



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 CO₂ 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, CO₂ 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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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, CO₂ 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

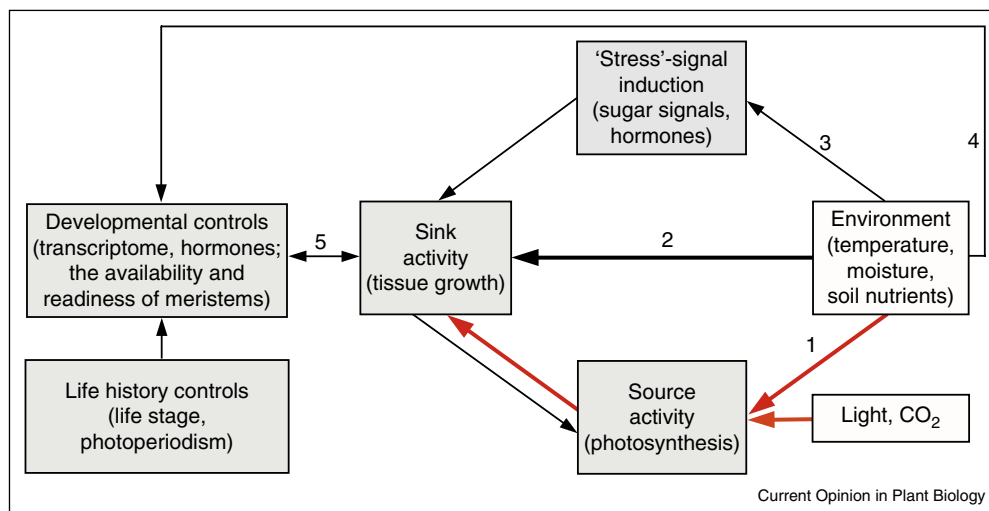
plant biomass is carbon), there are justified reasons to question the general assumption that photosynthesis is the rate controlling factor for plant growth. Just like C₄ plants are often believed to be more productive than C₃ plants, given the difference in photosynthetic capacity, although it is long known that such leaf level differences do not scale to ecosystem (field) level [3^{**},4,5], except under drought stress, when C₄ 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 CO₂, at multi-year time scales. This assessment will not account for conditions in which CO₂ is made the ultimately limiting resource by rising the availability of all other resources.

Stoichiometric constraints

Assuming a general, rate limiting role of net-CO₂-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 notable 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 CO₂ and N₂ (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 CO₂ can drive plants into nutrient limitation (e.g. [27,28]). The situation may have been different 18,000 years ago, when the atmospheric CO₂ 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 CO₂ 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.

In late successional systems one could plausibly argue that the composition of soil organic matter, including very recent organic debris, has become similar to the stoichiometry of living plants, decoupling the plant nutrient cycle from bedrock stoichiometry. Unless leaching has caused such stoichiometric relatedness to vanish, plants and their microbial partners could ‘mine’ such resources in the event of excess photoassimilate availability, but obviously this is only a short term option. Such ‘priming’ effects have been evidenced in CO₂ enrichment experiments [32,33,34], but the opposite has been suggested as well, namely (an at least transitory) microbial ‘locking’ of soil nutrients, when extra photoassimilates are exuded to the rhizosphere (e.g. [28,35]). So, it is advised to revisit the C priority in growth models [36].

Tissue level controls of C demand

The rather basic requirements for building a plant body are (besides having a plan), whether the plant is in a building stage (meristems available and ready for producing new cells), the availability of resources is matching demand, and whether resources reach the building site. The building process itself is one end of the pipeline (C sink activity), and with respect to carbon, leaf photosynthesis is the other one (C source activity). The two, must be in balance, and it is not *a priori* clear which side is driving and which is the driven. For instance, in well fertilized plants, the day-time rate of downloading of fresh photoassimilates from chloroplasts may, periodically, constrain substrate availability at building sites [37], while also explaining, why the afternoon rates of CO₂ assimilation are often reduced, compared to morning hours, at otherwise similar environmental conditions (endproduct feedback on photoassimilation; e.g. [38], see below), a diurnal asymmetry that becomes enlarged under elevated CO₂ and high light [39–41]. Starch accumulation in foliage exposed to CO₂ enriched air may even cause chloroplast damage, despite massive reductions in source capacity (down regulation of photosynthesis; [42,43]). So, it is an over-simplistic view at plant growth, assuming a dominant control of the capacity to assimilate CO₂ over growth [44]. The point I am advocating here is that the rate of growth and NPP are controlled by the rate of tissue formation, rather than CO₂ assimilation, while the common perception is the opposite, simply due to the availability of data, methods, theory and history. Similar views have been elaborated earlier (e.g. [8,44,45]), but failed to make any impact among plant ecologists and modellers, with far ranging consequences, including the understanding of the global carbon cycle.

