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Regression Smoothers for Estimating Parameters of Growth Analyses

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The objective of regression smoothers is to obtain predicted values of a dependent variable and its first derivative from empirical data without having to assume any particular functional relationship between the dependent and independent variables. An early variant of this type of analysis, specifically natural *B*-splines, was first applied to growth analyses by Parsons and Hunt in 1981 (*Annals of Botany* **48**: 341–352, 1981). The object of this paper is to describe and evaluate two recent advances in this area (cubic spline smoothers and loess smoothers) in the context of plant growth analysis and compare them to natural *B*-splines. The accuracies of these methods are evaluated using simulated data of a type that normally causes difficulties with other methods. A bootstrap procedure is described that improves the estimate of the optimal smoother parameter. It is shown that these smoothers can capture even subtle changes in relative growth rate. The method is then applied to growth data of *Holcus lanatus*.

Key words: *B*-splines, cubic spline smoothers, growth analyses, *Holcus lanatus*, loess, relative growth rate, RGR.

INTRODUCTION

Researchers interested in plant growth often have to estimate growth quantities from experimental data. At their simplest, such estimates may be of plant dry weight over time; but, more often, estimates of rates of change or relative rates of change are involved (Hunt, 1982). The parameters of growth analysis, such as relative growth rate, net assimilation rate or nitrogen productivity are now particularly important in plant ecology because they are state variables in influential models of plant ecophysiology and of vegetation structure and dynamics (for example Grime, 1979; Tilman, 1988).

The underlying assumption when obtaining such estimates is that there is an unknown systematic trend in the data which is disturbed by random errors. Unfortunately, there is no parametric growth function that can describe this underlying trend which is also generally applicable to different species and to different environmental conditions. Because of this, researchers generally rely on statistical curve-fitting techniques. Hunt (1982) described and compared a number of such methods used in plant growth analysis. Hunt and Parsons (1974) advocated step-wise polynomial regression of the (natural) log-transformed dry weights on time followed by differentiation to obtain rates of change. Unfortunately, this still forces the data into a particular parametric function which may result in over- or under-fitting (Parsons and Hunt, 1981). Poorter (1989) suggested calculating average relative growth rates over sequential time periods followed by step-wise polynomial regression but this does not avoid the problem of forcing nonlinear data into a particular parametric form. Parsons and Hunt (1981) made a major improvement when they introduced the method of cubic *B*-spline regression. The objective of this method was to approximate the data by a series of cubic polynomial regressions that are fitted to contiguous subsets of the data, with the added constraint that the first and second derivatives of successive polynomials agree at the 'knots' (the points where the successive polynomials touch). Although a parametric function is still used (a cubic polynomial), varying the number and placement of knots allows an almost infinite range of functions to be approximated.

The objective of the present paper is threefold. First, we wish to introduce two recent advances in form-free regression to plant biologists interested in plant growth. Second, we introduce a bootstrap procedure that improves the ability of these methods to capture accurately the underlying systematic trend in the growth trajectory. Finally, we evaluate the ability of these two methods as well as cubic *B*-splines to detect subtle changes in growth rate through the use of numerical simulations and an actual data set involving *Holcus lanatus*.

CUBIC SPLINE SMOOTHERS

There have been major improvements in the use of splines for form-free curve fitting since the publication of Parsons and Hunt (1981). These improvements remove much of the subjectivity in the choice of the number and positioning of knots and this method is now available in at least one commercially available statistical package (Statistical Sciences, 1994).

The theoretical and algorithmic details of cubic spline smoothing can be found in Wahba (1990). A comparison of

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this method with the *B*-splines regression method used by Parsons and Hunt (1981) can be found in chapter 2 of Hastie and Tibshirani (1990). An intuitive understanding of the technique is given here. First, interior knots are placed at each unique value of the independent variable (i.e. each unique harvest date for growth data). If cubic splines were fit to the data at this point by minimizing the residual sum of squares, one would obtain a very good 'fit' to the data but the predicted values would simply be the means of the (ln) dry weights at each harvest. This would result in a very 'wobbly' curve that is strongly affected by the random fluctuations in the data and that therefore obscures the underlying systematic trend.

To avoid this, a penalty function is introduced which adds additional constraints to the spline functions. Ordinary cubic splines are already constrained such that the first and second derivatives be continuous across the knot positions and the second derivative is zero beyond the extremes of the data. The penalty function attempts to minimize the integrated second derivatives of the splines. If the cubic splines were fit only by minimizing this penalty function the second derivatives would vanish and the result would be a straight line regression. The smoothing operation involves chosing the spline functions by minimizing a 'penalized' residual sum of squares (PRSS). The PRSS [eqn (1)] consists of two terms: the first term is the sum of squared deviations between the observed and predicted values and therefore measures the residual deviation between observed and predicted values, while the second term is the penalty function weighted by a smoothing parameter λ and therefore measures the degree of nonlinearity of the predicted values. The minimized PRSS for a given λ therefore represents the best compromise between the closeness of fit and the least nonlinearity.

$$PRSS = MIN[\Sigma(y-f(x))^2+\lambda\int(f''(x))^2]\,dt. \qquad (1)$$

Here $f(x)$ is the cubic splines function.

