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Comparison of yellow poplar growth models on the basis of derived growth analysis variables

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Summary

Quadratic and cubic polynomials, and Gompertz and Richards asymptotic models were fitted to yellow poplar growth data. These data included height, leaf area, leaf weight and new shoot weight for 23 weeks. Seven growth analysis variables were estimated from each function. The Gompertz and Richards models fitted the data best and provided the most accurate derived variables. However, the Richards model was more complex to fit.

Introduction

Several mathematical models have been used to fit growth data. These include polynomial models, asymptotic models and special approaches such as data segmentation and spline regression (Hunt 1982). Each approach has advantages and disadvantages depending on the growth data and the computer facilities available.

The objective of this study was to compare growth analysis variables calculated from four mathematical growth models (Hunt 1982), namely, the quadratic and cubic polynomials, and the Gompertz and Richards asymptotic models.

Materials and methods

Two hundred and fifty one-year-old yellow poplar (*Liriodendron tulipifera* L.) seedlings were potted in 15-cm pots containing a 2:1 (v:v) peat soil:sand mixture. The seedlings were randomly assigned a harvest date and placed on a greenhouse bench. The plants were maintained in a photoperiod of $\geq$ 15 h, watered three times a week and fertilized every two weeks with 100 ml of soluble fertilizer (N:P:K, 20:20:20).

Starting at bud-break, 10 seedlings were harvested weekly for 23 weeks. Height of new stem growth, leaf area, leaf weight and new stem weight were determined. Leaf area was measured with an electronic area meter and dry weight was determined by drying the tissue to constant weight at 100°C.

At the end of the collection period, leaf area, leaf weight, new growth dry weight (new stem plus leaf weight) and height data were transformed to natural logs and plotted over time. The following mathematical models were fitted to each of the four data sets:

Quadratic polynomial

$$\log_e Y = a + bt + ct^2$$

Cubic polynomial

$$\log_e Y = a + bt + ct^2 + dt^3$$

Gompertz function

$$\log_e Y = ae^{-be^{-ct}}$$

Richards function

$$\log_e Y = a(1 \pm e^{(b-ct)})^{-1/d}.$$

The parameters for the Gompertz and Richards functions were calculated with an iteration program that ran no more than 10 iterations. The data were transformed to natural logs to ensure homogeneity of the variance. The growth analysis variables were calculated with these models and with the following first derivative of each model:

Quadratic polynomial

$$\frac{d(\log_e Y)}{dt} = b + 2ct$$

Cubic polynomial

$$\frac{d(\log_e Y)}{dt} = b + 2ct + 3dt^2$$

Gompertz function

$$\frac{d(\log_e Y)}{dt} = abce^{-ct-be^{-ct}}$$

Richards function

$$\frac{d(\log_e Y)}{dt} = \frac{ace^{b-ct}}{d} \cdot (1 \pm e^{b-ct})^{-(1/d + 1)}$$

The growth analysis variables calculated were:

Relative growth rate (RGR) $= \frac{1}{W} \cdot \frac{dW}{dt}$

Relative leaf area growth rate (RLAGR) $= \frac{1}{A} \cdot \frac{dA}{dt}$

Relative leaf weight growth rate (RLWGR) $= \frac{1}{L} \cdot \frac{dL}{dt}$

Leaf area ratio (LAR) $= A/W$

Leaf weight ratio (LWR) $= L/W$

Specific leaf area (SLA) $= A/L$

Net assimilation rate (NAR) $= \frac{1}{A} \cdot \frac{dW}{dt}$

where A = leaf area (cm^2), L = leaf weight (g), W = new growth weight (g) and t = time (weeks).

Results and discussion

The growth data were fitted to each of the four mathematical models (Figure 1). In general, the index of fit (1 – (residual sums of squares/corrected total sum of squares)) for the Gompertz and Richards models was almost identical, followed closely by the cubic polynomial. The index of fit (Table 1) for the quadratic polynomial was 0.02–0.04 units lower. The asymptotic models and the cubic model were nearly identical up to the 22nd week when the cubic polynomial started to increase. The quadratic polynomial always had a higher intercept than the other functions but gave a lower estimate of the growth variable by the 23rd week.

The quadratic model is the simplest of the four models but expresses a clear departure from linearity with time. It provides a good fit for data that do not include the advanced stages of growth. The curvature of quadratics is uniform and the first derivative (relative growth rate) varies linearly with time. The quadratic model is not a good function to use when the data contain an asymptote.

