{max}-\sqrt{(\Phi_0*PPFD+A_{max})^2-4\theta*\Phi_0*PPFD*A_{max}}}{2\theta} - R_n \qquad \text{(Eqn.9)}$$

With A the photosynthetic rate (µmol m^{-2} s^{-1}), PPFD the Photosynthetic Photon Flux Density (µmol m^{-2} s^{-1}), Φ_0 the quantum yield at PPFD of 0 µmol m^{-2} s^{-1} (µmol $µmol^{-1}$), A_{max} the absolute maximum photosynthetic rate (µmol m^{-2} s^{-1}), θ the dimensionless convexity factor and R_n the dark respiration (µmol m^{-2} s^{-1}).

The percentage of limitation of A by g_s during the afternoon (> 6 hours after light onset) was calculated by estimating the maximal potential A without g_s limitation and comparing it with the measured A (Eqn. 2).

Statistical analysis and data processing

All data processing and statistical analysis was carried out in R (V 3.4.3). Genotypic differences were tested by applying one-way analysis of variance (ANOVA) with a post hoc Tukey HSD test. Segmented regression was performed on the whole-plant transpiration between -90 and 90 min relative to the onset of light. Data with no significant segmented regression (p-value Davies Test < 0.05, segmented R package, 7.5% of the data) and negative slopes (2.5% of the data) were removed. Transpiration rate was calculated as the mean water loss every 30 min. To use the sigmoidal model (Eqn. 1) on whole-plant transpiration data, 1 min weight measurements were smoothed according to the Savitzky and Golay (1964) method with a filtering window of 21 and a fourth-order polynomial. Each day of whole-plant transpiration responses was regarded as a new replicate by incorporating a plant-specific factor and a date-specific factor as a random effect in a linear mixed model.

Supplemental Data

Supplemental Fig. S1 Correlation matrix of gas exchange and stomatal anatomy variables.

Supplemental Fig. S2 Maximum slope of stomatal conductance response (Sl_{max}) to an increase in light intensity from 100 µmol m^{-2} s^{-1} to 1000 µmol m^{-2} s^{-1} and to a decrease in light intensity from 1000 µmol µmol m^{-2} s^{-1} to 100 µmol m^{-2} s^{-1}

Supplemental Fig. S3 Stomatal limitation of photosynthesis (A) and timings until steady-state values of stomatal conductance (g_s), photosynthesis and maximum velocity of Rubisco for carboxylation (V_{cmax}) were reached after an increase in light intensity from 100 µmol m^{-2} s^{-1} to 1000 µmol m^{-2} s^{-1}.

Supplemental Fig. S4 Increase in photosynthesis (A) after increasing the light intensity from 100 µmol m^{-2} s^{-1} to 1000 µmol m^{-2} s^{-1}. A was considered limited until 95 % of steady-state A was reached.

Supplemental Fig. S5 Response of intrinsic water use efficiency ($_i$WUE) and the intracellular CO_2 (C_i) to a step increase and decrease in light intensity from 100 to 1000 µmol m^{-2} s^{-1} and back.

Supplemental Fig. S6 Mean intrinsic water use efficiency ($_i$WUE) after the increase in light intensity from 100 to 1000 µmol m^{-2} s^{-1} and the decrease to 100 µmol m^{-2} s^{-1} afterwards.

Supplemental Fig. S7 Stomatal density, stomatal length, guard cell size, subsidiary cell size and proportion of subsidiary cells of the five banana genotypes.

Supplemental Fig. S8 Gravimetric transpiration rate analysis of genotypes Cachaco and Mbwazirume under gradual increasing light intensity.

Supplemental Fig. S9 Modelled time constant (K_i) for the whole-plant transpiration rate increase of genotypes Cachaco and Mbwazirume after a step increase in light intensity from 0 to 120 µmol m^{-2} s^{-1}.

Supplemental Table S1 Modelled steady-state and light-induced variables of the stomatal conductance (g_s) response to a step increase and decrease in light intensity from 100 to 1000 µmol m^{-2} s^{-1} for five different banana genotypes.

Supplemental Table S2 Time to reach 95%, 90% and 50% of steady-state photosynthesis (A), stomatal conductance (g_s) and V_{cmax} after a step increase in light intensity from 100 to 1000 µmol m^{-2} s^{-1} for five different banana genotypes.

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Figure legends

Fig. 1 Response of stomatal conductance (g_s, orange) and photosynthesis (A, black) of five banana genotypes to a step increase in light intensity from 100 to 1000 µmol $m^{-2}s^{-1}$ followed by a decrease from 1000 to 100 µmol $m^{-2}s^{-1}$. Grey and white areas indicate time periods of 100 µmol m^{-2} s^{-1} and 1000 µmol $m^{-2}s^{-1}$, respectively. Dashed lines indicate when 95 % of steady-state A was reached. Points and error bars represent mean ± SE (n = 7-8).

Fig. 2 Modelled steady-state and light-induced variables of the stomatal conductance (g_s) response to a step increase and decrease in light intensity between 100 and 1000 µmol m^{-2} s^{-1} for five different banana genotypes (n = 7-8). (A) Steady-state g_s at 100 ($g_{s,100}$ faded colours) and 1000 µmol m^{-2} s^{-1} ($g_{s,1000}$ bold colors). (B) Time constant of g_s increase (K_i) for different genotypes. Different letters indicate significant differences between genotypes (post hoc Tukey HSD test, $P < 0.05$; A>B>C). (C) Time constant of g_s conductance decrease (K_d) for different genotypes. Different letters indicate significant differences between genotypes (post hoc Tukey HSD test, $P < 0.05$; A>B>C). (D) Significant correlation between K_i and K_d (Pearson's correlation, $R^2 = 0.41$, $P < 0.001$). K_i was significantly higher than K_d. The solid line shows the linear regression, the dashed line shows the 1:1 line. Points and error bars represent mean ± SE (n = 7-8). The bold middle line in boxplots represents the median. The box is confined by the first and third quartile and the whiskers extend to 1.5 times the interquartile distance. Points falling outside the whiskers are considered outliers and plotted as dots.