The ease by which gas exchange can be measured, caused other important components of growth such as cell production, or hormonal controls, or stress signalling to remain largely disregarded in models. Environmental constraints can induce hormone mediated (transcriptome) signal cascades that cause meristematic activity to cease before C

shortage comes into play, with sugars playing a central signalling role [11,46–48]. In the following, I will briefly re-visit the evidence that tissue formation itself exerts significant constraints on growth rate under water shortage or low temperature, irrespective of the constraints set by nutrient availability (discussed above).

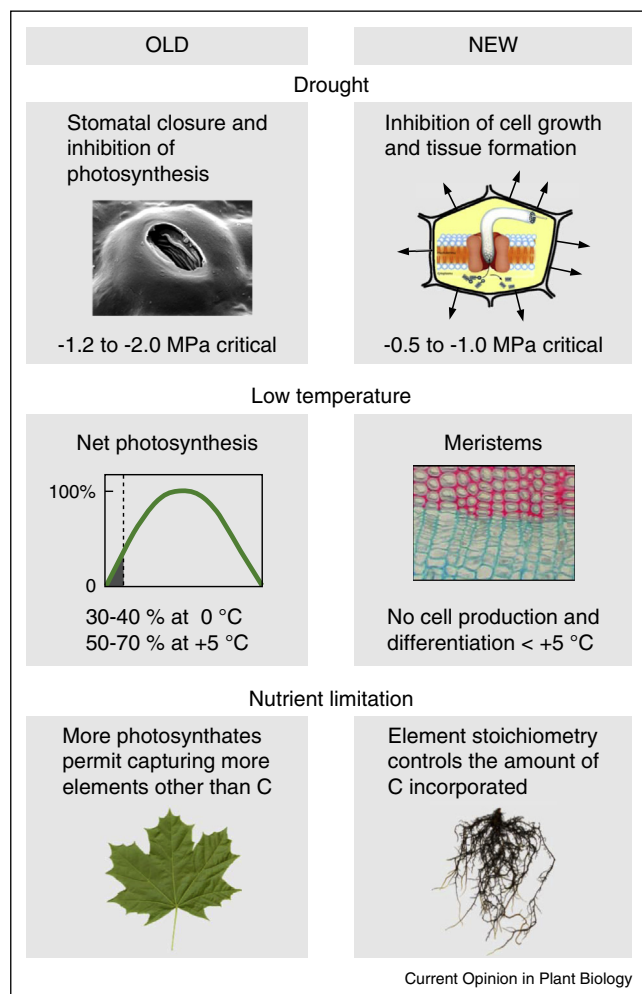
When growth is slow or zero in a green plant, the concentration of non-structural carbohydrates (NSC, i.e. starch and low molecular weight sugars) is commonly high and *vice versa* [49]. Temperate or Mediterranean evergreen species enter spring with a high pool of NSC. As soon as growth commences, NSC declines and reaches a minimum during peak shooting. In the humid tropics, the rainy season is a period of fast growth and reduced levels of reserves, the less humid, drier period, is a period of NSC accumulation and little or no growth, as was shown for an entire mature forest in Panama [50]. Another example for Douglas-fir: NSC is negatively correlated with the growth rate of branches [51].

The cessation of structural growth can be related to phenology, for instance, the reproductive cycle, or the late season transition to winter dormancy, or to external constraints such as low temperature, limited access to soil nutrients because of soil drying, or insufficient turgor for cell differentiation during dry periods. So, opposite to wide spread belief, periods of growth cessation for both, internal and external reasons, are commonly periods of carbon overflow (i.e. the potential for uptake exceeding the potential of structural investment) and high levels of storage pools (‘stored growth’). In all these cases, growth is low despite a high availability of mobile photoassimilates. This holds for wild species [49], and crops [52].

