Implications of carbon source-sink feedbacks for plant growth responses to environmental factors

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Summary Global models of vegetation dynamics are largely carbon (C) source-driven, with behaviour primarily determined by the environmental responses of photosynthesis. However, real plants operate as integrated wholes, with feedbacks between sources and sinks resulting in homeostatic concentrations of metabolites such as sugars. An approach to implementing such behaviour in a plant growth model is presented and its implications for responses to generic environmental factors assessed. The approach is based on Hill functions representing inhibition of C sources (net photosynthesis) and activation of sinks (structural growth) based on sugar concentrations. The model is parameterised for a mature tropical rainforest site and its qualitative behaviour is found to be consistent with experimental observations. Key findings are that sinks and sources strongly regulate each other. For example, doubling potential net photosynthesis (i.e. the rate that would occur without feedback) results in growth increasing by only 1/3 at equilibrium, with increased sugar concentration causing feedback-inhibition of photosynthesis. A source-only driven response, as in current global models, would result in close to a doubling of growth. Hence environmental factors that affect potential net photosynthesis, such as atmospheric CO_2, have greatly reduced effects on growth when homeostatic behaviour of sugars is considered. The implications of considering source-sink coupling for the behaviour of models of vegetation dynamics are likely to be profound.

Keywords: growth, model, source, sink, feedback, homeostasis, sucrose

1 Introduction

Plant growth can be characterised as the irreversible increase in cell number, biomass, and/or plant volume (Hilty et al. 2021). It determines the resource acquisition, competitivity, and reproductive output of individuals and plays a major role in the global carbon (C) cycle, estimated to currently sequester at least 80 Pg(C) yr^{-1} in terrestrial biomass annually (Graven et al. 2011), over 7x the estimated total anthropogenic emissions of C in 2023 (Friedlingstein et al. 2023).

Unlike in animals, growth in plants is typically modular and indeteminate (Brukhin and Morozova 2011). Growth requires a supply of resources, and the movement of carbohydrates and other nutrients within plants to support growth is commonly characterised as occurring from “sources” to “sinks” (Mason and Maskell 1928). C is mainly transported as a component of sucrose (Dominguez and Niittylä 2022), with mature leaves being the principal source organs. C sinks include the active meristems which import assimilates for growth and reproduction, as well as processes such as respiration and exudation (Kaitaniemi and Honkanen 1996; White et al. 2016). Storage tissues such as parenchyma can be a C source or sink, depending on the plant-level balance of supply and demand (Furze et al. 2019; MacNeill et al. 2017; Saddhe, Manuka, and Penna 2021).

The mechanisms determining the relationships between source and sink activities within plants, and the balance between different sinks, have been researched for many decades (e.g. Wardlaw 1990; Hartmann, Bahn, et al. 2020). Much of this work has been driven by the desire to improve crop production

through reducing limitations to growth (e.g. Wardlaw 1990; White et al. 2016; Fernie et al. 2020), but the underlying mechanisms determining source-sink relationships are also relevant to the future viability and productivity of plants growing in natural ecosystems in the context of environmental change (e.g. Hartmann, Bahn, et al. 2020; Shestakova et al. 2024), and the dynamics of the global carbon cycle (e.g. Fatichi et al. 2019; Friend et al. 2019). While understanding of carbohydrate metabolism is much more advanced in annuals such as *Arabidopsis* than perennials such as trees (Wingler and Henriques 2022), a key on-going debate in both agronomic and global-change research concerns whether C sources or sinks, especially growth sinks, are "in control" of dry matter production (e.g. White et al. 2016; Körner 2015; Camarero and Andrés 2014; Gessler and Zweifel 2024).

Sucrose, along with other assimilated sugars, performs three key roles at the whole-plant scale: (1) a reserve of energy and its supply to sink organs; (2) metabolic precursor and supply to sink organs; and (3) regulatory signalling (Fichtner et al. 2021; Saddhe, Manuka, and Penna 2021; Choudhary et al. 2022; Göbel and Fichtner 2023). Complex regulatory pathways maintain homeostasis in sucrose levels (Miret, Griffiths, and Paul 2024), and are the focus of much current research (e.g. Avidan et al. 2024; Chang and Zhu 2017). Sucrose homeostasis ensures energy and precursor supply rates to cells are compatible with their metabolic capacities and that overall osmotic balance is maintained (Saddhe, Manuka, and Penna 2021; Dominguez and Niittylä 2022). While many details of the regulatory networks responsible for sucrose homeostasis remain unknown, it is evident that feedbacks on source and sink activities play key roles (e.g. Avidan et al. 2024).

Boussingault (1868) is reported to have been the first to postulate that photosynthesis is regulated by its end products (Neales and Incoll 1968; Paul and Foyer 2001). Subsequent work has found that feedback regulation of photosynthesis is frequently observed (Ainsworth and Bush 2011), and is strongly linked to whole plant nitrogen status (Paul and Foyer 2001), although it may not occur when it is drought-stress that reduces growth (Gessler and Zweifel 2024). Promotion of C-source activities such as photosynthesis and storage remobilisation occurs when sugars are depleted, whereas promotion of sink activities such as cellular growth and biosynthesis occurs when sugars are abundant (Eveland and Jackson 2012; Avidan et al. 2024). Sucrose can be sensed directly, or a signal is expressed through glucose or UDP-glucose products, with these hexoses promoting organ growth and cell proliferation, while sucrose promotes differentiation and maturation (Borisjuk et al. 2002; Koch 2004). The relevance of these different regulatory roles can be seen in relation to their differential spatial distributions across developing wood (e.g. Uggla et al. 2001).

Evidence for source-sink feedbacks operating through these mechanisms in mature trees has been found using phloem girdling, compression, and chilling to alter rates of C supply to the cambial meristem (Rademacher, P. Fonti, LeMoine, M. Fonti, Basler, et al. 2021; Rademacher, P. Fonti, LeMoine, M. Fonti, Bowles, et al. 2022). Rademacher, P. Fonti, LeMoine, M. Fonti, Basler, et al. (2021), using phloem girdling and compression treatments, found wood formation in *Pinus strobus* was correlated with C supply. Stem regions with presumed increased C-supply experienced increased radial growth, mainly due to higher numbers of cells, with fewer cells produced in regions with constrained supply. Despite

large changes in growth, labile carbohydrate concentrations were relatively stable across the different stem regions, reflecting homeostasis, with respiration rates correlated with C-supply. Rademacher, P. Fonti, LeMoine, M. Fonti, Bowles, et al. (2022) used chilling to control phloem transport in mature *Acer rubrum* and also found large effects on radial growth. The treatment additionally caused increased leaf carbohydrate concentrations and downregulation of photosynthetic capacity.

