

4. Quotients, inverses and limits. Modelling photosynthesis

Almost everything about ordinary functions can be approached from either a graphical or an algebraic perspective. We saw in Lectures 1 and 2 that functions can be defined either in way. We saw in Lecture 1 that extrema can be found graphically, and we will discover in Lecture 16 that they can also be found algebraically. We saw in Lecture 3 that concavity can be determined graphically, and we will discover in Lecture 16 that it can also be determined algebraically. We saw in Lecture 1 that the inverse of a function can be found graphically, and we will discover in this lecture that it can also be found algebraically. First, however, we need to define another category of function combination.

Accordingly, let g and h have the same domain, and assume that 0 does not belong to the range of h . Then the **quotient** of g and h is the function $Q = g/h$ defined by $Q(x) = g(x)/h(x)$. Suppose, for example, that $g(x) = Ax$ and $h(x) = x + B$ define linear functions with positive parameters A, B on some domain where $x \geq 0$. Because $x \geq 0$ implies $x + B \geq B$ and $B > 0$, we have $h(x) > 0$, implying in particular that $h(x) \neq 0$; that is, 0 does not belong to the range of h . So a quotient Q is well defined by

$$(4.1) \quad Q(x) = \frac{Ax}{x+B}$$

A quotient of two linear functions is a special case of a **rational function**, i.e., a quotient of polynomials.

Plant scientists have used the relationship $y = Q(x)$ to model both the effect of potassium concentration on rate of ion absorption in roots (see, e.g., Fitter and Hay, 1987, pp. 89-90) and the effect of carbon dioxide concentration, or $[CO_2]$, on the rate of photosynthesis in leaves (e.g., Rabinowitch, 1951, p. 920). In the case of photosynthesis,

the independent variable x denotes interstitial $[CO_2]$ in micromoles per mole (which may differ from $[CO_2]$ in the surrounding air); the dependent variable $y = Q(x)$ denotes the rate in micromoles per square meter per second at which CO_2 is assimilated by a leaf; the

parameter A denotes the "saturation" rate of photosynthesis (in micromol $m^{-2} s^{-1}$); and the parameter B denotes the "half-saturation concentration" (in micromol mol^{-1} , same as for x). A lower value of B implies a higher "affinity" of the leaf for CO_2 ; it is called the half-saturation concentration because if $x = B$ then $y = A/2$ or

$$(4.2) \quad Q(B) = \frac{1}{2}A.$$

But why is A called the saturation rate? That is an interesting question, to which we will shortly return.

The actual values of A and B depend on temperature, light intensity and a number of other factors, but become largely irrelevant if we first of all "scale" y with respect to A and x with respect to B , i.e., if we first define a new independent variable u and a new dependent variable z by

$$(4.3) \quad z = \frac{y}{A}, \quad u = \frac{x}{B}.$$

Then, from (1) and $y = Q(x)$, we have

$$(4.4) \quad z = \frac{y}{A} = \frac{Q(x)}{A} = \frac{\frac{x+B}{x}}{A} = \frac{x+B}{x} = \frac{x/B + 1}{x/B} = \frac{u+1}{u}.$$

So in terms of scaled variables we have $z = K(u)$ where K

$$(4.5) \quad K(u) = \frac{u}{u+1}.$$

Note that $z = 1/2$ when $u = 1$; i.e., (2) becomes

The graph of the resulting quotient K is shown in Figure 1 for subdomain $[0, 19]$.

What is the full domain of K ? Although it doesn't make sense for a concentration to be negative, provided $u \geq 0$, there is no (mathematical) restriction on how large u can be. That is, (5) defines K on any interval of the form $[0, u^{\max}]$, no matter how large u^{\max} is. So K has domain $[0, \infty)$. Its domain is said to be infinite.

What kind of function is K ? From Figure 1, K is concave down, increasing, and therefore invertible. It is also smooth, and therefore continuous. A continuous function on a finite domain has a unique global maximum. But K has an infinite domain, which means that it need not have a maximum, and in fact it does not, because $K(u)$ gets larger and larger as u gets larger and larger. On the other hand, as u gets larger, $K(u)$ gets larger by smaller amounts, and it cannot exceed 1, because (5) implies that