Growth at low water availability

Beyond survival or tissue loss issues, coping with drought also means being able to sustain growth, with photosynthesis not representing the bottle neck process [53–55]. Muller *et al.* [11] summarized data for growth and carbon uptake under increasing water shortage, showing that growth ceases long before carbon uptake does, in every case tested. Of all processes related to plant growth, cell formation (specifically cell expansion and differentiation) is the most sensitive to any decline in turgor [44,56–58] and tissue formation is inhibited by drought long before carbon supply falls short because of drought induced limitations of gas exchange. This was already known in the 1980s [59–61], but did not receive the attention deserved, because technological developments made it so easy to measure gas exchange, with the consequence that a stomata-dominated cascade effect of C limitation, prevailed as the leading paradigm, counter existing evidence. Yet, water shortage first inhibits meristems (commonly at water potentials between –0.5 and –0.8 MPa), before carbon uptake becomes limiting (Figure 2). The prevention of photoinhibition (and thus damage to the photosynthetic machinery) by continued

Figure 2



A comparison of traditional and suggested novel priorities in plant growth control when nutrients, temperature or water availability constrain plant growth (or productivity). For details see the text. The inset picture on cell growth in the drought section was obtained (and modified) from Matyssek *et al.* [94], visualizing the interplay between cell wall growth (production of cellulose fibrils by protein complexes in the plasmalemma) and turgor (the rate of cell size expansion).

CO₂ fixation appears to have priority over a complete shut down of water loss, causing endproducts to accumulate (NSC storage). Any decline in the discharge of photoassimilates from chloroplasts induces down regulation of Rubisco [46,47,62–64].

Recently, it has become a hot topic, whether trees die from water shortage because of a depletion of C reserves (C starvation) or because of a failure of the hydraulic system [65,66], and several authors prioritized the old paradigm, assuming a dominant role of C starvation (e.g. [67]), although evidence points to a priority of hydration problems [68,69]. It usually remains unclear, whether conduits failed or whether the most sensitive tissue simply desiccated beyond a tolerance limit, because roots

became unable to cover the demand set by evaporative forcing. This is a field where cause and effect get easily confused (e.g. [70]) because a very long drought will not only lead into enhanced water shortage but also to reduced C reserves, but the latter (together with other symptoms) runs parallel to the first. Nobody has ever shown a causal link between mortality and C-starvation under drought. I disbelieve that such a link does exist, but rather think fatal desiccation comes before [71].

Growth at low temperature

Because the temperature response of A became so well studied, low temperature is often supposed to constrain growth through insufficient carbon assimilation. However, low temperature is affecting the rate of cell duplication or mitoses at levels that hardly affect A. At 5 °C most cool-adapted plants perform 50–70% of maximum, light saturated A, while growth stops. No higher plant has ever been found to grow near freezing point, where A is still running at c. 30% of maximum rate if water and light permit [49]. These constraints to tissue formation are found in all cold-adapted higher plants, including winter crops [72] and they explain the limit of tree growth at the alpine treeline [73,74]. Non-structural carbohydrates are accumulating as one approaches the treeline worldwide (hence, there is no C shortage; [75]) and detailed xylogenesis studies underpinned the 5 °C threshold for wood formation [76]. Trees are not more sensitive to low temperature than low stature plants, but due to their upright stature they are the first to be hit by declining ambient temperature, because of their close aerodynamic coupling to free air [77]. Roots also hardly grow below 5 °C [78], although the absolute limit for cell production may be around 2 °C [79]. So, similar to drought, low temperature is first constraining sink activity (Figure 2). In line with the initial effects of water shortage, low-temperature exposed plants reveal a carbon overflow, a fact already observed in the 19th century using iodine starch assays in cold exposed leaf tissue (reviewed in [49]).

Is atmospheric CO₂ concentration limiting plant growth?

If sink rather than source activity is controlling plant growth, CO₂ enrichment should not exert a 'fertilizing' effect. However, since A is not saturated at current atmospheric CO₂ concentration, it is often assumed that the current rise in CO₂ could enhance growth and net primary productivity (NPP, i.e. annual biomass accumulation) of the world's natural vegetation. This in turn, is often wrongly assumed to translate into enhanced C storage (C sequestration, net ecosystem productivity, NEP), but faster carbon assimilation does not scale to greater C pool size as is known from fast rotation tree plantations compared to old growth forests. Experimental CO₂ enrichment offers a test, whether the A → NPP cascade works that way, but it cannot contribute to identifying consequences of elevated CO₂ for NEP. In early experiments, plants were provided with unlimited

water, nutrients and/or space to expand into, and thus, often exhibited >20% greater biomass in one season. In perennial plants, such relative effects may accelerate over time in a sort of ‘compound interest’ response, provided resources remain unlimited (e.g. [80]). Yet, in the field, even fertilized and well watered cereal crops show much less than expected stimulation by a doubling of CO₂ concentration (7–12%; [81]), with soil water savings via stomata, rather than photosynthetic stimulation being the main cause of the remaining stimulation.