Despite overwhelming evidence that plants operate as integrated wholes, with source and sink activities feeding back on one another to maintain sugar homeostasis, global vegetation dynamics models (known as "Dynamic Global Vegetation Models": DGVMs), used as components of Earth system models (Arora et al. 2020) and as tools to analyse the global carbon budget (Sitch et al. 2024), assume a uni-directional relationship (sometimes with buffering from a storage pool), treating growth as the direct outcome of the supply of C from photosynthesis (Friend et al. 2019). Conceptually this can result in unrealistic behaviour for three broad, inter-linked, reasons: (1) sink environmental sensitivity (rates of sink and source activities respond differently to environmental factors), (2) sink capacity (growth rate at any one time is ultimately limited by meristem size and potential rates of cell proliferation and wall synthesis are under intrinsic metabolic controls), and (3) feedback on photosynthesis (if growth does not use all the available C, concentrations of labile C will increase and lead to down-regulation of source activities). However, the implications of, and methodology for, implementing source-sink feedback in DGVMs remain unclear.

Various frameworks have been suggested for integrating C sources and sinks in plant growth models (e.g. Friend et al. 2019; Gessler and Zweifel 2024), but these have not been formally assessed. Hayat et al. (2017) reviewed those tree growth models with explicit consideration of sink processes (e.g. Schiestl-Aalto et al. 2015), and while there had been many advances an approach integrating sources and sinks into a single framework was lacking. They therefore proposed and tested a new approach in which tree growth occurs from apical and lateral meristems, consuming C derived from photosynthesis, with a dynamic labile storage pool. The emphasis of the approach was on the geometric properties of the tree as it grows (height versus diameter), and controls thereof. It did not consider homeostasis of labile C or feedbacks between sources and sinks.

Other more recent models with explicit treatment of source and sink activities include Oswald and Aubrey (2023). Their approach is conceptually similar to the one described below with its emphasis on feedbacks regulating carbohydrate concentrations and implemntation using a simple mathematical approach. However, it uses somewhat different formulations and focuses on the seasonal dynamics of starch concentrations in response to supply and demand, rather than the effects of sugar feedbacks on environmental growth responses as here.

Formulating and assessing approaches to integrating C source-sink feedbacks within plant growth models is a priority, both to determine the conceptual framework for how such approaches might be constructed and to examine what the consequences might be for simulated growth responses to changes in potential source and sink activities (e.g. caused by effects of environmental factors). This paper explores the first-order implications of the effects of non-linear source-sink coupling through a common sugar

pool on growth responses to changes in potential source and sink activities. 'Potential' here refers to the activity of the source or sink when fully activated by the C-feedback, and is determined by the mass of the organ/tissue, its intrinsic metabolic machinery, and the effects of environmental and other non C-feedback factors (e.g. phytohormones). Responses of either source or sink activities to specific environmental factors are not considered. The aim here is to explore the general implications of the coupling for the behaviour of the system in response to variation in potential source and/or sink activity. Specific questions addressed include:

1) How can source-sink feedbacks and sugar homeostasis be represented?

2) How does the emergent behaviour of a homeostatic approach compare with a source-only driven approach?

3) How does this coupled behaviour compare with observed responses versus a source-only approach?

4) What insights into the behaviour of real plants (e.g. responses to atmospheric CO_2) can be derived from consideration of homeostatic behaviour?

5) What are the next steps in integrating the source-sink approach in a DGVM?

Below we introduce the approach to be considered, determine a realistic set of parameter values, examine the numerical time-dependent behaviour, explore the equilibrium behaviour of the proposed approach, and examine its response under conditions of C starvation or halted growth. Finally we discuss the implications of considering source-sink feedbacks in DGVMs in the manner proposed, and the next steps that will be required to move beyond source-only driven DGVMs.

2 Description

2.1 Governing equations

A parsimonious yet plausible theoretical approach to a biological system or process can generate conceptual understanding and provide a framework for more complete and mechanistic treatments. To gain insight into the consequences of source-sink feedbacks for plant growth responses to environmental variation and explore a potential approach for their inclusion in DGVMs, it is assumed that generic C sources and sinks are linked by a common sugar pool which can vary in size over time. The sugar is assumed to be sucrose, the source net photosynthesis, and the sink growth of structural mass (e.g. wood). The concentration of plant sucrose evolves with time according to,

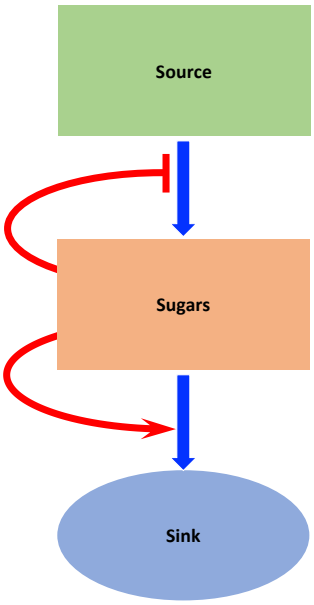

Figure 1: Schematic of source-sink feedbacks mediated by sugars. Blue arrows represent flows of sucrose, flat-headed red arrow represents an inhibition signal, and pointed red arrow represents an activation signal. Sugars inhibit source activity and promote sink activity, resulting in homeostasis in their own concentration.

$$M\frac{\partial[Su]}{\partial t} = q_{in} - q_{out} \tag{1}$$

where $[Su]$ is the mean plant sucrose concentration over all structural mass, q_{in} is the source term, q_{out} the sink term, and M is the total structural dry mass. The equation is written as a partial differential equation partly because it assumes mass is fixed (the framework does not consider growth in mass, conversion to heartwood, or litter losses).

Homeostasis requires coordinated adjustments to C source and sink rates. These adjustments are assumed to be achieved by sucrose inhibiting net photosynthesis and activating growth, as represented in Figure 1.

