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Plant growth and the optimal sharing of photosynthetic products with a mycorrhizal symbiont

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ABSTRACT

Questions: What fraction of photosynthetic products should a plant allocate to a mycorrhizal symbiont to maximize its own fitness?

Mathematical methods: Maximization of plant shoot biomass at equilibrium as a function of the fraction of photosynthetic carbon allocated to a mycorrhizal symbiont in a system consisting of two ordinary differential equations describing the growth of the plant and the symbiont.

Key assumptions: During growth, the plant maintains an optimal ratio of the rates at which carbon and nutrients become available by varying the ratio of its shoot and root biomass. Plant fitness is maximized by maximizing shoot biomass at equilibrium.

Conclusions: Sharing of photosynthetic products with a mycorrhizal symbiont is optimal if and only if the cost-efficiency of the mycorrhiza in terms of the rate of nutrient acquisition per unit of carbon cost is sufficiently large and in particular exceeds that of uninfected roots. If the cost-efficiency of uninfected roots is very low, then symbiosis with the mycorrhiza is obligatory for plant survival.

Keywords: mycorrhiza, optimization model, plant growth model, symbiosis

INTRODUCTION

Symbiotic mycorrhizal fungi benefit a plant by increasing the rate of absorption of mineral nutrient in the roots (Koide, 1991). Mycorrhizal fungi may also impose a cost for the plant in terms of carbon utilization, because the respiration rate of infected roots tends to be higher than that of uninfected roots (Jones *et al.*, 1991; Marschner, 1995; Smith and Read, 1997). Tuomi *et al.* (2001) formulated a model for the optimal balance of the benefits and the costs of mycorrhizal infection. In particular, they found that plants supporting mycorrhizal fungi may evolve even if they are less cost-efficient than uninfected plants in terms of acquired mineral nutrient per unit of carbon cost. We present a model for plant growth and the optimal

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sharing of photosynthetic products with a mycorrhizal symbiont that gives a different result.

Carbon and nutrients are essential and non-substitutable resources so that the availability of one resource defines a maximum possible plant growth rate irrespective of the availability of the other resource (Begon *et al.*, 1996). As in the model of Tuomi *et al.* (2001), we assume that there exists a specific ratio of the rates of nutrient and carbon acquisition where plant growth is limited by both resources at the same time. We refer to this specific ratio as the 'optimal' nutrient–carbon ratio. Our model differs from that of Tuomi *et al.* (2001) in two important ways, however: First, we assume that during growth the plant maintains the optimal nutrient–carbon ratio by continually adjusting its root–shoot ratio, while in the model of Tuomi *et al.* (2001) the root–shoot ratio is fixed, and the ratio of the rates at which carbon and nutrients become available is regulated by varying the fraction of infected roots instead. Secondly, in our model plant size reaches an equilibrium as opposed to unlimited growth in the model of Tuomi *et al.* (2001), so that instead of maximizing plant growth rate as a function of the proportion of infected roots, we maximize the equilibrium shoot biomass as a function of the proportion of carbon shared with the mycorrhiza.

In contrast with the results of Tuomi *et al.* (2001), we find that at the optimum a plant will support mycorrhizal infection if and only if the fungus is more cost-effective in terms of acquired mineral nutrient per unit of carbon cost than uninfected roots, and provided the cost-efficiency of the fungus exceeds a given minimum threshold value. This conclusion holds even if the mycorrhiza has a lower rate of nutrient acquisition per biomass than uninfected roots.

MODEL

Let W denote plant biomass and M mycorrhizal biomass, both measured as the amount of carbon present in living tissue. Plant biomass W we write as the sum of shoot biomass S and root biomass R:

$$W = S + R \tag{1}$$

where 'root' refers to the nutrient-absorbing part of the root system only, and therefore can be replaced by such terms as 'short root', 'fine root' or 'rootlet' (Ruotsalainen *et al.*, 2002). The rest of the plant, with some abuse of terminology, is referred to as the 'shoot'.

The growth of W and M is modelled by the differential equations

$$\begin{aligned} \dot{W} &= (1 - x)\varphi(S) - \mu S - \nu R \\ \dot{M} &= x\varphi(S) - \lambda M \end{aligned} \tag{2}$$

where $\varphi(S)$ is the rate of carbon acquisition by photosynthesis as a function of shoot biomass, $x \in [0, 1]$ is the fraction of carbon allocated to the mycorrhiza, and λ, μ and ν are respiration rates per unit of biomass for, respectively, the mycorrhiza, the shoot and the root. In (2) we implicitly assume that the mycorrhiza is carbon-limited and that spores of the mycorrhiza are ubiquitous, so that mycorrhizal biomass can increase even if $M = 0$ whenever sufficient carbon is available.

Furthermore, let $\chi(R)$ and $\psi(M)$ denote the rates of acquisition of nutrients as they become available to the plant through, respectively, the roots and the mycorrhiza. We assume that

$$\frac{\chi(R)+\psi(M)}{\varphi(S)} = r^* \quad \text{and} \quad \chi(R) > 0 \tag{3}$$

or

$$\frac{\psi(M)}{\varphi(S)} \geq r^* \quad \text{and} \quad \chi(R) = 0 \tag{4}$$

for some positive constant r^*. These equations mean that during growth, the plant tries to maintain a constant ratio of the rates at which nutrients and carbon become available by continually adjusting its R/S ratio. We refer to r^* as the optimal nutrient–carbon ratio. In (3), nutrients and carbon acquisition are optimally balanced, and plant growth is limited by both carbon and nutrients at the same time. In (4), the plant receives an excess of nutrients via the mycorrhiza so that plant growth is carbon-limited, and the optimal nutrient–carbon balance cannot be attained but is approximated as much as possible by minimizing nutrient absorption by the roots.

