

Light-mediated constraints on leaf function correlate with leaf structure among deciduous and evergreen tree species

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Summary Leaf structure has been shown to be an important determinant of leaf photosynthetic characteristics, yet the nature of this relationship remains ambiguous. It has been suggested that intra-leaf shading of chloroplasts may explain the negative influence of increasing leaf thickness/density on mass-based photosynthesis. To explore further the importance of light-mediated functional limitations conferred by leaf structure, we examined photosynthetic responses to high unidirectional and bidirectional irradiances among broad- and needle-leaves ranging widely in mass per area (LMA). Except for leaves with the lowest LMA ($< 40 \text{ g m}^{-2}$), photosynthesis increased in bidirectional irradiance, and the ratio of unidirectional to bidirectional photosynthesis (A_u/A_b) was strongly and negatively related to LMA, approaching 0.5 for the thickest/densest leaves. Bidirectional illumination also increased stomatal conductance, but the magnitude of stomatal response was modest and uncorrelated with LMA. Consequently, the ratio of intercellular CO_2 partial pressures during unidirectional versus bidirectional irradiation was positively related to LMA. Hence, it appears that many C_3 leaves may not be “light saturated” under high unidirectional illumination. The negative, exponential A_u/A_b –LMA relationship in this study supports the notion that, as LMA increases, an increasing fraction of leaf chloroplasts are functioning at subsaturating irradiance under unidirectional light.

Keywords: intra-leaf chloroplast shading, leaf mass per area, light-saturated photosynthesis.

Introduction

Numerous studies have demonstrated that structural and biochemical traits govern the photosynthetic capacity of a leaf (Mooney and Gulmon 1979, Gulmon and Chu 1981, Field 1983, Field and Mooney 1986, Evans 1989, Schulze et al. 1994, Hollinger 1996, Reich et al. 1997, 1998, Poorter and Evans 1998, Garnier et al. 1999, Peterson et al. 1999a). For example, when expressed on a mass basis, variation in light-saturated photosynthesis within and among species and functional groups is positively related to leaf N concentration and negatively related to leaf mass per area (LMA) (Field and Mooney 1986, Reich et al. 1997, 1999, Green 1998).

However, the exact nature of this relationship between leaf

structure and function remains ambiguous (Reich et al. 1998, Peterson et al. 1999a, Shipley and Lechowicz 2000). Specifically, why does light-saturated photosynthesis per unit leaf mass or nitrogen tend to decrease in thicker or denser leaves? Various mechanisms have been suggested, including (i) differences in the amount of light reflected (and thus, absorbed) by leaves at a given photosynthetic photon flux density (PPFD) (Osborne and Raven 1986, Poorter and Evans 1998); (ii) variation in the proportion of organic N compounds allocated to photosynthetic versus non-photosynthetic functions (Evans 1989, Poorter and Evans 1998, Reich et al. 1999); (iii) differential partitioning of leaf N between light harvesting, electron transport and CO_2 fixation (Reich et al. 1997, Poorter and Evans 1998); (iv) greater resistance to CO_2 diffusion in thicker leaves (Lloyd et al. 1992, Parkhurst 1994, Poorter and Evans 1998, Garnier et al. 1999); and (v) intra-leaf self-shading of chloroplasts (Jarvis 1981, Osborne and Raven 1986, Terashima and Hikosaka 1995, Reich et al. 1997).

Recent studies indicate that the influence of leaf structure on photosynthesis may be largely independent from that of biochemistry (Green 1998, Reich et al. 1998, Peterson et al. 1999a, 1999b). These findings suggest a general underlying mechanism such as inhibited CO_2 diffusion or intra-leaf shading of chloroplasts, and there are proponents for each possibility (e.g., Lloyd et al. 1992, Shipley and Lechowicz 2000). Shipley and Lechowicz (2000) argue that intra-leaf light attenuation plays a principal role, and this contention is supported by other data (Outlaw and Fisher 1975, Cannell 1989, Nishio et al. 1993, Stenberg et al. 1995), including observations that photosynthesis is stimulated considerably in both broad- and needle-leaf tree species when light is distributed evenly across all leaf surfaces rather than unidirectionally (Zelawski et al. 1973, Oker-Blom et al. 1992, Evans et al. 1993). In other words, at least under conditions typically imposed during photosynthetic measurements, high irradiance may not saturate the electron transport capacity of many leaves.