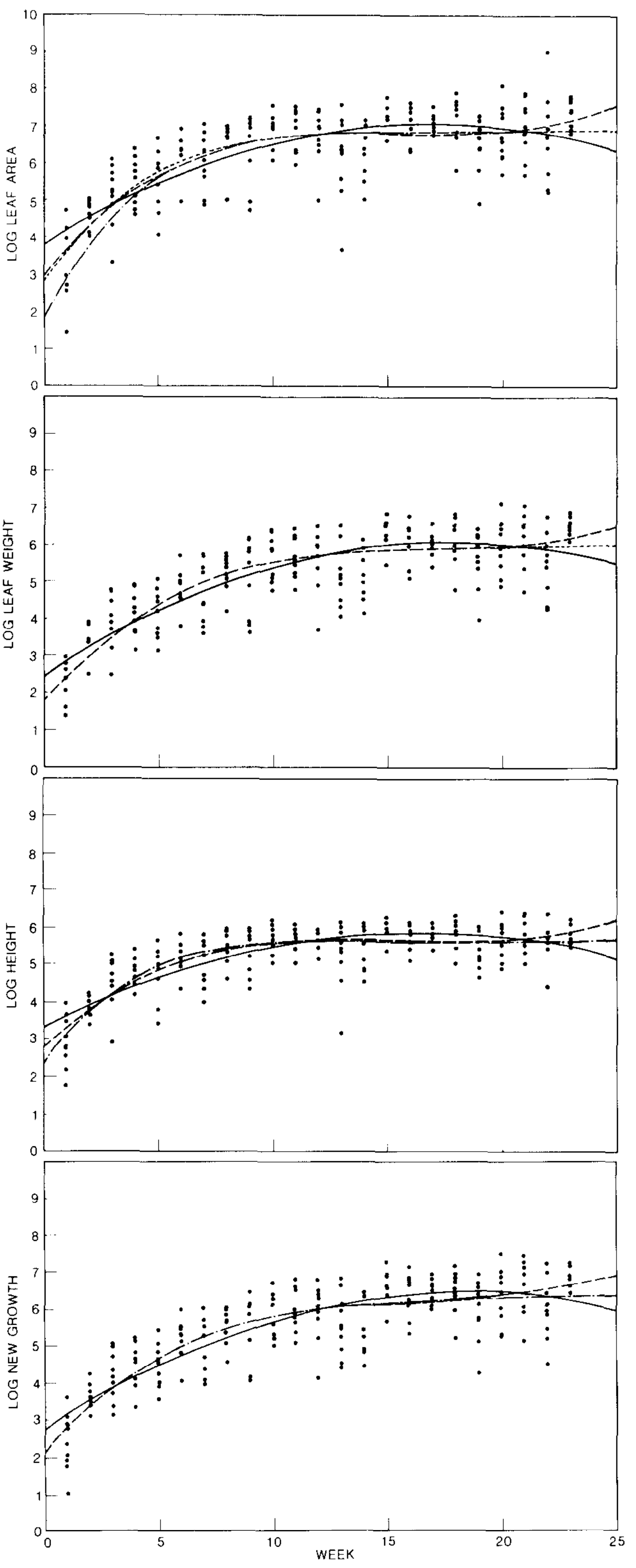
The cubic polynomial fitted the four growth variables slightly better than the quadratic polynomial. Its main lack of fit occurred after 20 weeks when the estimates of variables tend to increase. This inherent feature of the cubic polynomial is even more important when calculating growth rate. Although it initially falls with time in concordance with the data, it later increases after approximately 18 weeks when an examination of the data suggests that it should approach zero. The cubic polynomial has often been used to describe growth data, but as emphasized by Hughes and Freeman (1967) care must be used when data at the ends of the data set are interpreted.

The Gompertz and Richards models have a distinct advantage over the polynomial model with this set of data because both functions will fit data that possess an asymptote. The main difference between the two models is in the point of inflection of the curve. With the three-parameter Gompertz model, the point of inflection is always at 0.368 times the maximum value whereas with the four-parameter Richards model it may occur at any point. In the present data set, which does not include an inflection point because of the logarithmic transformation,

Table 1. Index of fit[1] for growth models.

Variable	Growth model			
	Quadratic	Cubic	Gompertz	Richards
Leaf weight	0.656	0.681	0.679	0.679
Leaf area	0.561	0.600	0.604	0.602
New growth weight	0.665	0.687	0.684	0.685
New height growth	0.581	0.630	0.643	0.643

[1] Index of fit = 1 – (residual sums of squares/corrected total sums of squares).