Fig. 3 Limitation of photosynthesis (A) after the increase in light intensity from 100 to 1000 µmol m^{-2} s^{-1}. (A) Time to reach 95 % of the steady-state A for five different banana genotypes. (B) Percentage limitation of A after the increase in light intensity. Different letters indicate significant differences between genotypes (post hoc Tukey HSD test, $P < 0.05$; n = 7-8; A>B). The bold middle line in boxplots represents the median. The box is confined by the first and third quartile and the whiskers extend to 1.5 times the interquartile distance. Points falling outside the whiskers are considered outliers and plotted as dots.

Fig. 4 Relation between abaxial stomatal density and the time constant describing the speed of stomatal conductance increase (K_i) after the light intensity increase from 100 to 1000 µmol m^{-2} s^{-1}. There was no significant correlation (Pearson's correlation test), caused by the outlying genotype Cachaco. Points and error bars represent mean ± SE (n = 7-8).

Fig. 5 Gravimetric transpiration rate analysis of genotypes Cachaco and Mbwazirume at dawn after a step increase in light intensity from 0 to 120 µmol m^{-2} s^{-1}. (A) A breakpoint was identified in whole-plant transpiration after the step increase in light intensity. The timing of the breakpoint in transpiration after dawn differed significantly between the genotype Cachaco and Mbwazirume (n = 24, P < 0.01, linear mixed-effects model with plant-specific and date-specific random effect). (B) Transpiration rate after dawn increased faster in Mbwazirume compared to Cachaco. Before dawn transpiration rates did not differ significantly. Similarly transpiration rates do not differ significantly after 90 minutes (24 datapoints per per time range for both Cachaco and Mbwazirume, * for P <0.05, ** for P <0.01, linear mixed-effects model with plant-specific and date-specific random effect). Grey areas indicate the time before dawn .. The bold middle line in boxplots represents the median The box is confined by the first and third quartile and the whiskers extend to 1.5 times the interquartile distance.

Fig. 6 Morning response of stomatal conductance (g_s) and photosynthesis (A) of the genotypes Cachaco and Mbwazirume. (A) Time course of the g_s response to a gradual increase in light intensity at dawn (black line). Data are the mean ± SE (n = 4). (B) The time constant of g_s increase (K_i) during the first 90 min after dawn was significantly higher in Cachaco. (C) The difference in g_s rapidity at dawn did not result in different A between both genotypes. Data represents the mean ± SE (n = 4). (D) The mean intrinsic water use efficiency ($_i$WUE) during the first 90 min after dawn was significantly higher in Cachaco compared to Mbwazirume. The grey area indicates the time before dawn. PPFD, Photosynthetic Photon Flux Density. (Student's *t* test , *for P <0.05, ** for P <0.01).

Fig. 7 Mean diurnal time course of measured photosynthesis ($A_{measured}$) and maximal photosynthesis (A_{max} , black line) under fluctuating light conditions for Mbwazirume and Cachaco. The A_{max} at each light intensity was determined by a modelled light response curve. The nonrectangular hyperbola-based model of Prioul & Chartier (1997) was optimized as described by Lobo et al. (2013). Grey areas indicate times of darkness, red areas indicate the difference between maximal A and measured A. Data are the mean ± SE (n = 4).

Fig. 8 Diurnal time course of gas exchange parameters of the genotypes Mbwazirume and Cachaco under fluctuating light conditions. (A) stomatal conductance (g_s), (B) photosynthesis (A) and (C) intrinsic water use efficiency ($_i$WUE) The light intensity fluctuated throughout the

day (black line). The significance of the time constant of g_s increase or decrease (K) and the maximal slope of g_s increase or decrease (Sl_{max}) is shown (Student's t test , *for P <0.05 and ** for P <0.01 for faster g_s rapidity in Mbwazirume compared to Cachaco). Throughout the day, g_s kinetics were faster for the genotype Mbwazirume compared to Cachaco, but differences were dependent on the target light intensity, the magnitude of change, the g_s prior to the intensity change and the time of the day. Grey areas indicate times of darkness. Green areas indicate the analyzed time frame of the g_s rapidity response. Blue areas indicate time points with significant differences in A or $_i$WUE between both genotypes (Student's t test, $P < 0.05$). PPFD, Photosynthetic Photon Flux Density. Data are the mean ± SE (n = 4).

Fig. 9 Average diurnal gas exchange parameters of the genotypes Mbwazirume and Cachaco under fluctuating light conditions illustrated in Fig. 8. (A) stomatal conductance (g_s), (B) photosynthesis (A) and (C) intrinsic water use efficiency (iWUE) . (D) The percentage limitation of A during the afternoon (> 6 hours after light onset). (Student's t test, * for $P < 0.05$, n = 4).