Thus, there is compelling evidence that intra-leaf light attenuation may limit the utilization of a leaf's full photosynthetic capacity. However, the importance of this constraint has not been examined as a function of leaf morphology, and we believe that such an effort could help clarify the role of light in this context. Accordingly, in the present paper we summarize results of an experiment designed to assess the relationship be-

tween light limitation of photosynthesis and leaf thickness/density. Specifically, we tested the hypothesis that the proportion of total photosynthetic potential realized under unidirectional irradiance (calculated as the ratio of photosynthetic rates under unidirectional versus bidirectional irradiance) is negatively related to LMA across a wide range of tree species and functional groups.

Materials and methods

Leaf photosynthesis in unidirectional and bidirectional irradiance

To explore the potential importance of light-mediated limitations on leaf function, photosynthetic rates of leaves from 12 tree species/hybrids were measured during both unidirectional and bidirectional illumination in July 1999. We chose species/hybrids on the University of Wisconsin-Madison campus that collectively spanned a wide range of leaf structural (i.e., LMA) and functional attributes (i.e., mass-based photosynthetic rate). One-year-old foliage was sampled from two evergreen needle-leaved conifers (*Pinus resinosa* Ait. (red pine) and *Pinus strobus* L. (white pine)), and fully expanded, first-flush leaves were measured on 10 deciduous broad-leaved hardwoods (*Acer platanoides* L. (Norway maple), *Catalpa speciosa* Warder (northern catalpa), *Juglans nigra* L. (black walnut), *Malus ioensis* Wood (prairie crab apple), *Populus deltoides* Bartr. (eastern cottonwood), *Populus nigra* L. × *P. maximowiczii* A. Henry, *Populus tremuloides* Michx. (quaking aspen), *Prunus serotina* Ehrh. (black cherry), *Robinia pseudoacacia* L. (black locust) and *Tilia americana* L. (American basswood)).

Leaf gas exchange was measured with a Li-Cor 6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE), using the broad-leaf cuvette with a clear bottom window to permit simultaneous illumination from both the cuvette top and bottom (bidirectional irradiance). Because the clear-bottom cuvette lacks a leaf thermocouple, leaf temperature was calculated by an energy balance approach (Li-Cor 1995). All leaves were measured at a cuvette air temperature of 25 °C and a CO₂ partial pressure (*p*) of 37 Pa on sunny days between 0900 and 1200 h. On average, leaf temperature during bidirectional irradiance exceeded that during unidirectional irradiance by 1.2 °C (SE = 0.05 °C).

Broad-leaves were measured *in situ* and illuminated on the adaxial surface for unidirectional treatments. Conifer needles were removed from shoots and arrayed in the cuvette to prevent inter-needle shading (Kramer and Clark 1947, Zelawski 1973, Oker-Blom 1985, Sprugel 1989) as well as light “leakage” into and possible light reflection from the cuvette bottom. During unidirectional measurements, the bottom cuvette window was covered with black cloth. Preliminary tests (D.S. Green and E.L. Kruger, unpublished data) revealed no discernible decline in gas exchange rates of detached pine needles during the time required for the sequence of unidirectional and bidirectional measurements. Typically, 3 min or less were required to attain a stable reading for both light conditions on

leaves that had received direct sunlight for at least 5 min before measurement (to induce photosynthetic enzymes).

Leaves were sampled from a variety of light environments (e.g., deep shade to full sun), which provided a wide range in LMA (Field 1983, Oren et al. 1986, Hollinger 1989, Harley and Baldocchi 1995, Green 1998). For all samples, leaves were first measured under unidirectional irradiance. Photosynthetic photon flux density (PPFD) for all unidirectional measurements was 1800 μmol m⁻² s⁻¹, which was provided by the blue-red LED array on the broad-leaf cuvette. Previous assessments of leaf light response across a wide range of broad- and needle-leaved species and light environments indicated that, in most cases, maximum photosynthesis under unidirectional light is attained at a PPFD of 1800 μmol m⁻² s⁻¹ (Green 1998, Green et al. 2001). However, particularly for members of the genus *Populus*, this generality may not always hold true. Thus, to check the validity of this assumption, unidirectional net photosynthesis was compared at a PPFD of 1800 versus 2500 μmol m⁻² s⁻¹ for 10 leaves of eastern cottonwood and quaking aspen. On average, net photosynthesis at 2500 μmol m⁻² s⁻¹ was only slightly higher (3.6% ± 0.3) than that at 1800 μmol m⁻² s⁻¹ (data not shown).