We take

$$\begin{aligned} \chi(R) &= \alpha R \\ \psi(M) &= \beta M \\ \varphi(S) &= \gamma S^{\theta} \end{aligned} \tag{5}$$

for positive α, β and γ and $\theta \in (0, 1)$. While the rates of nutrient acquisition by the root and the mycorrhiza are thus proportional to their respective biomass, the rate of photosynthesis is assumed to be a decelerating function of shoot biomass (e.g. as a consequence of self-shading).

To find the optimal proportion of carbon shared with the mycorrhiza, assuming that plant fitness increases with shoot biomass, we first prove that (2) subject to the constraint (3) or (4) has a unique stable equilibrium and then maximize the corresponding value of S as a function of x.

RESULTS

Using (1), (3), (4) and (5) we can eliminate W and R from (2), which then can be rewritten as

$$\dot{S} = \begin{cases} \dfrac{\gamma[\alpha(1-x)+\beta x - \nu r^*]\, S^{\theta} - \alpha\mu S - \beta(\lambda-\nu)M}{\alpha + r^*\gamma^{\theta} S^{\theta-1}} & \text{if} \quad 0 \leq M < \dfrac{r^*\gamma S^{\theta}}{\beta} \\ (1-x)\gamma S^{\theta} - \mu S & \text{if} \quad \dfrac{r^*\gamma S^{\theta}}{\beta} \leq M \end{cases} \tag{6}$$

$$\dot{M} = x\gamma S^{\theta} - \lambda M$$

The right-hand side of (6) has a discontinuity at $M = r^*\gamma S^{\theta}/\beta$, corresponding to the switch from condition (3) to (4). We refer to the corresponding curve in the (S, M)-plane as the discontinuity boundary.

A sample of various types of dynamics of (6) is given in Fig. 1. The positive quadrant of the (S, M)-plane is forward invariant, all forward orbits are bounded, and the origin is always an equilibrium. Equation (6) is readily solved analytically for non-trivial equilibrium

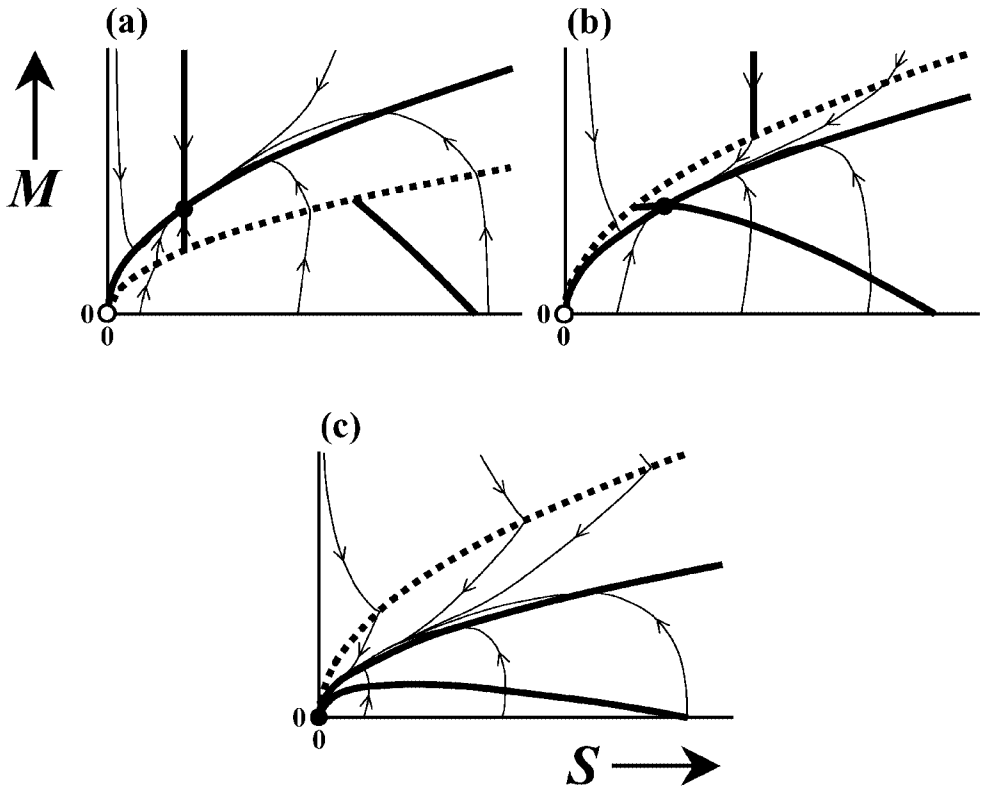

Fig. 1. Different types of dynamics. The dotted curve is the discontinuity boundary, the thick solid curves are the zero-clines (i.e. where $\dot{S} = 0$ or $M = 0$) and the thin curves are examples of orbits. Solid circles indicate stable equilibria, and open circles unstable equilibria. (a) $r^*(\lambda/\beta) < x < 1$ and $\lambda > \nu$. (b) $0 < (1-x)(\alpha/\nu) + x(\beta/\lambda) - r^*$ and $0 < x < r^*(\lambda/\beta)$ and $\lambda > \nu$. (c) $0 > (1-x)(\alpha/\nu) + x(\beta/\lambda) - r^*$ and $0 < x < r^*(\lambda/\beta)$ and $\lambda > \nu$.

