The Mathematical Treatment of Leaf Venation: the Variation in Secondary Vein Length along the Midrib

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INTRODUCTION

Leaf morphology has been quantified and treated mathematically in various contexts, including taxonomy (e.g. Melville, 1955; Jensen et al., 2002), differential growth and allometry (e.g. Melville, 1953; Phillips, 1983; Verwijst and Wen, 1996), leaf area estimation (e.g. Carbonneau, 1976; Verwijst and Wen, 1996) and the branching and development of veins (e.g. Slade, 1957). Morphometric analyses may be variously accomplished (Jensen et al., 2002), but notably in terms of lines, outlines, angles and landmarks (Dickinson and Phipps, 1984; Dickinson et al., 1987; Jensen, 1990; Jensen et al., 2002). Outlines may be captured as rectangular coordinates (Melville, 1937) or Fourier coefficients (Kincaid and Schneider, 1983; Dickinson et al., 1987) and, even when non-fractal, analysed in terms of fractal dimensions (Mancuso, 2002).

Certain dicotyledonous leaves and leaflets are tempting subjects for a quite different kind of quantitative treatment in that they have easily measurable secondary veins running, often more-or-less straight, from midrib (primary vein) to leaf edge. These are classified as simple craspedodromous (Hickey, 1973). This paper is just about leaves and leaflets of this kind. They are especially characteristic of many temperate trees where plication occurs between secondary veins before formation of tertiary veins in the bud. Most of the tree leaves treated here are illustrated with line drawings by Farrar (1995). Kobayashi et al. (1998) studied the geometry of primary and secondary veins in such leaves of Fagus sylvatica and Carpinus betulus, seen as unfolding mechanical structures. However, most quantitative work on growth and venation has been on other kinds of leaf, usually with distances measured across the main transport routes. Where vein lengths are well defined, a mathematical treatment is possible that is unlike all those of the previous paragraph.

Figure 1 illustrates the measurements that concern us here. Using the symbols of Burton (1960), the length of a secondary vein is \( p \), and the distance from its origin on the midrib to the leaf tip is \( l \). The length of the half-lamina is \( L \), so that \( \sqrt{L^2 + l^2} \) varies from 0 to 1. If \( p \) is seen as varying continuously with \( l \), it has a maximum value of \( P \) and, where \( l \) is \( L/2 \), its value is now denoted ‘\( P_{mid} \)’. The ratio \( P_{mid}/L \) is \( B \).

Where a vein is curved, \( p \) refers to true length, not the shorter distance between ends.

In these terms, there are obvious interspecific differences. Thus the longest secondary veins are near the leaf base in Tilia vulgaris and near the middle of the midrib in Castanea sativa. Within a single species, both \( B \) and the positioning (\( IL \)) of the longest secondary veins vary too, doing so progressively from leaf to leaf along single shoots in F. sylvatica (Burton, 1960). Nevertheless, figure 2 of Burton (1960) shows, partly independently of detailed mathemat-

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ical analysis, that there are common features in different species that demand explanation, notably a relationship between $P/L$ and the corresponding value of $ll/L$. The latter quantity was incorrectly given in that paper as $ll/(L - l)$.

Burton (1960) also found that a single general equation may be used to describe the relationship between secondary vein length and vein position in at least 14 species belonging to seven families. This is as follows:

$$p = B2^{x+y}(L - l)/L^{x+y-1}$$  \hspace{1cm} (1)

where $x$ and $y$ are constant for any given half-lamina. With all lengths expressed as fractions of $L$, this may be written as:

$$pL = B2^{x+y}(lL)^{(1 - l/L)^y}$$  \hspace{1cm} (2)

Alternatively,

$$pl = B2^{x+y}(ll/L)^{(1 - l/L)^y}$$  \hspace{1cm} (3)

The maximum value of $p$, i.e. $P$, occurs where $l/l/(L - l)$ equals $x/y$ and is given by:

$$pl = B(2x)^{(2y)}(x + y)^{xy}$$  \hspace{1cm} (4)

Equation (1) has the following logarithmic form:

$$\log p = \log K_1 + xlog l + ylog(L - l)$$  \hspace{1cm} (5)

where $K_1$ is $(B2^{x+y}/L^{x+y-1})$.