For bidirectional measurements, a PPFD of 1800 μmol m⁻² s⁻¹ was again provided to the upper surface(s) by the blue-red LED array, and the lower surface(s) was simultaneously exposed to sunlight of a similar PPFD (between 1750 and 1880 μmol m⁻² s⁻¹, after accounting for light attenuation by the clear bottom window, measured with an LI-190 Quantum Sensor, Li-Cor). Immediately following gas exchange assessments, foliage was measured for one-sided (broad-leaf) or projected (needle-leaf) area, oven-dried at 70 °C to a constant mass and weighed to calculate LMA (g m⁻²). Comparisons of photosynthetic response to sunlight versus LED irradiance were conducted on leaves of eastern cottonwood and white pine (*n* = 3 for both species) at high, unidirectional PPFD (~1800 μmol m⁻² s⁻¹). Photosynthesis did not differ between light sources for either species (*P* > 0.36), and the ratio of photosynthesis under sunlight versus LED light averaged 0.97 (SE = 0.02) across all samples.

Photosynthetic response to bidirectional irradiance in elevated CO₂

Photosynthesis in the shade-acclimated leaves may be inhibited by exposure to high irradiance (Powles 1984, Nishio et al. 1994, Sun et al. 1996, Schiefthaler et al. 1999). Therefore, to explore the possibility that photoinhibition could restrict net photosynthetic responses to bidirectional illumination in low- to moderate-LMA leaves, we conducted additional unidirectional/bidirectional assessments on Norway maple foliage (LMA range: 33.7 to 86.3 g m⁻²) while maintaining an intercellular *p* (*p_i*) exceeding 100 Pa (cuvette chamber *p* = 150 Pa). Preliminary tests indicated that this *p_i* was saturating for Norway maple leaves (Table 1). Theoretically, at a saturating *p_i*, the capacity of a leaf to process light (i.e., maximum electron transport rate) is often the primary factor limiting photosynthesis (Farquhar and von Caemmerer 1982). If a leaf is vulner-

Table 1. Mass-based photosynthesis (A_{mass}), stomatal conductance (g) and intercellular CO_2 partial pressure (p_i) of leaves under high unidirectional and bidirectional PPFD. Leaves spanning a wide range of mass per area (LMA) were sampled from 12 tree species/hybrids. Unidirectional measurements were conducted at a photosynthetic photon flux density (PPFD) of $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$, and bidirectional measurements were conducted at a PPFD of $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$ on adaxial and abaxial leaf surfaces. Unidirectional and bidirectional measurements were conducted at a cuvette chamber CO_2 partial pressure (p_c) of 37 Pa and, for Norway maple, 150 Pa.