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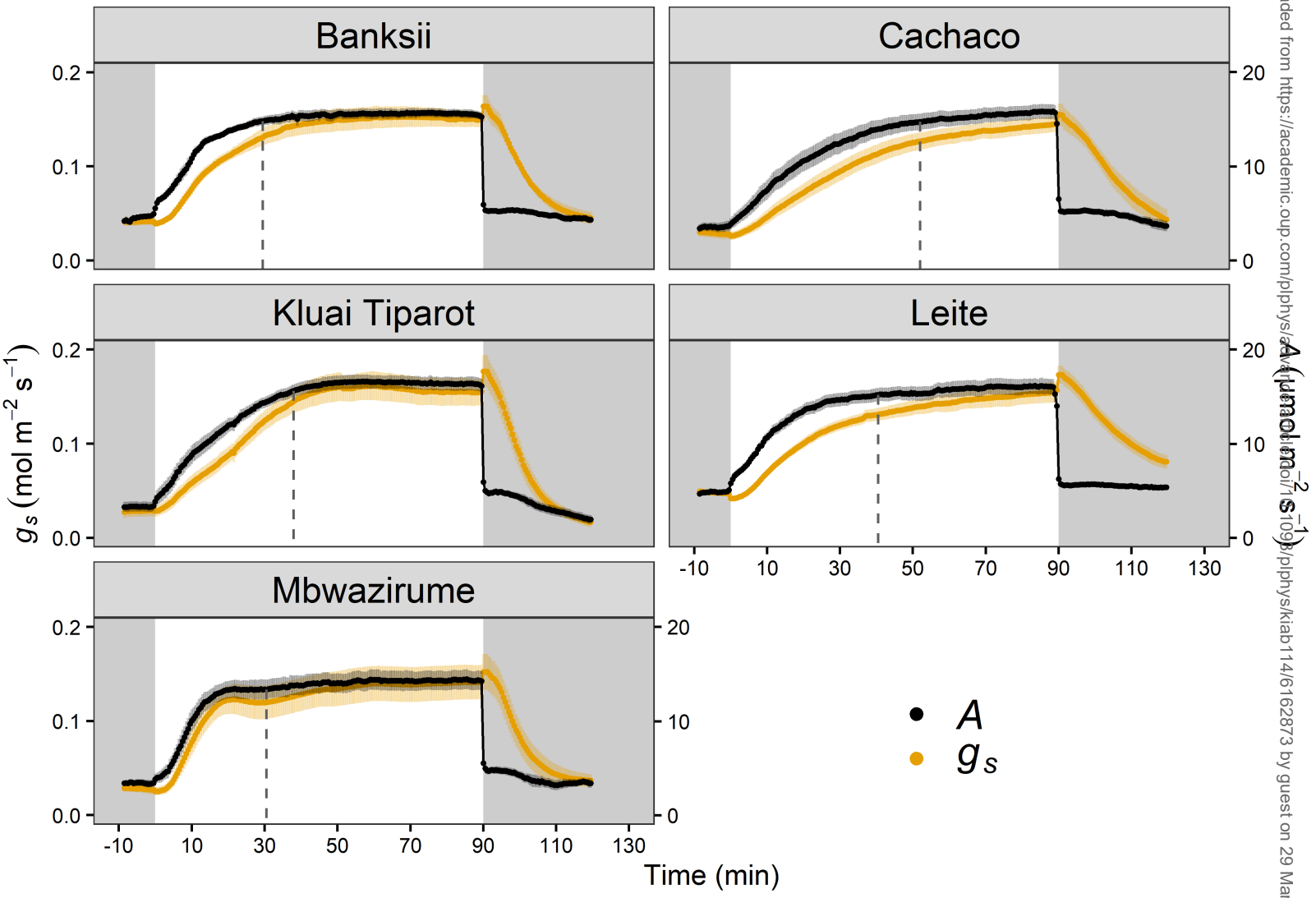