These equations are purely empirical – suggested by a glimpsed rose leaflet resembling a graph in a school algebra book. Its formula evolved to become eqn (1), with attention shifting from leaf outlines to vein lengths (and thus away from rose leaflets where the lengths are ill-defined). Inclusion of the term $L^{x+y-1}$ made eqn (1) dimensionless, with all parameters independent of leaf size (a point better illustrated by eqn 2). The number 2 was introduced because the term $K_1L^{x+y-1}$ for all leaves collectively was found to increase in proportion to $2^{xy}$. The parameter $B$, equal to $K_1L^{x+y-1}/2^{xy}$, was therefore defined for its independence of $x$ and $y$ rather than for its equality with the ratio $p_{mid}/L$. In data for 14 species, $B$ varied between 0-2 and 0-45, with a mean of 0-32 (Burton, 1960). For $F.$ sylvatica, Rubus fruticosus and perhaps Betula alba, $x$ and $y$ seem to show approximately linear relationships, such that $y$ is zero when $x$ is 1 (Burton, 1960). Lower values of $x$ were not found in any species.

For a given leaf, eqn (5) allows $\log K_1$, $x$ and $y$ to be estimated by linear regression. Burton (1960) estimated them by selecting three points on the curve of $p$ against $l$ and thus obtaining three simultaneous equations to be solved for $\log K_1$, $x$ and $y$. If their solution did not yield a good fit to the whole data set, the process was repeated. Because the calculations were laborious, it was suggested that the equations were unsuited to studies involving many leaves, but that was the view of an amateur before the widespread availability of computers. Non-linear regression is now easy and confirms, with inconsequential differences in detail, most of the values of $x$, $y$ and $B$ in table 1 of Burton (1960). However, for $T.$ vulgaris, while the calculated values of $p$ are correct, $B$ should have been tabulated as 0-39 rather than 0-35 (see Fig. 3).

As originally defined, $L$ is simply the length of a half-lamina as measured, hereafter denoted $L_m$. Sometimes, however, it is preferable or necessary to use a slightly different value, $L_c$, that is a fourth fitted parameter (i.e. in addition to $B$, $x$ and $y$). This is necessary when a half-lamina does not extend basally beyond the basal secondary vein, as, for example, in Corylus avellana. For such a vein, $l = L_m$, but $p$ is obviously not zero. Then eqn (1) can only apply if $L > L_m$, and $L_c$ obtained by non-linear regression is an appropriate value. Although extra parameters are in principle best avoided if they do not greatly improve the data fit, $L_c$ may be used in place of $L_m$ more generally. In fact, for many leaves, $L_c$ was found to be the same as $L_m$ within the limits of measurement precision, or not to differ statistically from it. However, for some other leaves, $L_c$ was significantly longer or shorter than $L_m$. For example, in the case of the data for the half-lamina of $B.$ alba given by Burton (1960), the calculated value of $p$ for the basal secondary vein (at $l = 72$ mm) is 30% too high when $L$ is taken as $L_m$ (72.5 mm), but is exactly right when $L$ is taken as $L_c$ (72.01 mm). Betula alba is a species in which $p$ is very

![Fig. 1. Diagram of a half-lamina to illustrate the vein length, $p$, the vein’s position on the midrib measured as distance $l$, and the total length of the half-lamina, $L$. $P$ is the hypothetical maximum vein length as calculated from the fitted curve and eqn (4). A vein for which $l$ equals $L/2$ would have length $p_{mid}$ equal to $BL$. Vein spacings are arbitrary.](image1)

![Fig. 2. Relationship between maximum lengths of secondary veins, $P$ (plotted as $PB_{Lm}$, where $B$ is constant for each half-lamina and $L_m$ is its length), and their distances from the leaf-tips, $l$ (plotted as $ll_{Lm}$). The broken lines represent limiting values based on data of Burton (1960). The circles correspond to individual half-leaves of another eight species.](image2)
sensitive to \((L - l)\) near the lamina base (as is generally true when \(x/y\) is high).