Genus/Species	p_c (Pa)	LMA (g m^{-2})	Unidirectional irradiance			Bidirectional irradiance		
			A_{mass} ($\text{nmol g}^{-1} \text{s}^{-1}$)	g ($\text{mol m}^{-2} \text{s}^{-1}$)	p_i (Pa)	A_{mass} ($\text{nmol g}^{-1} \text{s}^{-1}$)	g ($\text{mol m}^{-2} \text{s}^{-1}$)	p_i (Pa)
<i>Populus deltoides</i>	37	76.3	303	0.551	28.6	429	0.832	27.4
	37	84.3	261	0.877	31.5	368	1.649	30.8
	37	97.8	260	0.793	29.8	349	1.427	28.7
	37	93.7	273	0.859	30.2	348	1.305	28.7
<i>Populus hybrid</i> ¹	37	72.9	327	0.315	25.0	364	0.365	23.7
	37	96.8	291	0.870	29.3	377	1.529	26.8
	37	100.5	261	0.621	28.0	336	0.819	27.0
	37	101.0	182	0.527	30.4	232	0.727	28.9
<i>Populus tremuloides</i>	37	78.6	327	0.628	28.1	403	0.666	26.4
	37	98.8	249	0.662	28.9	332	0.799	26.9
<i>Acer platanoides</i>	37	50.9	139	0.106	28.6	172	0.119	27.5
	37	64.1	181	0.225	28.2	229	0.222	26.5
<i>Catalpa speciosa</i>	37	33.7	326	0.175	26.9	323	0.203	27.8
	37	34.9	347	0.226	28.1	347	0.239	28.4
<i>Juglans nigra</i>	37	72.2	263	0.276	24.8	310	0.269	22.9
<i>Malus ioensis</i>	37	67.1	130	0.111	24.4	146	0.121	23.5
	37	139.8	117	0.348	28.2	165	0.351	24.5
<i>Prunus serotina</i>	37	42.4	245	0.175	28.6	264	0.209	28.3
<i>Robinia pseudoacacia</i>	37	35.2	554	0.484	29.2	574	0.414	28.1
	37	61.9	259	0.281	27.2	280	0.268	25.9
<i>Tilia americana</i>	37	68.4	162	0.256	29.9	189	0.281	29.2
	37	55.5	105	0.123	28.6	135	0.131	28.0
<i>Pinus resinosa</i>	37	279.2	28	0.141	28.2	51	0.168	24.2
	37	312.8	38	0.229	29.8	61	0.279	22.0
	37	337.5	29	0.358	32.9	55	0.380	27.6
<i>Pinus strobus</i>	37	156.0	72	0.224	28.2	113	0.238	23.7
	37	182.0	52	0.133	25.4	84	0.151	21.7
	37	188.0	60	0.273	28.9	101	0.303	25.5
<i>Acer platanoides</i>	150	33.7	356	0.109	123.0	374	0.103	121.5
	150	39.6	371	0.113	123.0	409	0.109	121.2
	150	56.8	463	0.148	110.0	598	0.159	104.1
	150	66.9	193	0.089	117.0	236	0.093	114.0
	150	86.3	265	0.088	107.3	380	0.103	102.1

¹ *Populus nigra* \times *P. maximowiczii*.

able to photoinhibition, excessive PPFD may impair the light-harvesting apparatus, and at a saturating p_i this injury should be manifested by decreases in photosynthesis (as a result of depressed electron transport rates). Thus, a net decrease in CO_2 -saturated photosynthesis under bidirectional PPFD would be evidence that, at ambient p , photoinhibition is restricting the net photosynthetic response to bidirectional illumination. On the other hand, a neutral or positive response of CO_2 -saturated photosynthesis to bidirectional light would not necessarily rule out the possibility of photoinhibition, as it is conceivable that increased electron transport in inner "shaded" leaf regions may offset any decreases caused by photodamage. However, especially in thin leaves, it seems unlikely that a neutral response to bidirectional light would result from a situation in which substantial photoinhibition in one re-

gion of the leaf offset a concomitant light-mediated increase in photosynthesis elsewhere.

Results

The net photosynthetic rate (A_{mass} ; $\text{nmol g}^{-1} \text{s}^{-1}$) of a leaf in high, bidirectional irradiance was assumed to reflect its "light-saturated" functional capacity (at a given external p). We estimated the proportion of total photosynthetic capacity utilized under unidirectional light with the ratio of unidirectional to bidirectional photosynthesis (A_u/A_b). Except for leaves with the lowest LMA, photosynthesis increased in bidirectional irradiance (Table 1, Figure 1), and A_u/A_b was strongly and negatively related to LMA ($r^2 = 0.86$, $P < 0.0001$), approaching 0.5 for the thickest/densest leaves. Sto-

matal conductance (g ; $\text{mol m}^{-2} \text{s}^{-1}$) generally increased in bidirectional irradiance (Table 1). However, the ratio of unidirectional versus bidirectional g (g_u/g_b), which averaged 0.86 (SE = 0.03), was not correlated with LMA ($P = 0.98$). The increased conductance in bidirectional irradiance was associated with a decrease in p_i in all but the thinnest leaves. Moreover, the ratio of p_i under unidirectional versus bidirectional irradiance was positively related to LMA (Figure 1, $r^2 = 0.75$, $P < 0.0001$).