$$1 - K(u) = 1 - \frac{u+1}{1} = \frac{u+1}{1} \tag{4.7}$$

which is positive. We say that 1 is an upper bound of K . But if $K(u)$ cannot exceed 1, then it also cannot exceed 2, which makes 2 an upper bound of K as well. For that matter, so are 3 and 10. What makes 1 special is that it is the least such bound: there is no number smaller than 1 that always exceeds $K(u)$. So we say that 1 is the **least upper bound** of K . There is, however, more to be said. As u becomes indefinitely large, $K(u)$ becomes arbitrarily close to 1. As so often in calculus, there are two perspectives from which to view this statement. We can first of all view it graphically. In Figure 1(a), the dashed line corresponds to $z = 1$ and the curve to $z = K(u)$. So $1 - K(u)$ is the vertical distance between the dashed line and the curve. The further you move to the right (as far as you please, way off the page), the smaller the distance becomes, until eventually you move so far to the right that, for all practical purposes, the curve and the line are indistinguishable. We say that the distance approaches zero as u becomes indefinitely large, for which the mathematical shorthand is

$$\lim_{u \rightarrow \infty} 1 - K(u) = 0. \tag{4.8}$$

But to say that the distance between $K(u)$ and 1 approaches zero as u becomes indefinitely large is just another way of saying that $K(u)$ approaches 1 as u becomes indefinitely large, for which the mathematical shorthand is

$$\lim_{u \rightarrow \infty} K(u) = 1. \tag{4.9}$$

We say that the **limit** of $K(u)$ as u tends to infinity equals 1. We also say that $z = 1$ is a **horizontal asymptote** to the graph of K in Figure 1(a). We can also view the above result algebraically. If u becomes indefinitely large, then it is all the more true that $u + 1$ becomes indefinitely large, which means that $1/(u + 1)$ becomes arbitrarily small, or approaches zero. That is,

$$\lim_{u \rightarrow \infty} \frac{1}{u+1} = 0. \tag{4.10}$$

By (7), (10) is equivalent to (8), and therefore again implies (9). What is the range of K ? Because, from Figure 1(a), K eventually reaches every value between 0 and 1 except 1 itself, the range of K is $[0, 1]$ with the endpoint 1 removed. A possible mathematical shorthand for " $[0, 1]$ with the endpoint 1 removed" is $[0, 1] - \{1\}$, but a much more elegant one is $[0, 1)$. So the range of K is $[0, 1)$. More generally, [a, b)

denotes the "half-open" interval $[a, b]$ and $(a, b]$ denotes the "half-open" interval $[a, b] - \{a\}$, whereas (a, b) denotes the completely open interval $[a, b] - \{a\} - \{b\}$.

We have thus established that K is an increasing function with domain $[0, \infty)$ and range $[0, 1]$. It is therefore invertible, and if L denotes the inverse function, then L has domain $[0, 1]$ and range $[0, \infty)$. The graph of L is readily determined by the method of Lecture 1 and is shown in Figure 1(b). Note that, as z approaches 1 from the left, $L(z)$ becomes indefinitely large, for which mathematical shorthand is either

$$(4.11a) \quad \lim_{z \rightarrow 1^-} L(z) = \infty$$

or simply

$$(4.11b) \quad L(1^-) = \infty.$$

We also say that $z = 1$ is a **vertical asymptote** to the graph of L . Note that L is concave up whereas K is concave down (but both functions are increasing).

We have found the inverse graphically, but we can also find it algebraically. In general, finding the inverse L of a function K means rewriting $z = K(u)$ as $u = L(z)$. So, in this particular case, finding the inverse L of K means solving $z = u/(1+u)$ for u in terms of z . But $z = u/(1+u)$ is the same thing as $z(1+u) = u$ or $z + zu = u$, implying $z = u(1-z)$ or $u = z/(1-z)$. Thus the inverse of K is defined algebraically on $[0, 1)$ by

$$(4.12) \quad L(z) = \frac{z}{1-z}.$$

See Exercises 1-3 for further practice.

We now return to whether A in (1) should be called the saturation rate, because in practice we think of a saturation rate as a rate that can actually be achieved. According to our model, $K(u)$ is always strictly less than 1, even when u is extremely large, and so it follows from (4)-(5) that $Q(x)$ is always strictly less than A , even when $[CO_2]$ is very high. In practice, however, the photosynthetic reaction appears to saturate at quite moderate concentrations of CO_2 , for example, at 40-50 micromol/liter under 407 lux in the water plant *Cabomba caroliniana* (Rabinowitch, 1951, p. 897). More generally, there appears to exist a concentration C such that