Given eqns (2) and (4), figure 2 of Burton (1960) may now be adapted and corrected. Figure 2 shows \(P/B_{L_m}\) plotted against corresponding values of \(I_{L_m}\). The enclosed area encompasses all values of \(x\) and \(y\) found by Burton (1960). These indices, when graphed, all lay within a polygon defined by the coordinates \((1, 0), (1.5, 0), (1.1, 1.2), (2.1, 0.8)\) and \((2.3, 2.5)\). It is inevitable that \(P/B_{L_m} = 1\) when \(I_{L_m} = 0.5\), so the significant feature of Fig. 2 is the smallness of the enclosed area, almost all of which is for \(I_{L_m} > 0.5\). The original figure showed, not \(P/B_{L_m}\) but \(P/I_{L_m}\) normalized to the mean \(B\) value of 0.32 (i.e. \(0.32P/B_{L_m}\)). It also showed points for single leaves of 34 species, i.e. \(P/I_{L_m}\) without this normalization, emphasizing in a different way the likely existence of a common morphological pattern. In Fig. 2 those points are replaced by others described in the Results section.

As already indicated, many past investigations have been more concerned with actual leaf shapes. Conventional graphs of \(p\) against \(l\) do not show these, notably because the secondary veins in real leaves are usually angled forward. Real leaf outlines may also be, for example, lobed or extended at the lamina base. However, for real or calculated values of \(p\) and \(l\), one may derive a ‘vein-tip outline’ (looking sometimes like the leaf outline in Fig. 1) that ignores these complications. For given angles \(\alpha\) between straight secondary and primary veins, the shortest distance from vein tip to midrib is then \(psin\alpha\), while the corresponding value of \(l\) is reduced by \(pcos\alpha\). In \(F. sylvatica\) and \(Carpinus betulus\), the angles are typically 30–50°, decreasing gradually from base to tip of leaf (Kobayashi et al., 1998). Such vein-tip outlines may be useful in modelling leaf shapes and areas, but are not pursued here.

The main aim of this paper is to explore further this general mathematical approach and to indicate how it might be useful in future studies. The intention is not to characterize species completely, but to explore various issues arising in the application of the equations. Two points considered are whether \(x\) does always exceed 1.0, and whether \(y\) is typically proportional to \((x - 1)\) for individual trees.

**MATERIALS AND METHODS**

Measurements were made on leaves from the following species: *Alnus glutinosa* (L.) Gaertner, *A. viridis* (Chaix) DC and *Corylus avellana* L. (Betulaceae); *Sorbus aria* (L.) Crantz and *Crataegus monogyna* Jacq. (Rosaceae); *Hamamelis mollis* Oliver and *Corylopsis
veitchiana* Bean (Hamamelidaceae); *Castanea sativa* Miller (Fagaceae); *Ulmus glabra* Hudson and *U. procera* Salisb. (Ulmaceae); and *Tetrastigma voinierianum* Gagnepain (Vitaceae). Secondary veins were straightened for measurement if
nec} necessary. Although greater precision was sometimes achieved, measurements were usually made to the nearest 0·5 mm or 1 mm.

Equations were fitted to the data by non-linear regression (Motulsky and Ransnas, 1987) using the statistical program DataFit 8·0 (Oakdale Engineering). The half-lamina length, \( L_0 \), was taken sometimes as the measured value (\( L_m \)) and sometimes as a calculated fourth parameter (\( L_c \)). In a few special instances, \( x \) was taken as exactly 1. Although these three versions of the regression model yielded different parameters for any given half-lamina, the corresponding fitted curves were sometimes barely distinguishable when plotted and were thus, to the precision of the measurements, identical. Whether differences between \( L_m \) and \( L_c \) were statistically significant was tested by taking the fourth parameter as \((L_m - L_c)\) instead of \( L_c \) and comparing it with zero. Goodness-of-fit is reported in terms of \( R^2 \), the coefficient of determination adjusted for the number of regression parameters, \( n_1 \), and the number of data pairs, \( n_2 \). It is calculated from the correlation coefficient, \( R \), as \( \frac{(n_2 - 1)R^2 - n_1}{(n_2 - 1 - n_1)} \), with \( R^2 < R^2 \). This measure is independent of leaf size.

Relationships between \( x \) and \( y \) for given species are expressed, not in terms of either of the conventional regression lines (here invalid, since the variables have equal status), but of a line between them through the means of \( x \) and \( y \), its gradient being equal to the geometric mean of the regression gradients. As is often the case with regression lines, there is no theoretical basis for assuming linearity.