The functional forms of the feedbacks represented by the red arrows in Figure 1 are assumed symmetric and approximated by Hill equations (Hill 1910; Gesztelyi et al. 2012). Hill equations are frequently used to represent biological-control interactions (e.g. transcription factor regulation of gene expression: Alon 2020). They are biologically interpretable as a dose-response function where 'cooperativity' plays an important role. Coorperativity refers to the unit number of regulator required to initiate a unit molecular response, and is a frequent property of gene transcription regulation (Alon 2020). Sucrose acts as both a transcriptional and a translational regulator (e.g. Lastdrager, Hanson, and Smeekens 2014) and affects the phospho-proteome through the protein kinase complex SnRK1 (Leene et al. 2022). Because all of these processes ultimately result in up- or down-regulation of coordinated transcription factor networks, Hill equations are likely to be an appropriate way to represent source-sink interactions, albeit at a highly-aggregated level compared to the actual control pathways. The continuous and sigmoidal form of

the Hill equations as used here ensures both stability and continuity compared to linear functions, yet are easy to parameterise as they only have two parameters.

The Hill equation describing the activating effect of sucrose on sinks, f_a (a scalar), is,

$$f_a = \frac{[Su]^n}{{K_{Su}}^n + [Su]^n} \tag{2}$$

where K_{Su} is the value of [*Su*] at which sink activity is at half its potential rate and the exponent n is the "Hill coefficient", which determines the strength of the control (and is related to the cooperativity of the interaction, with higher values producing stronger control). K_{Su} can be considered as the neutral sucrose concentration in that the activities of the sources and sinks are equally activated when $[Su] = K_{Su}$. At the neutral sucrose concentration the sources and sinks are neither inhibited nor activated, proceeding at their default rates, which are defined as 50% of their potential rates (given by α and β).

For simplicity, spatial variation in sugar concentrations and finite transport between organs and tissues is not considered. However it is acknowledged that spatial variation in concentrations (Furze et al. 2019) and transport limitations (Aluko et al. 2021), especially in large plants such as mature trees, will influence source-sink relations, and indeed key roles in some models of C partitioning between organs such as that of Thornley (1972). Here we are interested in the first-order behaviour of the system under a set of broad assumptions. A mean sucrose concentration is assumed to be sufficient as an indicator of whole-plant source-sink balance.

The inhibiting effect of sucrose on sources, f_i (a scalar), is given by,

$$f_i = \frac{{K_{Su}}^n}{{K_{Su}}^n + [Su]^n} = 1 - f_a \tag{3}$$

We assume linear effects of these feedback strengths on source and sink activities. q_{in} is therefore related to f_i and q_{out} is related to f_a according to,

$$\begin{aligned} q_{in} &= f_i \alpha \\ q_{out} &= f_a \beta \end{aligned} \tag{4}$$

where α and β are the rates of net photosynthesis and growth, respectively, when fully activated. Sink activity is limited to consideration of only growth in order to keep things as simple as possible. In a complete treatment, α and β would depend on the environment and developmental processes (see below), and are therefore more correctly denoted $\alpha(t)$ and $\beta(t)$, but are considered constant in time for now. Neutral values of f_i and f_a are 0.5 (scalar), and therefore α and β will be 2x their neutral rates (i.e. their rates when sugars are at the neutral value, K_{Su}). If f_i and f_a were fixed at their neutral values, source and sink activities would be able to vary independently from one another in response to environmental factors resulting in and non-homeostatic behaviour in sugar concentrations.

In real plants, the effect of f_i on net photosynthesis (q_{in}) could be realised through controls on foliage

area through, for example, increased leaf senescence (Paul and Foyer 2001), and/or controls on the quantity of photosynthetic apparatus per unit area and its activity through expression of photosynthetic genes (e.g. Sheen 1990), but the precise mechanisms are not considered explicitly. Similarly, the effect of f_a on growth could be realised through regulation of cambial cell proliferation, volume increase, and wall deposition, as well as of apical growth (e.g. Kiba et al. 2019; Avidan et al. 2024).

By implication, α will be determined by the resources available to produce foliage, photosynthetic apparatus, and potential rates of carboxylation/sucrose production per unit investment, and therefore include external factors such nutrient availability, atmospheric CO_2 concentration, and soil water (which limits leaf area and stomatal conductance), as well as available light and temperature. Similarly, β will be determined by meristem sizes and intrinsic maximum rates of cell division, enlargement, and wall thickening, as well as the effects on these processes of temperature, soil water, and nutrient availability. Viewed this way, f_i and f_a are acclimative process controls that influence the sucrose balance on timescales of hour to days - they regulate the activity of the sources and sinks, but their capacities are fixed by other factors, internal and external. To aid interpretation and insight we assume fixed structural mass, and hence meristem volume, and focus on the equilibrium condition. Growth of structure will eventually affect growth meristem size, for example, but these longer-term effects are not considered here in order to focus on the consequences for growth of the primary feedbacks responsible for sucrose homeostasis.

2.2 Parameter values and integration

A default set of parameter values is given in Table 1. The value for K_{Su} is taken as 2.88% of dry matter, the mean sugar concentration across foliage, branch, stem, coarse roots, and fine roots measured by Würth et al. (2005) across nine tropical forest species (individual compartment values were 4.0%, 3.9%, 2.6%, 2.3%, and 1.6% respectively). The Hill coefficient (n) is set to 4, the top of the range given as typical for regulation of gene transcription by Alon (2020), producing a fairly steep function (i.e. relatively tight homeostatic regulation). α and β, the potential rates of net photosynthesis and growth, are each set to 13.14×10^{-3} kg(Su) m^{-2} day^{-1}, equivalent to double the 10.1 Mg C ha^{-1} a^{-1} rate of NPP reported by Malhi et al. (2009) for a tropical rainforest site. The structural mass, M, is also taken from this source (i.e. 228 Mg(C) ha^{-1}), equivalent to 48.1 kg(DM) m^{-2}, assuming 0.474 g(C) g(DM)$^{-1}$ (Martin and Thomas 2011).

Equation 1 was integrated using Euler's method over a loop in a Fortran code. The justification for this first-order approach is that it is efficient and the set of equations converge stably to the equilibrium state for typical parameter values. von Neumann stability analysis indicates that stability requires that $\Delta t \leq 0.9\frac{KM}{\alpha+\beta}$ (Appendix 9.1). For the default parameter set in Table 1 this gives a value of $\Delta t \lesssim 46$ days.