solutions, which gives

$$S = \begin{cases} \left(\dfrac{\gamma}{\mu} \dfrac{\nu}{\alpha} \left[(1-x)\dfrac{\alpha}{\nu} + x\dfrac{\beta}{\lambda} - r^* \right] \right)^{\frac{1}{1-\theta}} & 0 \le x < r^* \dfrac{\lambda}{\beta} \\ \left((1-x)\dfrac{\gamma}{\mu} \right)^{\frac{1}{1-\theta}} & r^* \dfrac{\lambda}{\beta} \le x \le 1 \end{cases} \tag{7}$$

$$M = \frac{x\gamma S^{\theta}}{\lambda}$$

It follows that a non-trivial equilibrium exists, if and only if

$$0 < (1-x)\frac{\alpha}{\nu} + x\frac{\beta}{\lambda} - r^* \quad \text{and} \quad 0 \le x < r^* \frac{\lambda}{\beta} \tag{8}$$

or

$$r^* \frac{\lambda}{\beta} \leq x < 1 \tag{9}$$

Moreover, if it exists, then it is unique and given by (7). Under condition (8) the equilibrium lies below the discontinuity boundary (Fig. 1b), whereas under condition (9) the equilibrium lies on or above the discontinuity boundary (Fig. 1a).

In Appendix 2 we prove that if the non-trivial equilibrium exists, then it is locally attracting. In Appendix 3 we prove that the origin is unstable whenever the non-trivial equilibrium exists and that the origin is globally attracting if the non-trivial equilibrium does not exist. Thus, for every $x \in [0, 1]$, there exists one and only one equilibrium that is locally attracting. In Appendix 1, moreover, we prove that so-called pseudo-equilibria do not occur. (A pseudo-equilibrium is a point on the discontinuity boundary where the flows on both sides of the boundary are in exactly opposite directions and not tangent to the boundary.)

What is the optimal proportion of photosynthetic products shared with the mycorrhiza – that is, what value of x maximizes the equilibrium value of S? Let $\hat{S}(x)$ denote the value of S at the attracting equilibrium as a function of x. There are six qualitatively different configurations of the graph of $\hat{S}(x)$ depending only on the ordering of the quantities α/v, β/λ and r^*:

(a) If $0 < r^* < \beta/\lambda < \alpha/v$, then $\hat{S}(x) > 0$ for $0 \leq x < 1$, and $\hat{S}(x)$ is maximal for $x = 0$ (Fig. 2a).
(b) If $0 < r^* < \beta/\lambda = \alpha/v$, then $\hat{S}(x) > 0$ for $0 \leq x < 1$, and $\hat{S}(x)$ is maximal for all $0 \leq x \leq r^*$ (λ/β) (Fig. 2b).
(c) If $0 < r^* < \alpha/v < \beta/\lambda$, then $\hat{S}(x) > 0$ for $0 \leq x < 1$, and $\hat{S}(x)$ is maximal at $x = r^*$ (λ/β) (Fig. 2c).
(d) If $0 < \alpha/v < r^* < \beta/\lambda$, then $\hat{S}(x) > 0$ for $[(\alpha/v) - r^*]/[(\alpha/v) - (\beta/\lambda)] < x < 1$ and zero elsewhere, and $\hat{S}(x)$ is maximal for $x = r^*$ (λ/β) (Fig. 2d).
(e) If $0 < \beta/\lambda < r^* < \alpha/v$, then $\hat{S}(x) > 0$ for $0 \leq x < [(\alpha/v) - r^*]/[(\alpha/v) - (\beta/\lambda)]$ and zero elsewhere, and $\hat{S}(x)$ is maximal for $x = 0$ (Fig. 2e).
(f) If $0 < \alpha/v < \beta/\lambda < r^*$ or $0 < \beta/\lambda < \alpha/v < r^*$, then $\hat{S}(x) = 0$ for all x (Fig. 2f).

If $\hat{S}(x)$ has a strict maximum at a positive value of x [cases (c) and (d)], then the corresponding equilibrium lies on the discontinuity boundary (as in Fig. 3a), and hence $R = 0$. If $\hat{S}(x)$ has a strict maximum for $x = 0$ [cases (a) and (e)], then the corresponding equilibrium lies on the S-axis (as in Fig. 3b), and hence $M = 0$.

DISCUSSION

We have found that the optimal proportion of photosynthetic products shared with the mycorrhiza depends only on the relative magnitude of the following three quantities: (1) the cost-efficiency α/v of uninfected roots and (2) the cost-efficiency β/λ of the mycorrhiza (both in terms of the amount of nutrients acquired per unit of carbon cost), and (3) the optimal nutrient–carbon ratio r^*. The values of the other model parameters γ, μ and θ (affecting the rate of photosynthesis or the respiration by the plant shoot) turn out to be of no consequence whatsoever.