At a p_i exceeding 100 Pa, the response of photosynthesis to bidirectional irradiance was slight in low-LMA leaves and substantial in moderate-LMA leaves (Table 1). Similar tests among thin herbaceous leaves ($15\text{--}20 \text{ g m}^{-2}$) growing in deeply shaded forest understories ($\sim 1\text{--}5\%$ ambient PPFD) produced evidence of photodamage (i.e., decreased photosynthesis) under bidirectional irradiance (data not shown). Thus, photoinhibition in thin leaves may partly explain their lack of net response to bidirectional irradiance, but the lack of a negative response in our assessments in high p_i indicates that photodamage was probably not significant across the sampled LMA range.

Discussion

A long-standing, widely held assumption is that, in ambient p_i , photosynthesis of nearly all C_3 leaves is light-saturated under

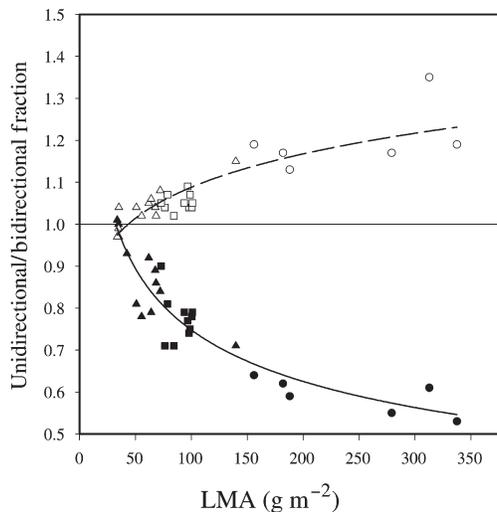


Figure 1. Ratios of photosynthesis (A_{mass}) and intercellular CO_2 partial pressure (p_i) under high unidirectional versus bidirectional irradiance as a function of mass per unit area (LMA) for leaves of 12 tree species/hybrids. Ratios of unidirectional to bidirectional A_{mass} (A_u/A_b , filled symbols) and p_i (p_u/p_b , open symbols) are as follows: genus *Populus* (squares); remaining hardwood species (triangles); and genus *Pinus* (circles). Relationships between unidirectional/bidirectional ratios and LMA were examined by linear regression using the General Linear Models procedure in the SAS Statistical Package (SAS Institute 2000) on log-log transformed data. The regression for the A_u/A_b -LMA relationship (solid line) is $\ln(A_u/A_b) = 0.87 - 0.25\ln(\text{LMA})$, $r^2 = 0.86$, $P < 0.0001$. The regression for the p_u/p_b -LMA relationship (dashed line) is $\ln(p_u/p_b) = -0.36 + 0.10\ln(\text{LMA})$, $r^2 = 0.75$, $P < 0.0001$.

unidirectional irradiance equal to or less than peak ambient PPFD (Maximov 1938, Björkman 1981, Nishio et al. 1993, Poorter and Evans 1998), about $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ or less at mid-latitudes. However, only the lowest LMA leaves in this study attained peak photosynthesis under unidirectional irradiance, and photoinhibition did not appear to explain their lack of response to bidirectional light. Additionally, the proportional gap between unidirectional and bidirectional photosynthesis increased with leaf thickness/density such that the highest LMA leaves were essentially unifacial, with each surface acting as an independent functional plane. Consequently, our hypothesis appears to be supported, and the photosynthetic apparatus of leaves across a wide range of C_3 plants may be light limited in conventional unidirectional assessments, even at PPFDs exceeding traditional "light-saturation" values.

However, bidirectional light may exert an influence on photosynthesis directly (e.g., as a result of the reduction in intra-leaf self shading of chloroplasts), indirectly (e.g., through the enhancement of the CO_2 supply by increasing g and p_i), or through a combination of both. Indeed, p_i under current atmospheric conditions may limit photosynthesis in C_3 plants (Lambers et al. 1998), but increases in photosynthesis under bidirectional light were achieved in this study despite decreases in p_i . The largest relative increases were associated with the greatest relative reductions in p_i . Thus, it seems unlikely that limitations to CO_2 diffusion are primarily responsible for the negative relationship between mass-based photosynthesis and LMA under unidirectional irradiance (Wong 1985, Nishio et al. 1993, 1994, Green 1998, Reich et al. 1998).