Table 1: Parameters and their default values. "DM" is structural dry matter. Area units refer to ground area.

Description	Symbol	Value	Units
Neutral sucrose fraction	K_{Su}	0.028	fraction of DM
Hill coefficient	n	4	unitless
Potential rate of net photosynthesis	$\alpha(t)^1$	13.14×10^{-3}	kg(Su) m^{-2} day^{-1}
Potential rate of growth	$\beta(t)^1$	13.14×10^{-3}	kg(Su) m^{-2} day^{-1}
Structural mass	M	48.1	kg(DM) m^{-2}
Timestep	Δt	1	day

[1]The t denotes that these parameters can change over time with environmental conditions and/or developmental controls.

3 Results

3.1 Test for convergence

The behaviour of the model using the default parameters in Table 1 is shown in Figure 2 for a range of initial sucrose concentrations. The integration is stable due to the feedbacks, with convergence to K_{Su} occurring over ca. 300 days. This relative slow response results from the large structural mass compared to the input flux, with the daily flux being <1% of the equilibrium total Su mass. $[Su]$ is strongly buffered in relation to sources and sinks on a daily timescale, but feedbacks generate homeostatic convergence over weeks to months from a perturbed state.

3.2 Equilibrium condition

The equilibrium condition allows unbiased quantification of model sensitivity to parameters and impacts of source-sink feedbacks. Non-equilibrium states are harder to evaluate quantitatively as the state depends on the distance from equilibrium. Furthermore, sucrose concentrations should remain close to equilibrium under the default parameter set given the strong homeostatic effect of source-sink feedbacks (see next section). At equilibrium,

$$\frac{\partial [Su]}{\partial t} = 0 \tag{5}$$

Taking into account sucrose feedbacks (Equations 3) and assuming fixed mass, the relationship of equilibrium growth rate with potential net photosynthesis and potential growth rates reduces to (see Appendix 9.2 for derivation),

$$q_{out} = \frac{\alpha\beta}{\alpha + \beta} \tag{6}$$

The response of equilibrium growth rate to potential growth and net photosynthesis rates is therefore independent of the strength of the feedbacks (i.e. the Hill coefficient, n). The rate of change in growth

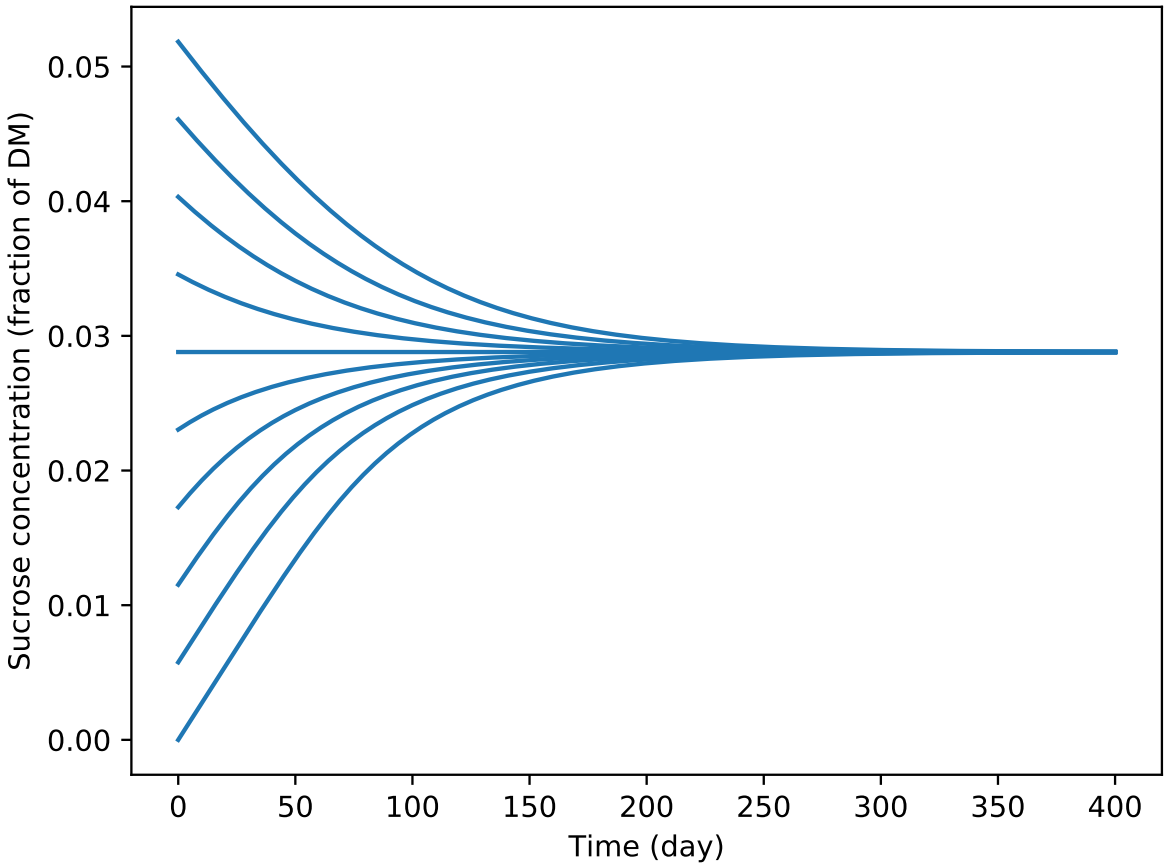

Figure 2: Simulated evolution of sucrose concentration over time using Equation 1 when initialised with different values for Su. Parameter values as in Table 1.

rate with change in α is (see Appendix 9.2 for derivation),

$$\frac{\partial q_{out}}{\partial \alpha} = \frac{\beta^2}{(\alpha + \beta)^2} \tag{7}$$

indicating a steeply increasing effect of variation in α on growth rate as α tends to zero. This makes sense as under conditions of low α growth becomes more source-limited.

3.3 Responses to source-sink coupling

The responses of the model equilibrium state and rates to variation in potential source or sink rates, α or β, are shown in Figure 3 using the set of remaining default parameters in Table 1.