RESULTS

The trend shown by the enclosed area in Fig. 2 may be checked for other species without recourse to equations. To illustrate this (in a different way from that used originally), \( P/L_{2m} \) and the corresponding values of \( \frac{L_m}{L_2} \), were estimated from plotted curves, without equation-fitting, for single leaves of eight species not listed by Burton (1960). The data points all lie within the area based on previous measurements. The species are \( A. glutinosa \), \( A. viridis \), \( C. avellana \), \( S. aria \), \( C. monogyna \), \( H. mollis \), \( C. veitchiana \) and \( T. voinierianum \). For \( T. voinierianum \), the central leaflet was used. To avoid bias, the leaves were chosen before \( P/L_m \) and \( \frac{L_m}{L_2} \) were calculated.

Data of that sort are less our concern than is the application of eqn (1), and this proved successful in all species studied. Figure 3 shows relationships between \( p/l \) and \( L_m/L_2 \) to illustrate some of the diversity in curve shapes that has been encountered. The reason for plotting \( p/l \) as in eqn (3), rather than \( p/L_m \) as in eqn (2), is explained below. More detailed results are given next for six species. Means are presented ± standard deviation (s.d.).

**Corylus avellana**

In \( C. avellana \) the basal secondary veins originate virtually at the lamina bases, so that \( L_0 \) has to be taken as \( L_c \) (see above). In 22 half-laminas from a single tree (with \( L_m = 84-116 \) mm), \( L_m/L_c \) was found to be 1·00001–1·026 (with differences between \( L_c \) and \( L_m \) often tiny in relation to measurement precision). Mean (± s.d.) \( R_2 \) was 0·9977 ± 0·0024 (range 0·9921–0·9999), with many curves fitting to within the precision of the measurements. The mean of \( B \) was 0·36 ± 0·02. Means of \( x \) and \( y \) were, respectively, 1·38 ± 0·12 and 0·24 ± 0·07. Values of \( x \) and \( y \) were correlated (\( r = 0·71 \), \( P < 0·001 \)), with the mean relationship between them given by the equation \( y = 0·59(x - 0·97) \). Values of \( y \) also correlated with those of \( L_m/L_c \) (\( r = 0·90 \), with the mean relationship between them given by the equation \( y = 9·63(L_m/L_c - 0·98) \). Since this must affect the relationship between \( y \) and \( x \), the latter was recalculated just for those 17 half-leaves where \( L_m/L_c < 1·01 \). The resulting equation is \( y = 0·35(x - 0·76) \). There were 8–11 (mean 9·5) measurable secondary veins per half-lamina (\( n_2 \)).

**Ulmus procera** and **U. glabra**

Hybridization of the British species of \( U. glabra \), with their differing and variable leaf forms (Melville, 1955; Stace, 1991), complicates identification but could itself be studied in terms of the equation parameters. Here we merely compare three small trees, A, B and C, with obviously different foliage (that represented in Fig. 3 being a fourth). If not hybrids, tree A is \( U. procera \) and the others are \( U. glabra \). Tree A has smaller but relatively broader leaves than tree B growing beside it. For 13 half-leaves from tree A, \( L_m \) averaged 63 ± 14 mm. For eight leaves from tree B, \( L_m \) averaged 133 ± 24 mm. The respective numbers of measurable veins averaged 10·3 ± 1·7 and 17·4 ± 2·6, with some positive dependence on \( L_m \) in each group. Because \( p \) changes steeply with \( l \) near the lamina base, precise values of \( L_c \) matter, but to within the accuracy of measurement, \( L_c \) equalled \( L_m \) in these examples. Therefore the question of a dependence of \( y \) on \( L_m/L_c \), as in \( C. avellana \), does not arise here. Mean values of \( B \) were 0·38 ± 0·05 in tree A and 0·27 ± 0·05 in tree B. The indices \( x \) and \( y \) did not differ significantly in trees A and B, with the means of \( x \) being 1·52 ± 0·24 and 1·61 ± 0·31, respectively, and the corresponding means of \( y \) being 0·39 ± 0·11 and 0·50 ±
values of long veins to be estimated, these being 42% and 14%. The
0.9595), it does allow the apparent extra lengths of the two
peaks. This point was also explored using