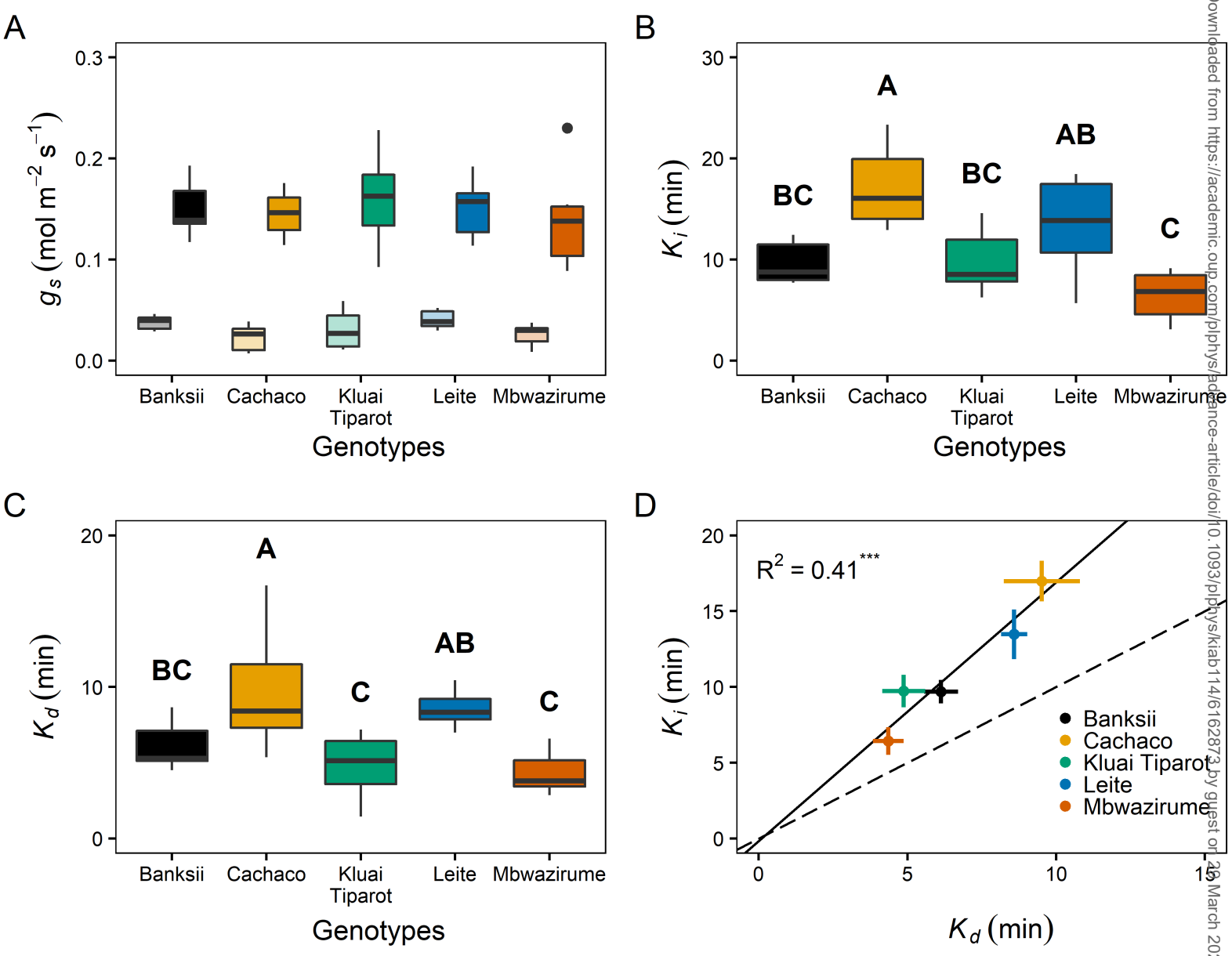

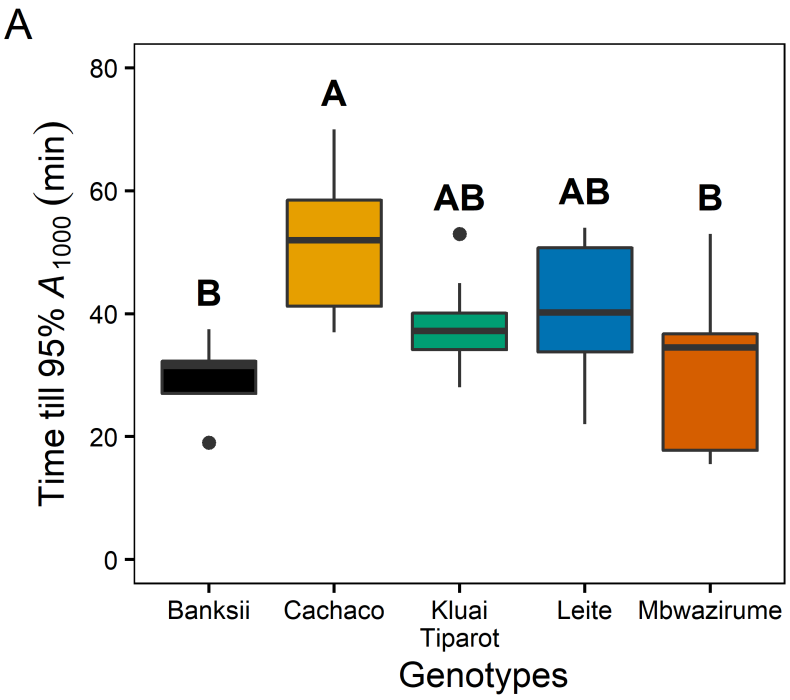

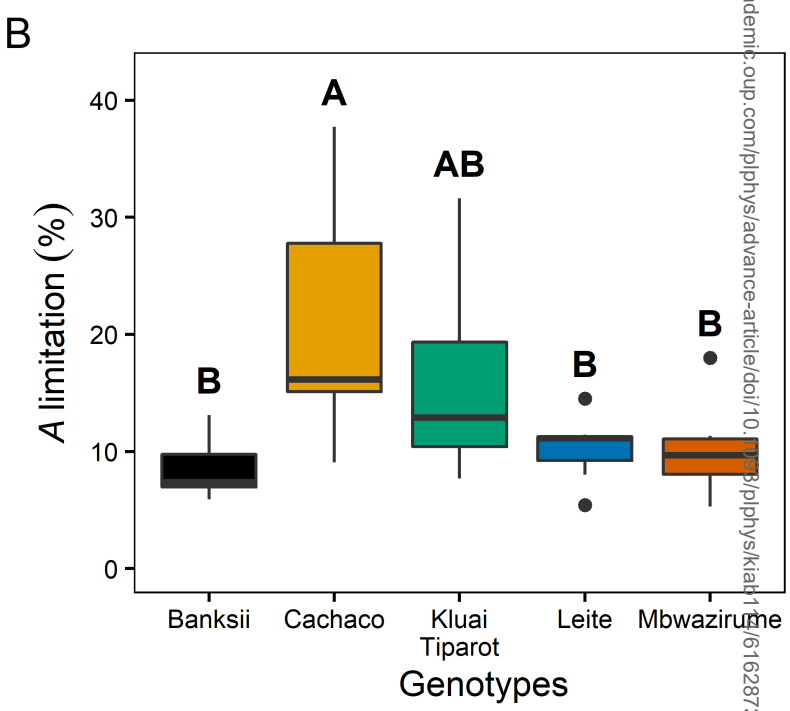

