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Current Opinion in Plant Biology

Paradigm shift in plant growth control

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For plants to grow they need resources and appropriate conditions that these resources are converted into biomass. While acknowledging the importance of co-drivers, the classical view is still that carbon, that is, photosynthetic CO_2 uptake, ranks above any other drivers of plant growth. Hence, theory and modelling of growth traditionally is carbon centric. Here, I suggest that this view is not reflecting reality, but emerged from the availability of methods and process understanding at leaf level. In most cases, poorly understood processes of tissue formation and cell growth are governing carbon demand, and thus, CO_2 uptake. Carbon can only be converted into biomass to the extent chemical elements other than carbon, temperature or cell turgor permit.

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Current Opinion in Plant Biology 2015, **25**:107–114

This review comes from a themed issue on **Physiology and metabolism**

Edited by **Steven Smith** and **Sam Zeeman**

http://dx.doi.org/10.1016/j.pbi.2015.05.003

Introduction

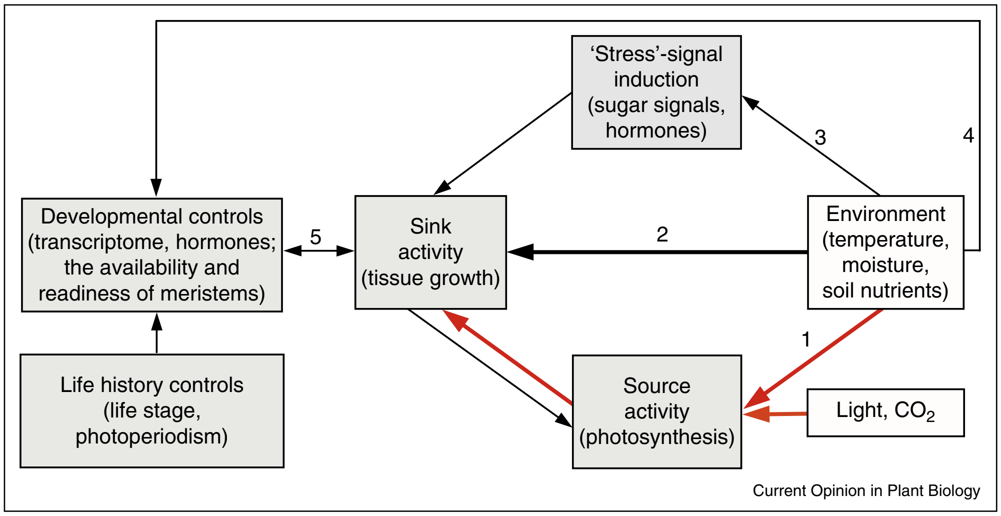
The progress in scientific understanding is strongly influenced by the historical sequence of discoveries, the resulting paradigms and by the availability of methods. Break through discoveries have a long shadow and technical options open new avenues, but they may also confine the scientific mind to the doable. The functional understanding of plant growth, that is, how plants accumulate dry matter, is a good example. Following from Priestley's discovery of oxygen in 1774, Jan Ingenhousz, Jean Senebier and Theodore de Saussure's revolutionary discovery between 1779 and 1804 that plants 'eat air' [1,2] instead of sucking the bulk of their dry matter from the substrate (as was believed before) had a lasting impact on the public and scientific understanding of plant growth. Since those early days, CO_2 has been known as the substrate for photosynthesis, with plant growth considered the inevitable outcome. While there is no question that plant growth builds upon photosynthates (half of plant biomass is carbon), there are justified reasons to question the general assumption that photosynthesis is the rate controlling factor for plant growth. Just like C_4 plants are often believed to be more productive than C_3 plants, given the difference in photosynthetic capacity, although it is long known that such leaf level differences do not scale to ecosystem (field) level [3••,4,5], except under drought stress, when C_4 species are more successful. Crop physiology back to the 1980s has disproven a direct linkage between the capacity for carbon uptake per unit leaf area and growth rate or yield, with tissue (leaf) duration and leaf area ratio as well as the regulation of development (phenology) identified as critical [7•,8••,9•].

