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# Path Curves and Plant Buds: An Introduction to the Work of Lawrence Edwards

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IIASA Professional Paper
July 1979

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Lawrence Edwards

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PP-79-5

International Institute for Applied Systems Analysis
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PATH CURVES AND PLANT BUDS
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To discover in the world of nature the geometrical forms of our own thinking is one of Man's most exciting experiences. A child delights in the hexagonal symmetry of a snow flake, and Kepler and thousands after him have joyed in the beauty of the laws of planetary motion. These experiences stir us, for they reveal that behind material nature there is a creative world in which we can participate through our thinking.

Such experiences are even more moving when they come from the world of living forms. The work of Lawrence Edwards [1] on plant buds offers the finest example known to me. In over four-fifths of the species he has examined, the bud profiles are fit extremely closely by a family of curves known as *path curves*, for they are the paths taken by points under repeated application of a projective transformation of three-dimensional space.

Edwards' own description [1] of the mathematics of these curves flows beautifully, but has proven perplexing to readers not well acquainted with these matters. I have therefore undertaken to provide an introduction to his work in terms of mathematics which is widely known. In the first section, we explain the construction of the bud-form curves. This section uses only plane geometry and suffices to understand the computations actually made by Edwards. It does not explain what these curves have to do with projective geometry. That is the business of section 2, which uses coordinate geometry and vectors and matrices for expressing linear equations. It also makes use of the idea of characteristic roots and vectors of a matrix. Still, this section does not give us algebraic equations for the path curves; Section 3 handles these matters, but it is necessary to use a bit more mathematics, namely linear differential equations and the elementary properties of complex numbers. With these formulae in hand, we turn, in the final section, to the statistical fitting of the path curves. Here we use data kindly provided by Edwards and fit path curves by least squares. For many species, the average absolute percentage error is less than two percent.

The first section should be intelligible to any interested reader; and the last section is intelligible without reading the intermediate sections if one will accept the formula derived for the path curves.

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1 I am indebted to Martin Levin for introducing me to this subject. Martin McCrea suggested the importance of homogeneous coordinates. My greatest debt, of course, is to Lawrence Edwards, who has painstakingly written answers to many questions and has shared the data he has accumulated over years of work. David McDonald of the Computer Service staff of the International Institute of Applied Systems Analysis has given the paper its elegant form. Calculations were done on the Institute's computer.

## 1 CONSTRUCTION OF A PLANT-BUD PATH CURVE

We plunge immediately into the construction of the bud-form curve. On a line a pick points O, A, and B, as in Figure 1. Our first task is to find the point C on this line such that

$$OC/OB = OB/OA = \lambda_1$$

that is to say, we are looking for the point C that makes the distance from O grow by the same percent between B and C as it did between A and B. Draw a line c parallel to a and choose V on c so that the line from V to O will be perpendicular to c. Draw a line d passing through O and not identical with a. Draw VB and mark its intersection with d by B'. Draw the line of AB' and mark its intersection with c by P. Draw PB and mark its intersection with d by C'. Draw the line of VC' and mark its intersection with a by C. C is the desired point.

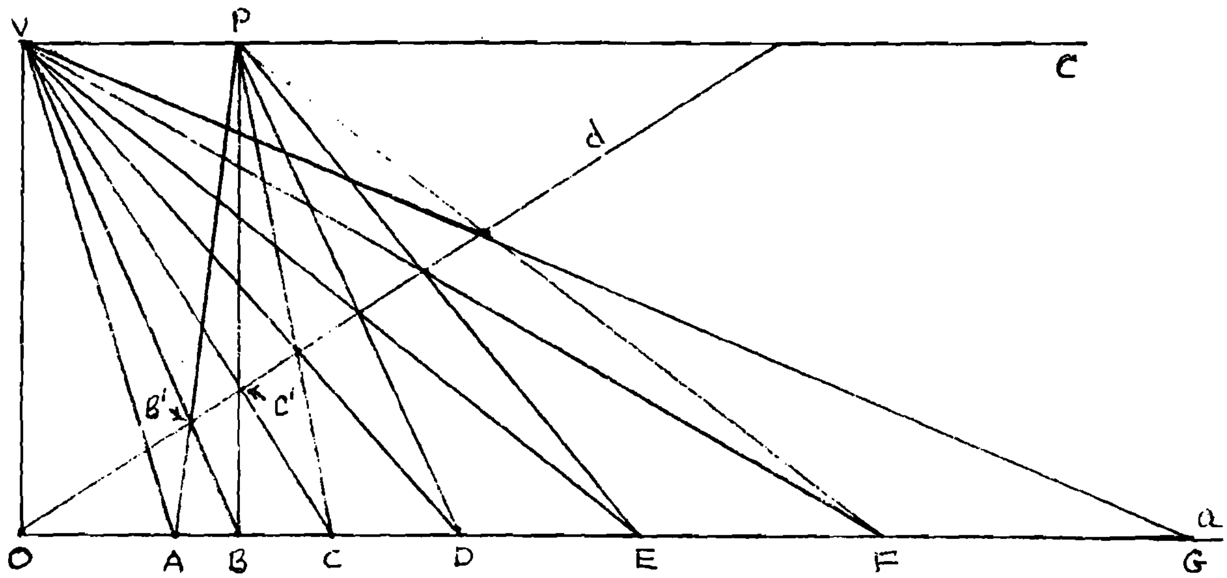


Figure 1 Construction of the Bud-form curve

Proof: By similarity of triangles

(a) $OA/AB' = PR/PB'$ $OB/BC' = PR/PC'$

(b) $AB/AB' = VP/PB' \qquad BC/BC' = VP/PC'$

Adding the two left-hand equations together and adding the two right-hand equations gives

$$(OA+AB)/AB' = (VP+PR)/PB' \qquad (OB+BC)/BC' = (VP+PR)/PC'$$

or

(c) $OB/AB' = VR/PB' \qquad OC/BC' = VR/PC'$ .

Dividing (c) by (a) gives

$$OB/OA = VR/PR \qquad OC/OB = VR/PR$$

and therefore, since the right sides of both of these equations are the same,

$$OB/OA = OC/OB$$

as was to be demonstrated.

An expanding sequence of points A,B,C,D,E, etc. can be constructed on the line a in this way. We say that $\lambda_1$ is the multiplier of this sequence. Similarly, in Figure 2, we construct a shrinking series of points A",B",C",D", ... along the line c. Let $\lambda_2$ = VB"/VA" be the multiplier on c. Now in Figure 3, we combine figure 1 and 2, but to avoid confusion we show only the lines passing through V and O. Where the line to A meets the line to A' mark the point x. Think now of x stepping along from line to line on the expanding sequence of lines and, simultaneously, on the contracting sequence. Its "footprints" will fall on the circled points of figure 3.

Now suppose that, instead of having multiplier $\lambda_1$ on a and multiplier $\lambda_2$ on c, we had multipliers of $\lambda_1^{1/2}$ on a and $\lambda_2^{1/2}$ on c. Then two steps of this "walk" are equivalent to one of the original. All of the "footprints" of x on the first walk remain footprints on the second, but the second has an extra print between each pair of the first. If we took a walk with $\lambda_1^{1/3}$ on a and $\lambda_2^{1/3}$ on c, then x would make two footprints between each pair of the original ones. With $\lambda_1^{2/3}$ and $\lambda_2^{2/3}$, x would have every other one of these footprints. Clearly x is traversing the same "path" on all of the walks; only its step-length differs. For all of the step-lengths, the ratio

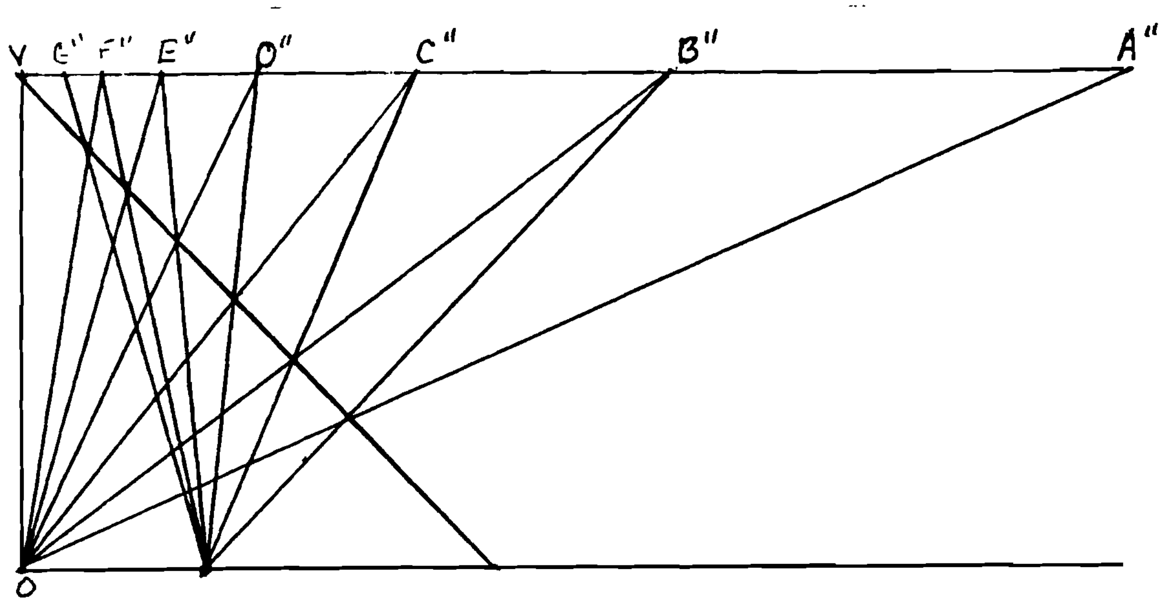


Figure 2 Shrinking series of points A

$$\lambda = \log \lambda_2^{\alpha} / \log \lambda_1^{\alpha} = \log \lambda_2 / \log \lambda_1$$

remains the same and characterizes the path itself.

It is these path curves which Edwards has shown to give the profile of plant buds. For a particular species, he collects numerous buds at the point just before opening. Then, using tweezers and a magnifying glass, he carefully removes the outer petals and reveals the form of the inner inflorescence. If a tiny petal budges, the specimen is lost. He then photographs the bud and enlarges it to be four inches high. At half-inch intervals along the vertical axis of the enlarged bud he measures the diameter. These measurements on at least seven buds of the species are averaged and plotted as in Figure 4. These measurements for 150 species and varieties are given in the appendix. They are radii in inches of the 4-inch high buds, starting from the top.