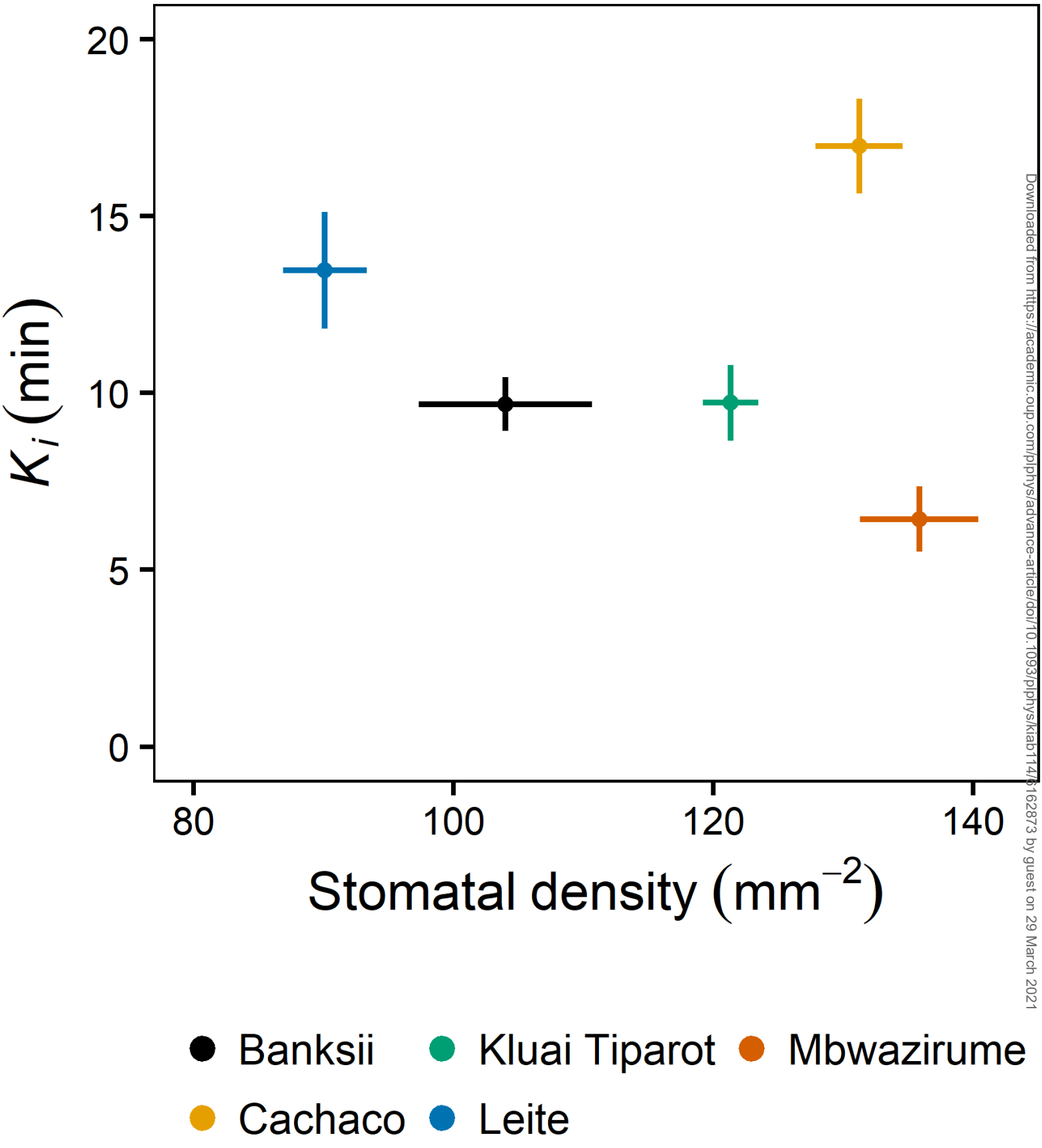

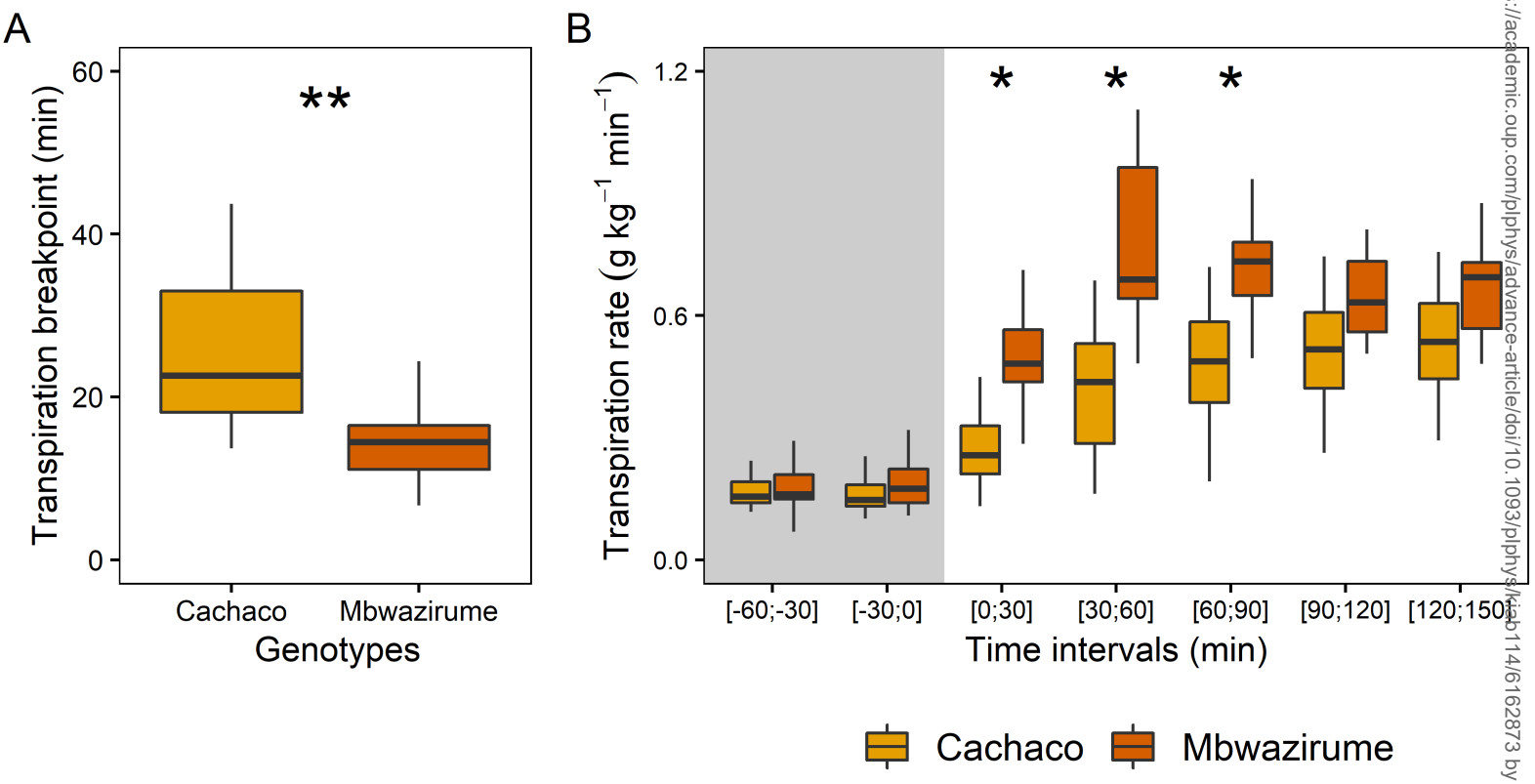

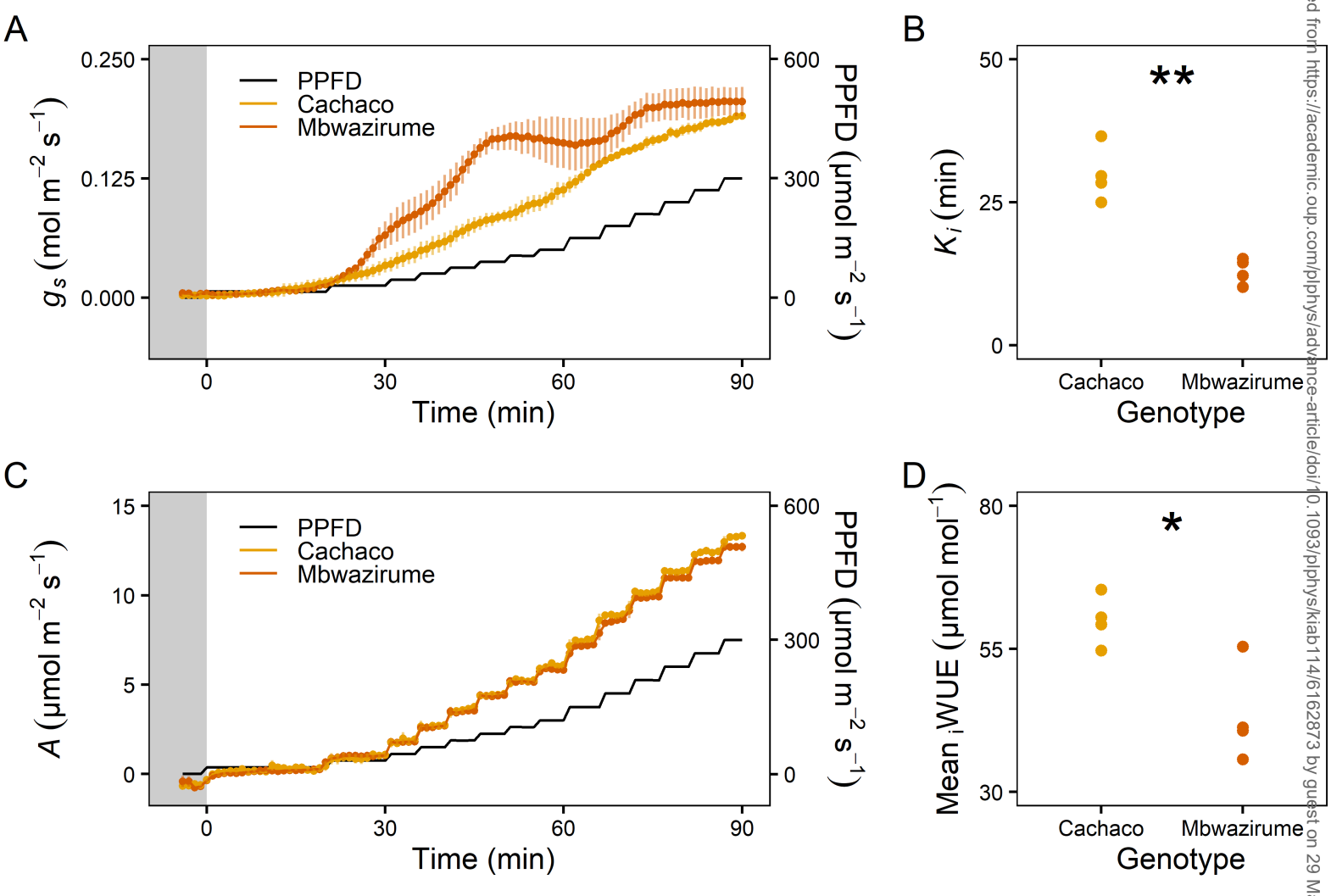