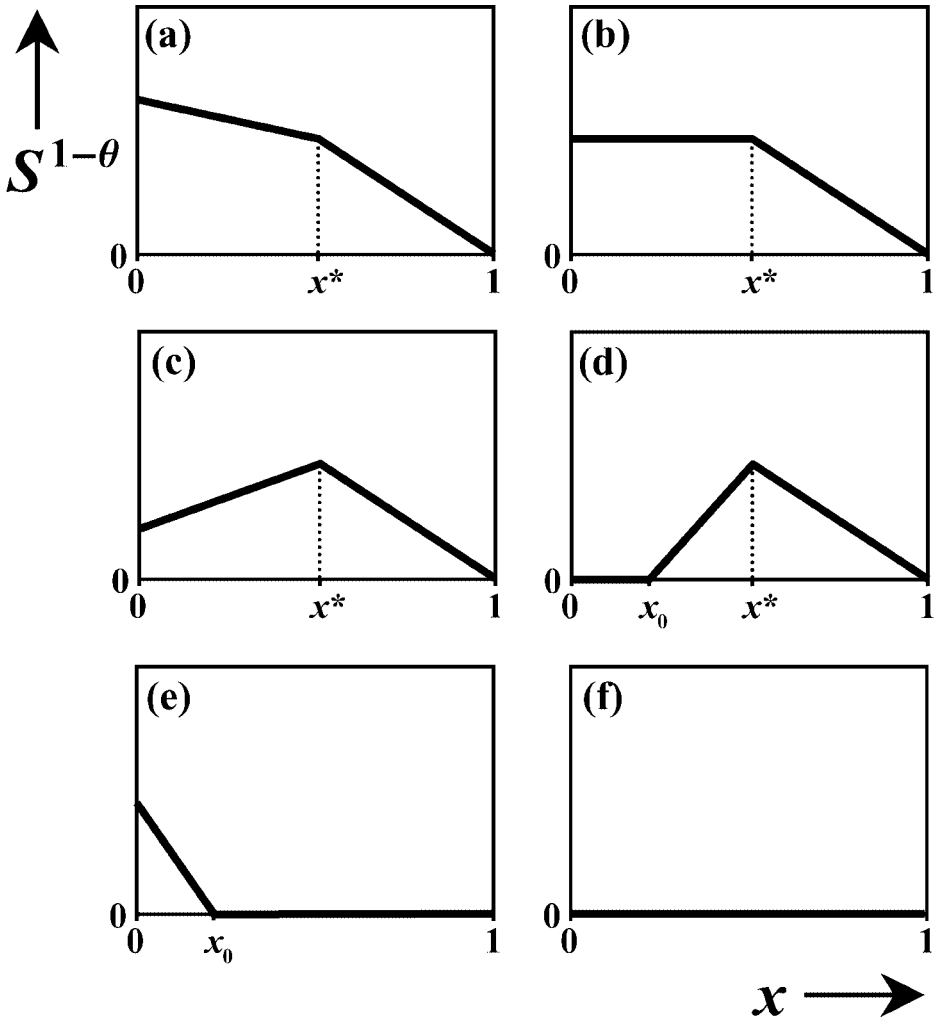

Fig. 2. Graph of $\hat{S}^{1-\theta}$ as a function of x with $x^* = r^*(\lambda/\beta)$ and $x_0 = [(\alpha/\nu) - r^*]/[(\alpha/\nu) - (\beta/\lambda)]$. (a) $0 < r^* < \beta/\lambda < \alpha/\nu$, (b) $0 < r^* < \beta/\lambda = \alpha/\nu$, (c) $0 < r^* < \alpha/\nu < \beta/\lambda$, (d) $0 < \alpha/\nu < r^* < \beta/\lambda$, (e) $0 < \beta/\lambda < r^* < \alpha/\nu$, and (f) $0 < \alpha/\nu < \beta/\lambda < r^*$ or $0 < \beta/\lambda < \alpha/\nu < r^*$.

To maximize shoot biomass, a plant in our model should share photosynthetic products with a mycorrhiza if and only if the cost-efficiency of the mycorrhiza is greater than that of uninfected roots and moreover exceeds the optimal nutrient–carbon ratio (Fig. 2c, d). If symbiosis is optimal, then the function of nutrient absorption is entirely delegated to the mycorrhiza (Fig. 3a). If the cost-efficiency of uninfected roots is greater than the optimal nutrient–carbon ratio, then the plant can also survive without the mycorrhiza (Fig. 2c), but otherwise symbiosis with the mycorrhiza is obligatory (Fig. 2d).

These results differ from those of Tuomi *et al.* (2001), who found that plants supporting mycorrhizal fungi may evolve even if they are less cost-efficient than uninfected plants. The most probable reason for this difference is that in the model of Tuomi *et al.* (2001) the

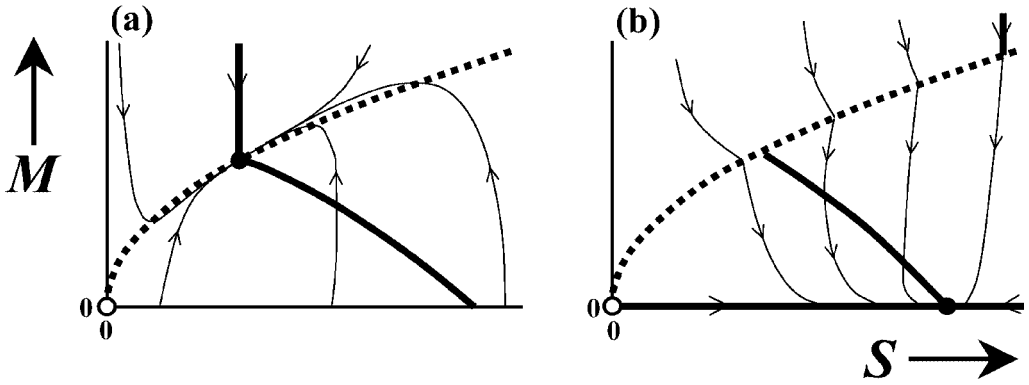

Fig. 3. Dynamics for the optimal value of x when (a) $\hat{S}(x) > 0$ and (b) $\hat{S}(x) = 0$.

root–shoot ratio is fixed, so that the only possibility of regulating the nutrient–carbon ratio is by changing the fraction of mycorrhiza-infected roots. In their model, therefore, symbiosis evolves as a means of attaining the optimal nutrient–carbon ratio. In our model, however, this mechanism does not work, because the optimal nutrient–carbon ratio is maintained by a variable root–shoot ratio.

