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Forum

Leaf photosynthesis: do endophytes have a say?

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Endophytes, both bacterial and fungal, constitute an integral component of the leaf ecosystem. Here we argue that the respiratory metabolism of endophytes in the intercellular spaces of leaves could have a significant role in enhancing leaf photosynthesis by enriching the internal CO_2 concentration, especially in C3 plants.

Endophytes, both bacterial and fungal, are an integral component of the microbiome of plants and occur internally in the aerial and below ground plant tissues. Although their evolutionary origins are unclear, endophytes exist asymptomatically in plants as commensals. For the purpose of this forum, we restrict our discussion to fungal endophytes only, although our thesis would hold true for bacterial endophytes as well. The fungal endophytes are either vertically transmitted across seed generations or horizontally acquired from the environment. The vertically transmitted endophytes, belonging to the family Clavicipitaceae, exhibit a narrow host range and infect only some cool-season grasses; by contrast, the horizontally transmitted endophytes, mostly belonging to the classes Pezizomycetes, Sordariomycetes, Dothideomycetes, and Eurotiomycetes, have a wide host range, infecting the leaves of many plant species through their wind-dispersed spores. The horizontally transmitted fungi have been extensively studied in the past couple of decades and have been shown to influence a range of plant fitness parameters including plant growth, tolerance to abiotic and biotic stresses, mineral nutrient uptake, and secondary metabolite production [1].

Here we argue that, besides the above functions, the horizontally transmitted foliar fungal endophytes could also directly influence two important components of the carbon budget in the leaf: namely, photosynthesis and photorespiration. Photosynthesis contributes positively to the carbon balance of plants, whereas photorespiration leads to carbon drain. We propose that the fungal endophytes in the intercellular spaces of the leaf mesophyll could play a major role in sustaining carbon fixation in leaves and ultimately in the success of the plant community as a whole. We identify several research gaps, which, when addressed, could contribute to an assessment of the role of endophytes in the carbon budget of leaves as proposed here. These could have implications for modeling and meeting the challenges of climate change effects.

Photosynthesis in the leaf

Fungal endophytes densely and uniformly colonize the intercellular spaces of leaves. Every 0.5-cm^2 area of a leaf lamina is colonized by one or more fungi such that the colonization frequency of fungal endophytes in a leaf ranges from 60% to 122% [2]. As heterotrophic microbes, such a dense presence in the leaf could substantially influence the leaf carbon balance, principally through the microbes' respiration, enriching carbon dioxide and depleting the oxygen content.

This is especially significant for C3 plants with their ribulose 1,5-bisphosphate carboxylase (RuBisCO) enzyme-catalyzed photosynthesis not being efficient due to the enzyme's dual and competing function as an oxygenase, leading to energy and carbon loss. Biochemical and anatomical alterations serve as CO_2-concentrating mechanisms to increase the level of CO_2 around RuBisCO; this enhances the carboxylation activity of the enzyme due to its dependence on the absolute CO_2 concentration following Michaelis–Menten kinetics [3]. Hence, it is conceivable that the increased substomatal CO_2 concentration due to the fungal respiration favors the carboxylase activity of RuBisCO while suppressing its oxygenase activity and thus effectively increasing photosynthesis and carbon-use efficiency. The fact that C3 plants are able to refix their mitochondrial respiratory CO_2 lends credence to this hypothesis [4].

Within a leaf, most fungal endophytes are localized in the upper and lower epidermal portions, with very few occurring in the deeper mesophyll tissue [5]. Respiratory CO_2 from such densely distributed fungal endophytes in the subepidermal regions (where photosynthetically active radiation is absorbed) could contribute to steepening the CO_2 concentration gradient between the subepidermal layer and chloroplast carboxylation sites [6]; this in turn would lead to greater diffusion of CO_2 to the chloroplasts leading to improved carbon assimilation. Simultaneously, the respiration of the densely distributed endophytes would be expected to directly lead to oxygen depletion, thus reducing photorespiration and increasing the carbon balance of the plants (Figure 1).

Central to the above arguments (on the respiratory activity of fungal endophytes) is, of course, the magnitude of the contribution of the fungal endophytes towards CO_2 enrichment and O_2 depletion in the subepidermal regions of the leaf. Probably due to methodological constraints, there are as yet no experimental data on this aspect of endophyte–plant host interaction. However, extrapolation of estimates from axenic cultures of the endophytes in culture flasks suggests that the contribution may be nontrivial. The endophyte-mediated enhancement of internal CO_2 would be especially relevant in stressful

