Growth modelling — New developments

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Abstract

Recent refinements in methods being used to develop growth models in New Zealand are described. These include new approaches to the modelling of site occupancy and fertilising, and computational improvements in parameter estimation. The desirability of models that are mathematically tractable as well as realistic is emphasized.

Introduction

A series of regional growth models for radiata pine in New Zealand is being developed. The models consist of systems of differential equations using stand-level variables. Parameters are estimated by maximum-likelihood.

This growth modelling program has been reviewed recently (García 1988a). Goulding (1986) surveys these and other growth models available in New Zealand. Conceptual aspects have also been discussed by García (1988b). Only a very brief sketch of the general methodology will be given here, followed by a description of some new work.

General methods

The models, in their simplest form, describe the state of a stand at any time by three variables: top height (H), basal area (B), and number of trees per hectare (N). Growth and natural mortality are given by three differential

equations:

$$\frac{\mathrm{d}H}{\mathrm{d}t} = f_1(H) \tag{1a}$$

$$\frac{\mathrm{d}B}{\mathrm{d}t} = f_2(H, B, N) \tag{1b}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = f_3(H, B, N) \tag{1c}$$

The form of the equations has been selected so that they are able to approximate observed growth patterns, and they can be integrated analytically. Analytical integration, among other benefits, makes feasible the use of efficient parameter estimation procedures.

For parameter estimation, random processes are included in equations (1) to represent the variation of observed variable values. A likelihood function can then be computed. Again, this is done in a way that is not unrealistic, and at the same time results in a closed-form expression for the likelihood. A numerical maximisation of the likelihood function is then carried out to obtain the parameter estimates.

Growth multipliers

An extension to (1) has been found useful. It consists of multiplying some or all of the equations by functions of an additional state variable. Applications to modelling site occupancy and fertiliser effects are described below. A similar approach could be used to include genetic gains and other variables.

Site occupancy

Under heavy thinning and pruning regimes, the three variables H, B and N may not be sufficient to adequately describe the state of a stand. Immediately following thinning or pruning a stand will not be fully utilising the site potential, and would grow more slowly than another stand with the same H, B, and N, but not recently treated (García 1979, 1984).

An additional state variable representing the degree of "site occupancy" may improve growth prediction in these circumstances. Lack of data and

the cost of measurement make impractical at this stage the use of variables such as foliage biomass or leaf area index, which might be appropriate. We can, however, use a proxy that we shall call "relative closure" and denote by R . This variable is not necessarily observable at all times. We need only to assume that it is 1 for closed stands fully occupying the site, and that it is reduced by thinning in proportion to the basal area removed. R may be also be reduced by pruning, by an amount related to the crown length removed. After thinning or pruning, R recovers approaching 1 as the stand closes. Diameter growth and mortality rates depend on the current value of R . Note that we make no assumptions about the mechanism of site occupancy; below ground (roots) as well as above ground (foliage) processes may be involved.

The relative closure variable may be included as a straightforward extension of our differential equations (1) to more than three dimensions. This was done, with satisfactory results, in models for the Hawkes Bay and Auckland Clays regions (García 1984, 1988a). One potential problem with this, however, is that the predicted growth may not always decrease with decreasing R. In fact, for small enough R the growth predicted by these models increases, although this happens well outside of the range of the data.

A better-behaved model can be obtained by extending (1) as follows:

$$\frac{\mathrm{d}H}{\mathrm{d}t} = f_1(H) \tag{2a}$$

$$\frac{\mathrm{d}B}{\mathrm{d}t} = g(R) f_2(B, N, H) \tag{2b}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = g(R) f_3(B, N, H) \tag{2c}$$

$$\frac{\mathrm{d}R}{\mathrm{d}t} = h(R) \tag{2d}$$

Here $g(R)$ is the growth and mortality reduction factor due to less than full closure. The function $h(R)$ specifies the rate of recovery of the relative closure.

It can be seen that with the substitution

$$\mathrm{d}s = g(R)\,\mathrm{d}t\ , \tag{3}$$

equations (2b) and (2c) take the same form as (1b) and (1c). Therefore, if (1a) to (1c) are integrable, (2a) to (2c) can be integrated in the same way as

functions of t and s . With suitable functions for $g(R)$ and $h(R)$, closed-form solutions in terms of t can be obtained.

The function $g(R)$ must be strictly increasing between 0 for $R = 0$, and 1 for $R = 1$. It is known that small reductions in closure have negligible effect, so that it is also desirable that the derivative of $g(R)$ at $R = 1$ should be zero. Appropriate functions are

$$g(R) = 1 - (1 - R)^m \ . \tag{4}$$

More convenient is a cubic of the form

$$\begin{aligned} g(R) &= R[a + (3 - 2a)R + (a - 2)R^2] \\ &= 1 - (1 - R)^2[1 - (a - 2)R] \ . \end{aligned} \tag{5}$$

The parameter a is the slope at the origin, and curves of suitable shape are obtained for values of a between 0 and 3. Equation (5) includes (4) for $m = 2$ and $m = 3$.