Edwards then takes two points on the profile, say T and E in figure 4, draws lines from O and V through them, and computes the multipliers $\lambda_1$ and $\lambda_2$ on a and c respectively, and then calculates

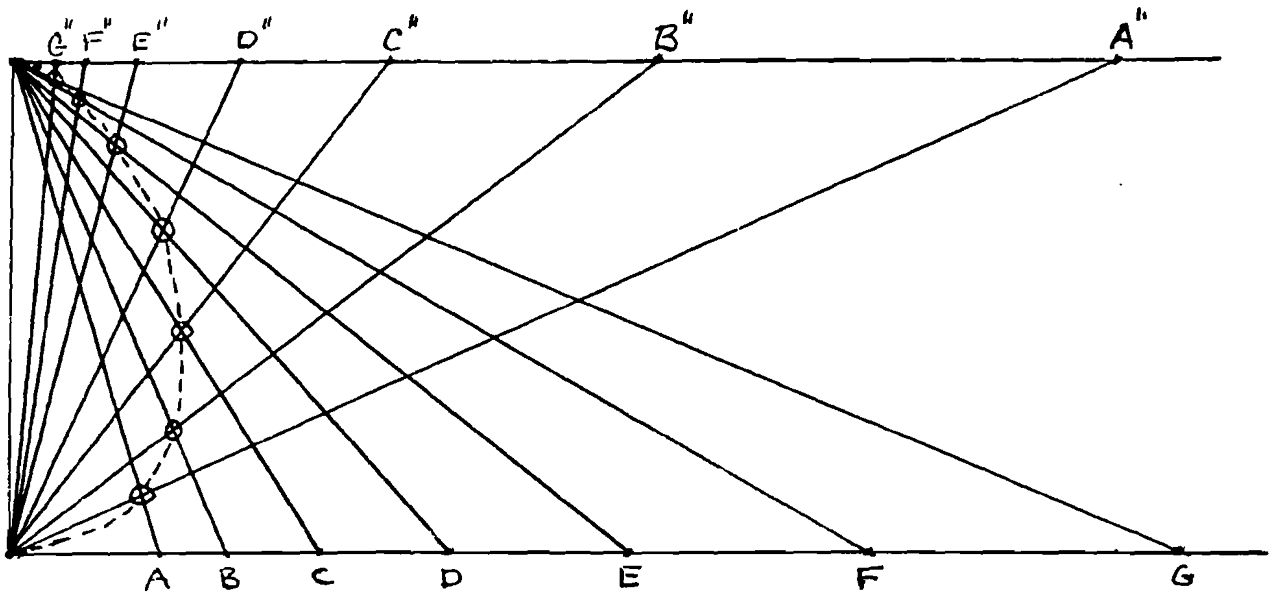


Figure 3 Figures 1 & 2 combined

$$\lambda = \log \lambda_2 / \log \lambda_1 .$$

If the profile is a perfect path curve, each pair of points gives the same value of $\lambda$. (Of course, it is not necessary actually to draw the figure; the value of $\lambda$ for a pair of points can be easily calculated directly from the measurements of the diameters without introducing any drafting error.) For ease of computation, Edwards takes the midpoint, marked T, in conjunction with each of the other points. For fifty-five species and varieties, Edwards reports in [2] the average absolute percentage deviations of the resulting six $\lambda$'s from their mean. He also indicates that deviations in $\lambda$ of ten percent or less mean extremely close fit to a path curve. Thirty of the species have average deviations of less than 10 percent; twenty of them have average deviations between 10 and 20 percent, four, between 20 and 30 percent, and only one over 30 percent.

We shall present in section 4 the results of fitting the path curves to Edwards' data in another way, minimizing the sum of the squared percentage errors between observed and "theoretical" values of the bud diameters. We present there also the average absolute error in the fit, which makes it easy even for the inexperienced to appreciate the extraordinary closeness of fit.

Although we have constructed the particular bud-form path curve, we have not seen its connection with projective transformations, nor have we developed the algebraic formula necessary for statistical fitting to the diameters, nor have we

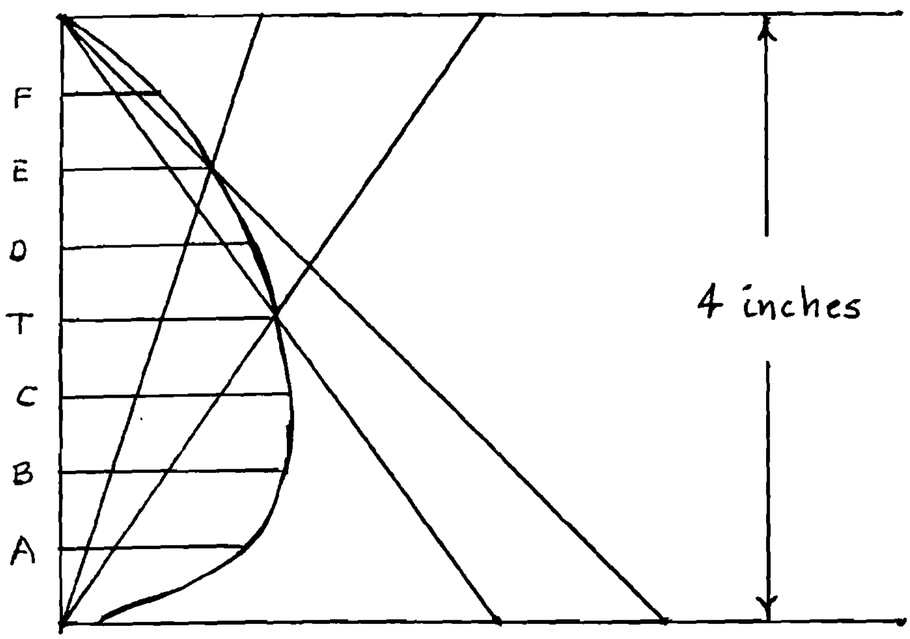


Figure 4 Plot of Bud measurements after averaging

seen how to generalize from two-dimensional figures to path curves in three dimensions. The next two sections concern these matters.

## 2 PROJECTIVE TRANSFORMATIONS AND HOMOGENEOUS COORDINATES

Projective geometry deals with the properties of figures which are preserved under projective transformation. Figure 5 shows a typical projective transformation of the line a into itself. The transformation is determined by a second line, d, and two points, p and q, not on a or d. The transformation of the point x is then found as follows. Draw the line determined by p and x; where it intersects d, mark the point x'. Draw the line determined by x' and q and mark x" where this line intersects a . This x" is the image of x under the transformation. Any point x is transformed into a unique x", and any x" comes from a unique x.

Figure 1 also shows an example of a projective transformation of the line a, with point A being transformed into B; B, into C; C, into D; and so on. Figure 6 shows yet another special case of a projective transformation of a line. This one

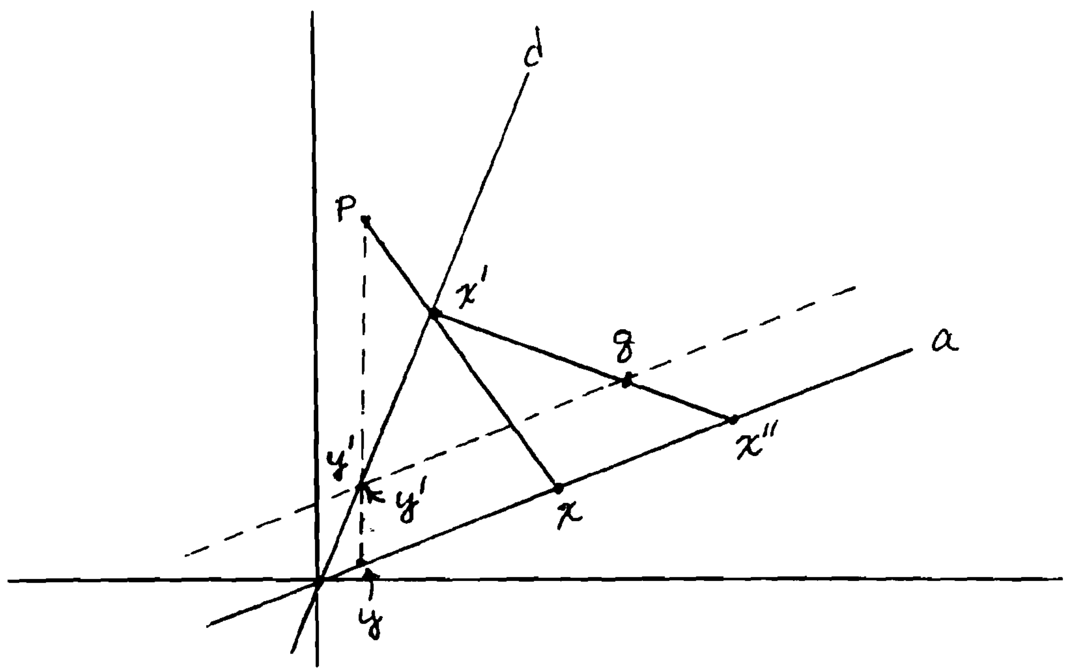


Figure 5  A Typical Projective Transformation

gives the solution of the the problem of representing in proper perspective on the plane a row of equally spaced telephone poles. It uses the fact that any three parallel lines in space will all meet at one point on the plane (or appear as parallel).

Let us return now to figure 5 and notice that if we happen to start from the particular point marked y, we will find that the line from y' to q is parallel to a. We say, however, that the two parallel lines determine the point at infinity or "intersect" at the point at infinity on a, which is, of course, also the point at infinity on the line through y' and q. Consequently, we see that parallel lines must all have the same point at infinity.

If we use ordinary, Cartesian coordinates, this point can only be written as $(\infty,\infty)$. But the point at infinity on the line d can also be written only as $(\infty,\infty)$. This notation is most unfortunate, for it gives the impression that a and d intersect at infinity, when, in fact, they intersect at (0,0). Consequently, projective geometry requires a coordinate system which can distinguish between the different points at infinity. This distiction is achieved by adding one more coordinate and agreeing that all multiples of the same vector represent the same point. Thus the vectors

$$\begin{matrix} 3 \\ 1 \\ 1 \end{matrix} \quad \text{or} \quad \begin{matrix} 6 \\ 2 \\ 2 \end{matrix} \quad \text{or} \quad \begin{matrix} 1 \\ 1/3 \\ 1/3 \end{matrix}$$

all denote the same point, and we shall write $x \approx y$ to mean that the vectors x and

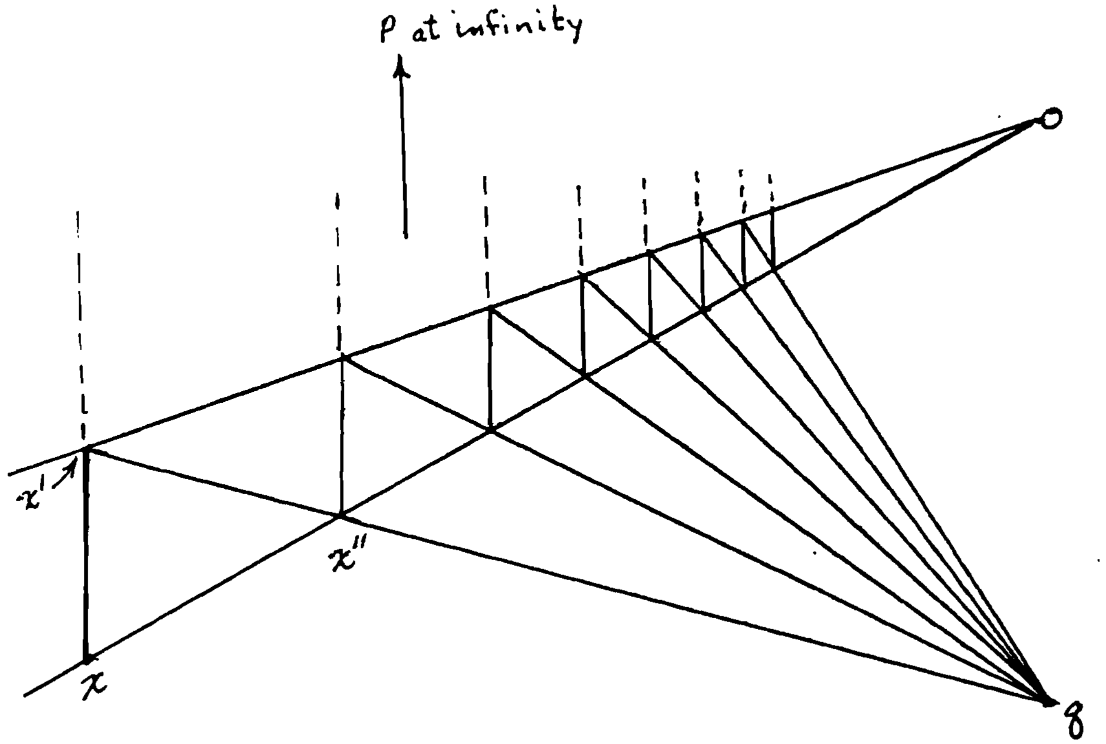


Figure 6 A Special Case of a Projective Transformation

y denote the same point.