In this essay, I will summarize evidence against the assumption of a growth limiting role of photosynthesis (source activity) under normal daylight conditions in the field, and will advocate a broader perception of what crop research and plant physiology have already arrived at, namely that tissue growth itself (sink activity) may be limited more than the provision of the carbohydrate building blocks produced by photosynthesis [6,7•,10, 11••]. There are five pathways through which tissue growth can be regulated, four of which are under environmental control, of which only one operates via carbon source activity, with the three other ones commonly dominating, when temperature, moisture or soil nutrients become restrictive (Figure 1). Here I will focus on the direct action of environmental drivers on tissue growth (pathway 2 in Figure 1) *versus* the classical assumption of a dominating role of pathway 1, with only brief comments on pathways 3 and 4. I will close by discussing the dilemma that leaf photosynthesis is almost always operating below light saturation, whereas net primary production, NPP, is commonly not constrained by the capacity of leaves to assimilate CO_2, at multi-year time scales. This assessment will not account for conditions in which CO_2 is made the ultimately limiting resource by rising the availability of all other resources.

Stoichiometric constraints

Assuming a general, rate limiting role of net-CO_2-assimilation (A) in plant growth and net primary production, is perhaps one of the most common first principles upon which the theory of plant growth is founded, and thus, it became the starting point of the majority of plant growth, vegetation and productivity models. This is quite surprising, because soon after the discovery of photosynthesis, Liebig (1840; reviewed by [12]) popularized the accumulating awareness that crop yield is commonly limited by mineral elements (he assumed 10, today ca. 20 chemical elements other than C, H and O are considered essential

Figure 1



The major pathways through which environmental conditions influence plant growth [1,2,3••,4]. Red arrows indicate source control over growth [1]. This review highlights the significance of the other control pathways, which commonly dominate under stress [2,3••,4]. The feedback of sink activity on source activity has a long distance (phloem) and a short distance (chloroplast, starch/sugar) signal chain, with the latter linked to the first. The possible feedback from sink activity to nutrient availability has been omitted for clarity. Under non-limiting environmental conditions, growth is regulated via 5 only. The reverse arrow between sink activity and development indicates the influence of plant size on phenology (e.g. minimum size to flower).

for plant, microbe and animal life), with the growth response function similar to a saturating light response function of A [13]. It was Ingestad's [14•,15] great discovery that it is not the concentration of mineral nutrients in the soil solution which matters, but the nutrient addition (release) rate, which controls plant availability. Hence, classical soil nutrient assays are not very helpful, apart from fertilizer driven cropping or horticulture systems.

It is hardly reflected in the novel literature that in 1862, Liebig arrived at a global terrestrial productivity estimate of 60 Gt C per year (close to modern calculations) based on soil nutrients only [16]. It is broadly accepted that (with noteable exceptions) nitrogen is the most important rate limiting soil nutrient in early successional and agricultural settings [17,18]. In late successional systems other elements such as P, K, Mg, Mn, Mo, etc. often tied to the N cycle, may be critical for growth rate and NPP [19,20]. This is not the place to review the nutrient limitation literature, but my point here is to simply recall the triviality that C can only be invested into biomass to the extent, chemical elements other than C permit. Basic stoichiometric laws do not permit significant departures from element ratios, specific for certain tissue types and plant species [21–25] and these constraints even include C incorporation in soil humus (e.g. [26]). The rate of release of these nutrients from substrate is far more difficult to assess, predict and model, than is the capture of carbon, and the pool size of these mineral resources in the soil is finite, whereas those of CO_2 and N_2 (not its soluble forms) are potentially infinite. So, except for conditions where nutrients are added, carbon is unlikely the rate controlling factor for plant growth, and should nutrients have not been growth controlling in the first place, elevated CO_2 can drive plants into nutrient limitation (e.g. [27,28]). The situation may have been different 18,000 years ago, when the atmospheric CO_2 concentration was 180 ppm or until the mid 18th century, when 280 ppm prevailed, compare to the current 400 ppm world, significantly exceeding the past ca. 1 Mio year average of 240 ppm (discussed in [29]).

Why did modellers adopt a carbon centric view and place C at the top of the hierarchy of plant growth control, that is, in a 'master', rather than in a 'slave' position? I think, this happened for two reasons. First, there is the de Saussure legacy, the mathematical beauty and excellent understanding of the related CO_2 uptake processes [30], and the inexistence of similarly straight forward algorithms for mineral nutrient uptake and tissue growth. Second, because of the intuitively plausible outcome of statistical productivity models (for fertilized crops) such as the classic by Monteith [31•], in which yield correlates linearly with the accumulation (dose) of solar radiation. However, the dose of solar radiation is a surrogate for calendar date (hence development), the progression of the season (hence time), accumulated warmth, potential evaporation, etc. Each of these factors or variable combinations could be similarly predictive, with the actual mechanisms remaining unaccounted for.