The smoothing parameter determines the degree to which the splines attempt to minimize the error sum of squares versus minimizing the degree of nonlinearity. As λ approaches zero, the penalty function becomes unimportant and the solution tends to an interpolating function of the means. As λ approaches infinity, the penalty term dominates, forcing the second derivatives to zero everywhere and the solution is a least-squares linear regression line.

The best predicted values would be those that accurately describe the underlying systematic trend in the data while ignoring the random fluctuations around this trend. If λ is too small, then the predicted values would be sensitive to the random fluctuations in the data, and this problem would be accentuated for the estimated derivatives. If λ is too large, then the systematic trend would be distorted. A common choice for λ is the value that minimizes the cross-validation score (Hastie and Tibshirani, 1990; Wahba, 1990), which is a measure of the predictive residual standard error. This is because the regression degrees of freedom increases, and the

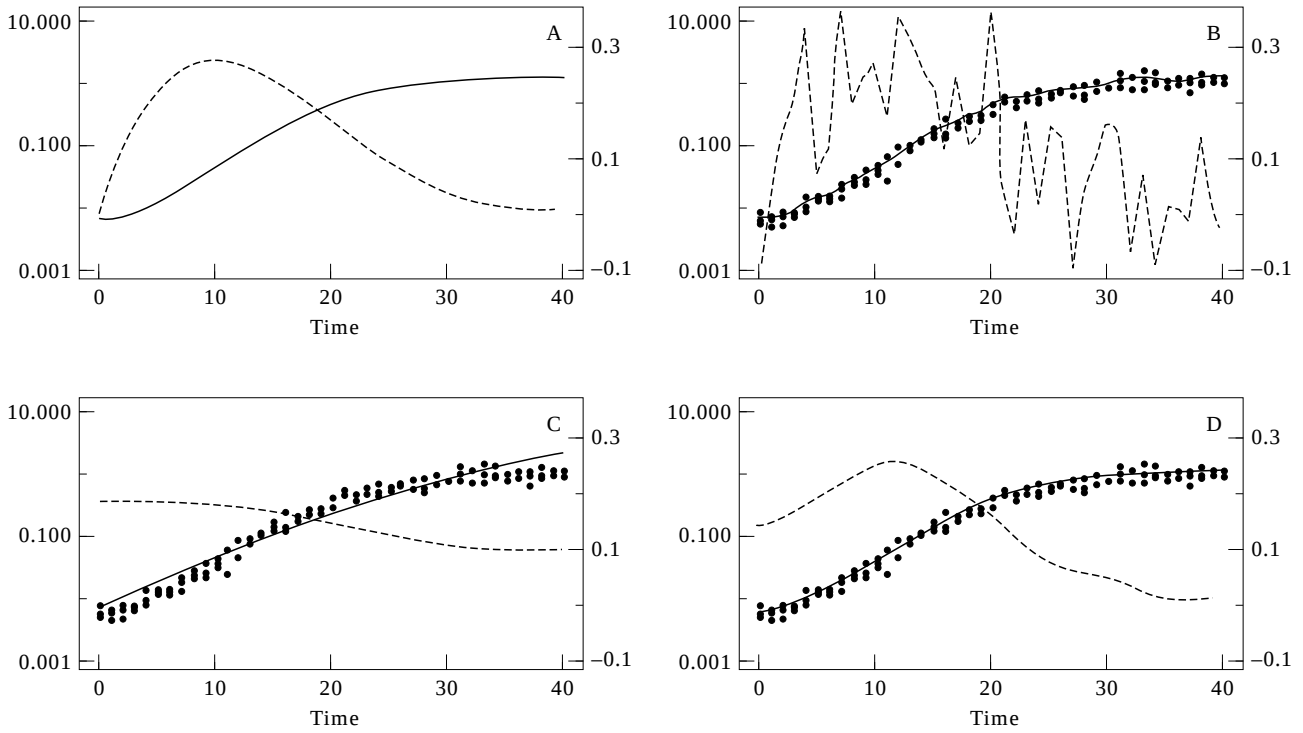

FIG. 1. The left scale of the abscissa gives values of plant dry weight on a logarithmic scale, the right scale gives relative growth rates (g g d^{-1}). Solid lines show the true underlying trends in plant weight while broken lines show the true trends in relative growth rate. (●) Normally distributed random samples ($\sigma = 0{\cdot}2$) around this trend. A, True values of 'plants' whose relative growth rates follow a beta distribution. B, Predictions of the cubic spline smoother when the smoother parameter is too small. C, Predictions of the cubic spline smoother when the smoothing parameter is too large. D, Predictions of cubic spline smoother with an optimal smoothing parameter, chosen by cross-validation.