For plotting, one picks a normalization, a row vector h, and plots the first two coordinates of the vector x/hx. The most common choice for h is h = (0,0,1), so that one plots $(x_1/x_3, x_1/x_3)$. Any other choice of h is equally valid, though of course the homogeneous representation of a point depends upon which h is used. For example, the point represented by the Cartesian coordinates (1,1) may be represented by (1,1,1) if h = (0,0,1), but by (1,1,-1) if h = (1,1,1). Only the vector (0,0,0) never arises as the homogeneous representation of a point.

If we think of the homogeneous coordinates of a figure as the Cartesian coordinates of a three-dimensional figure, then the normalization amounts to a projection through the origin onto the plane hx = 1. Then, in plotting only the first two coordinates, we are, in effect, looking at this planar figure from infinitely far out on the $x_3$ axis. More formally, we are projecting onto the plane

$$0x_1 + 0x_2 + 1x_3 = 1$$

from the point$(0,0,\infty)$.

Thus, plotting from homogeneous coordinates is formally equivalent to projection of a figure in three-dimensional space onto a plane.

In what follows, we shall denote the column vectors for the homogeneous coordinates of points with letters from p to z; row vectors for equations we denote with letters from a to h; and scalars we denote with k, m, and n.

In homogeneous coordinates, the points on the line connecting x and y may be written as mx + ny for any values of m and n. In the plane, the equation of a line may be written ax = 0, where x gives the homogeneous coordinates of points on the line. This equation corresponds to the equation

$$a_1x_1 + a_2x_2 = 1$$

in Cartesian coordinates; we just set $x_3 = 1$ and $a_3 = -1$, with h = (0,0,1). Similarly, in three-dimensional space, the equation of any plane can be written as ax = 0, where x is a four-element vector giving the homogeneous coordinates of points on the plane.

Let us now consider the transformation, not of a line, as in figure 5, but of an entire plane by a projective transformation. That is, let us start with a point x in plane A, project it through point p into point x' in a plane B, and then project x' through a point q back into plane A at x". (The points p and q must not lie in A or B.) We shall show that this transformation, which is quite non-linear in Cartesian coordinates, is linear in homogeneous coordinates and may be represented by u" = Cu, where u and u" are homogeneous coordinates of the original and transformed (or image) points, respectively, and C is a square matrix. It will prove convenient to take as plane A the "horizontal" plane with $x_3 = 0$ in its Cartesian coordinates.

The line from x through p is given by the points mx + np, where x and p are 4-element column vectors, homogeneous coordinates of points in three-dimensional space. The requirement that the point x' lie in B we may write as bx' = 0, so

$$bx' = b(mx + np) = 0$$

hence

$$n = - mbx/bp$$

and

$$x' = mx - m(bx/bp)p$$

for all m, so we may as well take m = 1. The line from x' through q is therefore all points of the form

$$m(x - (bx/bp)p) + nq$$

for all m and n. The requirement that $x_3'' = 0$ — i.e., the requirement that x lie in the plane A — implies that x" is given by the m and n that satisfy

$$-m(bx/bp)p_3 + nq_3 = 0$$

since $x_3 = 0$. Therefore, for x"

$$n = m(bx/bp)k$$

where $k = p_3/q_3$, so that

$$x'' = m(x - (bx/bp)p + k(bx/bp)q).$$

Since this equation is valid for all m, we may pick m = (bp) and write

$$x'' = (bp)x - (bx)p + k(bx)q.$$

Since (bx) is a scalar, (bx)p = p(bx) = [pb]x, where [ ] marks a square matrix. Likewise, (bx)q = [qb]x, so

$$x'' = ((bp)I - [pb] + k[qb])x$$

where I is the identity matrix. If we now denote the entire matrix on the right of this equation by B, the equation becomes just

$$x'' = Bx.$$

Furthermore, because both $x_3 = 0$ and $x_3'' = 0$, we can strike out the third row and column of B to get a 3-by-3 matrix C such that

$$u'' = Cu \tag{1}$$

for the three-element vectors u" and u derived by striking out the third coordinate of x" and x. Thus, u and u" are just the homogeneous coordinates of points in the plane A.

We have therefore shown that *a projective transformation of a plane into itself is represented by a linear transformation of its homogeneous coordinates.* Though we have conducted this proof in three dimensions, it immediately generalizes to n dimensions by just replacing "three" or "3" by "n".

The matrix C produced above has a certain structure, which, however, need not detain us, for it will disappear if we insert, after projecting onto plane B, projection onto a third plane C through a point r before returning to A. For the matrix of this transformation, we can only say that it is non-singular; no point transforms into the non-point (0,0,0).

What does a projective transformation of the plane look like geometrically? From matrix theory, we know that that a 3-by-3 matrix will have three characteristic vectors, $v_1$, $v_2$, and $v_3$, with corresponding characteristic values $m_1$, $m_2$, and $m_3$. For each of these

$$Cv_i = m_i v_i$$

But mv and v are the homogeneous coordinates of the same point. Therefore these characteristic vectors are the fixed points of the transformation. In this section, we shall assume that all three characteristic values are real and distinct. (In the next section we shall treat also complex characteristic values.) With this assumption, we can plot the three fixed points as in Figure 7.

Now any point on the line a determined by $v_1$ and $v_2$ is transformed into a point on this line, for

$$C(n_1 v_1 + n_2 v_2) = n_1 m_1 v_1 + n_2 m_2 v_2 .$$

We express this fact by saying that the line a is invariant under the transformation. The lines b and c determined by $v_1$,$v_3$ and $v_2$,$v_3$ are likewise invariant. These three invariant lines have been drawn on figure 7.

What can we say about the transformation of the line a into itself? Well, it is precisely a projective transformation of the type described by figure 5 with the point $v_3$ of figure 7 playing the same role as the point q in figure 5. We may take d to be any line through $v_1$ not containing $v_2$ or $v_3$. We then choose p on c and such that

$$1 - (dv_2/dp) = m_2/m_1 \qquad (2)$$

or

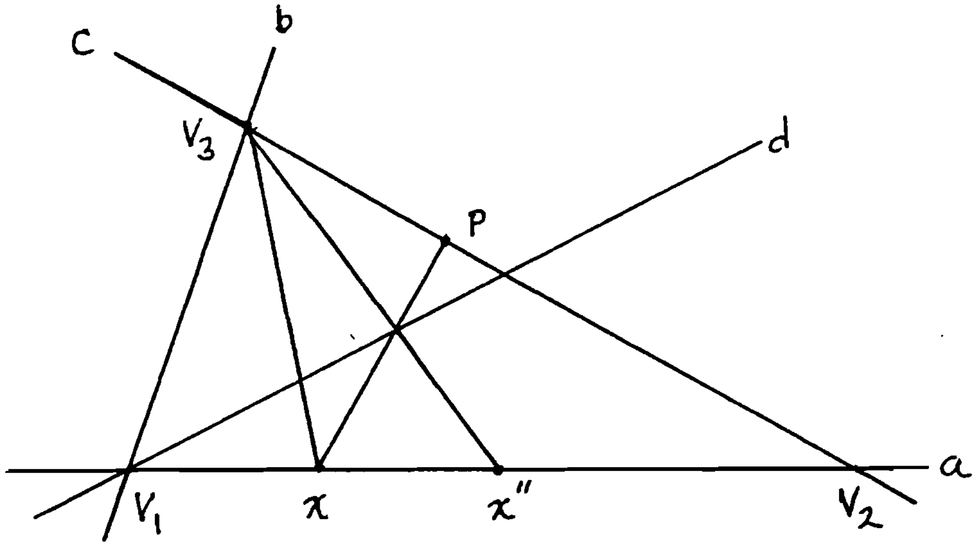


Figure 7 The Fixed Points of the Transformation

$$dp = bv_2/(1 - m_2/m_1).$$

To check that this geometrical construction will give the same transformation as does the matrix C, let us pick the point

$$x = n_1 v_1 + n_2 v_2$$

on a and find its image, x", in both ways. The matrix transformation gives immediately

$$x'' \approx C(n_1 v_1 + n_2 v_2) = n_1 m_1 v_1 + n_2 m_2 v_2. \qquad (3)$$

The transformation a la figure 5 gives first

$$x' \approx x - (dx/dp)p$$

(Clearly this x' is on the line of x and p and dx' = 0.) Next,

$$x'' \approx x' - (ax'/aq)q.$$

Since ax = 0,

$$ax' = -(dx/dp)(ap)$$

so

$$x'' \approx x - (dx/dp)p + (dx/dp)(ap/aq)q.$$

Similarly,

$$v_2 = p - (ap/aq)q$$

So

$$x'' \approx x - (dx/dp)v_2$$

$$x'' \approx n_1 v_1 + n_2 v_2 - ((n_1 dv_1 + n_2 dv_2)/(dp))v_2 .$$

But $dv_1 = 0$, so

$$x'' \approx n_1 v_1 + n_2(1 - dv_2/dp)v_2$$

or, by using (2),

$$x'' \approx n_1 v_1 + n_2(m_2/m_1)v_2 . \qquad (4)$$

Multiplying through by $m_1$ gives

$$x'' \approx m_1 n_1 v_1 + n_2 m_2 v_2$$

which is exactly the expression for x" which we obtained in (3) from the matrix transformation.

Thus, the projective transformation of the plane given by

$$x'' = Cx$$

induces a projective transformation on each of the lines connecting its three fixed points. Edwards refers to the ratio $m_2/m_1$ in (4) as the multiplier of the transformation along a, and denotes it by $\lambda_1$. The multipliers $\lambda_2 = m_3/m_2$ and $\lambda_3 = m_1/m_3$ on the two other invariant lines are similarly defined, and the identity

$$\lambda_1\lambda_2\lambda_3 = 1$$

becomes obvious.

If we know the transformation of two of the invariant lines, we can easily determine geometrically the transformation of the entire plane. In Figure 8, for example, let us suppose that we know the transformation induced by C on the lines a and c. Whither will the point x be transformed? From $v_3$, project x onto a at point y. This y will be transformed to some other point on a, say y", and $v_3$ is transformed into itself. Now the transformation induced by the matrix takes lines into lines:

$$C(k_1u_1 + k_2u_2) = k_1(Cu_1) + k_2(Cu_2)$$

for any k's and u's. Therefore, the line through $v_3$ and y will be transformed into the (dashed) line through $v_3$ and y".