In only three instances did

Alnus glutinosa: a special case?
The broad leaves of A. glutinosa, with their retuse or
Furthermore, the base of the lamina often tapers in a way
that raises doubts about the validity of \( L_m \) as the best
measure of \( L \). Indeed, for all but one of 16 half-laminas, \( L_c \)
was found to be shorter than \( L_m \) (by 6% on average). Mean
\( L \) for these data (with \( L = L_c \)) was 0.50 ± 0.06, which
is higher than for A. viridis and for other species studied
(Burton, 1960). Corresponding means for \( x \) and \( y \) were,
respectively, 1.02 ± 0.14 and 0.34 ± 0.12. These means
differ little from those for A. viridis, but nine values of \( x \)
were less than 1 (0.85–0.99). This would seem a more
serious challenge to the suggested generalization that \( x \) is
always greater than 1. Therefore, for the nine half-laminas
with \( x < 1 \), eqn (1) was refitted with \( x = 1 \), again with
\( L = L_c \).
Mean \( R_c^2 \) was little lowered by this constraint (from 0.9898

Alnus viridis

Alnus viridis conforms well to eqn (1). For nine half-
laminas, with \( L \) taken as \( L_m \), mean values of \( B, x \) and \( y \) were,
respectively, 0.35 ± 0.01, 1.04 ± 0.09 and 0.22 ± 0.05. In
three cases, \( x \) was less than 1 (i.e. 0.91–0.99), with two of
these corresponding to low values of \( R_c^2 \) (0.9827 and
0.9780, compared with the mean of 0.9918 ± 0.0071).
In other words, two of these low \( x \) values are associated with
a poor fit. This point was also explored using \( L_c \) instead of
\( L_m \).
In only three instances did \( L_c/L_m \) differ significantly from 1
(with values of 0.99, 1.05 and 1.06). With \( L = L_c \), mean
values of \( B, x \) and \( y \) averaged 0.35 ± 0.01, 1.14 ± 0.11 and
0.35 ± 0.16, respectively, with only one value of \( x \) less than 1
(i.e. 0.95), and that not significantly so. Mean \( R_c^2 \) was
0.9975 ± 0.0012, implying a better data fit with \( L_c \) than with
\( L_m \). The coefficient of correlation between \( x \) and \( y \) was 0.66
with \( L = L_m \), and 0.84 with \( L = L_c \). With \( L = L_m \), the average
relationship between \( x \) and \( y \) is given by the equation \( y = \)
0.50(\( x - 0.60 \)). With \( L = L_c \), the equivalent equation is \( y =
1.43(x - 0.89) \). In neither case is \( y \) proportional to \( x - 1 \),
therefore. The numbers of secondary veins per half-lamina
(n2) averaged 8.8 ± 2.4, correlating with \( L_m \) (\( r = 0.97, P <
0.001 \)).

Crataegus monogyna

In this species there are typically only four or five
measurable secondary veins per half-leaf and \( p \) increases
monotonically with \( l \). It is therefore unsurprising that eqn (1) generally fits well. The exact value of \( L_m \) is sometimes unclear through tapering of the lamina at its base, and \( L_c \) cannot be estimated using DataFit for only four data-pairs. Nevertheless, \( C. monogyna \) is of interest in that \( x \) may sometimes be significantly less than 1, and that is the main reason for including this species here. Twelve half-leaves were studied, with \( L_m \) measured to where the lamina narrowed most abruptly. Means of \( L_m \), \( B \) and \( R^2 \) were, respectively, 48.5 ± 10.1 mm, 0.40 ± 0.03 and 0.9972 ± 0.0046. The means of \( x \) and \( y \) were, respectively, 0.98 ± 0.08 and 0.08 ± 0.03, the two being slightly correlated \((r = 0.38)\). In five cases, \( x < 1.00 \).

**DISCUSSION**

Further evidence has been obtained for the general applicability of eqn (1) and its variants in appropriate leaves. Amongst questions to be discussed now are the following. What do the indices \( x \) and \( y \) signify? Are the equations of more than descriptive value, and how might they relate to the processes of growth? Is there a better equation? What uses are there to this mathematical approach?