The recovery function $h(R)$ could be expected to be zero at $R = 0$ (no growth), then increase with R as closure increases, and finally decrease to 0 for $R = 1$, so that R tends to 1 asymptotically. Alternatively, it may be thought of as affected by closure in the same way as the growth rate,

$$h(R) = g(R)k(R) \ ,$$

where $k(R)$ is initially constant (derivative zero at $R = 0$), and then decreases to zero as the stand reaches full closure. The logistic

$$h(R) = bR(1 - R) \tag{6}$$

satisfies these conditions, and leads to a closed-form solution in conjunction with (5).

With this choice of functions, (2d) can be integrated giving R as a function of t and the initial R , substituted into (3), and (3) integrated with respect to t , to obtain the relationship between the "adjusted time" s and the real time t . A more convenient form for computation was obtained by rewriting (3) as

$$\mathrm{d}s = \mathrm{d}t - [1 - g(R)]/h(R)\mathrm{d}R \ . \tag{7}$$

Then, substituting (5) and (6) and integrating,

$$s - s_0 = t - t_0 - [\ln(R/R_0) + (1 - a)(R - R_0) + (a/2 - 1)(R^2 - R_0^2)]/b \ .$$

Note that integrating the alternative form

$$\mathrm{d}s = [g(R)/h(R)]\,\mathrm{d}R$$

leads to numerical difficulties when R tends to 1.

A slight variation on this model (described below) has been fitted to data from radiata pine in the Pumice Plateau. The model includes also an estimated relationship between canopy depth removed in pruning and reduction in R . Another difference with previous models is that R is initialised with a small value for young stands. Specifically, stands start at an age corresponding to top height 1.4 m (to avoid problems related to basal area being undefined before then), with an R value proportional to the number of trees per hectare. That is, the initial closure corresponds to a small area utilised by each tree (a parameter estimated from the growth data). It is hoped that consistent modelling of young and old open stands would improve predictions for both.

All the parameters were estimated simultaneously by maximum likelihood. Considering the indirect nature of the estimates, it is perhaps surprising that the values obtained are reasonable. The value for a in (5) was 2.65, and the initial R per tree at 1.4 m implies full closure at a spacing of 48 cm. The effect of a 50% reduction in closure is negligible after about two years. It appears that the model extrapolates well to very young stands, without the need for the separate relationships used in previous models.

At this stage, no multiplier has been included in (2a). Therefore, very severe treatments that could affect the top height growth may not be modelled correctly.

Fertiliser effects

For the Auckland Clays region, a model was developed with data from stands that had been "adequately" fertilised with phosphorous. Multiplier functions were then added to predict the effect of lower phosphorous levels.

The model is similar to (2), with R representing the foliar P content. A multiplier function, with different parameter values, was also included in (2a), since the fertiliser had been found to affect both height and diameter growth but to different degrees. (The model included also a relative closure

variable, and the height growth multiplier was applied to the closure recovery equation as well).

In this instance, the growth multipliers $g\,(R\,)$ represent the growth reduction due to a less than adequate level of foliar P. This function should cross the R axis at a value below which there is no growth (estimated at 0.06% of foliar P), then increase up to a value of 1 at the level of P typically present in the plots used for the initial model (about 0.13%), and finally tend to a horizontal asymptote slightly above 1. Hyperbolae of the form

$$g(R) = (R - 0.06)/(aR - 0.13a + 0.07)$$

are suitable. The parameters a were estimated from the ratios of the growth in fertilizer experiment plots to the growth predicted by the initial model.

Equation (2d) describes here the decay in foliar P after fertilising. As a first approximation, an exponential decay down to an equilibrium level of 0.06% was satisfactory:

$$h(R) = b(0.06 - R)\ .$$

With these functions, (3) or (7) can be integrated to obtain "adjusted" or "physiological" times for phosphorous-deficient stands.

Variations

The actual models implemented differed slightly from the description given above. Although the deterministic model (2) can be solved as shown, it was not obvious how to extend this to the stochastic model needed for computing the likelihood. Therefore, the multipliers were applied after a transformation of these equations.

With our model form for (1), it is possible to find certain transformations of the state variables such that the equations are "uncoupled":

$$\frac{\mathrm{d}H}{\mathrm{d}t} = f_1(H) \tag{8a}$$

$$\frac{\mathrm{d}u}{\mathrm{d}t} = f_2'(u) \tag{8b}$$

$$\frac{\mathrm{d}v}{\mathrm{d}t} = f_3'(v)\ . \tag{8c}$$

Here u and v are functions of B , N and H [e.g. equation (2.3.4) of García 1979]. Variability is modelled by random processes added to the right-hand sides of (8).