Likewise, the line through $v_1$ and z will be transformed into the dashed line through $v_1$ and z". Since x", the image of x under the transformation, must lie on both the dashed lines, its location is fully determined.

We obtain our old friend figure 3, the cornerstone of Edwards' work, if we happen to have

$$v_1 = \begin{pmatrix}0\\0\\1\end{pmatrix} \quad v_2 = \begin{pmatrix}1\\0\\0\end{pmatrix} \quad v_3 = \begin{pmatrix}0\\1\\1\end{pmatrix}$$

Then $v_2$ is the point at infinity on the horizontal axis, so the "triangle" appears exactly as the lines a, b, and c of figure 3. If we rewrite formula (4) taking $n_1 = 1$ and $n_2 = n$, so that

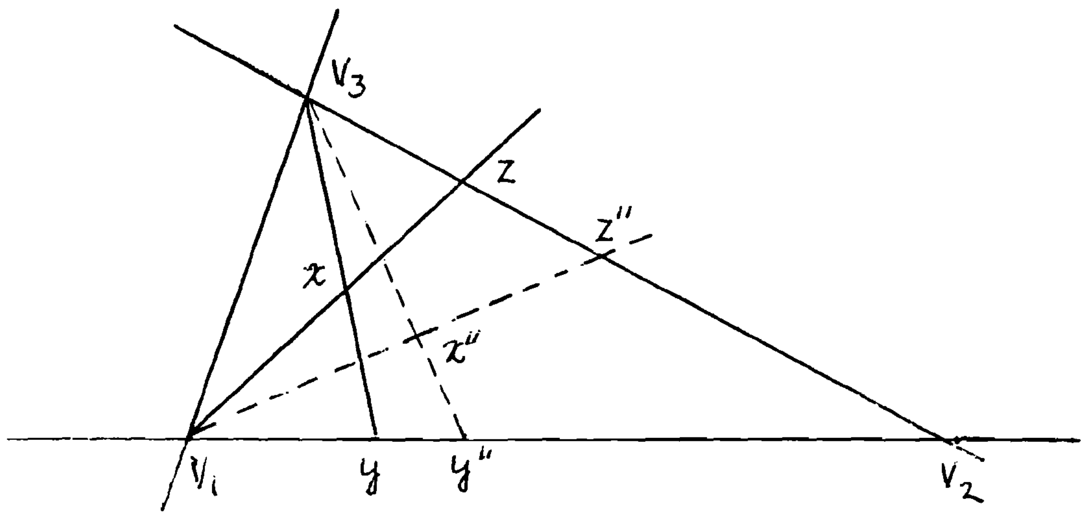


Figure 8 The Transformation Induced by C on the lines a & c

$$x'' = v_1 + n\lambda_1 v_2 .$$

then we see that the point on a at distance n from $v_1$ is transformed into the point at $\lambda_1$ n; and this point, into the one at distance $\lambda_1^2$ n, and so on, exactly as in figure 3. Similarly, the distance of a point on c from $v_3$ is changing by the multiplier $\lambda_2$, just as in figure 3. Thus, we have finally succeeded in showing that figure 3 does, in fact, represent successive applications of a projective transformation.

## 3 CONTINUOUS PATH CURVES

We now want to think of taking walks with shorter and shorter steps taken faster and faster. We therefore introduce a continuous parameter t and consider the sequence of projective transformations described by

$$x(t + \Delta t) = (I + A\Delta t)\, x(t) \qquad t = 0,\ \Delta t,\ 2\,t, \ldots$$

Here $\Delta t$ is a fixed, finite change in t; $I+A\Delta t$ is the matrix C of equation (1) and x(t) and $x(t+\Delta t)$ correspond to u and u" of equation (1). They are n+1 dimensional vectors giving the homogeneous coordinates of points in n-dimensional space relative to some normalization vector, h. If we fix A and take $\Delta t$ smaller and smaller, we do not, in fact, always walk along the same "path" as described at the end of section I; instead, the route changes slightly with each shorter t, but these routes converge to a limiting, continuous path. On each walk we have

$$(x(t + \Delta t) - x(t))/\Delta t = Ax(t)$$

and as $\Delta t \to 0$, we obtain the differential equations

$$\dot{x}(t) = Ax(t) \tag{5}$$

where the dot over x denotes the derivative with respect to t.

This is a system of n+1, linear, homogeneous equations with constant coefficients. Its solution is well-known, and we need only review it here. We can then easily show that it is, indeed, the path followed by infinitely many finite-step walks, and, in fact, that all such walks take such a path.

The general solution to the system (5) is

$$x(t) = \sum_{i=1}^{n+1} k_i v_i e^{(m_i t)} \tag{6}$$

where the k's are constants depending on initial conditions, and the v's and m's are characteristic vectors and values of the matrix A, as we shall explain. If x(t) is a solution of (5), kx(t) is also a solution, as is readily checked. Likewise, the sum of two solutions is a solution. Consequently, to investigate whether (6) is a solution of (5), we need only know the conditions for $ve^{mt}$ to be a solution. For this we must have

$$x = mve^{mt} = Ave^{mt} \qquad \textit{for all } t.$$

Therefore, we must have

$$mv = Av \quad or \quad (A - mI)v = 0 .$$

If this last equation is to have a solution other than v = 0, the matrix (A - mI) must be singular, so the determinant |A-mI| must be zero. The expansion of the determinant produces a polynomial of degree n+1 in m, which will have n+1 roots. These roots are the m's of (6). We shall assume that they are distinct, and this assumption is sufficient to guarantee that the v's are linearly independent. Let V be the matrix of the v's. Then $V^{-1}AV = M$, where M is a diagonal matrix having the m's, the characteristic values of A, down the diagonal.

We can now ask, first, are there finite-step walks which move along the curve given by (6)? Indeed there are, for we can pick any t and calculate by (6) the points x(0), x( t), x(2 t), etc. Can we find a matrix C which will give a walk with these footprints? Yes. Let

$$e^{(m_i \Delta t)} = f_i; \tag{7}$$

then from (6) we see that

$$x(j\Delta t) = \sum_{i=1}^{n+1} k_i v_i f_i^j .$$

Now define C = $VFV^{-1}$ where F is the diagonal matrix made from the $f_i$. Then from (6)

$$Cx(j\Delta t) = \sum_{i=1}^{n+1} k_i VFe_i f_i^j = VKF^j$$

where $e_i$ is the ith column of I and K is the diagonal matrix of the $k_i$ from (6). Then

$$Cx(j\Delta t) = VFV^{-1}VKF^j = VFKF^j = VKF^{j+1} = x((j+1)\Delta t)$$

so that C walks along precisely this path.

Conversely, given C, we can define F by F = $V^{-1}CV$, where V is the matrix of characteristic vectors of C, and then use (7) to define $m_i$ for a given $\Delta t$. The given C will walk along the path determined by (6) with these v's and m's.

Let us now look at a few special cases. First with n = 3, suppose that we have

$$V = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 1 & 1 \end{pmatrix}$$

and $k_2 = k_3 = 1$ and $k_1 = 1$. If we then write out the formula for each component of x(t) by (6); normalize with the vector h = (0,0,1); call the first component of the normalized vector r(t), and the second h(t); then divide numerator and denominator of the expressions for r(t) and h(t) by $\exp(m_3)$; choose the units of t so that $m_2 - m_3 = 1$; and define $m = m_1 - m_3$, we finally obtain

$$r(t) = k\, e^{mt}/(e^t + 1) \tag{8}$$

$$h(t) = e^t/(e^t + 1) \tag{9}$$

These are the parametric equations of the bud forms, with r as the radius of the bud at height h. When t = 0, h = 1/2 and r = k, so k is the radius of the bud at mid height. Figure 9 shows such a curve. Its connection with figure 3 becomes apparent if we draw a line from (0,0) through (r,h) to intersect the horizontal line at h = 1 at the point whose distance from the vertical axis is $ke^{(m-1)t}$. Clearly this distance is growing exponentially, just as in figure 3. Likewise, the intersection of the line from (0,1) through (r,h) intersects the horizontal axis at $ke^{mt}$, so this distance from the origin is expanding exponentially, just as in figure 3. Therefore, (8) and (9) do indeed give the continuous form of the path on which x was walking in figure 3. With step lenght of $\Delta t$, the multipliers on the top and bottom lines are $e^{(m-1)\Delta t}$ and $e^{m\Delta t}$, respectively. Now $\lambda$ is the ratio of the logarithms of these multipliers, so

$$\lambda = (m - 1)/m.$$

For statistical fitting it is convenient to divide (9) into (8) to get

$$r(t)/h(t) = ke^{(m-1)t} \tag{10}$$

or, in logarithmic form

$$log\, r(t) - log\, \mathrm{h}(\mathrm{t}) = \log \mathrm{k} + (\mathrm{m}-1)\mathrm{t}. \tag{11}$$

We also solve (9) for t in terms of h, thus

$$t = log[h(t)/(1 - h(t))]. \tag{12}$$

Now given observations on r at various values of h, we compute by (12) the values of t corresponding to these h's and then fit (11) by least squares. Note that the r, h, and t in (11) are known, and we seek log k and m-1 to give the closest fit to (11). Results are given in the next section.

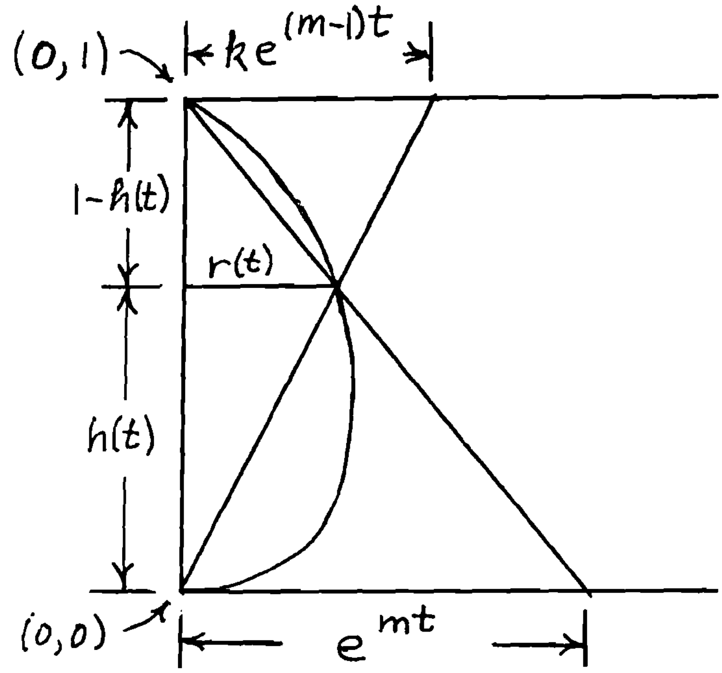


Figure 9 Plotting the Parametric Equations

We need to comment briefly on the case of complex roots in (6). If they occur, they occur in conjugate pairs, and it is easy to see that the corresponding v's are also conjugate. Furthermore, since the initial point is real, the corresponding k's must also be conjugate. We then use the definition

$$e^{(a + ib)t} = e^{at}(\cos(bt) + i\,\sin(bt)).$$

Clearly, the exponential functions of conjugates are conjugate, so the vectors on the right of (6) occur in conjugate pairs and their imaginary components cancel in the summation. Suppose then we have the following V matrix

$$V = \begin{pmatrix} 1 & 1 & 0 \\ -i & i & 0 \\ 0 & 0 & 1 \end{pmatrix} .$$

For simplicity, let us suppose that all the k's of (6) are 1.0, and that $m_1 = a + ib$, $m_2 = a - ib$, and $m_3 = m$. Then (6) gives just

$$x_1(t) = 2\,e^{at} \cos(bt)$$

$$x_2(t) = 2\,e^{at} \sin(bt)$$

$$x_3(t) = e^{mt} .$$

If we now normalize with h = (0,0,1), we get a logarithmic spiral. Thus this curve, also found in nature, is a path curve.