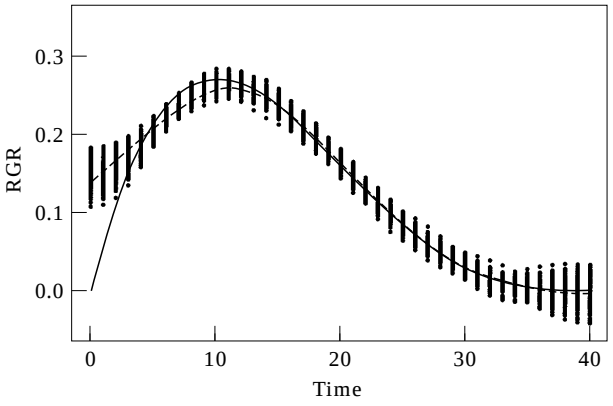

FIG. 2. Simulation results of 500 random data sets whose systematic component is shown in Fig. 1A. Each solid circle is a predicted relative growth rate obtained from a cubic spline smooth using cross-validation. The solid line is the true trend in relative growth rate and the broken line is the average trend of the data.

residual degrees of freedom decreases, as λ decreases (see Chambers and Hastie, 1992, for a discussion of the calculation of degrees of freedom in the context of cubic spline smoothers and loess). If λ is too large then the sum of squared deviations will be large. Subsequent decreases in λ will result in large decreases in the sum of squared deviations for only modest decreases in the residual degrees of freedom, thus decreasing the residual standard error. However, once the underlying systematic trend has been accurately described, further decreases in λ will only marginally decrease the sum of squared deviations while still decreasing the residual degrees of freedom, thus increasing the residual standard error. Note that the optimal λ, as determined by cross-validation, provides an asymptotically correct value. In data sets likely to be encountered in studies of plant growth, the cross-validation λ may sometimes result in over- or under-fitting (Wahba, 1990). We have found, using numerical simulations, that using the modal cross-validation λ obtained from bootstrapped samples (Leger, Politis and Romano, 1992; Dixon, 1994) overcomes this problem even in data sets in which the λ obtained from the sample itself is not optimal. The S-PLUS statistical program (Statistical Sciences, 1994) implements the cubic spline smoother using the 'smooth.spline' function. Estimated first and second derivatives are obtained though the 'predict.smooth.spline' function.

LOESS REGRESSION

Loess, or local regression (Cleveland and Devlin 1988), is another recent advance in form-free regression. An intuitive description of the algorithm is as follows. For a given