The meanings of \( x \) and \( y \)

Whereas the parameter \( B = p_{mid}/L \) is a simple length ratio, \( x \) and \( y \) correspond individually to no obvious common-language descriptors. Indeed, they must be considered together in relation to all relevant aspects of leaf form, including notably both the relative length of the hypothetical longest secondary vein \((P/L)\) and its position (given by \( x/y \)). The following relationships are implied by the equations. For given values of \( P/BL \) equal to \((2x)+(2y)/(x+y)\), realistic values of \( x \) and \( y \) show nearly linear positive relationships with each other. For a given value of \( xy \), that of \( P/BL \) increases with \( x \) and \( y \), while, for values of \( l \) less than \( L/2 \), those of \( p/B \) decrease. The gradient of the graph of \( p \) against \( l \), i.e. \( dp/dl \), equals \( 2Bx \) when \( l = L/2 \). The ratio of \( p \) values where \( l = 0.75L \) and \( l = 0.25L \) is \( 3^{1/2} \).

Values of \( x \) had previously been found always to exceed 1 (Burton, 1960) and most new values do so too. Moreover, the contrary evidence in relation to \( A. viridis \) and \( A. glutinosa \) can all be attributed to ‘errors’ (i.e. growth irregularities plus measurement errors). As to the low values of \( x \) in some leaves of \( C. monogyna \), these are not readily dismissed as due either to errors of measurement or to the stated uncertainties regarding \( L \), but they may be explained by modest growth irregularities. For example, the lowest value (0.87) would rise to 1.00 if 3 mm (6% of \( L_m \)) were added to the leaf tip, increasing all measurements of \( l \) and \( L_m \) by the same amount. Alternatively, a lesser discrepancy at the leaf tip could be combined with discrepancies in \( p \).

For the moment, one can only conclude that values of \( x \) less than 1 are uncommon, and perhaps not biologically significant. This suggests that the processes of growth lead to a final dependence of \( p \) on \( l \) that arises in two functionally distinct ways, relating separately to \( l \) and \( l^{-1} \). This idea lies behind eqn (3) and the plots of \( pl/l \) against \( ll/L_m \) in Fig. 3.

In the special case that \( x = 1 \) and \( y = 0\), \( pl/l \) is constant \((= 2B)\) for all secondary veins of a given leaf. This situation could arise, for example, with acropetal initiation of secondary veins during initial growth of the midrib, together with proportionate increases in \( p \) and \( l \) subsequently. More generally, eqn (3) may perhaps be interpreted, therefore, in terms of a basically similar growth pattern, but modified by non-proportionate changes in \( p \), \( l \) and \( (L-l) \) that lead to the term \( 2^{1+\gamma}(ll/L)_x^\gamma(1-(ll/L))_y^\gamma \). Power relationships amongst biological measures are both common (as in many examples of allometry) and expected (Apple and Korostyshhevskij, 1980).

For \( F. sylvatica \), \( R. fruticosus \) and much less clearly \( B. alba \), Burton (1960) found approximate linear relationships between \( x \) and \( y \) such that \( y \) would be zero if \( x \) were 1. Positive correlations have also been found for \( C. avellana \), \( U. procera \), \( U. glabra \), \( A. viridis \), \( A. glutinosa \) and \( C. monogyna \), but the relationships, taken as rectilinear, correspond, on extrapolation, to \( x < 1 \) when \( y = 0 \). What do they mean? Because some correlation amongst parameters is inherent in curve-fitting (Motulsky and Ransnas, 1987), the correlations between \( x \) and \( y \) could result partly from irregularities or ‘errors’ in leaf growth, i.e. departures from the supposed ideal of eqn (1), from measurement errors, or from inappropriate choices of \( L \).