Finally, we go to three-dimensional space -- described by 4-element homogeneous coordinates -- and consider the equations with

$$V = \begin{pmatrix} 1 & 1 & 0 & 0 \\ -i & i & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix} .$$

The first three components will be as in the previous example, and the fourth will be another exponential function. Normalizing with h = (0,0,1,1) gives a family of three-dimensional curves that wind around a bud shape, as described in Edwards' second article. [3]

Here we see how the three-dimensional form of the bud whispers of the fourth dimension. Many plants look much alike in their first two leaves before they expand in infinite variety of shapes in their leaves and stems. Then in the bud, they again contract, again touch back to the archetypal plant and let a higher dimension breathe through them before they open into the glory of the blossom. In the bud, the plant meditates; in the blossom, it works in this world.

## 4 HOW THE CURVES FIT THE BUDS

To fit a path curve to a bud profile, we find the values of log k and m-1 to minimize

$$\sum_{i=1}^{7} [\log r_i - \log h_i - ( \log k + (m-1)t_i)]^2$$

where the $r_i$ are the observed values of the radius of the bud at the chosen heights $h_i$, and $t_i$ is defined by (12) as

$$t_i = \log[h_i/(1 - h_i)], \quad i = 1,2,...,7.$$

A slight complication is added by uncertainty about where the bottom of the bud is. The bud is always attached to the plant, so it cannot come down to a zero radius at h = 0. Therefore, there is some uncertainty about where the bottom of the bud is. On each photograph, Edwards extrapolates freehand the path-curve-like part of the profile downwards to a point at the bottom. Consequently, this lower point is somewhat uncertain. The seven observations of the radii, therefore, may not be at the heights

$$h_i = 1 - i/8$$

but at the heights

$$h_i = 1 - i/8b$$

where b is the true length of the bud. I follow Edwards's practice of varying b and picking the b that gives the best fit. The variation in length, however, has been limited to five percent on either side of the "best guess" length estimated by Edwards by eye.

The results of fitting are shown in the accompanying tables. Edwards has collected bud profiles not only where he lives, in Scotland, but also on his travels in New Zealand and Australia. He gave me the data grouped by country, and I have left it in this grouping. In the tables, the first column gives the value of m - 1, the parameter actually estimated by regression; the second column gives the value of λ derived from m -1. The third column, labelled "ro", gives the value of k in the regression. (The notation ro recalls the fact that it is the "theoretical" radius at h = 1/2, which corresponds to t = 0.) The column labeled "|er|" gives the average absolute error for the fit. The units are in hundredths of an inch on a bud shape about four inches high. The column labeled "emax" gives the maximum absolute error, also in hundredths of an inch. The "ape" column give the average absolute percentage error. The "rho" column gives the autocorrelation of errors along the curve. (Values of rho close to zero are good; they indicate that relatively large errors in the same direction do not tend to occur next to one another along the bud height. Thus, low values of rho indicate that the errors are "noise" in the observations rather than evidence of systematic deviation from path-curve forms.) Finally, the column labeled "length" gives the optimal-fit, theoretical length as a percent of the best-guess, free-hand estimate of the length of the bud.

Buds have not been excluded, after taking measurements, because they gave a poor fit. On the other hand, some plants have non-symmetric buds which are obviously not path curves, and Edwards has not gone to the trouble to measure them to prove the obvious. (The outer budcase of the rhododendron, a beautiful, big bud visible all winter, was measured but was not a good path curve and is not given here. The inner inflorescence, however, is a good path curve. It was actually this plant from which Edwards learned to measure the inner shape, not the outer case.) In New Zealand and Australia, Edwards was often unable to identify the plant whose buds he collected. The accuracy with which these plants, quite unrelated to those of Edwards's home country, produce path curves shows that this capacity is little connected with family lines, but comes directly from the nature of the plant kingdom.

Of the 150 species or varieties in the tables, 125 have an emax of less than 4 hundredths of an inch. That is, for these 125, the maximum deviation is less than one percent of the height of the bud. No bud had a maximum deviation of as much as two percent of the height. The average absolute percentage error was under two percent for 109 of the buds; for only two of them did it slightly exceed four percent. (The buds are higher than wide, so the errors are a larger percent of the radius than of the height.)

Edwards has asked his classes to draw buds or to draw ovals flat at one end and pointed at the other. Only three or four percent of the results were path curves in the range of accuracy with which plants produce them. I have tried drawing bud-form path curves with only slightly better results. I suggest the reader try a few freehand curves for himself. He can then take two points on the curve, and -- using the method of figure 3 -- check other points. Whether or not he proves no better at it than I am, he may share my amazement that plants all over the world are out there producing path curves by the billion. And if he shares my amazement, he may share my joy.

## APPENDIX: RESULTS OF FITTING A PATH CURVE TO BUD PROFILES

Scotland

| bud | m - 1 | lambda | ro | $\lvert er \rvert$ | emax | ape | rho | length |
|---|---|---|---|---|---|---|---|---|
| aubresia | 0.436 | 1.29 | 1.11 | 0.91 | 1.54 | 0.91 | 0.24 | 96. |
| blackberry | 0.481 | 1.08 | 1.83 | 1.03 | 3.66 | 0.72 | -0.31 | 102. |
| bluebell single bud | 0.478 | 1.09 | 0.72 | 2.01 | 3.45 | 3.39 | 0.35 | 95. |
| bluebell inflor. | 0.445 | 1.25 | 0.72 | 1.03 | 1.66 | 1.73 | 0.55 | 95. |
| buttercup i | 0.309 | 2.24 | 1.80 | 1.03 | 2.97 | 0.66 | -0.11 | 105. |
| buttercup ii | 0.364 | 1.75 | 2.27 | 2.06 | 4.01 | 1.12 | 0.03 | 101. |
| campanula | 0.446 | 1.24 | 0.89 | 0.71 | 1.98 | 0.93 | 0.30 | 95. |
| campion, pink | 0.260 | 2.85 | 0.96 | 0.88 | 2.05 | 1.18 | 0.24 | 98. |
| campion, white | 0.271 | 2.69 | 0.99 | 2.68 | 4.06 | 3.26 | 0.52 | 95. |
| celandine | 0.416 | 1.41 | 1.52 | 1.89 | 4.21 | 1.59 | 0.04 | 99. |
| cherry, ornamental | 0.411 | 1.44 | 1.23 | 0.75 | 1.41 | 0.77 | -0.02 | 99. |
| cherry, wild | 0.470 | 1.13 | 1.70 | 1.15 | 3.81 | 0.77 | -0.24 | 96. |
| chickweed i | 0.353 | 1.83 | 0.62 | 0.70 | 1.58 | 1.31 | -0.44 | 95. |
| chickweed ii | 0.337 | 1.97 | 0.83 | 0.27 | 0.72 | 0.38 | -0.09 | 103. |
| clematis | 0.187 | 4.34 | 0.68 | 0.99 | 1.70 | 1.83 | 0.31 | 104. |
| columbine | 0.148 | 5.75 | 0.68 | 1.61 | 2.91 | 3.16 | 0.24 | 104. |
| comfrey | 0.542 | 0.85 | 0.62 | 0.49 | 0.73 | 0.89 | 0.05 | 95. |
| convolvulus | 0.253 | 2.94 | 0.47 | 0.60 | 1.30 | 1.53 | 0.21 | 103. |
| cornflower | 0.327 | 2.05 | 1.30 | 0.48 | 1.22 | 0.41 | -0.14 | 103. |
| creeping jenny | 0.300 | 2.34 | 0.94 | 0.62 | 1.23 | 0.84 | -0.01 | 102. |
| crowsfoot | 0.460 | 1.18 | 1.53 | 3.08 | 4.85 | 2.30 | 0.52 | 95. |
| currant, flowering i | 0.308 | 2.25 | 1.08 | 2.48 | 4.96 | 2.57 | 0.23 | 105. |
| currant, flowering ii | 0.319 | 2.14 | 1.06 | 2.24 | 4.68 | 2.46 | 0.16 | 105. |
| currant, flowering iii | 0.377 | 1.65 | 1.03 | 1.40 | 2.65 | 1.58 | 0.53 | 105. |
| daffodil | 0.523 | 0.91 | 0.50 | 1.14 | 1.85 | 2.73 | 0.40 | 95. |
| elm leafbud | 0.357 | 1.80 | 0.85 | 0.66 | 2.33 | 0.86 | -0.42 | 102. |
| forsythea | 0.343 | 1.92 | 0.67 | 1.18 | 2.82 | 2.05 | 0.27 | 102. |
| fuschia | 0.257 | 2.88 | 0.53 | 1.53 | 3.49 | 3.73 | 0.30 | 100. |
| garden briar rose | 0.195 | 4.13 | 0.76 | 1.53 | 3.57 | 2.42 | 0.36 | 104. |
| garlic | 0.194 | 4.16 | 0.80 | 2.27 | 3.93 | 3.18 | 0.58 | 105. |
| geranium | 0.396 | 1.53 | 1.04 | 0.87 | 1.84 | 0.96 | -0.10 | 103. |
| grape hyacinth inflores | 0.374 | 1.67 | 0.73 | 1.76 | 3.11 | 2.97 | 0.23 | 96. |
| hawthorn | 0.504 | 0.98 | 1.82 | 1.01 | 2.63 | 0.68 | -0.40 | 101. |
| honesty | 0.468 | 1.14 | 0.71 | 0.70 | 1.66 | 1.10 | -0.45 | 99. |
| hypericum | 0.335 | 1.99 | 1.21 | 1.27 | 3.23 | 1.25 | 0.30 | 100. |
| ivy leafbud | 0.428 | 1.33 | 1.15 | 0.65 | 1.40 | 0.64 | -0.19 | 101. |
| jasmine, winter | 0.325 | 2.07 | 0.84 | 0.67 | 1.30 | 0.92 | 0.41 | 100. |
| kale (flower bud) | 0.441 | 1.27 | 1.18 | 0.77 | 1.92 | 0.78 | 0.30 | 99. |
| knapweed | 0.453 | 1.21 | 1.54 | 0.88 | 2.64 | 0.66 | 0.02 | 101. |
| larch (male flower bud) | 0.455 | 1.20 | 1.60 | 0.89 | 2.06 | 0.69 | -0.27 | 98. |
| lime leafbud | 0.357 | 1.80 | 0.75 | 0.54 | 1.51 | 0.89 | 0.24 | 101. |
| mahonia | 0.485 | 1.06 | 0.85 | 0.85 | 1.45 | 1.17 | 0.23 | 95. |
| narcissus | 0.349 | 1.86 | 0.53 | 0.68 | 1.09 | 1.64 | 0.43 | 95. |
| phlox, dwarf | 0.410 | 1.44 | 0.74 | 1.59 | 4.63 | 2.46 | -0.08 | 102. |
| potentilla | 0.447 | 1.24 | 1.75 | 1.10 | 2.29 | 0.72 | 0.24 | 98. |
| oak leafbud | 0.281 | 2.56 | 0.84 | 0.96 | 2.25 | 1.52 | 0.27 | 105. |
| poplar (leaf bud) | 0.263 | 2.80 | 0.64 | 0.50 | 1.21 | 0.98 | 0.19 | 105. |
| poppy | 0.277 | 2.62 | 1.00 | 1.44 | 2.67 | 1.59 | 0.31 | 105. |
| poppy (another variety) | 0.346 | 1.89 | 0.96 | 0.92 | 2.29 | 1.14 | 0.04 | 105. |
| primrose | 0.369 | 1.71 | 1.04 | 2.61 | 5.87 | 3.14 | 0.28 | 100. |
| pussy willow (catkin) | 0.434 | 1.31 | 0.53 | 0.57 | 1.05 | 1.21 | 0.48 | 95. |
| red may | 0.511 | 0.96 | 1.90 | 1.01 | 3.29 | 0.57 | -0.11 | 99. |
| rhododendron | 0.344 | 1.91 | 1.24 | 0.85 | 2.77 | 0.77 | -0.18 | 105. |
| sage | 0.212 | 3.71 | 1.10 | 2.91 | 3.91 | 3.55 | 0.23 | 105. |