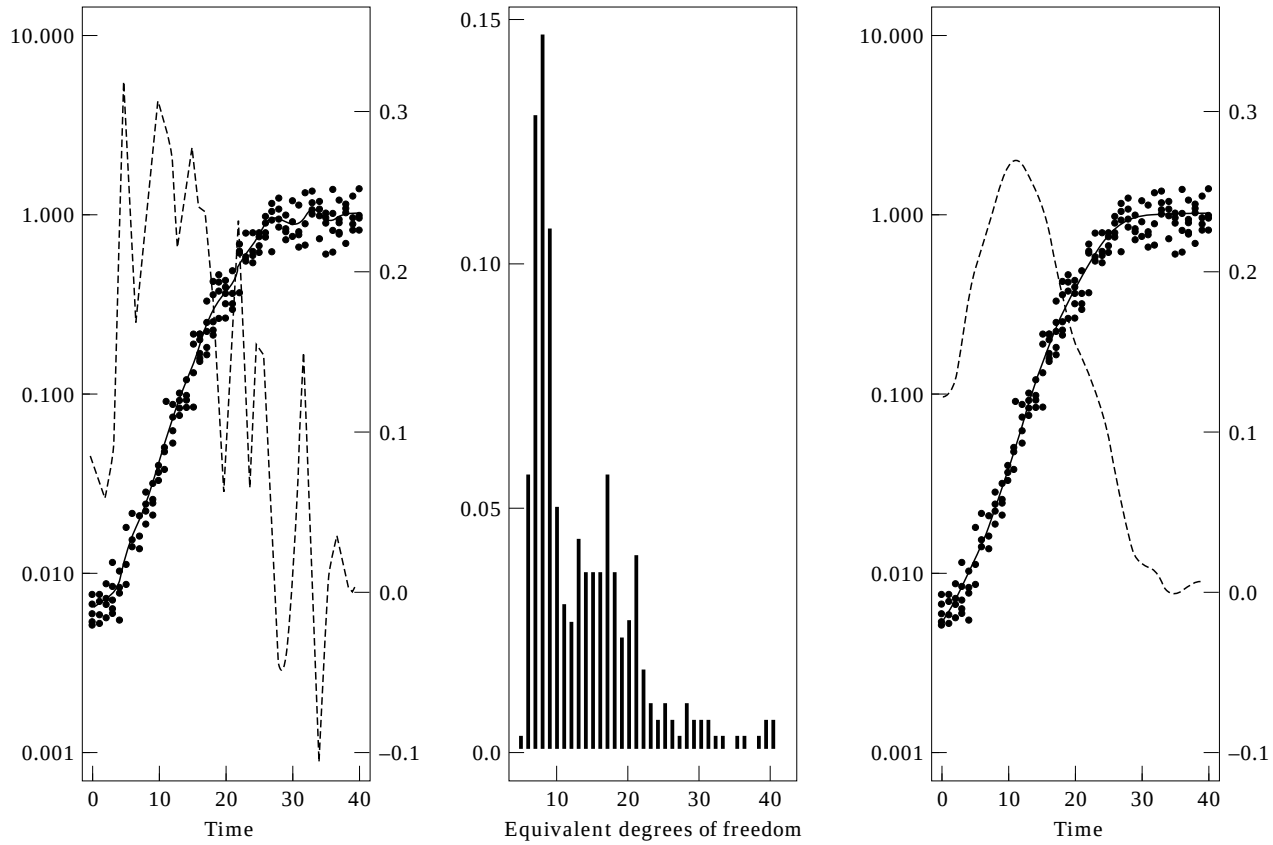

FIG. 3. A, One (relatively rare) data set from Fig. 2 in which cross-validation results in a severely under-smoothed curve. B, The distribution of the equivalent regression degrees of freedom, obtained from cross-validation, over 400 bootstrap data sets taken from the data shown in (A). C, The same data as in (A), but fitted using the modal equivalent degrees of freedom (eight) from the bootstrap data sets.

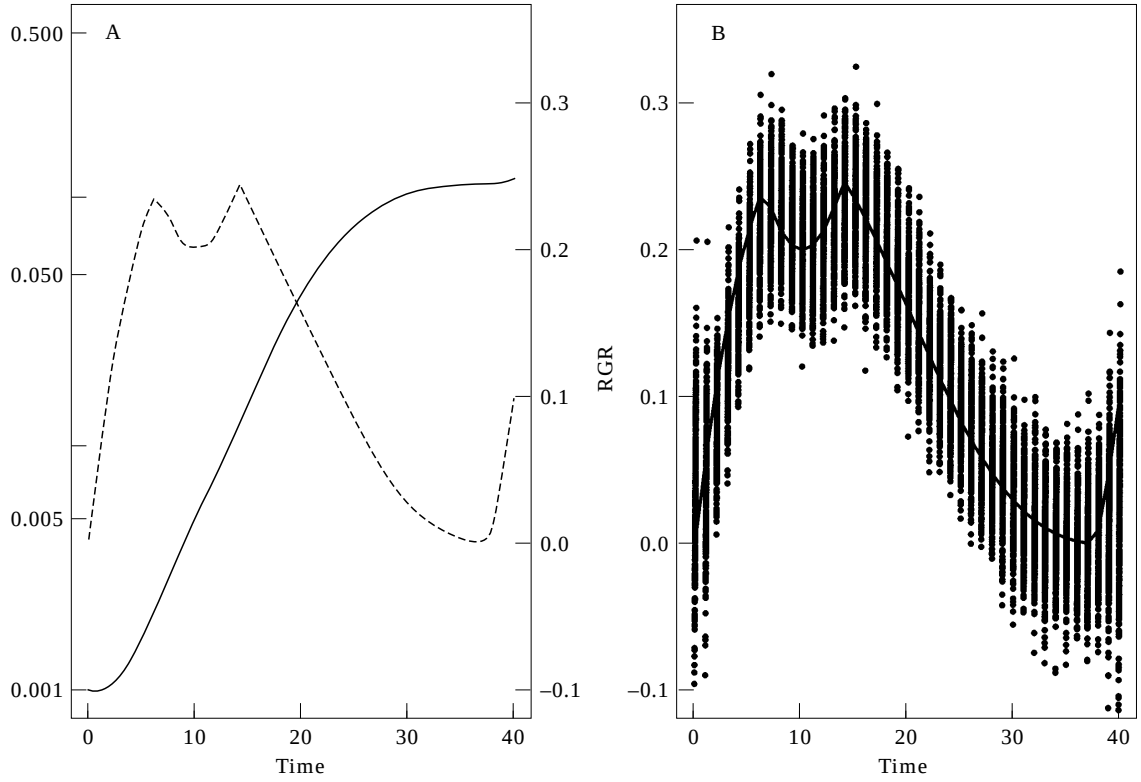

FIG. 4. A, The true values of plant dry weight (——) and relative growth rate (– – – –) for a plant with a complicated growth trajectory. B, The predicted values of relative growth rate (●) for 500 simulated data sets in which the random component was generated from a normal distribution with $\sigma = 0{\cdot}20$. The solid line shows the true values.