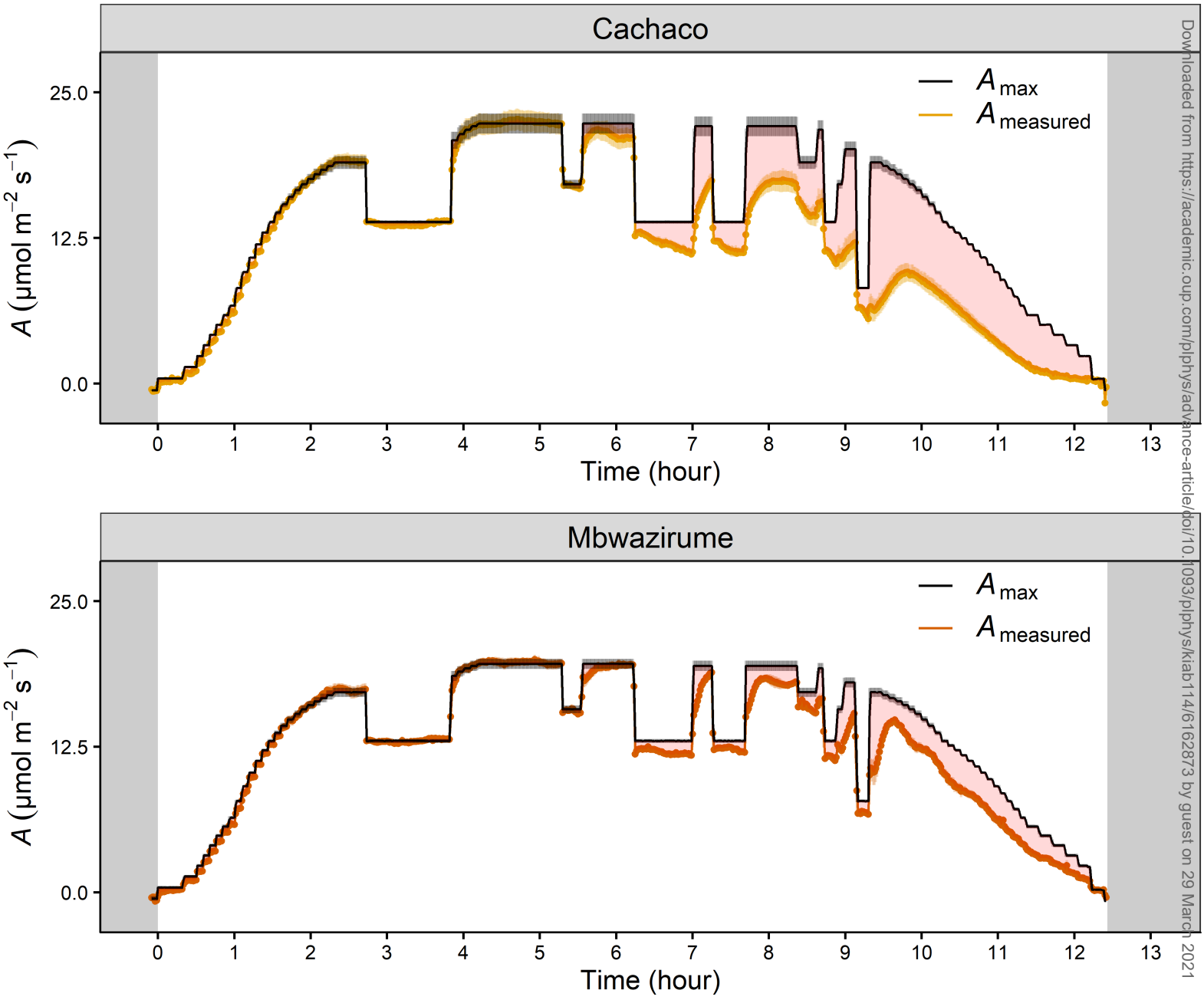

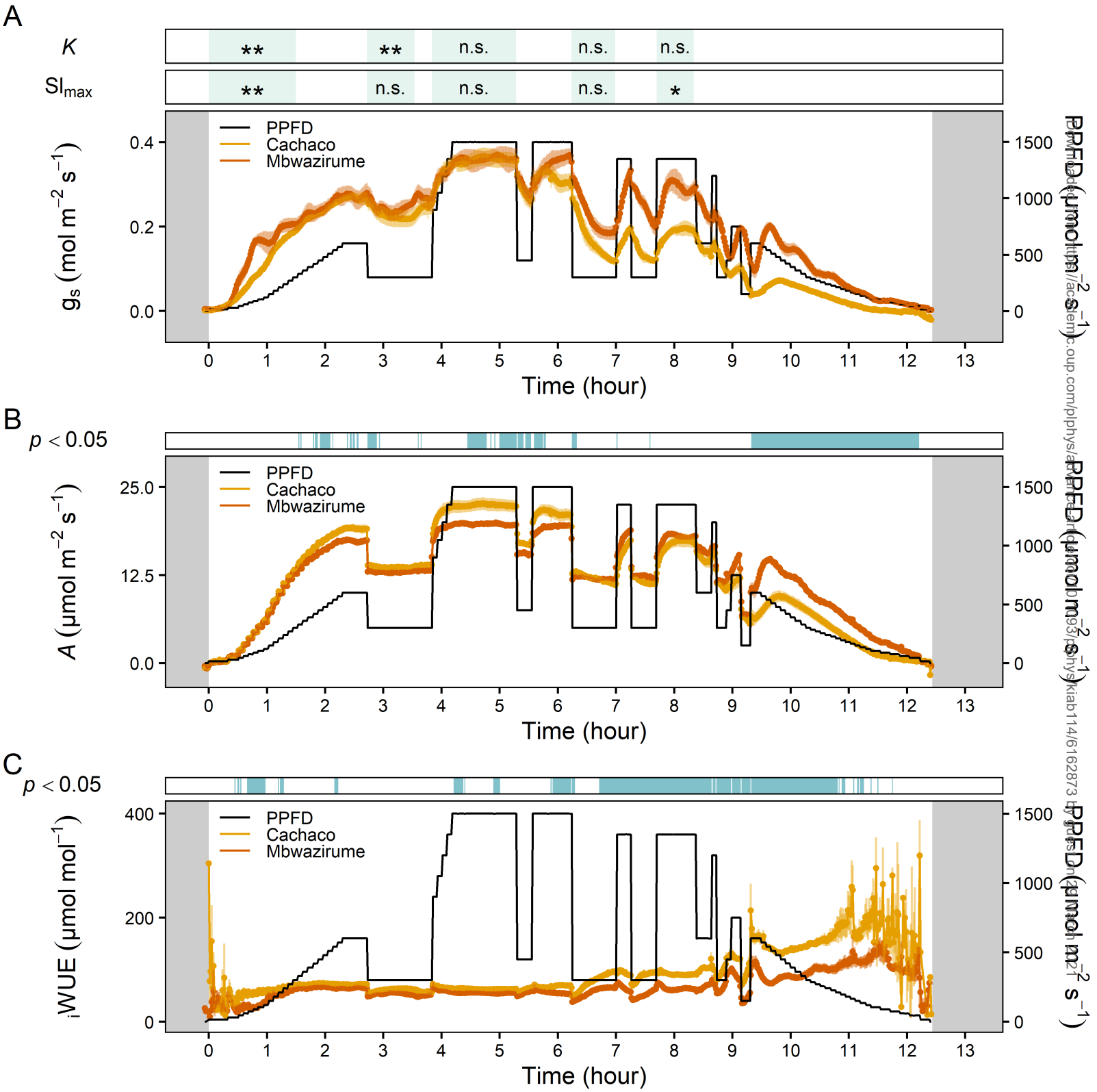
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