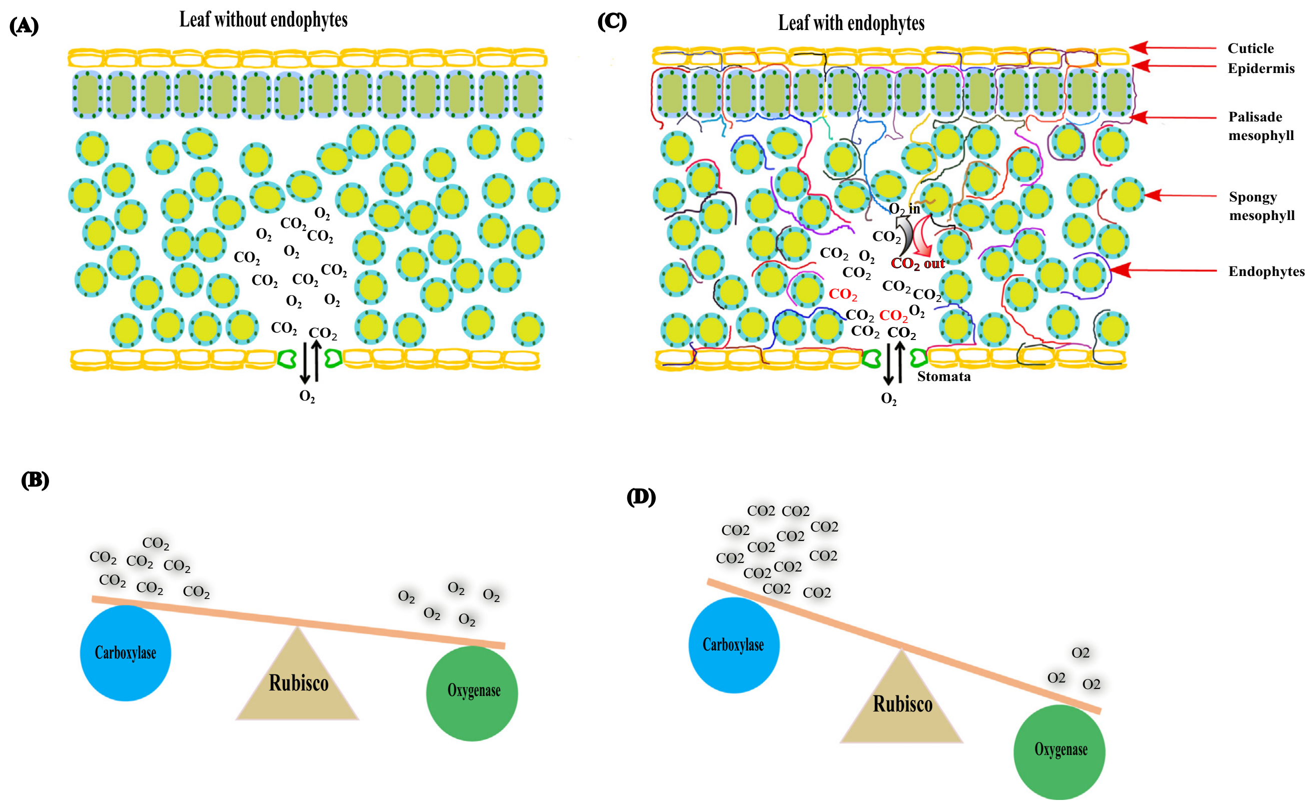

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Figure 1. Schematic diagram showing the consequences of leaf endophytes for carbon balance in the leaf. (A) Depicting a leaf without endophytes and the normal gas exchange of CO_2 and O_2 through the stomata. (B) The corresponding influence on the relative carboxylase and oxygenase activity of ribulose 1,5-bisphosphate carboxylase (RuBisCO) in a leaf without endophytes. (C) A leaf with endophytes. The internal CO_2 concentration is enriched, while O_2 is depleted by endophyte respiration. (D) Consequently, the relative carboxylase activity of RuBisCO compared with a leaf without endophytes is enhanced.

environments where stomatal conductance is generally low. Under these situations, the enhanced CO_2 concentrations can lead to significant gains in mesophyll efficiency.

Extending the possible positive role of fungal endophytes in photosynthesis, it is reasonable to argue that the decreased photosynthesis in fungicide-treated plants [7] could be partially due to the loss of their endophytes. Although the mechanism is unclear, several studies have indicated that colonization of crop plants with selected bacterial or fungal endophytes significantly increased their net leaf photosynthesis compared with plants that were not enriched with the endophytes (Table S1 in the supplemental information online). It would be worthwhile to study whether such an increase is indeed facilitated by increased internal CO_2 concentration in the leaf. Studying foliar fungal endophytes of the so-called 'super-performing plants', which exhibit very high photosynthesis with high solar radiance, may throw light on fungal endophyte-influenced photosynthesis [8]. The fungal endophyte-enabled carbon gain could also have a multiplier effect on plant biomass, if one were to consider that many fungal endophytes are known to produce auxins. These auxins, along with that produced by the plant, may delay leaf senescence and thereby contribute to enhanced plant productivity [5].

In summary, the high density of fungal endophyte infection, the constant presence of fungal endophyte's in a plant's endobiome, and their long evolutionary history of association with the leaf (fungal endophytes existed about 300 million years ago [9]) could possibly have compensated for the intrinsic inefficiency of RuBisCO, thus aiding in the survival of the photosynthetically less efficient C3 plants.

Concluding remarks

Several strategies, such as photorespiratory bypass, converting C3 photosynthesis to C4 metabolism, and increasing RuBisCO production, have been proposed to increase photosynthesis especially under current climate change conditions [10]. Given that most plants are invariably colonized by fungal endophytes, it would be of interest to explore whether they could be used as an alternative to improve net leaf photosynthetic rates. Endophytes could improve the CO_2:O_2 ratios in leaf mesophyll intercellular spaces and thereby contribute substantially to the maintenance of a positive carbon balance in the plant. Furthermore, it is known that higher CO_2 inside the leaves would lead to a reduction in stomatal conductance and hence transpiration. This would increase the intrinsic water use efficiency and hence drought adaptation. Clearly, more studies are needed to substantiate this view to harness the potential of fungal endophytes in leaf photosynthesis.

Acknowledgments

The authors thank M.S. Sheshasayee and Nataraja Karaba for constructive comments. M.S.A. was supported by a CSIR Junior Research Fellowship, Government of India.

Declaration of interests

No interests are declared.

Supplemental information

Supplemental information associated with this article can be found online at https://doi.org/10.1016/j.tplants.2022.07.009.

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https://doi.org/10.1016/j.tplants.2022.07.009

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