Scotland cont.

| bud | m - 1 | lambda | ro | \|er\| | emax | ape | rho | length |
|---|---|---|---|---|---|---|---|---|
| sea thrift | 0.290 | 2.45 | 1.16 | 1.01 | 2.06 | 1.11 | -0.14 | 100. |
| sibirica | 0.447 | 1.24 | 0.81 | 0.56 | 1.74 | 0.92 | -0.15 | 98. |
| snowdrop | 0.402 | 1.49 | 0.60 | 1.43 | 2.23 | 3.07 | 0.27 | 95. |
| speedwell | 0.299 | 2.35 | 0.93 | 0.80 | 2.09 | 0.97 | 0.09 | 105. |
| star of bethlehem | 0.380 | 1.63 | 0.69 | 0.53 | 1.02 | 0.92 | 0.47 | 95. |
| stitchwort | 0.371 | 1.70 | 0.76 | 1.12 | 2.04 | 1.86 | 0.07 | 99. |
| strawberry, wild | 0.386 | 1.59 | 1.25 | 0.88 | 1.54 | 0.77 | -0.11 | 104. |
| summer snow | 0.450 | 1.22 | 0.87 | 0.59 | 1.21 | 0.82 | 0.01 | 98. |
| summer snow ii | 0.422 | 1.37 | 0.84 | 0.67 | 1.79 | 0.94 | -0.43 | 96. |
| sycamore flower bud | 0.450 | 1.22 | 0.92 | 0.81 | 1.34 | 1.04 | 0.32 | 95. |
| sycamore leafbud | 0.404 | 1.47 | 0.91 | 0.47 | 1.19 | 0.59 | 0.12 | 95. |
| syringa | 0.322 | 2.11 | 0.90 | 2.74 | 5.20 | 3.55 | 0.54 | 105. |
| veronica | 0.386 | 1.59 | 0.80 | 0.94 | 2.06 | 1.31 | -0.02 | 101. |
| water lily | 0.312 | 2.20 | 0.83 | 0.73 | 1.40 | 1.03 | -0.18 | 103. |
| whortleberry | 0.343 | 1.92 | 1.37 | 3.67 | 5.93 | 3.35 | 0.25 | 95. |
| wild iris | 0.421 | 1.38 | 0.48 | 0.97 | 1.97 | 2.31 | 0.34 | 97. |
| wood sorrel | 0.349 | 1.86 | 0.88 | 0.68 | 1.45 | 0.94 | -0.09 | 101. |
| wood sorrel (dif. year) | 0.345 | 1.90 | 0.69 | 0.45 | 0.88 | 0.77 | 0.35 | 99. |

Australia

| bud | m - 1 | lambda | ro | !er! | emax | ape | rho | length |
|---|---|---|---|---|---|---|---|---|
| boromia | 0.385 | 1.59 | 1.82 | 0.92 | 1.73 | 0.58 | 0.39 | 101. |
| camelia | 0.324 | 2.09 | 1.42 | 1.68 | 4.16 | 1.39 | 0.14 | 104. |
| Christmas bells ? | 0.435 | 1.30 | 1.08 | 0.54 | 1.57 | 0.56 | -0.41 | 99. |
| clematis, bush | 0.366 | 1.73 | 0.92 | 1.23 | 2.65 | 1.52 | 0.18 | 105. |
| epocris | 0.198 | 4.04 | 0.68 | 0.59 | 1.37 | 1.00 | -0.05 | 103. |
| eriostemon i | 0.389 | 1.57 | 1.00 | 1.15 | 2.56 | 1.39 | 0.10 | 101. |
| eriostemon ii | 0.392 | 1.55 | 1.30 | 2.17 | 3.70 | 1.93 | 0.51 | 95. |
| eriostemon iii | 0.347 | 1.88 | 0.99 | 1.58 | 2.95 | 2.12 | 0.09 | 95. |
| eucalyptus i | 0.404 | 1.48 | 1.34 | 1.83 | 2.84 | 1.69 | 0.21 | 95. |
| eucalyptus ii | 0.137 | 6.31 | 1.14 | 1.58 | 3.39 | 1.68 | 0.39 | 105. |
| gardenia | 0.340 | 1.95 | 0.99 | 0.89 | 1.70 | 1.23 | 0.13 | 100. |
| hibertia stricta | 0.244 | 3.09 | 1.08 | 0.88 | 2.36 | 1.10 | -0.27 | 103. |
| hibiscus i | 0.343 | 1.91 | 0.80 | 0.44 | 1.17 | 0.61 | 0.05 | 100. |
| hibiscus ii | 0.440 | 1.27 | 1.57 | 0.64 | 1.86 | 0.48 | 0.03 | 99. |
| hibiscus iii | 0.292 | 2.43 | 0.78 | 1.09 | 3.17 | 1.56 | -0.06 | 95. |
| mallow | 0.265 | 2.78 | 0.70 | 1.01 | 1.82 | 1.99 | 0.12 | 99. |
| wild vine | 0.129 | 6.78 | 0.81 | 2.17 | 4.14 | 2.81 | 0.18 | 105. |
| unidentified i | 0.299 | 2.35 | 0.90 | 2.13 | 2.87 | 3.21 | 0.25 | 95. |
| unidentified ii | 0.360 | 1.77 | 1.62 | 0.57 | 1.35 | 0.39 | 0.10 | 99. |
| unidentified iii | 0.387 | 1.58 | 0.65 | 0.73 | 2.17 | 1.26 | 0.21 | 95. |
| unidentified iv | 0.410 | 1.44 | 0.98 | 0.75 | 1.47 | 0.94 | -0.07 | 98. |
| unidentified v | 0.148 | 5.74 | 0.87 | 3.46 | 6.46 | 4.25 | 0.18 | 105. |
| unidentified vi | 0.377 | 1.65 | 0.85 | 0.90 | 1.50 | 1.33 | 0.09 | 102. |
| unidentified vii | 0.376 | 1.66 | 0.85 | 1.11 | 2.88 | 1.42 | 0.01 | 95. |
| unidentified viii | 0.494 | 1.03 | 0.85 | 1.80 | 4.04 | 2.50 | -0.06 | 95. |
| unidentified ix | 0.395 | 1.53 | 0.84 | 0.61 | 0.99 | 0.88 | 0.28 | 98. |
| unidentified x | 0.377 | 1.65 | 0.98 | 0.71 | 1.43 | 0.80 | -0.22 | 99. |
| unidentified xi | 0.353 | 1.84 | 0.98 | 0.61 | 1.04 | 0.67 | 0.04 | 103. |
| unidentified xii | 0.373 | 1.68 | 1.01 | 1.13 | 3.06 | 1.23 | -0.03 | 96. |
| unidentified xiii | 0.559 | 0.79 | 1.55 | 3.52 | 6.15 | 2.57 | 0.34 | 101. |
| unidentified xiv | 0.251 | 2.99 | 0.46 | 0.27 | 0.54 | 0.81 | -0.08 | 97. |