Do light-mediated limitations on leaf function, particularly under unidirectional irradiance, increase with LMA as a result of the self-shading of leaf chloroplasts? Numerous studies have shown that unidirectional light gradients within leaves can be severe, even in relatively thin leaves (Osborne and Raven 1986, Cui et al. 1991, Fukshansky and Remisowsky 1992, Vogelmann 1993, DeLucia et al. 1996). Vogelmann et al. (1989) measured a 90% attenuation of unidirectional light by the initial 50 μm of the leaf (about one-third of the leaf thickness) at wavelengths of 450 and 680 nm in *Medicago sativa* L. They also found that at a relative leaf thickness of 0.6 (where the adaxial surface = 0.0 and the abaxial surface = 1.0), PPFD at 680 nm was only about 4% of incident values, whereas PPFD at 550 nm remained at about 20% of incident values. At a relative thickness of 1.0, virtually all PPFD at 680 nm had been attenuated, whereas about 10% of the PPFD at 550 nm remained. Thus, nearly all PPFD transmitted to the abaxial surface of the leaf was in the least efficient portion of the photosynthetic light spectrum. Hence, photosynthesis of chloroplasts in deeper leaf regions under high unidirectional irradiance may be limited by both light quantity and quality.

Osborne and Raven (1986) proposed that steep unidirectional PPFD profiles produce strong light limitations in abaxial leaf chloroplasts, whereas adaxial chloroplasts may be saturated or photoinhibited. The negative, exponential A_u/A_b -LMA curve in this study supports the notion that an increasing fraction of leaf chloroplasts are functioning at subsaturating

PPFD under unidirectional light as LMA increases. Patterns of CO₂ assimilation may be uncoupled from unidirectional leaf light gradients. Several studies have shown that the photosynthetic potential in the spongy mesophyll may approach or equal that of the palisade mesophyll in broad leaf C₃ species (Mokronosov et al. 1973, Outlaw and Fisher 1975, Nishio et al. 1993). Nishio et al. (1993) found that peak CO₂ assimilation occurred in the mid-section of spinach leaves. Additionally, many needle-leaved species display symmetrical photosynthetic capacity subtending adaxial and abaxial surfaces (Esau 1977). These findings indicate that multidirectional light likely facilitates more efficient utilization of whole-leaf biochemical capacity in many C₃ leaves, perhaps as a result of an increase in RuBP production associated with greater electron transport capacity.

Correspondingly, whereas intra-leaf shading of chloroplasts may provide a general mechanistic explanation for much of the light-mediated influence of leaf structure on function, the specific importance of whole-leaf light absorption may differ between functionally symmetrical and asymmetrical leaves (DeLucia et al. 1991, Evans et al. 1993, Vogelmann 1993) as a result of unbalanced chloroplast distributions across adaxial and abaxial leaf surfaces. The A_u/A_b-LMA relationship observed here, then, is not suggested as a "universal" trend. However, even functionally asymmetrical leaves are likely to be more efficient in bidirectional light than under single-sided irradiance (Evans et al. 1993). Thus, the inclusion of multidirectional light environments could prove useful in assessments of leaf photosynthesis (Osborne and Raven 1986, Vogelmann 1993) and associated estimates of light-, nutrient- and water-use efficiencies.

Although photosynthetic performance may vary due to numerous factors other than light limitations (Mooney and Gulmon 1979, Gulmon and Chu 1981, Field 1983, Field and Mooney 1986, Evans 1989, Schulze et al. 1994, Hollinger 1996, Reich et al. 1997, 1998, Poorter and Evans 1998, Garnier et al. 1999, Peterson et al. 1999a), our data raise important questions about light-mediated controls on leaf photosynthetic efficiency. For instance, does photosynthetic performance under whole-leaf illumination reflect "real world" CO₂ assimilation potential, or are leaves simply inefficiently constructed (Poorter and Evans 1998)? Preliminary modeling of average daily photosynthesis in unshaded thick (i.e., unifacial) leaves using multidirectional PPFD distributions (measured on clear days) indicates that actual leaf photosynthesis may exceed estimates based on unidirectional light by as much as 50% (D.S. Green and E.L. Kruger, unpublished data). Given the magnitude of such a disparity, this issue and its implications for plant carbon balance deserve further attention.

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