ordered x_i (normally harvest dates i in the context of growth analysis), an estimation of the expected value of y_i [normally ln (plant weight) at harvest i in the context of growth analysis] is obtained from a weighted linear or quadratic regression. However, the regression is 'local' because the estimation of the expected value $\bar{y}_i$ associated with a given x_i is obtained after assigning weights, based on the tricube weight function (Cleveland, 1979), to the independent variables and these weights differ for each harvest date. The weights are both a decreasing function of the distance of each independent variable (harvest date) from x_i (the harvest date for which the predicted plant dry weight is sought) and a smoothing parameter which defines a 'neighbourhood size'; i.e. the proportion of all independent variables (harvest dates) beyond which the weights become zero. This 'neighbourhood size' is called the 'span'. Thus, data points close to x_i contribute more to the regression than points farther from x_i, and points beyond the neighbourhood size do not contribute at all to the fit. A separate weighted regression (with different weights as described above) is fit for each unique x_i giving a set of predicted y values. This procedure is implemented in the 'loess' function of S-PLUS (Statistical Sciences, 1994). As with cubic spline smoothers, the degree of nonlinearity will depend on the smoothing parameter defining the neighbourhood size, and can be objectively chosen as the value that minimizes the prediction standard error. Since the first derivatives are not printed in the 'loess' function, we give a short function, written in the S language, which can obtain these derivatives from the output of 'loess' (Appendix).

EVALUATION OF THESE METHODS FOR PLANT GROWTH ANALYSIS

Earlier papers (Hunt and Parsons, 1974; Parsons and Hunt, 1981; Poorter, 1989) have demonstrated their methods using actual data sets. Unfortunately, it is impossible to judge the ability of these methods to accurately capture the underlying systematic trend in the growth trajectory because, by definition, the 'true' values are unknown. Here, we apply natural *B*-splines, cubic spline smoothing and loess to two simulated data sets in which the true values are known. The first data set simulates a trajectory of relative growth rates similar to the pattern described in Hunt (1982, p. 192). Young plants often exhibit a short period of hyper-exponential growth in which the relative growth rate increases with time, followed by a slowing of growth in which the relative growth rate decreases (Hunt, 1982). To simulate this process, we model a plant whose relative growth rate (RGR) follows a beta function. Plant dry weight is 0·0001 g and RGR is zero at time zero. RGR increases rapidly to $0{\cdot}27\ \mathrm{g\,g^{-1}\,d^{-1}}$ at day 10 and then decreases nonlinearly to zero at time 40 [eqn (2)].

$$\frac{1}{W}\frac{\mathrm{d}W}{\mathrm{d}t} = 1 \times 10^{-6} t(40-t)^3,\ t = (0, 40). \qquad (2)$$