The responses of equilibrium net photosynthesis and of growth rate to varying potential net photosynthesis or potential growth rates are shown in Figure 3(a). By definition the two rates are equal at equilibrium. Also, the responses are the same whether potential net photosynthesis or potential growth

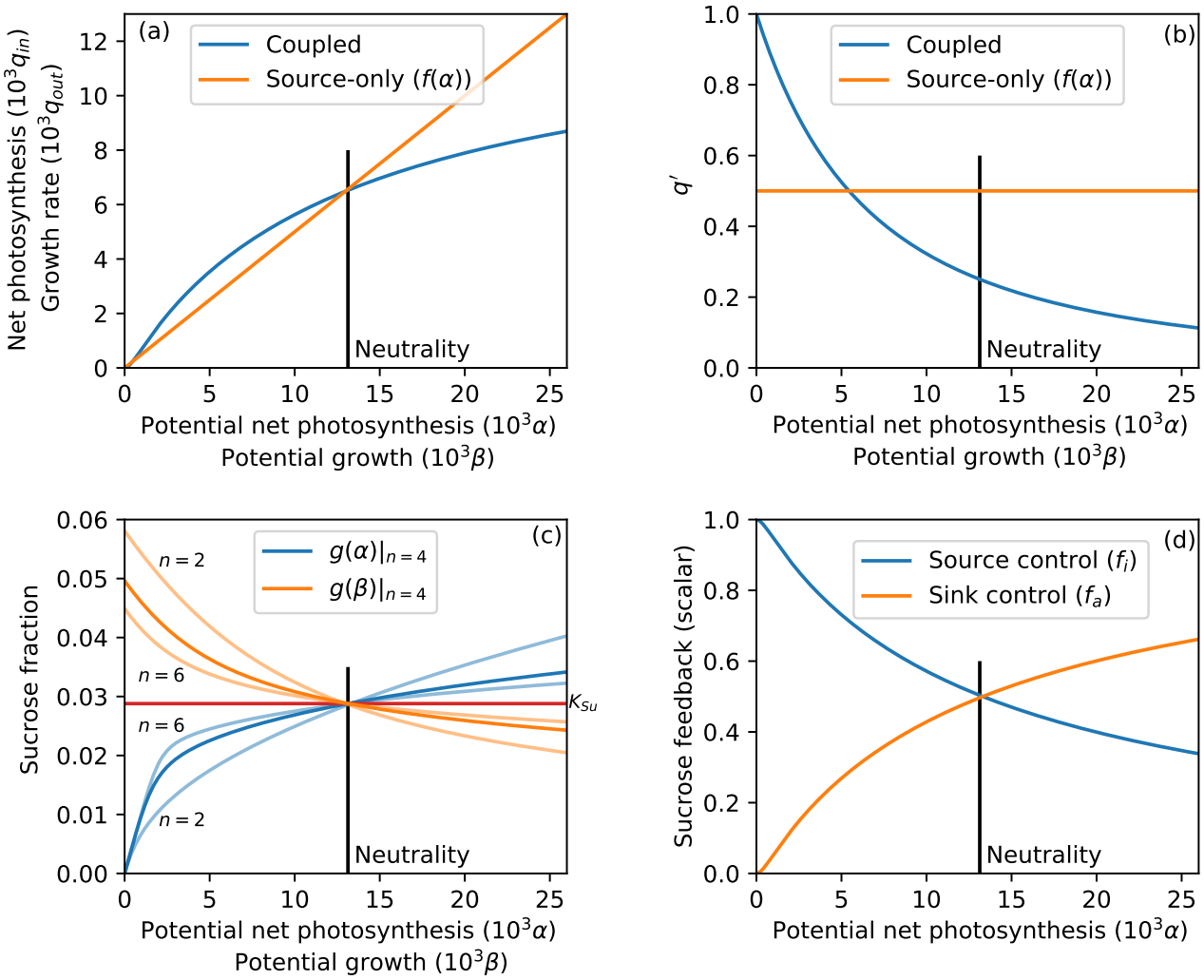

Figure 3: Simulated equilibrium rates states and rates using parameter values in Table 1, except where specified. (a) Responses of equilibrium net photosynthesis (q_{in}) and growth rate (q_{out}) to potential net photosynthesis rate (α) or potential growth rate (β) ('Coupled'). Also shown are the responses assuming net photosynthesis = $\alpha/2$ and growth rate is equal to net photosynthesis rate with no feedback effects ('Source-only ($f(\alpha)$)'). (b) Derivatives of the responses shown in (a). (c) Responses of equilibrium sucrose fraction to potential net photosynthesis ($g(\alpha)$) or potential growth rate ($g(\beta)$) with different values of Hill coefficient (n). (d) Responses of equilibrium sucrose feedback controls to potential net photosynthesis (α). All panels indicate the position of the neutral condition for the coupled model (i.e. $f_a = f_i$ and $Su = K_{Su}$) using a vertical black line.

rates are varied due to the symmetries in the feedback effects (Equation 3) and the flux-response functions (Equation 4) (see below). Therefore only one curve is shown. This curve shows strong saturation with potential source or sink activity, demonstrating the constraining effect of sources on sinks and sinks on sources, each imposing a limit on the other. Even when potential net photosynthesis or growth rate is double its default value, growth or net photosynthesis, respectively, increase to only 1/3 above their default rates, 2/3 of their potential rates (cf. Equation 6). Equilibrium growth has the upper limit of β as

α is increased (obviously the growth rate cannot exceed its potential), and vice versa.

Also shown is the response of the growth rate if it is assumed to equal net photosynthesis with no feedbacks (denoted $f(\alpha)$), similar to assumptions in source-centric approaches. This response is calibrated to equal the coupled response at the neutral condition (i.e. $f_a = f_i$ and $Su = K_{Su}$ in the coupled mode) to facilitate comparison, which requires net photosynthesis to be 1/2 of its potential. Above this neutral condition the two approaches diverge considerably as the effect of net photosynthesis capacity on growth saturates due to the limiting rate of potential growth in the coupled model. At double the default value of potential net photosynthesis, the rate of growth is 50% higher without feedbacks than with homeostatic coupling, and therefore the coupling reduces growth by 1/3 compared to the non-coupled assumption.

The derivatives of the responses in Figure 3(a) are shown in Figure 3(b). At the neutral point for the coupled model, the sensitivity of growth to variation in potential net photosynthesis is only 50% of the sensitivity if growth is entirely source-driven. The sensitivity of the coupled model only reaches that of the source-driven approach when potential net photosynthesis is reduced to 50% of its default value.