Effects of such ‘errors’ can be explored by modelling. A model half-lamina is first defined in exact accordance with eqn (1), with values of \( B \), \( L \), \( x \) and \( y \) and vein spacings appropriate to the species in question. Errors (random or otherwise) can then be applied to individual vein lengths over many trials, with the parameters being re-calculated each time. Estimates of \( x \) and \( y \) will be positively correlated, showing a greater variability when \( L \) is taken as \( L_c \) rather than as the value originally defined. If \( P/B \) happens to remain constant despite the errors, then the relationships are calculable from eqn (4). Alternatively, if values of \( ll/L \) corresponding to \( P \) stay constant, \( y/x \) is constant too. In fact, definitive relationships between \( x \) and \( y \) cannot be obtained in this way, since they depend on the details of the model (including the initially chosen ‘true’ values of \( x \) and \( y \)), but what can be said is that they can be broadly similar to relationships observed for real leaves. Thus, with \( L = L_{m} \), \( y \) may be approximately proportional to \((x - c) \), where \( c \) is a constant between about 0-2 and 0-80. Modelling thus suggests that the observed correlations between \( x \) and \( y \) could be partly due to ‘errors’ of growth or measurement. However, the smoothness of real data curves suggests that these ‘errors’ are unlikely to be large and random. Thus, in \( A. viridis \) with \( L = L_{c} \), the standard deviations of the residuals averaged only 0.42 mm ± 0.17 mm, compared with the typical measurement-precision of 0.5 or 1 mm. Put differently, the absolute residuals for only six of the 66 secondary veins of eight half-leaves exceeded 0.5 mm (maximum 1-4 mm). (In the seventh half-leaf, half the absolute residuals lay in this range.)

Such error-modelling cannot, in any case, explain all correlations between \( x \) and \( y \). Thus the two curves for \( U. glabra \) in Fig. 5A seem too distinct in shape, and values of \( x \) and \( y \) in \( F. sylvatica \) and \( R. fruticosus \) (Burton, 1960) imply clear variations in leaf form. In \( F. sylvatica \), the ratio \( x/y \),
estimated as \( ll(L_m - l) \) when \( p = P \), may increase progressively from the tip to the base of a shoot (Burton, 1960), again implying meaningful variations in \( x \) and \( y \). Conspicuous leaf heteroblasty along shoots is well known (e.g. Dickinson and Phipps, 1984; Dickinson et al., 1987) and occurs in Ulmus (Stace, 1991). Error-modelling and the data for A. viridis both show that estimates of \( x \) and \( y \) vary more when calculated for \( L = L_c \) than for \( L = L_m \). Therefore, biologically meaningful variations in \( x \) and \( y \) may be best studied in species where \( L \) values are most certain, and where the values of \( ll/L \) corresponding to \( P \) vary substantially and are not close to 1.

Published studies on leaf growth

Mathematical descriptions of mature leaf forms should ultimately help in the quantitative modelling of prior growth. Much is known of leaf growth (e.g. Nelson and Dengler, 1997; Poethig, 1997; McConnell and Barton, 2003), but not enough for present purposes. Indeed, most information is for other species, not all with appropriate venation. Of particular interest is whether the initiation of secondary veins is acropetal, as suggested above. It is so in Cercis siliquastrum and Prunus serrulata (Slade, 1957), in Sorbus alnifolia and S. hybrida (Merrill, 1979) and for most, if not all, of the 14–16 secondary veins in Ostrya virginiana (Franck, 1979). The sequence is basipetal in Populus deltoides (Isebrands and Larson, 1980), as in Arabidopsis and some other herbaceous dicotyledons (Telfer and Poethig, 1994). Isebrands and Larson (1980) quantified progressive increases in the spacing of secondary veins in very early leaves of P. deltoides, but length changes are more easily studied in leaves no longer in the bud. At that late stage, alterations in leaf outline are often small to the casual eye. In P. × eumericana Taylor et al. (2003) measured changes (sometimes negative) in the areas between successive secondary veins during leaf expansion. Wolf et al. (1986) mapped quantitative patterns of leaf expansion in Vitis vinifera. In Antirrhinum a front of cell-cycle arrest moves gradually from leaf tip to base (Nath et al., 2003).