We now discuss the potential significance of our two main assumptions. First, we assume in our model that the optimal nutrient–carbon ratio r^* is a constant. In reality, however, the demand for nutrients and carbon could change during plant growth and development in such a way that the optimal nutrient–carbon ratio depends on plant age or size. If we make r^* a function of, for example, the biomass of the root, the shoot or both, then the shape and the position of the discontinuity boundary in the (M, S)-plane between the regions defined by conditions (3) and (4) become different. Moreover, the dynamics below (but not above) the discontinuity boundary changes as well, so that conclusions of the model concerning the optimal allocation of carbon to the mycorrhiza need not remain the same.

Secondly, in our model plant size reaches an equilibrium, and to calculate the optimal proportion of shared carbon we maximize shoot biomass at the equilibrium. This approach presumes that plant fitness is positively correlated with shoot biomass, that the equilibrium is reached fast, and that the plant does not reproduce before the equilibrium has been reached. If these assumptions are not satisfied, then another fitness criterion should be used, namely one that accounts also for root mass and that integrates reproduction during plant growth and not only at the equilibrium. This involves choosing a different output from the model as a function of the proportion of shared carbon, and although the growth dynamics of the model stay the same, the predictions may very well be different from those presented here.

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APPENDIX 1

Equation (6) is an example of a so-called Filippov system – that is, a system of differential equations with piece-wise continuous right-hand sides (Filippov, 1988). In such systems, the behaviour of solutions at the discontinuity boundaries warrants special attention. For a concise introduction to two-dimensional Filippov systems including further references, we refer the reader to Kuznetsov *et al.* (2003).

For the present model, let

$$H(S, M) = M - r^* \frac{\gamma}{\beta} S^{\theta} \tag{A1}$$

and hence

$$\dot{H}(S, M) = \dot{M} - r^* \frac{\gamma}{\beta} \theta S^{\theta - 1} \dot{S} \tag{A2}$$

To simplify notation, we usually write H and $\dot{H}$ instead of $H(S, M)$ and $\dot{H}(S, M)$ with explicit arguments. Furthermore, let

$$\Sigma = \{(S, M) \in \mathbb{R}^2_+ : H = 0\} \tag{A3}$$

denote the discontinuity boundary (dotted curve in Fig. 1), and let Σ_+ and Σ_- denote the regions above and below Σ, respectively. For any point $(S_0, M_0) \in \Sigma$, let $\lim_+ \dot{H}$ and $\lim_- \dot{H}$ denote the limit of $\dot{H}$ as $(S, M) \to (S_0, M_0)$ in Σ_+ and Σ_-, respectively.

Since $H > 0$ in Σ_+, and $H < 0$ in Σ_-, it follows that if $\lim_+ \dot{H} < (>) 0$, then there exists an orbit in Σ_+, transversally to Σ, that leaves (enters) Σ_+ at (S_0, M_0) with a non-vanishing speed (i.e. $\lim_+ \dot{S}$ and $\lim_+ \dot{M}$ are not both zero). If $\lim_+ \dot{H} = 0$, then the orbit is either tangent to Σ, or (S_0, M_0) is a *boundary equilibrium* of Σ_+ (i.e. both $\lim_+ \dot{S}$ and $\lim_+ \dot{M}$ are zero). Similarly, if $\lim_- \dot{H} < (>) 0$, then there exists an orbit in Σ_- that enters (leaves) Σ_- at (S_0, M_0) with a non-vanishing speed and transversally to Σ, while if $\lim_- \dot{H} = 0$, then the orbit is either tangent to Σ, or (S_0, M_0) is a boundary equilibrium of Σ_-.

A point $(S_0, M_0) \in \Sigma$ is a *crossing point* if $\lim_+ \dot{H}$ and $\lim_- \dot{H}$ have the same sign but are not zero. At such a point there exists an orbit that actually crosses the discontinuity boundary with a non-vanishing speed. A point in Σ that is not a crossing point is a *sliding point*. An

important special kind of sliding point is the *pseudo-equilibrium* where two orbits transversal to Σ and with exactly opposite flows on opposite sides of Σ meet at the discontinuity boundary. Thus, at a pseudo-equilibrium, $\lim_{+} \dot{H}$ and $\lim_{-} \dot{H}$ are not zero and have opposite signs. Pseudo-equilibria are important as possible stationary points of the dynamics.

Proposition 1. *Σ does not contain a pseudo-equilibrium. If $x\beta - r^*\lambda + r^*\theta\mu \le 0$, then all points in Σ with $S > 0$ are crossing points where orbits leave Σ_+ and enter Σ_-. If $x\beta - r^*\lambda + r^*\theta\mu > 0$, then all points in Σ with $0 < S < S^*$ and*

$$S^* = \left(\frac{(1-x)r^*\theta\gamma}{x\beta - r^*\lambda + r^*\theta\mu}\right)^{\frac{1}{1-\theta}} \tag{A4}$$

are crossing points where orbits leave Σ_+ and enter Σ_-, while all points in Σ with $S > S^*$ are crossing points where orbits leave Σ_- and enter Σ_+.