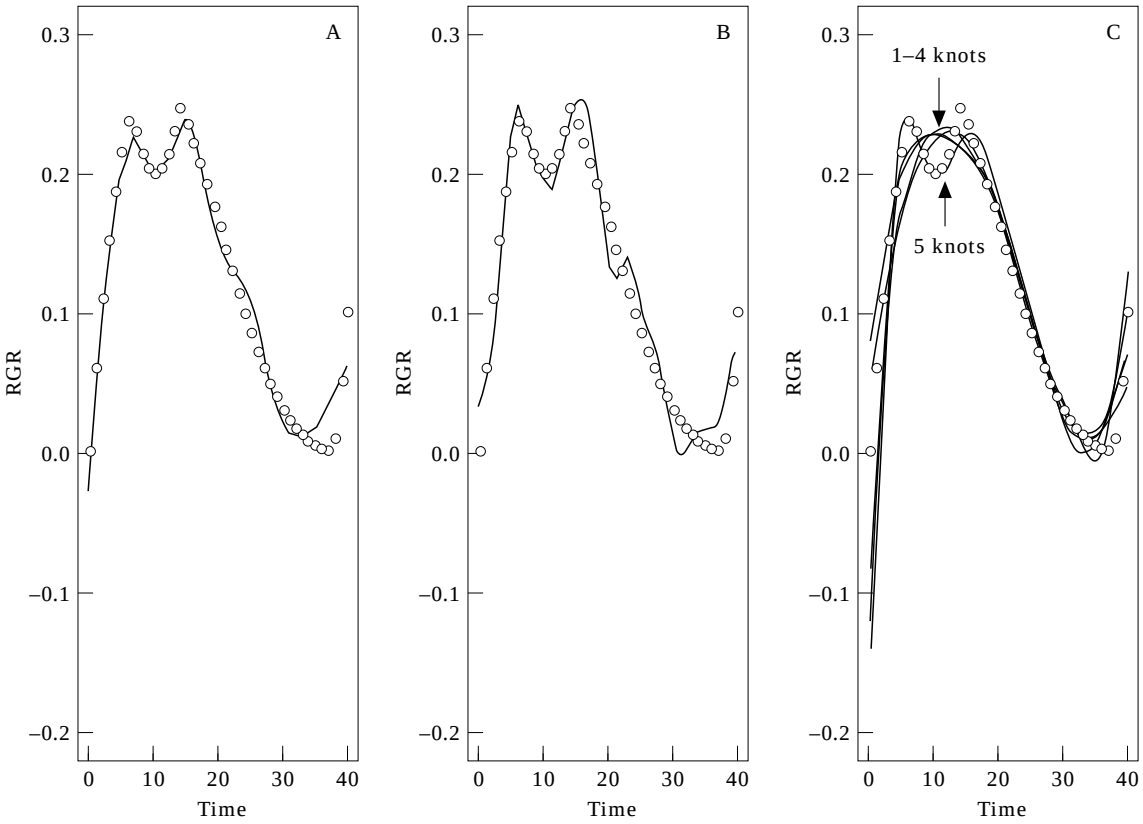

FIG. 5. Open circles show the true values of RGR from Fig. 4A. A, the loess curve obtained with an optimal span of 0·3; B, the cubic spline smoother curve obtained with an optimal regression degrees of freedom of 13; C, five curves obtained from the *B*-spline regression with from one to four knots, respectively. The thicker line in the right hand graph is the curve with five knot positions.

Integrating this equation gives the trajectory of the (natural) log-transformed dry weights over time [eqn (3)].

$$\ln(W) = 1 \times 10^{-6}\left[\frac{(40-t)^5}{5} - 40\frac{(40-t)^4}{4} - 9{\cdot}2\right]. \quad (3)$$

As an example, consider 80 plants, all of whose growth trajectories follow eqn (3) but in which each plant has an added independent random component from a normal distribution with a mean of zero and a standard deviation of 0·2. An example is shown in Fig. 1A. If the cubic spline smoothing parameter is set too low ($\lambda = 1{\cdot}92 \times 10^{-7}$, with 1 equivalent error degree of freedom) then the predicted values are sensitive to the random variations (Fig. 1B), and this effect is accentuated in the predicted relative growth rates. If the smoothing parameter is set too high ($\lambda =$ 0·41914, with 37·5 equivalent error degrees of freedom) then the predicted values misrepresent the true systematic trend (Fig. 1C) and underestimates the true RGR over the first half of the graph while overestimating it over the second half of the graph. The smoothing parameter that minimizes the predictive standard error ($\lambda = 0{\cdot}00158$, with 33 equivalent error degrees of freedom) accurately captures most of the systematic trend (Fig. 1D). Figure 2 shows the distribution of RGR values obtained from 500 random data sets, each generated as described above. It is clear that the cubic spline smoother accurately captured the true trend over most of the 'growth' period.

Figure 3A shows one of the 500 random data sets in which the cross-validation λ severely under-smooths the data, as shown by the very jagged, rapidly changing RGR values. Fig. 3B shows the distribution of the regression degrees of freedom associated with the optimal cross-validation λ for each of 400 bootstrapped samples of this data set. Although cross-validation of the data shown in Fig. 3A suggested a regression degrees of freedom of almost 20, the most common value of the bootstrapped data sets was 8 (therefore 32 equivalent error degrees of freedom). Figure 3C shows this same data as shown in Fig. 3A, but with a smoothing parameter producing eight equivalent degrees of freedom for the cubic spline smoother. The bootstrapped value provides a much better fit.

Figure 2 clearly shows that the estimated relative growth rates predicted by the cubic spline smoother have a bias at the beginning of the harvest period. This is due to the fact that the first derivative (RGR) is increasing very rapidly at this part of the curve but the algorithm has few 'data' to use. Since natural cubic splines—both smoother splines and the regression splines used in Parsons and Hunt (1981)—require the second derivatives to be zero beyond the first boundary knot, this is equivalent to making RGR constant before time zero. This bias is often found when the derivatives are changing rapidly near the extremes of the curve. However, it is asking too much to expect accurate estimates of a rate of change from this method at the very first harvest date when no information of earlier values is