Equilibrium sucrose fraction for the full coupled model increases with α and decreases with β, equalling K_{Su} at their default values (Figure 3(c)). Source-sink feedbacks are highly effective at maintaining homeostatic sucrose levels across a wide range of potential net photosynthesis and growth rates. For example, a 50% increase in α from its default value results in f_{Su} increasing by only ca.11%. Similarly, an increase in potential growth (i.e. β) of 50% reduces f_{Su} by only ca.10%. Figure 3(c) also shows the equilibrium sucrose responses for different values of the Hill coefficient (n), which could be calibrated from observed behaviour in sugar concentration with respect to environmental conditions such as atmospheric CO_2.

Figure 3(d) shows the responses of the feedback signals to potential net photosynthesis for the full model when at equilibrium. Controls are stronger when α is below its default value than above, representing a starvation response. The responses to changing potential growth are the inverse of these responses (not shown), with source control increasing and sink control decreasing with sink strength.

3.4 Dynamic responses to starvation or halted growth

The dynamic consequences for the model of halted source or sink were investigated in order to assess the temporal dynamics and compare with real-world observations. These scenarios represent either constrained photosynthesis ('starvation', e.g. due to defoliation) or constrained growth (e.g. due to intense drought directly affecting xylogenesis), respectively. For both, the fully coupled model was integrated using the parameters in Table 1 for 500 days to bring it to equilibrium from an initial state with no sucrose (cf. Figure 2). For the first, the C source was then switched off by setting q_{in} = 0, and the resulting behaviour of the growth sink (q_{out}; 'Starvation') and sucrose pool ($[Su]$) are shown in Figure 4. Growth declines steeply as sucrose concentrations fall, reaching 50% of the equilibrium rate after 171 days, or nearly 6 months. Such a response is consistent with the observed effects of defoliation on radial increment in mature trees (e.g. Naidoo and Lechowicz 2001; Hilmers et al. 2023). Starvation causes sucrose to decline as growth continues, consistent with observations (e.g. Z. Wang, Zhou, and C. Wang 2021).

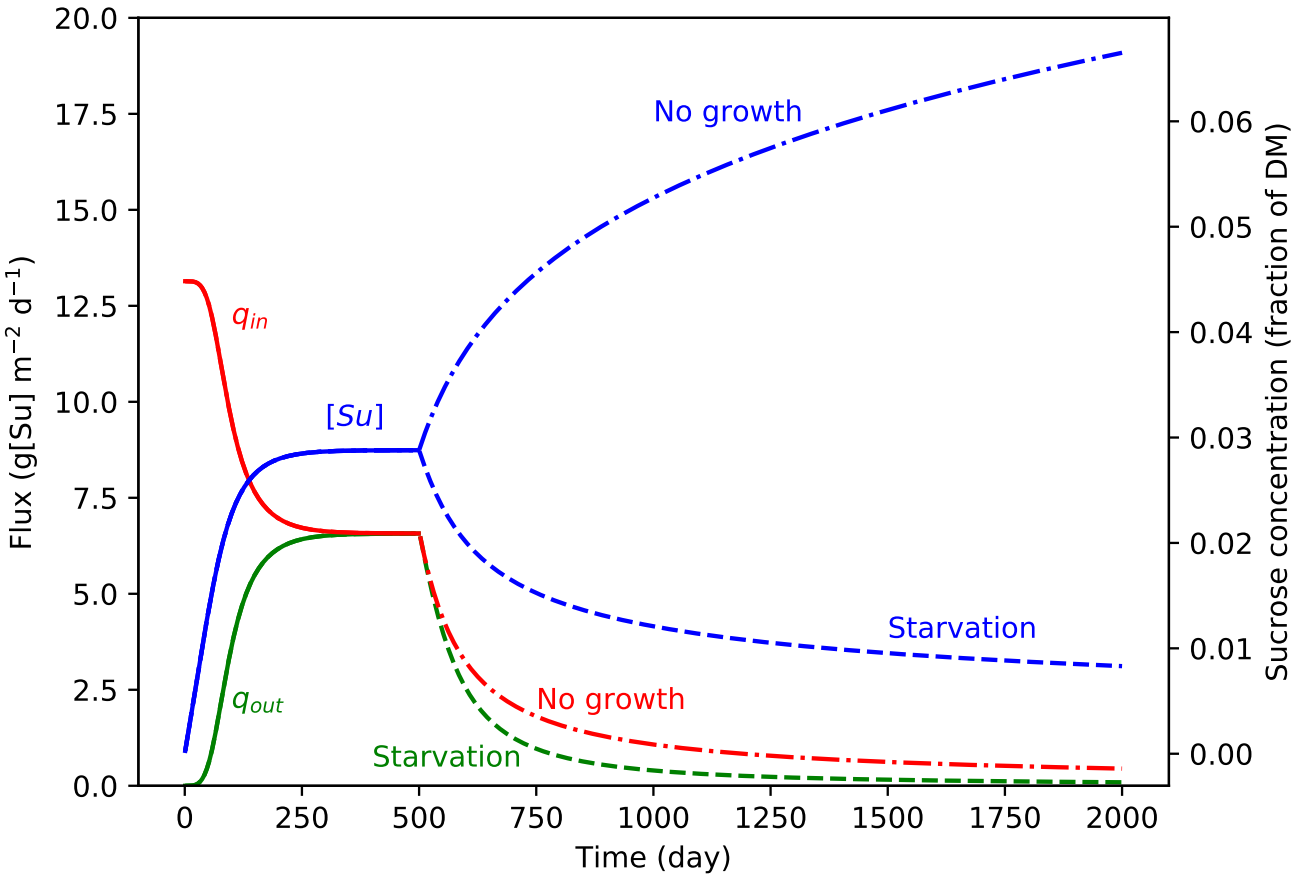

Figure 4: Simulated dynamic source and sink fluxes and sucrose concentrations using parameter values in Table 1 for a spin-up of 500 days, after which either q_{in} ('Starvation') or q_{out} ('No growth') is set to 0.