New Zealand

| bud | m - 1 | lambda | ro | \|er\| | emax | ape | rho | length |
|---|---|---|---|---|---|---|---|---|
| apple | 0.463 | 1.16 | 1.32 | 0.50 | 1.09 | 0.44 | -0.22 | 98. |
| berberis | 0.575 | 0.74 | 1.53 | 1.69 | 3.40 | 1.28 | -0.06 | 98. |
| cabbage (flower plant) | 0.438 | 1.28 | 1.40 | 0.80 | 1.39 | 0.70 | -0.18 | 101. |
| cabbage tree | 0.609 | 0.64 | 1.02 | 1.09 | 2.04 | 1.18 | 0.16 | 95. |
| california fuschia | 0.248 | 3.04 | 1.06 | 0.72 | 1.84 | 0.70 | -0.08 | 104. |
| camelia | 0.346 | 1.89 | 1.50 | 1.95 | 4.45 | 1.56 | 0.16 | 105. |
| chinese lantern | 0.401 | 1.49 | 1.47 | 0.60 | 1.58 | 0.50 | -0.25 | 100. |
| clematis, bush | 0.413 | 1.42 | 1.29 | 1.55 | 2.55 | 1.50 | 0.18 | 104. |
| cress | 0.477 | 1.10 | 1.23 | 1.83 | 3.43 | 1.75 | 0.24 | 97. |
| daphne | 0.385 | 1.60 | 0.86 | 0.57 | 0.89 | 0.77 | -0.16 | 100. |
| diosma | 0.268 | 2.73 | 0.77 | 2.66 | 5.68 | 4.11 | 0.47 | 105. |
| flax | 0.210 | 3.76 | 0.76 | 2.00 | 4.17 | 3.21 | 0.13 | 105. |
| fremontia | 0.190 | 4.26 | 1.18 | 2.12 | 5.15 | 1.81 | 0.33 | 105. |
| geranium | 0.384 | 1.60 | 0.90 | 0.87 | 3.07 | 1.13 | -0.28 | 105. |
| ginger | 0.519 | 0.93 | 0.94 | 1.83 | 3.20 | 2.25 | 0.61 | 95. |
| holly | 0.620 | 0.61 | 1.53 | 0.72 | 1.51 | 0.51 | 0.32 | 99. |
| horopito | 0.327 | 2.06 | 2.48 | 2.77 | 5.11 | 1.25 | 0.28 | 102. |
| indian hawthorn, pink | 0.264 | 2.79 | 1.28 | 1.07 | 2.34 | 1.16 | -0.09 | 100. |
| indian hawthorn, white | 0.274 | 2.65 | 1.14 | 2.00 | 3.25 | 1.98 | 0.33 | 105. |
| iris, new zealand | 0.479 | 1.09 | 1.12 | 0.41 | 0.94 | 0.44 | -0.06 | 96. |
| jasmine, minature | 0.294 | 2.40 | 1.09 | 1.21 | 2.50 | 1.30 | -0.35 | 95. |
| japonica | 0.323 | 2.10 | 1.35 | 1.32 | 2.76 | 1.15 | 0.35 | 99. |
| karaka | 0.397 | 1.52 | 1.55 | 0.62 | 1.11 | 0.44 | -0.04 | 97. |
| keria | 0.240 | 3.17 | 0.81 | 0.40 | 0.86 | 0.64 | -0.08 | 101. |
| lady´s smock | 0.399 | 1.51 | 0.69 | 1.05 | 2.33 | 1.94 | 0.04 | 97. |
| lemon | 0.553 | 0.81 | 1.50 | 1.79 | 2.72 | 1.39 | 0.16 | 99. |
| magnolia | 0.315 | 2.18 | 0.65 | 1.03 | 2.61 | 1.92 | 0.33 | 99. |
| magnolia stellata | 0.314 | 2.18 | 0.63 | 2.23 | 4.45 | 4.32 | 0.37 | 103. |
| magnolia,port wine | 0.333 | 2.00 | 1.09 | 0.38 | 0.62 | 0.39 | -0.36 | 101. |
| malus | 0.453 | 1.21 | 1.18 | 0.58 | 1.61 | 0.57 | 0.11 | 98. |
| maori privet | 0.279 | 2.58 | 1.71 | 3.47 | 7.48 | 2.35 | 0.38 | 104. |
| ngaio | 0.378 | 1.64 | 0.94 | 1.41 | 2.47 | 1.68 | -0.07 | 99. |
| oxalis | 0.384 | 1.61 | 0.50 | 0.42 | 0.55 | 0.97 | -0.12 | 99. |
| peach | 0.396 | 1.52 | 1.45 | 1.42 | 5.28 | 1.06 | -0.15 | 102. |
| periwinkle | 0.245 | 3.07 | 0.87 | 2.91 | 4.84 | 4.38 | 0.43 | 95. |
| pimpernel, scarlet | 0.313 | 2.20 | 0.92 | 2.09 | 3.37 | 2.88 | 0.23 | 96. |
| poroporo | 0.517 | 0.93 | 1.13 | 0.50 | 1.32 | 0.50 | 0.37 | 95. |
| quince | 0.251 | 2.98 | 1.04 | 1.63 | 3.11 | 1.85 | 0.47 | 105. |
| rose, wild | 0.196 | 4.10 | 0.91 | 2.24 | 3.48 | 2.95 | 0.20 | 105. |
| tawari | 0.318 | 2.14 | 1.75 | 0.97 | 2.31 | 0.68 | -0.20 | 103. |
| vibernum | 0.425 | 1.35 | 1.74 | 1.65 | 2.86 | 1.05 | 0.04 | 102. |
| wiegela | 0.544 | 0.84 | 0.89 | 0.81 | 1.57 | 1.04 | 0.28 | 97. |
| unidentified i | 0.354 | 1.83 | 1.70 | 2.13 | 5.13 | 1.44 | 0.18 | 103. |
| unidentified ii | 0.606 | 0.65 | 0.93 | 1.33 | 2.76 | 1.64 | 0.29 | 104. |
| unidentified iii | 0.195 | 4.13 | 0.55 | 1.54 | 3.14 | 3.55 | 0.30 | 102. |
| unidentified ivte mata? | 0.336 | 1.97 | 0.59 | 0.38 | 0.89 | 0.71 | -0.42 | 100. |
| unidentified v | 0.412 | 1.43 | 1.92 | 1.80 | 3.25 | 1.09 | 0.35 | 97. |

Scotland *Data*

| | F | E | D | T | C | B | A |
|---|---|---|---|---|---|---|---|
| aubresia | 0.630 | 0.880 | 1.043 | 1.120 | 1.110 | 1.045 | 0.910 |
| blackberry | 1.180 | 1.570 | 1.760 | 1.830 | 1.780 | 1.550 | 1.200 |
| bluebell single bud | 0.470 | 0.580 | 0.654 | 0.700 | 0.590 | 0.650 | 0.590 |
| bluebell inflor. | 0.430 | 0.570 | 0.650 | 0.700 | 0.715 | 0.690 | 0.600 |
| buttercup i | 0.840 | 1.300 | 1.650 | 1.830 | 1.940 | 1.870 | 1.570 |
| buttercup ii | 1.180 | 1.670 | 2.040 | 2.250 | 2.360 | 2.310 | 1.910 |
| campanula | 0.520 | 0.710 | 0.820 | 0.880 | 0.870 | 0.840 | 0.740 |
| campion, pink | 0.400 | 0.620 | 0.795 | 0.940 | 1.040 | 1.100 | 1.030 |
| campion, white | 0.430 | 0.640 | 0.790 | 0.940 | 1.040 | 1.130 | 1.110 |
| celandine | 0.875 | 1.150 | 1.375 | 1.520 | 1.555 | 1.460 | 1.210 |
| cherry, ornamental | 0.670 | 0.975 | 1.145 | 1.220 | 1.245 | 1.185 | 0.985 |
| cherry, wild | 1.040 | 1.405 | 1.615 | 1.710 | 1.690 | 1.535 | 1.330 |
| chickweed i | 0.305 | 0.440 | 0.540 | 0.630 | 0.640 | 0.650 | 0.590 |
| chickweed ii | 0.410 | 0.610 | 0.750 | 0.840 | 0.880 | 0.960 | 0.710 |
| clematis | 0.260 | 0.420 | 0.560 | 0.680 | 0.790 | 0.850 | 0.800 |
| columbine | 0.250 | 0.395 | 0.540 | 0.690 | 0.820 | 0.910 | 0.880 |
| comfrey | 0.435 | 0.565 | 0.620 | 0.620 | 0.600 | 0.540 | 0.440 |
| convolvulus | 0.200 | 0.310 | 0.400 | 0.460 | 0.520 | 0.540 | 0.480 |
| cornflower | 0.630 | 0.950 | 1.160 | 1.320 | 1.385 | 1.350 | 1.135 |
| creeping jenny | 0.433 | 0.650 | 0.825 | 0.955 | 1.024 | 1.010 | 0.890 |
| crowsfoot | 0.930 | 1.260 | 1.400 | 1.470 | 1.480 | 1.460 | 1.250 |
| currant, flowering i | 0.515 | 0.755 | 0.944 | 1.100 | 1.210 | 1.170 | 0.910 |
| currant, flowering ii | 0.524 | 0.760 | 0.915 | 1.100 | 1.170 | 1.120 | 0.890 |
| currant, flowering iii | 0.545 | 0.790 | 0.970 | 1.065 | 1.090 | 0.990 | 0.745 |
| daffodil | 0.355 | 0.430 | 0.480 | 0.485 | 0.475 | 0.440 | 0.380 |
| elm leafbud | 0.430 | 0.640 | 0.770 | 0.855 | 0.890 | 0.830 | 0.725 |
| forsythea | 0.340 | 0.490 | 0.580 | 0.656 | 0.700 | 0.710 | 0.575 |
| fuschia | 0.235 | 0.340 | 0.420 | 0.525 | 0.600 | 0.620 | 0.565 |
| garden briar rose | 0.300 | 0.480 | 0.620 | 0.760 | 0.880 | 0.965 | 0.985 |
| garlic | 0.290 | 0.500 | 0.710 | 0.860 | 0.946 | 0.958 | 0.885 |
| geranium | 0.574 | 0.795 | 0.970 | 1.064 | 1.064 | 0.980 | 0.790 |
| grape hyacinth inflores | 0.390 | 0.520 | 0.630 | 0.700 | 0.760 | 0.770 | 0.660 |
| hawthorn | 1.230 | 1.550 | 1.770 | 1.820 | 1.760 | 1.540 | 1.160 |
| honesty | 0.440 | 0.590 | 0.690 | 0.715 | 0.715 | 0.630 | 0.520 |
| hypericum | 0.590 | 0.870 | 1.040 | 1.190 | 1.270 | 1.280 | 1.100 |
| ivy leafbud | 0.670 | 0.920 | 1.080 | 1.170 | 1.160 | 1.060 | 0.860 |
| jasmine, winter | 0.400 | 0.600 | 0.730 | 0.825 | 0.890 | 0.390 | 0.780 |
| kale (flower bud) | 0.705 | 0.950 | 1.090 | 1.180 | 1.190 | 1.110 | 0.900 |
| knapweed | 0.940 | 1.260 | 1.450 | 1.540 | 1.550 | 1.390 | 1.080 |
| larch (male flower bud) | 0.945 | 1.325 | 1.505 | 1.590 | 1.595 | 1.460 | 1.210 |
| lime leafbud | 0.385 | 0.555 | 0.665 | 0.755 | 0.790 | 0.765 | 0.545 |
| mahonia | 0.540 | 0.700 | 0.790 | 0.835 | 0.840 | 0.790 | 0.645 |
| narcissus | 0.260 | 0.370 | 0.450 | 0.510 | 0.545 | 0.550 | 0.510 |
| phlox, dwarf | 0.425 | 0.580 | 0.670 | 0.730 | 0.750 | 0.745 | 0.540 |
| potentilla | 1.020 | 1.420 | 1.650 | 1.765 | 1.730 | 1.620 | 1.340 |
| oak leafbud | 0.385 | 0.575 | 0.720 | 0.850 | 0.920 | 0.920 | 0.780 |
| poplar (leaf bud) | 0.280 | 0.435 | 0.550 | 0.650 | 0.715 | 0.710 | 0.620 |
| poppy | 0.440 | 0.675 | 0.890 | 1.040 | 1.120 | 1.095 | 0.915 |
| poppy (another variety) | 0.475 | 0.725 | 0.885 | 0.980 | 1.005 | 0.935 | 0.765 |
| primrose | 0.565 | 0.755 | 0.880 | 1.020 | 1.075 | 1.085 | 0.885 |
| pussy willow (catkin) | 0.305 | 0.425 | 0.490 | 0.520 | 0.530 | 0.510 | 0.455 |
| red may | 1.280 | 1.650 | 1.840 | 1.935 | 1.840 | 1.630 | 1.270 |
| rhododendron | 0.620 | 0.930 | 1.140 | 1.260 | 1.300 | 1.215 | 1.090 |
| sage | 0.400 | 0.760 | 0.990 | 1.170 | 1.260 | 1.290 | 1.190 |

*radii in inches*

Scotland cont.