Alternative equations

In a mature half-lamina of the type under consideration, \( p \) rises steadily from zero at the leaf tip to a single maximum, then falls towards zero at or just beyond the base. Equation (1) has appropriate characteristics, and is flexible enough to match most data (Fig. 3), doing so with no more than the minimum number of parameters (\( B, x, y \) and, if necessary, \( L_c \)). Furthermore, its logarithmic version, eqn (5), is useful when a non-linear regression program is unavailable. All this is not to say that other equations might not be as valid, however. In illustration, here is one possibility:

\[
p = BL_c^3 \left[ 4(K_2 - 0.5)(llL_c)(1 - llL_c)(K_2 - llL_c)K_3 \right]^{K_3} \tag{6}
\]

where \( L_c, K_2 \) and \( K_3 \) are new constants, \( L_c^3 \) is equivalent to \( L_c \), and \( K_2 > 1 \). This is formulated to include \( BL_c^3 \) as a distinct term. We may compare the results of applying eqn (6) and (1) to the tabulated data of Burton (1960). Then \( K_3 \) slightly exceeds \( x \) (by 8 % on average). Mean \( R^2 \) is 0.9956 with eqn (1) and 0.9947 with eqn (6). In most plots of \( p \) against \( l \), the two lines are barely distinguishable over the relevant ranges of \( l \), but eqn (1) is favoured in that \( L_c \) is near \( L_m \) for all nine data sets (mean \( L_c/L_m = 1.019 \pm 0.043 \); range 0.993–1.128), while \( L_c \) exceeds \( L_m \) in each case (mean \( L_c/L_m = 1.066 \pm 0.103 \); range 1.006–1.336). Although other equations can be found that fit the same data quite well, it is not true that any equation yielding similar shapes of curve will do so.

The choice of equation may depend largely on convenience and on the desirability of minimizing the number of parameters, but objectives matter too. Thus eqns (1)–(6) may be satisfactory for descriptive purposes, but growth studies may eventually suggest different formulae. An important aim has been the simple one of exploring the appropriateness of applying just one equation to diverse species, whatever that equation might be. So far the evidence favours doing so. On physiological grounds, however, it may ultimately prove necessary to consider, not just the chosen linear measurements, but also, say, angles, cell numbers, or areas. At present, however, there is no reason to discard eqn (1) and its variants.

Usefulness of the mathematical approach

Despite the importance of leaf characteristics in taxonomy, it is not obvious that the equations would be useful there, for the parameters are few and insufficiently constant for any one species. Although the contours illustrated in Fig. 3 do differ, the examples were chosen to that end. Rather, it is not variety, but the conformity of so many species to a common pattern that equation-fitting embraces.

The greatest value of this general approach may eventually lie in the quantitative understanding of coordinated growth processes. The particular regularity in leaf form discussed here should also be understood in the broader context of morphological regularities in dicotyledonous leaves generally. Thus, many other kinds of undivided leaf, with less easily defined vein lengths, do have similar outlines inasmuch as they are broadest near the middle or base and taper distally. In divided leaves, the equations may apply to individual leaflets, as in Rubus and Aesculus (Burton, 1960) and in T. voinierianum. Occasionally, as in Rubus, a pair of lateral leaflets may be incompletely separated, and one may then ask how far the resulting pattern of vein lengths accords with the equations. The same may be asked of the central lobes of simple palmate leaves, as of Acer. Resolving that could be one stage in understanding developmental processes in such leaves too. Here, as in the example of A. glutinosae, we have the possibility of using the equations in hypothesis testing.

Amongst leaves of a given species, and even along a single stem (Burton, 1960), there is variation in \( B, x \) and \( y \). An obvious approach to understanding these parameters is to explore how they might relate to other aspects of growth, including spatial and temporal variations in morphogens.
Conclusions

The leaves of many dicotyledonous species show similar mathematical relationships between the lengths of the secondary veins and their positions on the midrib. For each half-leaf the relationship is defined by four constants. How it relates to growth is unknown, but one may surmise that there is a general quantitative pattern to that also. One aspect of leaf development common to the relevant leaves, but established in a few species only, may be the acropetal initiation of secondary veins. The chosen equation should prove useful in guiding growth studies, not only by quantifying particular aspects of mature leaves, but by providing a descriptive norm against which to judge biologically significant departures from it. Ideal species for further study may be found amongst those showing highly variable leaf shape, and having their longest secondary veins originating not too near the lamina bases.

The leaves of A. glutinosa were suspected of not conforming with the equations, but were found to do so. However, it would be wrong to conclude that these equations always apply, and tree C (U. glabra) showed a conspicuous genetic departure from the usual pattern. Other tree species, e.g. those with palmatifid leaves, do so too obviously to have been treated here, but it is possible that the same mathematical approach, enhanced by an understanding of the relevant growth processes, might eventually shed light on these.

LITERATURE CITED