For testing the effect of constrained growth, the C sink was switched off by setting $q_{out} = 0$ at the end of the spin-up period. The effect of this imposed growth restriction is to cause a reduction in photosynthesis (q_{in}; 'No growth'), with a somewhat slower dynamic than the response of growth to zero photosynthesis (Figure 4). This asymmetry in effects of source and sink constraints is due to the asymmetry in the Hill equations. As sucrose levels fall with starvation, the activation of the sink falls, reaching 88.2% of its neutral value (i.e. 0.5) when halved. Increasing sucrose by the same amount from its neutral value increases activation by 67.0%. Hence declining sucrose levels have a stronger relative effect than when increasing, resulting in the asymmetry between the effects of starvation and no growth in Figure 4. Even after 1,500 days of zero growth, photosynthesis is continuing at 6.8% of its neutral value, whereas after the same period with no photosynthesis, growth has declined to only 1.4% of its neutral value.

Observational evidence for effects of restricted growth independently of external effects on photosynthesis is rare due to methodological challenges. Using phloem chilling in mature *Acer rubrum*, Rademacher, P. Fonti, LeMoine, M. Fonti, Bowles, et al. (2022) found reduced woody growth below the

chilling collars, accumulation of sugars in phloem and leaves above the collars, and reduced photosynthethis capacity, all consistent with the behaviour of the model under $q_{out} = 0$. The incomplete homeostasis found in these experiments also occurs in the model.

4 Discussion

Despite the knowledge that plants operate as integrated wholes, with strong coupling between sources and sinks, DGVMs are largely C source-only driven. While there have been numerous calls for the inclusion of explicit growth processes in DGVMs (e.g. Fatichi et al. 2019; Friend et al. 2019), approaches for doing this and for coupling growth to source activity require development and assessment. Additionally, the implications for growth responses of coupling of growth with source activity using such a mechanism require investigation. Here an approach based on the concept of homeostasis is described and analysed, with feedbacks from a common sucrose pool regulating source and sink activities. The approach is built around Hill functions representing aggregated controls on source and sink activities.

Using a realistic set of model parameters for a tropical rainforest site, the approach described here is effective at maintaining sucrose homeostasis while allowing for environmental effects on potential (i.e. fully activated) source and sink rates. Separation of feedback effects from potential source and sink rates (i.e. α and β) allows the effects of external environmental factors to be included while the system is still able to behave homeostatically. Maintenance of homeostasis through feedbacks constrains the extent to which changes in potential source or sink rates can affect overall growth (cf. Figure 3a). For example, the effect on growth of increasing potential net photosynthesis above the neutral value is strongly constrained by the potential growth rate.

An implication of these results is that the strong CO_2-fertilization effects on growth predicted by many DGVMs (e.g. Huntzinger et al. 2017) are likely to be unrealistic, with major consequences for projections of the future terrestrial C sink. Compared with the assumption of C source-driven growth, the equilibrium growth response to doubled net photosynthetic potential (e.g. due to increasing CO_2) is reduced from +100% to +33% in the fully coupled model. This response is reflected in experimental results, with the growth stimulation less than expected given the (initial) stimulation of photosynthesis due to, e.g., elevated CO_2 (Körner 2006). Variation in the growth response to CO_2 is often attributed to different levels of nutrient availability, which limits biomass production due to stoichiometric constraints (e.g. Jiang et al. 2024). This constraint is incorporated into a growing number of DGVMs (e.g. Zaehle and Friend 2010), but the consequences of dynamic coupling of sinks to sources as described here has not been explored. Our model approach allows for the incorporation of stoichiometric constraints through the β parameter, and the consequences for the coupled behaviour are simulated under the assumed mechanisms of coupled negative feedbacks to produce homeostasis in sucrose concentrations. This then allows for a treatment of the mechanistic interactions between C and nutrient constraints, such as of N and P.

The responses of the model to C starvation or halted growth, and the generic convergence simulations

shown in Figure 2, provide information regarding the temporal dynamics of the sugar pool (Figure 4). It is noteworthy that the response times are of the same order as a typical growing season. This suggests that total labile carbohydrates in mature trees will be dynamically and constantly converging to their equilibrium value, getting close to equilibrium during the growing season regardless of the starting point. However, a full assessment of the dynamics of carbohydrates during the course of the growing season (and interactions with phenology) requires separation of sugars and starch, and compartments within trees such as branches and roots (cf. Furze et al. 2019).

Inclusion of explicit growth in DGVMs has been advocated largely on the basis of evidence that growth processes can be more strongly regulated by environmental factors such as soil moisture and temperatures away from optima than photosynthesis (e.g. Gessler and Zweifel 2024). Coupling sources and sinks as described here widens this justification through demonstrating that even if sources are more strongly environmentally regulated than sinks, the growth response will still depend on feedbacks and hence sink capacity (which is never infinitely plastic), meaning growth processes need to be represented.

The homeostatic behaviour of the sucrose pool is consistent with observations and theory (e.g. Rademacher, P. Fonti, LeMoine, M. Fonti, Basler, et al. 2021; Miret, Griffiths, and Paul 2024). Therefore this component of the approach presented is presumably realistic to first order. The details of the feedback function forms are harder to verify, but at equilibrium are unlikely to be critical (N.B. the Hill coefficient does not affect the equilibrium responses to potential C source and sinks rates). It is the presence of the feedbacks themselves that govern the behaviour of the system, rather than the specific functional forms (Oswald and Aubrey 2023). For further refinement, observations of seasonal variation in sucrose levels would allow these functions to be constrained for non-equilibrium conditions. The main model development challenge therefore concerns how to extend the approach to include variation in α and β as functions of internal and external factors, and how to implement other direct influences on sucrose levels such as storage and respiration dynamics. The key to the first is distinguishing between feedback effects (that influence current activity within potential rates) and changes in potential rates themselves, which are governed by broader biological and environmental factors. This is the object of on-going work, in which the dynamic responses of the mass and activities of structural components (e.g. cambial meristem) are being formulated.

It would be valuable to explore experimentally the assumptions within, and insights derived from, the model presented here. In particular, the functional dynamics of homeostatic feedback could be explored by manipulating source and sink strength and measuring carbohydrate concentrations over time (cf. Figure 4). What are the response functions between source and sink activities and sucrose concentrations? Do Hill functions reproduce the observed behaviour? It would be important to explore homeostatic behaviour over a range of plant sizes, with the expectation that larger plants would be more buffered and potentially relatively more sink-limited (cf. Hayat et al. 2017). Another important consideration is the extent to which starch reserves buffer sucrose concentrations and whether starch synthesis is passive overflow or actively controlled (cf. Hartmann and Trumbore 2016). Experimental manipulation of source and sink activities in the context of starch-sucrose dynamics would be extremely interesting. Starch-deficient mutant hybrid aspen trees are starting to be used for such experiments (Wang et al. 2022), and are likely

to yield important information in future work.