A (μmol m−2 s−1)
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p < 0.05
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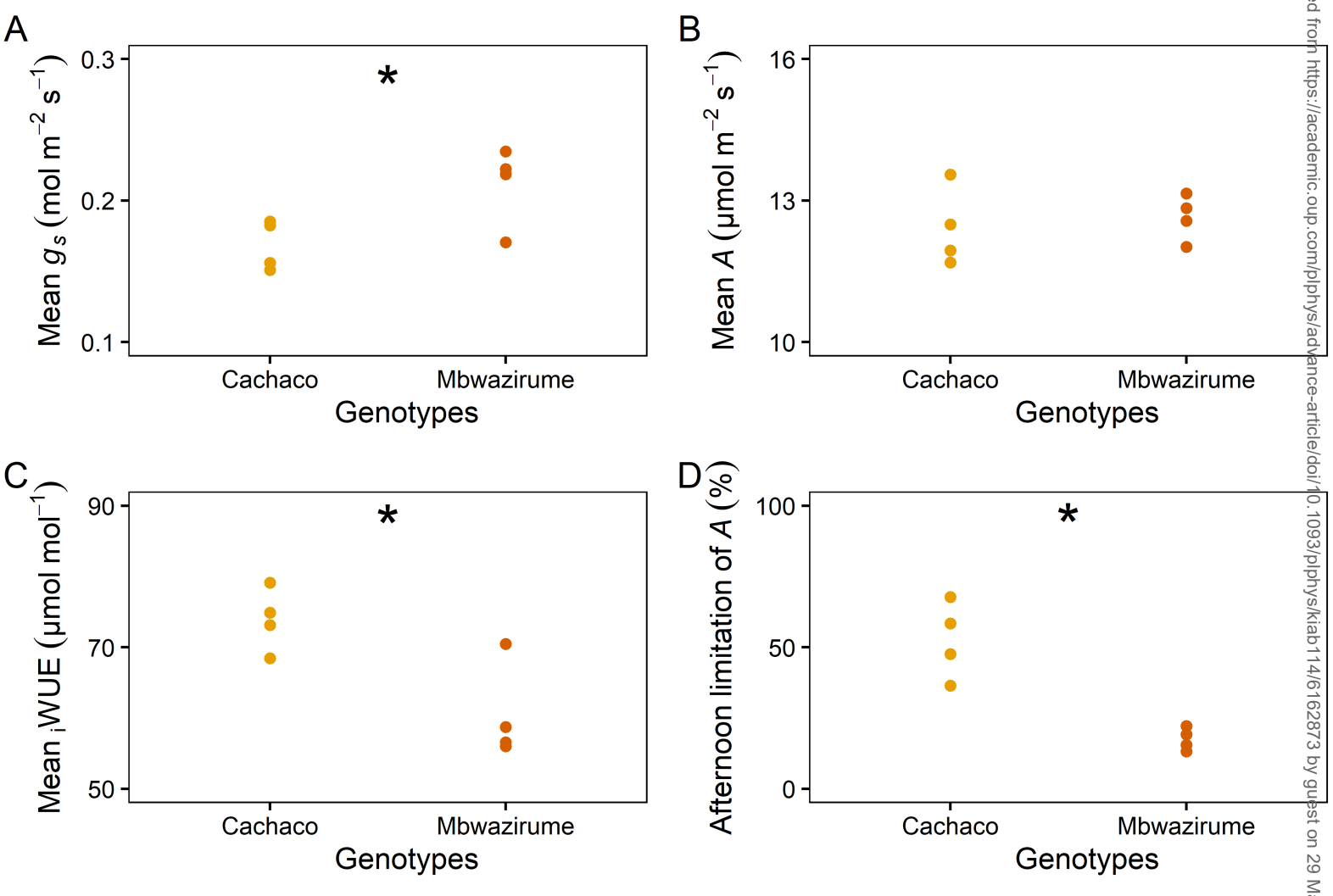

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