Proof. Let (S, M) be a point in Σ. To prove that Σ does not contain a pseudo-equilibrium, it is sufficient to show that $\lim_{+} \dot{H}$ and $\lim_{-} \dot{H}$ have the same sign. From (6) we find

$$\begin{aligned}
\lim_{+} \dot{H} &= \frac{r^*\theta\gamma S^\theta}{\beta}\left(\frac{x\beta - r^*\lambda}{r^*\theta} - [(1-x)\gamma S^{\theta-1} - \mu]\right) \\
\lim_{-} \dot{H} &= \frac{r^*\theta\gamma S^\theta}{\beta}\left(\frac{x\beta - r^*\lambda}{r^*\theta} - \frac{\alpha[(1-x)\gamma S^{\theta-1} - \mu] + (x\beta - r^*\lambda)\gamma S^{\theta-1}}{\alpha + r^*\theta\gamma S^{\theta-1}}\right)
\end{aligned} \tag{A5}$$

Suppose that $\lim_{+} \dot{H} < (=, >)\ 0$. Then

$$\frac{x\beta - r^*\lambda}{r^*\theta} < (=, >)\ \ (1-x)\gamma S^{\theta-1} - \mu \tag{A6}$$

so that

$$\begin{aligned}
&\frac{\alpha[(1-x)\gamma S^{\theta-1} - \mu] + (x\beta - r^*\lambda)\gamma S^{\theta-1}}{\alpha + r^*\theta\gamma S^{\theta-1}} > (=, <) \\
&\frac{\alpha\left(\dfrac{x\beta - r^*\lambda}{r^*\theta}\right) + (x\beta - r^*\lambda)\gamma S^{\theta-1}}{\alpha + r^*\theta\gamma S^{\theta-1}} = \\
&\frac{x\beta - r^*\lambda}{r^*\theta}
\end{aligned} \tag{A7}$$

Hence $\lim_{-} \dot{H} < (=, >)\ 0$ (i.e. $\lim_{-} \dot{H}$ has the same sign as $\lim_{+} \dot{H}$) and therefore Σ cannot contain a pseudo-equilibrium.

Rearranging (A6), we see that $\lim_{+} \dot{H} < (=, >)\ 0$, and hence $\lim_{-} \dot{H} < (=, >)\ 0$, if and only if,

$$\frac{x\beta - r^*\lambda + r^*\theta\mu}{(1-x)r^*\theta\gamma} < (=, >)\ S^{\theta-1} \tag{A8}$$

from which the rest of the proposition readily follows.

APPENDIX 2

Proposition 2. *The non-trivial equilibrium given by (7) is locally attracting whenever it exists.*

Proof. Necessary and sufficient conditions for the existence of the non-trivial equilibrium are given by (8) and (A5). We first consider the equilibrium under condition (8). That is, suppose that

$$0 < (1-x)\frac{\alpha}{\nu} + x\frac{\beta}{\lambda} - r^* \quad \text{and} \quad 0 \le x < r^*\frac{\lambda}{\beta} \tag{A9}$$

The equilibrium then lies below the discontinuity boundary. The Jacobi matrix J at the equilibrium is

$$J = \begin{pmatrix} \dfrac{\theta\gamma[(1-x)\,\alpha + x\beta - \nu r^*]S^{\theta-1} - \alpha\mu}{\alpha + r^*\gamma\theta S^{\theta-1}} & \dfrac{-\beta(\lambda-\nu)}{\alpha + r^*\gamma\theta S^{\theta-1}} \\ x\gamma\theta S^{\theta-1} & -\lambda \end{pmatrix} \tag{A10}$$

where

$$S^{1-\theta} = \frac{\gamma}{\mu}\frac{\nu}{\alpha}\left((1-x)\frac{\alpha}{\nu} + x\frac{\beta}{\lambda} - r^*\right) \tag{A11}$$

To prove local attraction, it is sufficient to show that the determinant of J is positive and the trace of J is negative:

$$\det J = \frac{\lambda\alpha\mu(1-\theta)}{\alpha + r^*\gamma\theta S^{\theta-1}} \tag{A12}$$

and

$$\operatorname{tr} J = \frac{\theta\gamma[(1-x)\alpha + x\beta - \nu r^*]S^{\theta-1} - \alpha\mu}{\alpha + r^*\gamma\theta S^{\theta-1}} - \lambda \tag{A13}$$

The determinant is obviously positive, so it suffices to show that the trace is negative. From (A9) we have $x\beta - \lambda r^* < 0$, and hence $x\beta - \lambda r^* < x\beta\,(\nu/\lambda)$. Adding $(1-x)\alpha - \nu r^*$ on both sides gives

$$(1-x)\alpha + x\beta - (\lambda+\nu)r^* < (1-x)\,\alpha + x\beta\frac{\nu}{\lambda} - \nu r^* \tag{A14}$$

Multiplication on the left by $\theta\gamma$ (which is less than one) and on the right by $\gamma[1 + (\lambda/\mu)]$ (which is greater than one) gives, after rearrangement of the right-hand side,

$$\theta\gamma[(1-x)\alpha - x\beta - (\lambda+\nu)r^*] < \alpha(\lambda+\mu)\frac{\gamma}{\mu}\frac{\nu}{\alpha}\left((1-x)\frac{\alpha}{\nu} + x\frac{\beta}{\lambda} - r^*\right) \tag{A15}$$

By (A11) this is equivalent to

$$\theta\gamma[(1-x)\alpha + x\beta - (\lambda+\nu)r^*] < \alpha(\lambda+\mu)S^{1-\theta} \tag{A16}$$

which can be rearranged as

$$\frac{\theta\gamma[(1-x)\alpha + x\beta - \nu r^*]S^{\theta-1} - \alpha\mu}{\alpha + r^*\gamma\theta S^{\theta-1}} - \lambda < 0 \tag{A17}$$

By (A13) the left-hand side is equal to tr J, which therefore is negative.

We thus have shown that if there exists a non-trivial equilibrium in the region below the discontinuity boundary, then it is locally attracting. Under condition (9) with strict inequalities, i.e.

$$r^* \frac{\lambda}{\beta} < x < 1 \tag{A18}$$

the non-trivial equilibrium lies above the discontinuity boundary, and the Jacobi matrix at the equilibrium then is given by

$$J = \begin{pmatrix} (1-x)\gamma\theta S^{\theta-1} - \mu & 0 \\ x\gamma\theta S^{\theta-1} & -\lambda \end{pmatrix} \tag{A19}$$

with

$$S^{1-\theta} = (1-x)\frac{\gamma}{\mu} \tag{A20}$$

Since by (A20)

$$(1-x)\gamma S^{\theta-1} - \mu = -\mu(1-\theta) < 0 \tag{A21}$$

it follows that the determinant of J is positive and the trace is negative, and therefore the equilibrium is locally attracting.