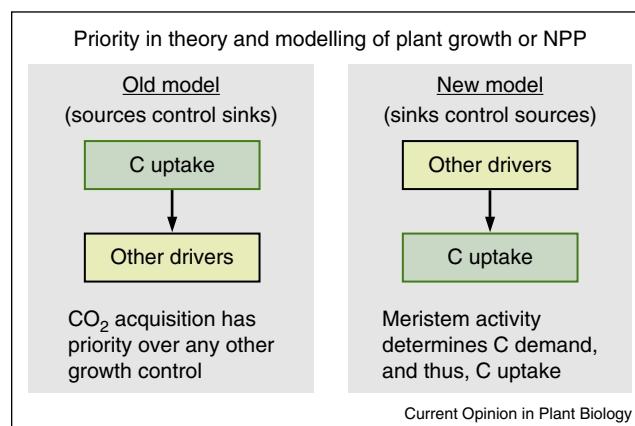
In tree stands on undisturbed ground, greater effects will always be obtained in young, expanding, compared to more mature systems [29], which commonly end up with little if any growth stimulation [82,83,84]. A pine plantation at the Duke FACE site, retained annual growth stimulation by elevated CO₂, with trees successfully foraging for extra nutrients [85] and still growing into denser canopies, but obviously, neither nutrient mining nor increases in canopy density can be sustained in the longer term. McCarthy *et al.* [86] showed that the growth signal is explained by LAI expansion. Hence, the outcome of CO₂ experiments will always depend on plant and vegetation type, nutrient availability, soil moisture, state of initial stand development (leaf area index, LAI, and root turnover) and study duration [29,87]. Large dendrological data sets for tropical trees revealed no stimulation of stem diameter growth in response to the past >100 years atmospheric CO₂ enrichment (e.g. [88,89]).

Leaves have C limitations, not ecosystems

The current debate on plant carbon limitation distills down to the question of whether leaf level responses of gas exchange scale to ecosystem scale net carbon capture, NEP (and further to net biosphere productivity, NBP). According to the latest carbon balance estimates of the globe [90] we are missing (by default) between 10 and 20 g C per m² of terrestrial land that carries ‘some’ vegetation (ca. 100 Mio km²). If we assume that this missing amount of carbon is due to a greater rate of carbon assimilation by particularly vigorous terrestrial vegetation, with an assumed mean annual NPP of ca. 1000 g C m⁻² a⁻¹, the net gain in NEP (C sequestration) would thus, correspond to 1–2% of that NPP, which contrasts the gain in A for a change from preindustrial 280 ppm to the current 400 ppm by more than 25%. As small as this global net C fixation might be (if it occurs in forests at all), it must find an end, given forest density per unit land area is limited and C sequestration to soil organic matter would co-sequester nutrients away from growth and thus constrain NPP. Part of that ‘missing carbon’ may be due to a still ongoing ramping up of forest density, forest expansion in the temperate zone and organic C export from land to ocean via rivers.

As the ‘missing carbon’ fraction of the total C released to the atmosphere is currently declining (more C remaining

Figure 3



The suggested shift in paradigm from a carbon centric (source) to a meristem (sink) oriented approach of explaining plant growth.

in the atmosphere or dissolved in oceans), it appears that the biosphere is approaching CO₂ saturation, despite the fact that most foliage operates far below its photosynthetic capacity, also because of mutual shading, imperfect leaf orientation to the sun or due to clouds. Yet, foliage has more functions than just capturing CO₂. In an evolutionary context, leaves shade out competing neighbours, store nutrients and buffer against herbivory and other losses. As long as ‘amortized’ foliage exerts no net carbon cost, suboptimal foliage illumination does not mean that there is C limitation at ecosystem or landscape scale [91].

With these examples, I am advocating a sink oriented view at plant growth, by accounting for chemical element stoichiometry in plant tissue and direct constraints to carbon sinks by drought and low temperature, that come into play before these drivers act upon carbon source activity. It is rather the norm than the exception that sink activity constrains source activity, causing growth (demand for carbon) to control photosynthesis (fixation of carbon), rather than the other way round ([92], Figure 3). Because in the long run, source activity and sink activity cannot be decoupled (the ‘functional convergence hypothesis’; [93]) a ‘big leaf’ model describes the joint action of both, but is unlikely to mirror the critical mechanisms that drive the carbon cycle [36].

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