$$(4.13) \quad Q(x) = A \quad \text{if } x \geq C.$$

We call C the saturation concentration. From (4)-(5), we can rewrite (13) as

$$(4.14) \quad K(u) = 1 \quad \text{if } u \geq c$$

where

$$(4.15) \quad c = \frac{B}{C}$$

is the ratio of full-saturation concentration to half-saturation concentration. For numerous species of plants, representative values of c can be inferred from Table 27.1 of Rabinowitch (1951, pp. 892-893). Most of these values fall between 2 and 5 (although some are higher). So any K satisfying (6) and (14) with $2 \leq c \leq 5$ is potentially a better photosynthesis model than (5). For example, we could take $c = 3.41$ and define

$$(4.16) \quad K(u) = \begin{cases} 0.586u\{1 - 0.146u\} & \text{if } 0 \leq u \leq 3.41 \\ 1 & \text{if } 3.41 \leq u < \infty \end{cases}$$

The graph of this join is plotted in Figure 2, with the rational function shown dotted for comparison. Note that even if the new K really is a better model for CO_2 assimilation rate versus $[CO_2]$ concentration, the old K may still be a better model for CO_2 assimilation rate versus other variables, e.g., light intensity; see, e.g., Coombs et al (1985, p. 89).

Note also that (5) and (16) both satisfy (9). That is, in either case it is true that $K(u)$ is arbitrarily close to 1 for indefinitely large u . But (5) and (16) satisfy (9) in different ways: In (5), K approaches 1 only asymptotically, whereas in (16) K equals 1 on $[c, \infty)$. In a sense, (16) satisfies (9) by default: $K(u)$ has no choice but to be arbitrarily close to 1 when it is also actually equal to 1.

References

- Coombs, J. et al (1985). *Techniques in Bioproduction and Photosynthesis*. Pergamon Press, Oxford.
- Fitter, A. H. & R. K. M. Hay (1987). *Environmental Physiology of Plants*. Academic Press, New York.
- Rabinowitch, Eugene I. (1951). *Photosynthesis and Related Processes*, Volume II, Part 1. Interscience Publishers, New York.

Exercises 4

4.1 Find, by algebraic methods, the inverse B of the function A defined by (2.2), i.e., $A(t) = 4\pi t^2 / 81$.

4.2 Verify that g and h in Table 2.1 are inverses of one another.

4.3 Verify that q and r in Table 2.1 are inverses of one another.

4.4* During the last 0.15 seconds – the atrial contraction phase – of a human cardiac cycle, the volume of the left ventricle increases by 9 ml. Let $R(t)$ denote recharge at any time t during this phase (so that, in particular, $R(0) = 0$ and $R(0.15) = 9$). It is modelled by

$$R(t) = \begin{cases} 800t^2 & \text{if } 0 \leq t \leq 0.075 \\ 9 - 2(3 - 20t)^2 & \text{if } 0.075 \leq t < 0.15 \end{cases}$$

(a) Using *Mathematica* or otherwise, sketch the graph on $[0, 0.15]$ of the join R . Why must R be invertible? What does its inverse tell you?
 (c) Find R 's inverse graphically.
 (d) Find R 's inverse algebraically.
 (e) Describe the concavity of both R and its inverse.

4.5* In a photosynthetic reaction, rate of assimilation (as a proportion of the saturation rate) at concentration x (measured in units of half-saturation concentration) is $K(x)$, where K is the join defined on $[0, \infty)$ by

$$K(x) = \begin{cases} \left(\frac{9}{8} - \frac{1}{2}\right)x - \frac{1}{4} & \text{if } 0 \leq x \leq 1 \\ 1 - \frac{1}{6x^2} & \text{if } 1 \leq x < \infty \end{cases}$$

(a) Using *Mathematica* or otherwise, sketch the graph of K on subdomain $[0, 10]$. Why must K be invertible? What does its inverse tell you?
 (c) Find K 's inverse graphically.
 (d) Find K 's inverse algebraically.
 (e) Describe the concavity of both K and its inverse.

Answers and Hints for Selected Exercises

4.1 $B(y) = \frac{9}{2} \sqrt{\frac{\pi}{y}}$

4.4 (b) R must be invertible because R is increasing. Call the inverse function Q. Let y be an arbitrary volume between 0 and 9 ml. Then Q(y) is the time (in seconds) when the recharge is y.