If $x = r^*(\lambda/\beta)$, then the equilibrium lies on the discontinuity boundary, and therefore the Jacobi matrix does not exist. Instead, we prove local stability using the phase-plane method (i.e. graphically) by inspection of the flow in the (S, M)-plane given by (6). Figure A1 gives the three possible local configurations of the flow under the various conditions formulated in the figure legend. The discontinuity boundary and the zero-cline $\dot{M} = 0$ coincide. Orbits starting in the indicated box eventually must enter the shaded regions, inside of which the orbit converges monotonically to the equilibrium.

APPENDIX 3

Proposition 3. *The origin is unstable if the non-trivial equilibrium exists but globally attracting if the non-trivial equilibrium does not exist.*

Proof. Suppose the non-trivial equilibrium exists. Then either (8) or (9) is satisfied. Since the origin lies on the discontinuity boundary Σ, we use the phase-plane method. We distinguish six qualitatively different local configurations of the flow near the origin (Fig. A2). The configurations are readily derived from (6) under the various conditions listed in the figure legend. It can be seen that arbitrarily close to the origin inside the shaded regions, orbits exist that eventually escape from the origin's neighbourhood. Hence the origin is unstable.

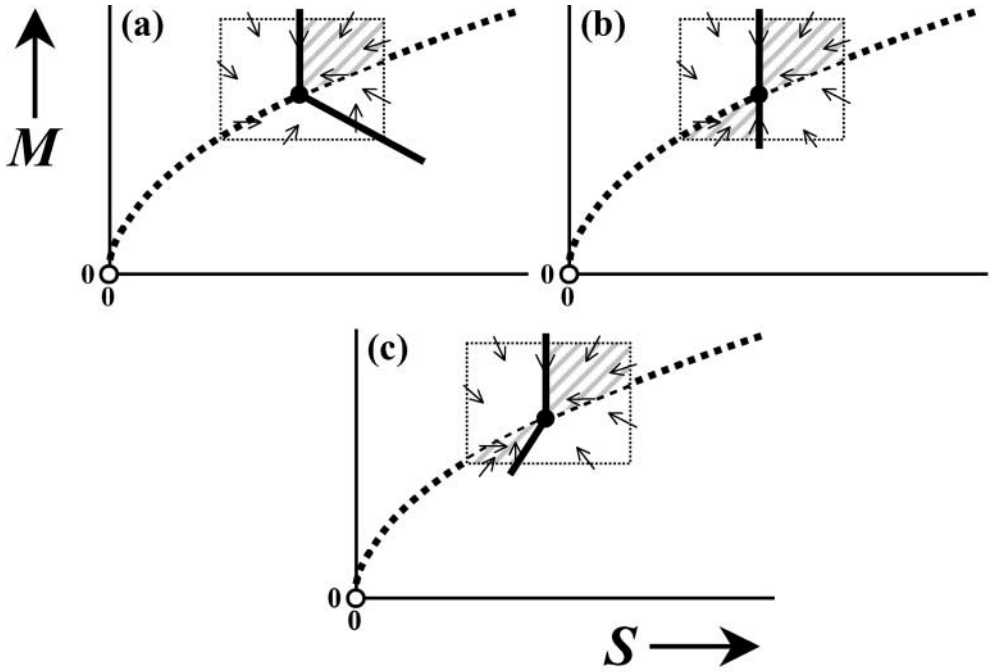

Fig. A1. Local configuration of the flow near the non-trivial equilibrium if $x = r^*(\lambda/\beta)$. The arrows indicate the flow direction in various parts of the plane. Orbits starting in the indicated box eventually must enter the shaded regions, inside of which the orbit converges monotonically to the equilibrium. (a) $\lambda > \nu$, (b) $\lambda = \nu$ and (c) $\lambda < \nu$.

Next, suppose the non-trivial equilibrium does not exist. Then, either $x = 1$ or

$$0 \geq (1-x)\frac{\alpha}{\nu} + x\frac{\beta}{\lambda} - r^* \quad \text{and} \quad 0 \leq x < r^*\frac{\lambda}{\beta} \tag{A22}$$

If $x = 1$, then $W \to 0$ as $t \to \infty$, and hence $S \to 0$, which in turn implies that $M \to 0$. The origin is thus globally attracting.

Under condition (A22) we distinguish two sub-cases. First, if $x\beta - r^*\lambda + r^*\theta\mu \leq 0$, we know from Proposition 1 in Appendix 1 that all points on the discontinuity boundary Σ are crossing points where orbits leave the region Σ_+ above the boundary and enter the region Σ_- below the boundary (Fig. A3a). An orbit that crosses the boundary into Σ_- cannot return to Σ_+. Since all orbits are bounded and there does not exist a non-trivial equilibrium, it follows from the Poincaré-Bendixon theorem that any orbit starting in Σ_-, or crossing into Σ_-, must converge to the boundary equilibrium at the origin.