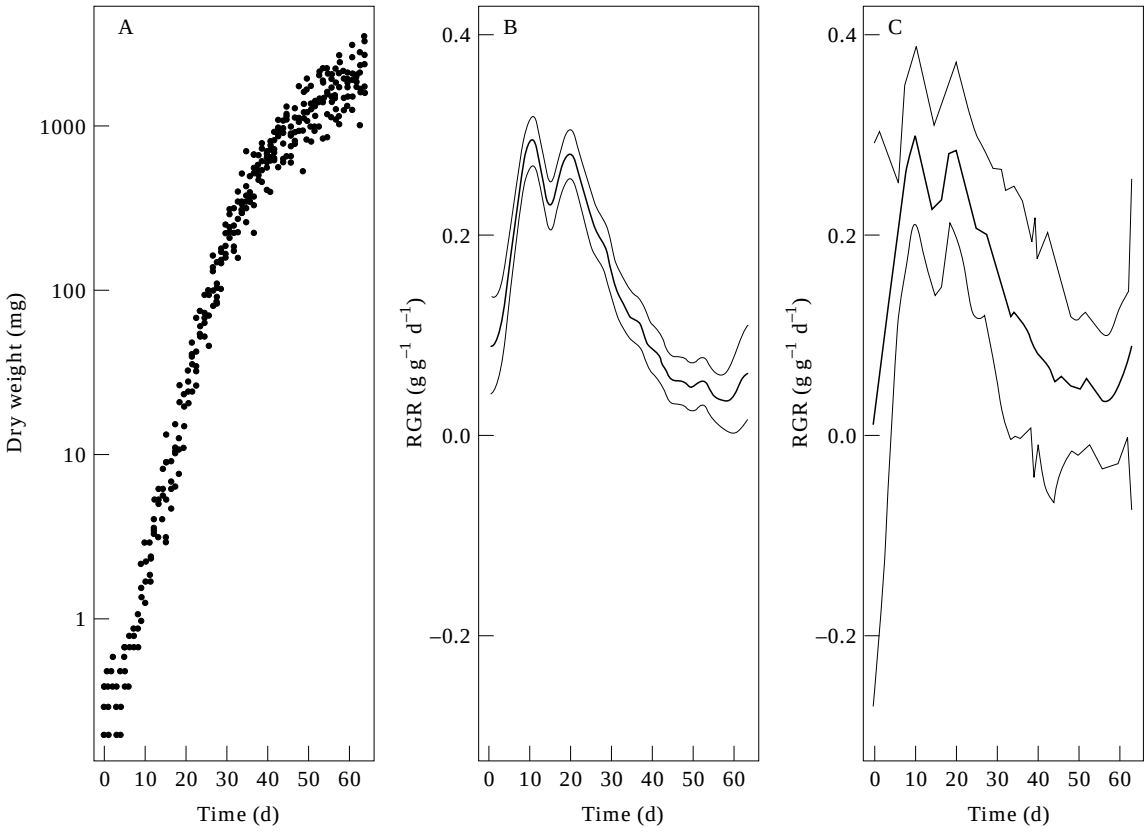

FIG. 6. A, Solid circles are the actual dry weights of 126 plants of *Holcus lanatus* L. grown in sand culture from seed and harvested over 63 d. B, The predicted relative growth rates (thicker line) based on cubic spline smoothers, with pointwise 95% confidence intervals. C, The predicted relative growth rates (thicker line) based on a loess smooth, along with pointwise 95% confidence intervals.

available. Although the bias persists at the second harvest period, the true values are within the confidence limits. The bias has largely disappeared by the third harvest. Because the loess algorithm does not have this requirement, this bias does not appear (Fig. 5A).

To explore further the ability of smoother splines to estimate relative growth rate, we then conducted a second simulation in which the RGR follows a beta function over most of its trajectory, but in which small rapid changes are introduced. From time 0 until 8, RGR follows the beta function given in eqn (1). From time 8 until 12 RGR follows a quadratic function [$\mathrm{RGR} = 5{\cdot}67 \times 10^{-3}(10-t)^2 + 0{\cdot}2$] after which it returns to the beta function until time 37. From time 37 until time 40, RGR follows a cubic equation [$\mathrm{RGR} = 0{\cdot}001\ (t-37)^3$]. We integrated this very complicated trajectory numerically over 0·1 time units. Figure 4A shows the true values of RGR and (ln) dry weight. Note that the two brief periods in which RGR deviates from the beta function are scarcely visible when looking at the plant weights; when random variation is added to these values, the deviation is all but indistinguishable from random fluctuations. Figure 4B shows the distribution of predicted values of RGR, as estimated by smoother splines, based on 500 randomly generated data sets of 41 'plants' each, whose error standard deviation is 0·2; the smoother splines were able to detect these subtle changes. To directly compare loess, cubic spline smoothers and *B*-spline regression, we generated a single random sample of 41 'plants' as described above and analysed this data set using all three methods. Figure 5 summarizes the results. Both the cubic spline smoother (Fig. 5B, with an optimal regression degrees of freedom of 13) and the *B*-spline regressions (Fig. 5C, with curves having from one to five knots) show a bias at the beginning of the 'harvest' period, but this disappears by the second (cubic spline smoother) or third (*B*-spline regression) 'harvest' period. The loess curve (Fig. 5A, with an optimal span of 0·3) does not show this bias. On the other hand, both loess and the cubic spline smoother underestimate the final rapid increase in RGR at the last three harvest periods, unlike the *B*-spline regression with five knots. The main disadvantage of the *B*-spline regression is that there is no way to choose the number of knots objectively, although Parsons and Hunt (1981) described a 'migration' procedure which could be used to optimize knot positions once knot number had been chosen. All of the *B*-spline curves with less than five knots completely miss the rapid quadratic decrease in RGR between 'harvest' times 5 and 15. Overall, all three methods captured the main trends in this complicated growth trajectory, but the loess curve seems to have produced the best overall result.

The S-PLUS statistical package, unlike the *B*-spline program of Parsons and Hunt (1981), does not automatically estimate confidence intervals for the first derivatives of either the smoother splines or loess. However, a method of

calculating the standard errors, and therefore confidence intervals, can be found in Hastie and Tibshirani (1990). Our Appendix lists a short function in the S language that implements this method.