(d) On subdomain [0, 0.075], R is defined by $y = R(t)$ where $R(t) = 800t^2$. R is increasing on this subdomain, and so its range is $[R(0), R(0.075)] = [0, 4.5]$. That means the inverse function has domain [0, 4.5]. Call the inverse Q. Then, on [0, 4.5], $t = Q(y)$ must be the same thing as $y = R(t)$. But $y = R(t)$ means $y = 800t^2$, which is the same thing as $t = \sqrt{2y}/40$.

So the inverse is defined on [0, 4.5] by $Q(y) = \sqrt{2y}/40$. On subdomain [0.075, 0.15], however, R is defined by $y = R(t)$ where $R(t) = 9 - 2(3 - 20t)^2$. R is increasing on this subdomain also, and so its range is $[R(0.075), R(0.15)] = [4.5, 9]$.

The inverse is still called Q, even though it is restricted to a different subdomain, namely, [4.5, 9]; and on that subdomain, $t = Q(y)$ is still be the same thing as $y = R(t)$. But $y = R(t)$ means $y = 9 - 2(3 - 20t)^2$, which is the same thing as $(3 - 20t)^2 = (9 - y)/2$ or $3 - 20t = \sqrt{(9 - y)/2}$ (because $3 \geq 20t$ if $t \leq 0.15$). So $t = (3 - \sqrt{(9 - y)/2})/20$, and the inverse is defined on [4.5, 9] by

$$Q(y) = \frac{1}{20} \left(3 - \sqrt{\frac{9 - y}{2}} \right).$$

We have now determined each component of Q. Combining our results, we obtain the join on [0, 9] defined by

$$Q(y) = \begin{cases} \frac{\sqrt{2y}}{40} & \text{if } 0 \leq y \leq 4.5 \\ \frac{1}{20} \left(3 - \sqrt{\frac{9 - y}{2}} \right) & \text{if } 4.5 \leq y < 9 \end{cases}$$

(e) R is concave up on [0, 0.075] and concave down on [0.075, 0.15]. Q is concave down on [0, 4.5] and concave up on [4.5, 9].

(b) K must be invertible because K is increasing.

(d) Call the inverse function L. Let y be an arbitrary assimilation rate. Then, on subdomain [0, 1], K is defined by $y = K(x)$ where

$$K(x) = \frac{9}{8} - \frac{1}{4} \left(x - \frac{3}{4} \right)^2.$$

K is increasing on this subdomain, and so its range is $[K(0), K(1)] = [0, 5/6]$. That means the inverse has subdomain $[0, 5/6]$ and subrange $[0, 1]$, with $x = L(y)$. But

$$y = \frac{9}{8} - \frac{1}{4} \left(x - \frac{3}{4} \right)^2 \Leftrightarrow \left(x - \frac{3}{4} \right)^2 = 2 \left(\frac{9}{8} - y \right) \Rightarrow x = \frac{3}{4} \pm \sqrt{2 \left(\frac{9}{8} - y \right)}$$

to begin with. This equation does not define a function because it is ambiguous, and a function is a rule for labelling things unambiguously. Rather, the above

equation defines two functions, each with domain $[0, 5/6]$, say \underline{L} defined by

$$\underline{L}(y) = \frac{3}{4} + \sqrt{2 \left(\frac{9}{8} - y \right)}$$

and \bar{L} defined by

$$\bar{L}(y) = \frac{3}{4} - \sqrt{2 \left(\frac{9}{8} - y \right)}.$$

Which of these two functions is the inverse of K? In other words, is $L = \underline{L}$, or is $L =$

? Well, you know that $L(y)$ must belong to $[0, 1]$. But $\bar{L}(y)$ is never less than $4/3$.

So it is always bigger than 1. So it cannot belong to $[0, 1]$. Therefore it must be the

case that $L = \underline{L}$. In other words,

$$L(y) = \frac{3}{4} - \sqrt{2 \left(\frac{9}{8} - y \right)}$$

on $[0, 5/6]$. Similarly, on subdomain $[5/6, 1]$ of L, we have

$$y = 1 - \frac{1}{6x^2} \Leftrightarrow \frac{1}{6x^2} = 1 - y \Leftrightarrow x = \sqrt{\frac{1}{6(1-y)}}.$$

So L is the join defined on $[0, 1]$ by

$$L(y) = \begin{cases} \frac{3}{4} - \sqrt{2 \left(\frac{9}{8} - y \right)} & \text{if } 0 \leq y \leq \frac{6}{5} \\ \sqrt{\frac{1}{6(1-y)}} & \text{if } \frac{6}{5} \leq y < 1 \end{cases}$$

(e) The inverse tells you the concentration at which a particular assimilation rate will be observed.