Secondly, if $x\beta - r^*\lambda + r^*\theta\mu > 0$, we know from Proposition 1 in Appendix 1 that there exists a number $S^* > 0$ such that all points on Σ with $0 < S < S^*$ are crossing points where orbits leave Σ_+ and enter Σ_-, while all points on Σ with $S > S^*$ are crossing points where orbits leave Σ_- and enter Σ_+ (Fig. A3b). From (A22) we have $x\beta < r^*\lambda$, so that the zero-cline of M (i.e. the curve $\dot{M} = 0$) lies below Σ. Therefore, we can construct the horizontal line segment with endpoints (S^*, M^*) on Σ and (S^{**}, M^*) on the curve $\dot{M} = 0$ with $S^{**} > S^*$,

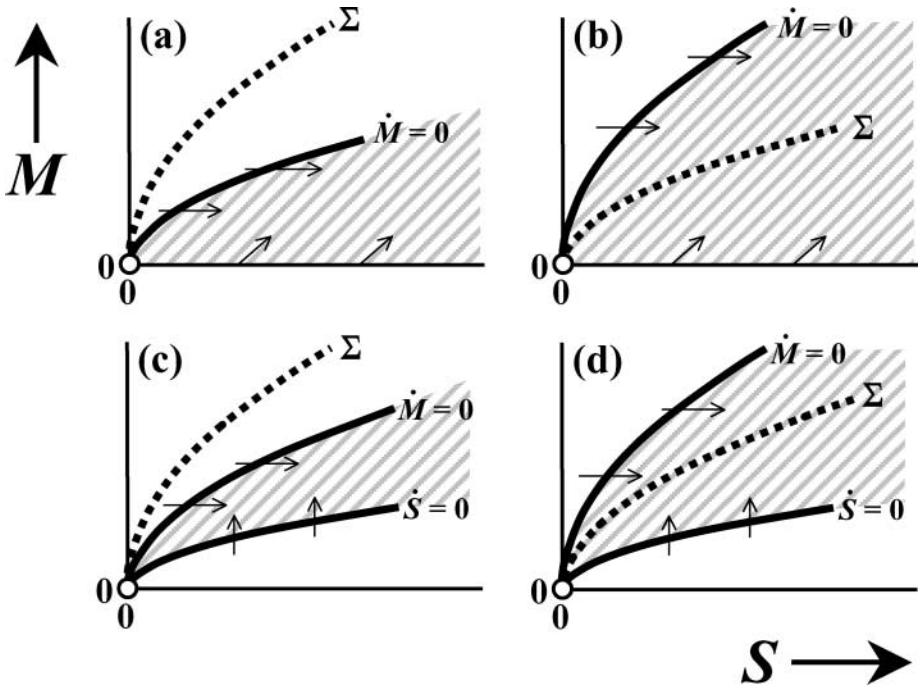

Fig. A2. Local configuration of the flow near the origin if the non-trivial equilibrium exists. Orbits starting in the shaded regions eventually escape from the origin's neighbourhood. (a) Condition (8) holds together with $\lambda \geq v$, or together with $\lambda < v$ and $(1-x)\alpha + x\beta - vr^* > 0$. (b) Condition (9) holds together with $\lambda \geq v$, or together with $\lambda < v$ and $(1-x)\alpha + x\beta - vr^* > 0$. (c) Condition (8) holds and $\lambda < v$ and $(1-x)\alpha + x\beta - vr^* \leq 0$. (d) Condition (9) holds and $\lambda < v$ and $(1-x)\alpha + x\beta - vr^* \leq 0$.

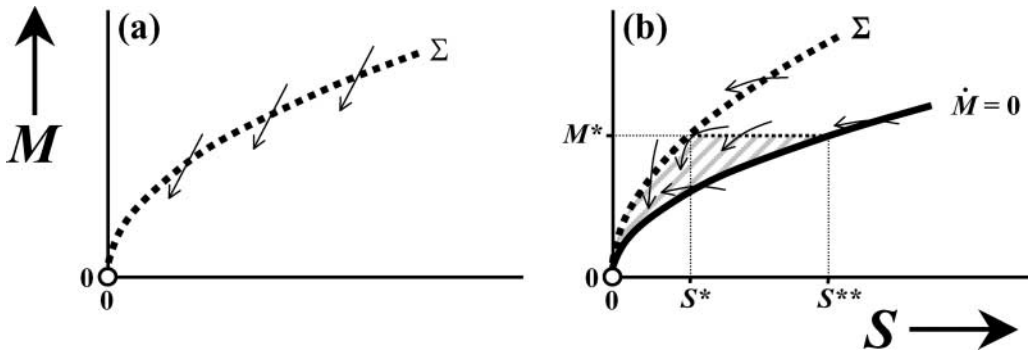

Fig. A3. Global dynamics if the non-trivial equilibrium does not exist. The zero-clines $\dot{S}=0$ and $\dot{M}=0$ have not been drawn, except in (b) where only the zero-cline $\dot{S}=0$ has been omitted. (a) $x\beta - r^*\lambda + r^*\theta\mu \leq 0$, (b) $x\beta - r^*\lambda + r^*\theta\mu > 0$. See Appendix 3 for further explanation.

and which is crossed by orbits from above (Fig. A3b). Moreover, from $0 \geq (1 - x)(\alpha/v) + x(\beta/\lambda) - r^*$ in (A22), it follows that $\dot{S} < 0$ on the curve $\dot{M} = 0$ for every $S > 0$. Thus, the shaded region in Fig. A3b between Σ, the curve $\dot{M} = 0$ and the line segment connecting the points (S^*, M^*) and (S^{**}, M^*) is forward invariant. An orbit starting in this region cannot leave, and since the region does not contain a non-trivial equilibrium, it follows from the Poincaré-Bendixon theorem that the orbit must converge to the origin. Orbits starting elsewhere may enter the shaded region eventually, or they may remain outside this region but inside Σ_-, or they may cross over to Σ_+ and remain there. The first of these three cases has already been considered. In the latter two cases, it follows again from the Poincaré-Bendixon theorem that the orbits converge to the origin.