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Environmental regulation of intrinsic photosynthetic capacity: an integrated view

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Environmental modulation of photosynthetic capacity is reviewed in the context of its assessment and its regulation, genetic differences among species and ecotypes, and links to plant stress tolerance and productivity. Modulation of intrinsic photosynthetic capacity matches investment in photosynthetic components to opportunity for CO_2 uptake and productivity in specific environments, with exceptionally high rates during particularly narrow windows of opportunity. Response varies among species and ecotypes and should be evaluated on multiple reference bases as well as chloroplast, leaf, and whole plant scales. Photosynthetic capacity, total foliar vascular transport capacity, and plant sink strength are modulated in concert. Switching among alternative target sinks and alternative foliar vascular architectures may provide avenues for co-optimization of productivity and stress tolerance.

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Introduction

Harnessing and conversion of sunlight into usable products by photosynthetic organisms drive the production of food, materials, and fuels. An organism's photosynthetic activity varies widely in response to natural fluctuations in available sunlight over time and among different environments. Additionally, photosynthetic organisms adjust their intrinsic photosynthetic capacity to optimize return of investment in photosynthetic components. For example, a plant growing in a shaded environment typically minimizes photosynthetic capacity. Intrinsic photosynthetic capacity also varies over the lifespan of the organism and between different organisms in the same environment.

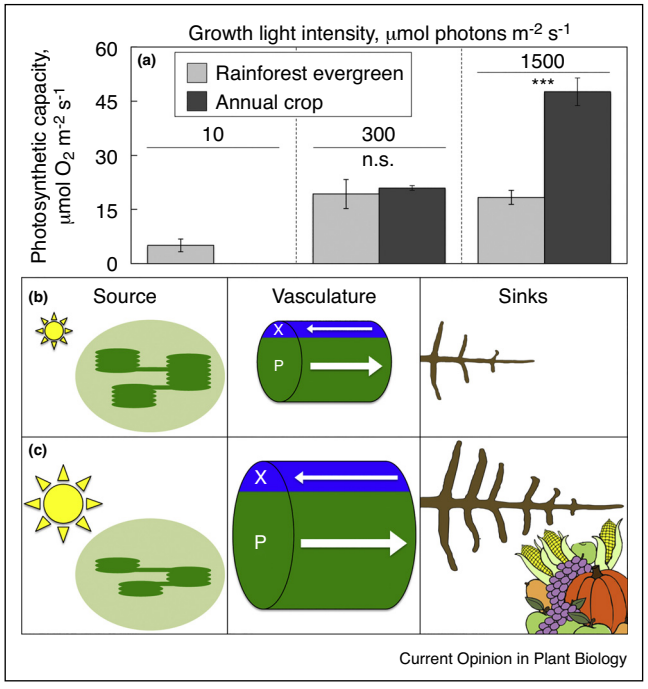
Photosynthetic capacity can be experimentally assessed as the light-saturated rate of either CO_2 uptake or photosynthetic electron transport from oxygen evolution. The latter metric allows determination of intrinsic photosynthetic capacity under CO_2 levels high enough to overcome all stomatal, cuticular, and mesophyll resistances to CO_2 flux [1]. The present review focuses on environmental regulation of light-saturated and CO_2-saturated intrinsic photosynthetic capacity as the rate of linear photosynthetic electron transport ascertained via oxygen evolution. The topic of constraints in CO_2 flux is beyond the scope of the present review; such limitations arise from low stomatal conductance under limiting water availability [2], can involve species-dependent differences in morphological traits that affect mesophyll conductance [3], and have been described in integrated hydraulic–stomatal–photosynthetic models [4].

Regulation of photosynthetic capacity by input and demand

Provided that other necessary resources are available, most species upregulate photosynthetic capacity in environments with high versus limiting light availability. However, even in high-light environments, slow-growing evergreen species – capable of dramatically downsizing their photosynthetic machinery in deep shade – tend to feature lower intrinsic photosynthetic capacities than fast-growing, shade-intolerant annuals (Figure 1a).

Intrinsic photosynthetic capacity is adjusted not only in response to inputs such as light availability, but also in response to the rate at which products of photosynthesis are exported from the leaf [5]. Such regulation of photosynthetic capacity by demand occurs via concomitant transcriptional gene regulation of proteins and other components of photosynthesis and is orchestrated by signals associated with the balance between photosynthesis as the source of sugars and the plant's sinks. High sink strength – high rates of sugar utilization for maintenance metabolism, storage, cell division, growth, and reproduction by sink tissues – leads to upregulation of photosynthesis, whereas low sink activity leads to sugar

Figure 1



(a) Differential acclimation patterns of photosynthetic capacity in response to growth light intensity in two species with different growth habits and schematic depiction of the concomitant acclimation to growth light intensity (**(b)** low light; **(c)** high light) of source strength (of mature photosynthesizing leaves), foliar vascular capacity for sugar and water transport, and sink strength (of tissues that utilize and/or store sugars). The species shown in (a) are the rainforest evergreen *Monstera deliciosa* Liebm and the annual crop spinach (data from Ref. [56]; a constant light intensity of 10 μmol photons m^{-2} s^{-1} was not sufficient to support growth of the annual species; intensities of 300 and 1500 μmol photons m^{-2} s^{-1} were the peak intensities in a sun-lit glasshouse). X, xylem; P, phloem; *** = statistically different at $P < 0.001$ via Student's *t*-tests.

accumulation in source leaves and feedback downregulation of photosynthesis ([6,7]; Figure 1b,c).

Photosynthetic organisms are able to differentially adjust photosynthetic electron transport and CO_2-fixation capacity by using electron acceptors other CO_2. Photosynthetic organisms employ a variety of alternative routes for electrons, ranging from reduction of nitrogen or sulfur compounds to the process of photorespiration and other alternative routes for electron flow [8,9].

Intrinsic photosynthetic capacity on different reference bases

In response to increased growth light intensity, photosynthetic capacity typically increases relative to light-harvesting capacity and chlorophyll content. However, in many other environmental contexts, levels of light-harvesting proteins and Calvin cycle proteins vary in concert. For instance, in leaves grown under low versus high soil nitrogen content (Figure 2a,b) and in green versus yellowing, senescing leaves (Figure 2c,d) under a common growth light intensity, photosynthetic capacity and chlorophyll content per leaf area varied in concert. To be able to assess variation of photosynthetic capacity under such parallel modulation of light-harvesting capacity and CO_2-fixation capacity, reference bases for photosynthetic capacity other than chlorophyll (*e.g.*, Figure 2b,d) are needed (such as per leaf area; Figure 2a,c). It should be noted that concomitant variation of both growth light intensity and nitrogen level leads to changes in the proportion of nitrogen allocated to thylakoid versus stromal proteins [10,11].

These principles are further illuminated by the response of photosynthetic capacity to growth temperature and growth light environment in two *Arabidopsis thaliana* (a winter annual) ecotypes: intrinsic photosynthetic capacities varied when expressed relative to either leaf area (Figure 3a) or chlorophyll content (Figure 3b), but not when expressed per leaf dry weight (Figure 3c). Such concomitant increases in photosynthetic capacity and leaf dry mass per leaf area are seen in many species in