The issue as to under which circumstances plants are C source- or sink-limited has been the subject of much discussion (e.g. Körner 2006). The analysis presented here, based on maintenance of sucrose homeostasis through feedbacks on sources and sinks, suggests that such a clear dichotomy does not reflect the dynamic and continuous nature of plant carbon allocation, where source and sink activities are dynamically regulated by both environmental and internal conditions, as well as the balance between source and sink demands. Growth and photosynthesis are coupled together. Their relative importance varies, however, as their potential rates vary, for example with environmental conditions, which helps to explain why experimental evidence is inconclusive as to whether C source or sink limits growth (a similar sentiment was expressed by Gessler and Zweifel (2024)). In our model, the relative effect of source and sink strength can be quantified as the derivative of growth with respect to α or β (as in Figure 3(b)). C source is more important than sink when $\alpha > \beta$ because then $\partial q_{out}/\partial\alpha > \partial q_{out}/\partial\beta$, and vice versa.

In conclusion, a parsimonious theoretical approach to coupling plant C source and sink activities through a shared sucrose pool has been presented and its implications assessed. Such coupling strongly constrains the response of growth to changes in C source activity and suggests a pathway to more realistic integration of whole-plant physiology and environmental controls in DGVMs. Future research will focus on extending this framework through developing detailed physiological dynamics of source and sink activities (i.e. replacing α and β by process-based representations at the individual plant scale) and integration of whole-plant growth into a DGVM.

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6 Competing interests

No competing interest is declared.

7 Author contributions

A.D.F. conceived of the study, wrote and ran the model, and wrote the first draft of the manuscript. P.R.T. derived the stability analysis and wrote the relevant section in the Supporting Information, as well as contributing to mathematical ideas in the main manuscript. All authors contributed to interpretation of model output and provided input to the final version of the manuscript.

8 Data availability

Model code can be found on GitHub: https://github.com/adfriend45/sucrose

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9 Supporting Information

9.1 von Neumann stability analysis

The numerical scheme for the sink–source model can be written:

$$N_{i+1} = N_i + \frac{\Delta t}{M}\left((\alpha+\beta)\frac{K_{Su}^n}{K_{Su}^n + N_i^n} - \beta\right) \tag{8}$$

Here N_i is the numerical approximation to Su_i at time $i\Delta t$. Further, we define $\epsilon_i = N_i - Su_i$ to be the numerical error introduced.

Hence, writing $N_i = Su_i + \epsilon_i$, and Taylor expanding Equation 8 to linear order in ϵ, we find that ϵ

obeys

$$\epsilon_{i+1} = \epsilon_i \left(1 - \frac{\Delta t}{M}(\alpha+\beta)\frac{cK_{Su}^n Su_i^{n-1}}{(K_{Su}^n + Su_i^n)^2}\right) \tag{9}$$

We define $G = \epsilon_{i+1}/\epsilon_i$ to be the error gain. To ensure that the error does not grow, we require $|G| \leq 1$, and to avoid oscillations in the sign of the error we require $G \geq 0$. Imposing both of these conditions on G, we find that we require

$$\left\{\frac{\Delta t}{M}(\alpha+\beta)\max_{\{Su\geq 0\}}\frac{cK_{Su}^c Su^{c-1}}{(K_{Su}^c + Su^c)^2} \leq 1\right\} \tag{10}$$

and

$$\left\{\frac{\Delta t}{M}(\alpha+\beta)\min_{\{S\geq 0\}}\frac{cK_{Su}^c S_u^{c-1}}{(K_{Su}^c + Su^c)^2} \geq 0\right\} \tag{11}$$

The second of these conditions is clearly true, so this is equivalent to requiring

$$\Delta t \leq \frac{4n}{n^2-1}\left(\frac{n-1}{n+1}\right)^{1/n}\frac{K_{Su}M}{\alpha+\beta} \approx 0.9\frac{K_{Su}M}{\alpha+\beta} \tag{12}$$

where the last approximate equality is for $n = 4$. Further, if α and β vary in time, then the stability condition (Equation 12) becomes

$$\Delta t \lesssim 0.9\frac{K_{Su}M}{\max(\alpha(t)+\beta(t))} \tag{13}$$

While Δt under this constraint for the parameter values in Table 1 is significantly larger than would be used in a typical implementation (e.g. a maximum of 6-hr to capture the diurnal solar cycle), grasses, for example, might have similar NPP but significantly lower M. Therefore it would be prudent to test for stability during a simulation and switching to a smaller Δt when necessary.

9.2 Equilibrium growth rate

At equilibrium source and sink fluxes are equal,

$$q_{in} = q_{out} \tag{14}$$

and therefore.

$$\frac{{K_{Su}}^n}{{K_{Su}}^n + [Su]^n}\alpha = \frac{[Su]^n}{{K_{Su}}^n + [Su]^n}\beta \tag{15}$$

Solving for equilibrium $[Su]^c$ gives,

$$[Su]^n = {K_{Su}}^n \alpha/\beta \tag{16}$$

substituting into the expression for q_{out} and simplifying,

$$
\begin{aligned}
q_{out} &= \frac{[Su]^n}{{K_{Su}}^n + [Su]^n}\beta \\
&= \frac{{K_{Su}}^n \alpha/\beta}{{K_{Su}}^n + {K_{Su}}^n \alpha/\beta}\beta \\
&= \frac{\alpha/\beta}{1 + \alpha/\beta}\beta \\
&= \frac{\alpha\beta}{\alpha + \beta}
\end{aligned} \tag{17}
$$

The derivative of q_{in} with respect to α can then be found using the quotient rule,

$$
\begin{aligned}
\frac{\partial q_{in}}{\partial \alpha} &= \frac{\beta(\alpha + \beta) - \alpha\beta \cdot 1}{(\alpha + \beta)^2} \\
&= \frac{\beta^2}{(\alpha + \beta)^2}
\end{aligned} \tag{18}
$$