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| sea thrift | 0.520 | 0.780 | 1.007 | 1.180 | 1.264 | 1.260 | 1.160 |
| sibirica | 0.490 | 0.640 | 0.756 | 0.810 | 0.810 | 0.760 | 0.625 |
| snowdrop | 0.344 | 0.440 | 0.525 | 0.590 | 0.610 | 0.600 | 0.550 |
| speedwell | 0.423 | 0.665 | 0.840 | 0.953 | 1.000 | 0.965 | 0.830 |
| star of bethlehem | 0.355 | 0.510 | 0.605 | 0.675 | 0.700 | 0.695 | 0.635 |
| stitchwort | 0.403 | 0.550 | 0.670 | 0.770 | 0.805 | 0.765 | 0.660 |
| strawberry, wild | 0.675 | 0.980 | 1.140 | 1.245 | 1.290 | 1.200 | 0.925 |
| summer snow | 0.510 | 0.720 | 0.825 | 0.865 | 0.860 | 0.810 | 0.665 |
| summer snow ii | 0.470 | 0.640 | 0.790 | 0.840 | 0.850 | 0.810 | 0.700 |
| sycamore flower bud | 0.545 | 0.730 | 0.840 | 0.900 | 0.910 | 0.880 | 0.745 |
| sycamore leafbud | 0.485 | 0.695 | 0.835 | 0.910 | 0.930 | 0.890 | 0.800 |
| syringa | 0.410 | 0.660 | 0.860 | 0.970 | 0.980 | 0.900 | 0.740 |
| veronica | 0.425 | 0.630 | 0.745 | 0.785 | 0.815 | 0.795 | 0.650 |
| water lily | 0.390 | 0.580 | 0.740 | 0.850 | 0.890 | 0.860 | 0.750 |
| whortleberry | 0.610 | 1.010 | 1.253 | 1.373 | 1.400 | 1.370 | 1.325 |
| wild iris | 0.260 | 0.380 | 0.460 | 0.500 | 0.486 | 0.446 | 0.397 |
| wood sorrel | 0.445 | 0.640 | 0.790 | 0.890 | 0.940 | 0.895 | 0.770 |
| wood sorrel (dif. year) | 0.330 | 0.500 | 0.620 | 0.690 | 0.715 | 0.700 | 0.625 |

Australia

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| boromia | 0.960 | 1.395 | 1.685 | 1.840 | 1.870 | 1.760 | 1.470 |
| camelia | 0.670 | 1.045 | 1.305 | 1.460 | 1.515 | 1.430 | 1.230 |
| Christmas bells ? | 0.630 | 0.860 | 1.010 | 1.075 | 1.100 | 1.010 | 0.830 |
| clematis, bush | 0.475 | 0.700 | 0.870 | 0.950 | 0.950 | 0.870 | 0.700 |
| epocris | 0.255 | 0.425 | 0.590 | 0.700 | 0.780 | 0.815 | 0.790 |
| eriostemon i | 0.550 | 0.760 | 0.905 | 0.995 | 1.025 | 1.000 | 0.800 |
| eriostemon ii | 0.695 | 0.970 | 1.150 | 1.245 | 1.300 | 1.320 | 1.180 |
| eriostemon iii | 0.490 | 0.675 | 0.840 | 0.965 | 1.030 | 1.055 | 0.940 |
| eucalyptus i | 0.740 | 1.000 | 1.195 | 1.310 | 1.360 | 1.355 | 1.180 |
| eucalyptus ii | 0.375 | 0.695 | 0.980 | 1.200 | 1.370 | 1.465 | 1.495 |
| gardenia | 0.495 | 7.050 | 0.870 | 0.995 | 1.050 | 1.030 | 0.905 |
| hibertia stricta | 0.450 | 0.695 | 0.935 | 1.105 | 1.210 | 1.230 | 1.130 |
| hibiscus i | 0.390 | 0.575 | 0.715 | 0.810 | 0.840 | 0.815 | 0.715 |
| hibiscus ii | 0.915 | 1.270 | 1.490 | 1.570 | 1.570 | 1.450 | 1.200 |
| hibiscus iii | 0.330 | 0.520 | 0.695 | 0.760 | 0.815 | 0.850 | 0.825 |
| mallow | 0.305 | 0.450 | 0.585 | 0.700 | 0.780 | 0.800 | 0.745 |
| wild vine | 0.275 | 0.460 | 0.660 | 0.850 | 1.015 | 1.095 | 1.050 |
| unidentified i | 0.415 | 0.575 | 0.735 | 0.855 | 0.955 | 0.990 | 0.950 |
| unidentified ii | 0.810 | 1.195 | 1.465 | 1.625 | 1.685 | 1.630 | 1.435 |
| unidentified iii | 0.340 | 0.485 | 0.585 | 0.620 | 0.660 | 0.660 | 0.590 |
| unidentified iv | 0.530 | 0.775 | 0.905 | 0.985 | 0.995 | 0.935 | 0.810 |
| unidentified v | 0.315 | 0.500 | 0.705 | 0.910 | 1.105 | 1.180 | 1.070 |
| unidentified vi | 0.460 | 0.635 | 0.770 | 0.845 | 0.885 | 0.840 | 0.685 |
| unidentified vii | 0.435 | 0.635 | 0.750 | 0.825 | 0.875 | 0.895 | 0.775 |
| unidentified viii | 0.535 | 0.740 | 0.825 | 0.855 | 0.825 | 0.735 | 0.670 |
| unidentified ix | 0.455 | 0.635 | 0.755 | 0.830 | 0.865 | 0.830 | 0.710 |
| unidentified x | 0.510 | 0.730 | 0.895 | 0.990 | 1.020 | 0.965 | 0.845 |
| unidentified xi | 0.495 | 0.730 | 0.900 | 1.000 | 1.020 | 0.975 | 0.815 |
| unidentified xii | 0.515 | 0.750 | 0.885 | 0.990 | 1.045 | 1.055 | 0.905 |
| unidentified xiii | 1.105 | 1.450 | 1.605 | 1.600 | 1.430 | 1.190 | 0.880 |
| unidentified xiv | 0.185 | 0.290 | 0.380 | 0.455 | 0.500 | 0.520 | 0.505 |

New Zealand

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| apple | 0.810 | 1.080 | 1.250 | 1.330 | 1.310 | 1.205 | 0.990 |
| berberis | 1.140 | 1.465 | 1.545 | 1.545 | 1.425 | 1.230 | 0.940 |
| cabbage (flower plant) | 0.815 | 1.150 | 1.325 | 1.395 | 1.400 | 1.275 | 1.020 |
| cabbage tree | 0.845 | 0.970 | 1.030 | 1.030 | 0.970 | 0.850 | 0.645 |
| california fuschia | 0.440 | 0.710 | 0.930 | 1.090 | 1.190 | 1.190 | 1.090 |
| camelia | 0.740 | 1.140 | 1.410 | 1.540 | 1.580 | 1.460 | 1.200 |
| chinese lantern | 0.810 | 1.130 | 1.360 | 1.480 | 1.510 | 1.420 | 1.180 |
| clematis, bush | 0.710 | 1.055 | 1.230 | 1.305 | 1.290 | 1.170 | 0.900 |
| cress | 0.745 | 1.040 | 1.195 | 1.250 | 1.210 | 1.085 | 0.920 |
| daphne | 0.460 | 0.650 | 0.785 | 0.870 | 0.895 | 0.840 | 0.715 |
| diosma | 0.310 | 0.540 | 0.700 | 0.840 | 0.865 | 0.820 | 0.710 |
| flax | 0.310 | 0.470 | 0.625 | 0.770 | 0.880 | 0.945 | 0.820 |
| fremontia | 0.445 | 0.730 | 1.010 | 1.250 | 1.425 | 1.455 | 1.335 |
| geranium | 0.490 | 0.700 | 0.840 | 0.915 | 0.920 | 0.825 | 0.665 |
| ginger | 0.650 | 0.830 | 0.890 | 0.910 | 0.900 | 0.845 | 0.705 |
| holly | 1.260 | 1.510 | 1.585 | 1.535 | 1.390 | 1.170 | 0.830 |
| horopito | 1.170 | 1.790 | 2.270 | 2.540 | 2.610 | 2.530 | 2.225 |
| indian hawthorn, pink | 0.545 | 0.830 | 1.085 | 1.290 | 1.405 | 1.430 | 1.340 |
| indian hawthorn, white | 0.495 | 0.780 | 1.045 | 1.200 | 1.270 | 1.230 | 1.070 |
| iris, new zealand | 0.705 | 0.925 | 1.060 | 1.115 | 1.110 | 1.030 | 0.850 |
| jasmine, minature | 0.470 | 0.710 | 0.930 | 1.075 | 1.160 | 1.160 | 1.140 |
| japonica | 0.620 | 0.965 | 1.220 | 1.365 | 1.420 | 1.410 | 1.285 |
| karaka | 0.825 | 1.175 | 1.420 | 1.550 | 1.580 | 1.520 | 1.330 |
| keria | 0.330 | 0.525 | 0.690 | 0.815 | 0.903 | 0.945 | 0.880 |
| lady's smock | 0.355 | 0.550 | 0.640 | 0.685 | 0.690 | 0.670 | 0.590 |
| lemon | 1.065 | 1.395 | 1.510 | 1.515 | 1.415 | 1.210 | 0.925 |
| magnolia | 0.290 | 0.465 | 0.600 | 0.660 | 0.690 | 0.680 | 0.630 |
| magnolia stellata | 0.320 | 0.440 | 0.520 | 0.615 | 0.695 | 0.695 | 0.570 |
| magnolia,port wine | 0.520 | 0.790 | 0.965 | 1.095 | 1.150 | 1.120 | 0.975 |
| malus | 0.700 | 0.965 | 1.125 | 1.175 | 1.170 | 1.085 | 0.900 |
| maori privet | 0.730 | 1.200 | 1.590 | 1.795 | 1.850 | 1.820 | 1.635 |
| ngaio | 0.480 | 0.720 | 0.865 | 0.915 | 0.940 | 0.950 | 0.800 |
| oxalis | 0.265 | 0.375 | 0.450 | 0.505 | 0.520 | 0.490 | 0.425 |
| peach | 0.795 | 1.135 | 1.345 | 1.400 | 1.485 | 1.405 | 1.118 |
| periwinkle | 0.370 | 0.530 | 0.670 | 0.815 | 0.940 | 1.020 | 1.020 |
| pimpernel, scarlet | 0.435 | 0.610 | 0.765 | 0.890 | 0.990 | 1.022 | 0.920 |
| poroporo | 0.760 | 0.985 | 1.095 | 1.125 | 1.090 | 1.010 | 0.830 |
| quince | 0.425 | 0.710 | 0.945 | 1.085 | 1.175 | 1.160 | 1.025 |
| rose, wild | 0.360 | 0.560 | 0.745 | 0.930 | 1.080 | 1.140 | 1.020 |
| tawari | 0.840 | 1.250 | 1.570 | 1.760 | 1.870 | 1.860 | 1.560 |
| vibernum | 1.010 | 1.420 | 1.610 | 1.720 | 1.760 | 1.640 | 1.260 |
| wiegela | 0.625 | 0.810 | 0.895 | 0.900 | 0.850 | 0.750 | 0.595 |
| unidentified i | 0.850 | 1.255 | 1.600 | 1.745 | 1.780 | 1.675 | 1.400 |
| unidentified ii | 0.750 | 0.920 | 0.980 | 0.935 | 0.820 | 0.660 | 0.420 |
| unidentified iii | 0.220 | 0.335 | 0.440 | 0.545 | 0.640 | 0.705 | 0.655 |
| unidentified ivte mata? | 0.285 | 0.435 | 0.525 | 0.590 | 0.635 | 0.615 | 0.540 |
| unidentified v | 1.070 | 1.480 | 1.730 | 1.875 | 1.960 | 1.890 | 1.600 |

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