ANALYSIS OF AN EMPIRICAL DATA SET

Finally, we re-analyse the data set presented in Hunt (1982) and Hunt and Lloyd (1987) consisting of daily replicate harvests over 63 d of *Holcus lanatus* grown in a growth chamber in sand culture using a modified Long Ashton solution. Hunt (1982) analysed these data using the original method of Parsons and Hunt (1981) based on three migrated knots; the resulting curve can be found in Fig. 8.6 of Hunt (1982) and in Fig. 4 of Hunt and Lloyd (1987). Figure 6 shows the estimated RGR using the smoother splines and loess. Both the smoother splines and loess clearly indicate a brief period of rapidly decreasing, and then increasing, RGR during days 8–15 that was missing in the original *B*-spline regression analysis. This pattern is similar to the second artificial pattern described above. Of course, with empirical data it is impossible to know with certainty whether this brief period of rapid change is 'real' but Fig. 5 clearly indicates that these methods are capable of detecting such changes. This figure also shows that the pointwise confidence intervals around the cubic spline smoother curve are much narrower than those around the loess curve.

CONCLUSION

The methods of cubic spline smoothers and loess represent versatile and accurate ways of form-free curve fitting that have the added advantage of being able to estimate smoothly changing first derivatives with less subjectivity than *B*-splines. Overall, all three methods capture the main trends in a complicated growth trajectory, but the loess curve seems to have produced the best overall result in our experience, although with larger confidence intervals. The application of these methods to growth analysis will result in more accurate descriptions of growth phenomena.

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APPENDIX

The following function, written in the S language, can be used with S-PLUS to calculate confidence intervals of the RGR values from a cubic smoother spline. Lines in italics and enclosed within exclamation marks are the equivalent lines for the loess curve; the code for the 'loess.deriv' are given later.

```
G.matrix←function(time, DF){
   !l.fit←loess(y∼x,span=op.value)
  deriv←loess.deriv(l.fit)!
  x←unique(time)
  n←length(x)
  G←matrix(0, n, n)
  S←G
  I←diag(n)
  for(i in 1:n){
  fit←smooth.spline(x, I[,i], df=DF)
    !fit2←loess(I[,i]∼x, span=op.value)!
  S[,i]←fit$y
  G[,i]←predict.smooth.spline(fit,x,deriv=1)$y
    !G[,i]←loess.deriv(fit2)[,3]!
  list(G=G, S=S)
}
```

The following is an example analysis in which y is ln(dry weight) and x is harvest day and the optimal λ is chosen by cross-validation.

```
y.fit←smooth.spline(x, y, cv=T)
```

(y.fit$y gives the predicted values of y at each unique harvest day. y.fit$df gives the equivalent degrees of freedom of the model and (unique(x)-y.fit$df) gives the residual degrees of freedom)

```
deriv.fit←predict.smooth.spline(y.fit,
y.fit$x, 1)
```

(deriv.fit$y gives the predicted first derivatives, i.e. RGR, at each unique harvest day)

```
SE.y←sqrt(diag(G.matrix(x,
y.fit$df)$S%*%t(G.matrix(x,
y.fit$df)$S))*y.fit$cv.crit)
```

(This gives the standard error of the predicted values of y at each unique harvest day)

```
SE.rgr←sqrt(diag(G.matrix(x,
y.fit$df)$G%*%t(G.matrix(x,
y.fit$df)$G)*y.fit$cv.crit)
```

(This gives the standard error of the predicted RGR at each unique harvest day)

Multiplying the standard errors by the appropriate value of a t distribution provides the pointwise confidence intervals.

```
loess.deriv←function(fit)
{
  aln←fit$surface$interpolator$all.numeric
  d←aln$parameter["d"]
  coef←matrix(aln$vval, ncol = d+1, byrow = T)%*%
    diag(c(1, 1/fit$surface$divisor))
  x←matrix(0, ncol = d, nrow = nrow(coef))
  vc←nv←2^d
  for(i in 1:d)
    x[1:vc, i]←rep(rep(aln$vert[c(i, i+d)],
    rep(2^(i−1), 2)), 2^(d−i))
  cell←matrix(1:vc, nrow = 1)
  i←nc←1
  while(i <=nc){
    s←aln$a[i]
    if(s > 0){
      cell←rbind(cell, cell[i, ], cell[i,
          ])
      z←x[cell[i, ], s]
      u1←(1:vc)[z==z[1]]
      u2←(1:vc)[z==z[vc]]
      newv←(nv+1):(nv+vc/2)
      cell[nc+1, u2]←cell[nc+2, u1]←
        newv
      x[newv, ]←x[cell[i, u1], ]
      x[newv, s]←aln$xi[i]
      nc←nc+2
      nv←nv+vc/2
    }
    i←i+1
    }
    x←x%*%diag(fit$surface$divisor)
    ret←cbind(x, coef)
    dimnames(ret)←list(NULL, c(fit$predictors$
      names.predictors, "fhat", paste("d.", fit$
      predictors$names.predictors, sep="")))
    ret[order(ret[, 1), ]
}
```