LOG LEAF AREA
LOG LEAF WEIGHT
LOG HEIGHT
LOG NEW GROWTH
WEEK
0
5
10
15
20
25

both functions fit the data equally well. As the Gompertz model has one less parameter it is probably the better model for this data set.

To compare growth analysis variables calculated from these models, variables were calculated for the 5th, 10th, 15th and 20th weeks (Table 2). This eliminated part of the wide variation that may be present at the extreme ends of regression

Table 2. Growth analytical variables calculated from the four growth models.

Variable	Growth model	Age (weeks)			
		5	10	15	20
RGR		*g g⁻¹ week⁻¹*			
	Quadratic	0.288	0.180	0.072	0.000
	Cubic	0.343	0.126	0.030	0.055
	Gompertz	0.346	0.130	0.042	0.013
	Richards	0.347	0.130	0.042	0.013
RLWGR		*g g⁻¹ week⁻¹*			
	Quadratic	0.295	0.181	0.066	0.000
	Cubic	0.353	0.124	0.022	0.047
	Gompertz	0.359	0.122	0.035	0.010
	Richards	0.352	0.123	0.035	0.010
RLAGR		*cm² cm⁻² week⁻¹*			
	Quadratic	0.272	0.160	0.047	0.000
	Cubic	0.342	0.091	0.000	0.051
	Gompertz	0.336	0.078	0.016	0.003
	Richards	0.344	0.078	0.015	0.003
SLA		*cm² g⁻¹*			
	Quadratic	356	320	292	264
	Cubic	368	329	277	259
	Gompertz	402	319	274	261
	Richards	399	325	274	258
LWR		*g g⁻¹*			
	Quadratic	0.73	0.73	0.72	0.70
	Cubic	0.73	0.75	0.73	0.70
	Gompertz	0.74	0.75	0.72	0.70
	Richards	0.75	0.74	0.72	0.70
LAR		*cm² g⁻¹*			
	Quadratic	258	236	211	184
	Cubic	270	246	203	180
	Gompertz	299	238	197	182
	Richards	299	240	197	183
NAR		*g cm⁻² week⁻¹ × 10⁻³*			
	Quadratic	1.116	0.763	0.341	0.000
	Cubic	1.270	0.512	0.148	0.306
	Gompertz	1.157	0.546	0.214	0.071
	Richards	1.160	0.542	0.213	0.071

Figure 1. Increase in $\log_e$ height, mm (a); $\log_e$ leaf area, cm^2 (b); $\log_e$ leaf weight, g (c), and $\log_e$ new growth weight, g (d) of yellow poplar seedlings with time. Quadratic model (———), cubic model (– – – –), Gompertz model (- - - - - -) and Richards model (– · – · –).

lines (Hughes and Freeman 1967). Relative growth rate (RGR), relative leaf weight growth rate (RLWGR) and relative leaf area growth rate (RLAGR) calculated from the quadratic model decreased linearly, dropping below zero before the 20th week. The growth analysis variables calculated from the cubic polynomial decreased until about the 15th week and then increased. Examination of the data suggests that neither of these trends accurately describes the data collected after 17–18 weeks. The growth analysis variables calculated by the Gompertz and Richards models decreased with time and approached zero by the 20th week. This is in agreement with the observed relationship between the measured growth variables and time.

The remaining four growth analysis variables are closely related. With all four models LWR was uniform but tended to decrease slightly by week 20. In each case, approximately 74% of the new growth weight was in the leaves in the 5th week. This dropped to approximately 70% by week 20, suggesting that more growth material was being allocated to the new stems in the 20th than in the 5th week.

All four models suggested that SLA decreased with time. However, the decrease ranged from approximately 100 $cm^2\ g^{-1}$ with the quadratic model to 140 $cm^2\ g^{-1}$ for the Gompertz and Richards models. These same relationships were also found in LAR because LAR = LWR × SLA and as LWR was nearly constant, LAR tended to follow SLA.

The final growth analysis variable calculated was NAR, which for the quadratic model rapidly decreased to zero, whereas for the cubic model it decreased up to the 15th week and then increased by the 20th week. Net assimilation rate calculated from the Gompertz and Richards models approached but did not reach zero. This suggests that at the later stages of growth when leaf growth has slowed or ceased, photosynthesis is also slowing or respiration is increasing, or both, which causes NAR to approach zero.

From this experiment the Gompertz and Richards models fitted the data best and provided the most accurate growth analytical variables. The Richards model, however, was more complex than necessary.

References

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