The multiplier functions were applied to equations (8b) and (8c), instead of (2b) and (2c). This allowed computations to be carried out with relatively minor alterations to the existing programs.

Contrary to (2), with this formulation the diameter growth does not necessarily drop to zero when the closure is zero. This is related to the already mentioned absence of a multiplier in (2a), and does not occur in the fertiliser model. On the other hand, (8) allows the flexibility of using a different multiplier for each equation.

Computing

As already indicated, the growth model parameters are estimated by direct maximisation of the log-likelihood function using a general-purpose numerical optimisation procedure (García 1984). The most efficient procedures, e.g. quasi-Newton or variable-metric methods, require the knowledge of the partial derivatives of the function with respect to the parameters. Because of the complexity of the function, it has not been practical to code the computation of the analytical derivatives, and finite difference approximations have been used instead.

The computation of finite differences, however, is costly, especially when the data sets and number of parameters are large. Each function evaluation performs a loop over all the observations. A gradient computation requires one or two function evaluations for each parameter, depending on if forward or central differences are used.

Recently, a computer program for the automatic generation of partial derivatives was developed. The program takes the Fortran subroutine that computes the function value, and produces another subroutine that computes the partial derivatives with respect to specified variables. For the Pumice Plateau growth model, this has reduced the CPU time used for typical parameter estimation runs from 8 hours to 1 hour, on a VAX 785. Between 15 and 20 parameters are estimated, using over 2000 observations.

Although a number of symbolic algebra systems, such as MACSYMA and

muMATH, can generate derivatives of mathematical expressions, what was required was to derivate functions computed by complex routines, including conditionals, loops, and intermediate variables. The basic idea originated from Wengert (1964), and a similar principle was implemented by hand in the height growth parameter estimation program (García 1983). In it each statement of the function evaluation routine is followed by statements to compute the derivatives of the left-hand-side variable (usually an intermediate variable). For example,

```
C = A * B
```

would be followed by

```
C1 = A1 * B + A * B1
C2 = A2 * B + A * B2
etc.,
```

where the `Ai` and `Bi` are partial derivatives with respect to parameter `i`, computed in previous statements (with obvious simplifications where the partials for some terms do not exist). The function derivatives sought follow the statement defining the final value of the function, at the end of the subroutine.

The derivative-generating program essentially automates this procedure. The statements computing derivatives precede instead of follow each function evaluation statement, to deal correctly with statements such as

```
A = A * B .
```

For each statement, the right-hand side expression is processed by a recursive descent parser. The program avoids generating many redundant computations, and an optimising Fortran compiler will eliminate many others. Certain situations involving loops and conditionals require more than one pass, and this is handled automatically. Some manual editing of the input and output Fortran routines may be needed, but this is usually simple and of a minor nature.

The system runs on a microcomputer under STSC's APL Plus or Pocket APL. It is a tribute to the power of the APL computer language that such a complex system could be implemented within a very short time.

Another factor facilitating growth model development has been the porting of the parameter estimation programs to a microcomputer. With a 20 MHz 80386 processor the CPU time used is not much higher that on the VAX 785, and the turn-around is much faster.

Concluding remarks

One school of thought in growth modelling searches for simple mathematical "laws", that all plants are supposed to follow. Examples of this are the 3/2 self-thinning rule, and the belief in particular growth curve equations. At the other extreme, with modern computing facilities it is easy to build very complex process-based models. Large numbers of equations are put together and output is generated by numerical simulation.

In relation to the first approach, it can be argued that there is nothing mathematical about plant growth, models being just convenient approximate representations of parts of the real world. Different equations can be equally "biologically meaningful" (or meaningless) as descriptions for observed relationships. For example, for all practical purposes equation (4) with $m = 2.5$ would be indistinguishable from (5) with $a = 2.58$. Even Newton's laws in physics, seen by many as the epitome of natural laws, have no theoretical basis whatsoever. They are just empirical approximations (and not very accurate under some conditions, as shown by Einstein). In the words of G.E.P. Box in a slightly different context, "all models are wrong, but some are useful".

A problem with complex aggregates of equations that can only be solved numerically, is that they can be almost as much of a "black box" as the real system. They may contribute little to our understanding of the system behavior ("The purpose of computing is insight, not numbers", R.W. Hamming). In addition, it can be difficult or impossible to obtain satisfactory parameter estimates. Some of these models effectively amount to hypotheses that cannot be invalidated with empirical data, being therefore of questionable scientific value.

Although there is a place for all types of models, much work needs to be done on models having both a rational basis and mathematical tractability. Building models with these properties, however, is a difficult art involving much trial and error. Mathematical expediency must not override the requirement of agreeing with the field data. To end with yet another quotation, we may paraphrase A. Einstein: a model "must be as simple as possible, but not simpler".

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