An expolinear model of the growth pattern of the apple fruit

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SUMMARY

The expolinear growth model of Goudriaan and Monteith (1990) is proposed as a new model for the inherent growth pattern of fruit of apple (*Malus domestica* Borkh.), defined as growth pattern under apparently non–limiting conditions. This function has three parameters: maximum relative growth rate, maximum absolute growth rate, and "lost time" (x intercept of the linear growth phase). Apple fruit growth (weight basis) at very low crop loads and apparently optimum environmental conditions, displays an early positive curvilinear growth followed by linear growth to harvest, and is described well by the expolinear function. The model also fits growth patterns of 'Empire' and 'Golden Delicious' apple fruit differing in the rate of growth in the exponential phase due to differences in the crop load. Estimates of cortical cell numbers in 'Empire' fruit from related studies suggest that during the linear phase in mid–season, different growth rates among crop load treatments were apparently controlled by differences in numbers of cells in the fruit, since estimated growth rates per cortical cell were essentially constant over several treatments.

THE growth pattern of the apple fruit has generally been described in texts or reviews as sigmoidal (Pratt, 1988; Faust, 1989), especially if diameter is the measure of growth, but plots of fresh weight data versus time may also show a late–season decline in fruit growth rates. However, a growth pattern of the apple fruit being curvilinear during the first 3–5 weeks followed by a linear increase in weight until harvest has also been reported by Blanpied (1966) and Assaf *et al.* (1982) and observed by the authors in lightly cropping trees. Recently Magein (1989) suggested that the apple growth pattern is a double sigmoid rather than simple sigmoid; however, the erratic nature of the timing and amplitude of the short "lag period" in the data presented casts doubt on the soundness of this proposal. Bollard (1970) emphasized the need to measure volume or

weight, especially in dry weight, rather than diameter as a more standard biological definition to properly express "growth." For apple fruit, fresh weight appears to be the most useful expression of growth over long periods since few reports use dry weight.

Recently modelling approaches have been used to describe apple fruit growth. Welte (1990) developed a complex differential dynamic simulation model for predicting final harvest size of 'Jonagold' apples that included temperature effects on growth rate within certain temperature ranges, daylength effects, crop load effects and other empirical factors. Although this complex was apparently effective at empirically fitting growth curve variations from year to year, it did not address the fundamental pattern of growth of the apple fruit. Schecter *et al.* (1993a and 1993b) have

modelled the seasonal growth curve with two linear sections approximating the phases of cell division and cell expansion. The linear portion late in the season fit well, but the early season growth appears to be clearly curvilinear.

This growth pattern resembles the shape modelled by an "expolinear" growth equation recently described by Goudriaan and Monteith (1990) to describe seasonal crop plant growth patterns that show an initial exponential increase in crop dry weight, followed by a linear growth phase. The early exponential growth is related to the exponential increase in light interception as leaves are produced. After canopy closure, the light interception becomes constant, and the growth is a linear function of light availability.

Similarly, the apple fruit grows in two phases, an early exponential cell division phase that typically lasts for about 3–5 weeks after bloom, followed by a cell expansion phase for the rest of the season (Bollard, 1970; Blanpied and Wilde, 1968; Pratt, 1988). It is proposed that the expolinear growth equation be evaluated as a mathematical description of the inherent growth pattern of the apple.

It is necessary to distinguish between the *inherent* or *potential* growth pattern (defined as the growth pattern of a fruit supplied with apparently optimal resources and having no competition) from the *actual* growth (i.e. growth under actual conditions of limited resources and/or competition from other fruits). In practice, to estimate the inherent growth pattern, fruit growth should be measured under conditions as close to optimum as possible as proposed by DeJong (1990) (i.e. growth of well exposed fruits with high seed counts on low–cropping, well pruned trees, thinned early, and without any indication of nutrient, water or pest stresses).

The objectives of this study were: (1) to evaluate the fit of the Goudriaan–Monteith expolinear model to growth of the apple growing under apparently optimum conditions with low crop competition, and (2) to evaluate how growth patterns and model parameters are affected by early and late thinning that affect final fruit size.

MATERIALS AND METHODS

Fruit growth data was gathered from mature 15 year old slender–spindle trained 'Empire' apple trees on M.9 rootstock in Geneva, NY in 1987. To provide as closely as possible the "optimum" conditions needed to express the inherent growth pattern, several trees were hand thinned at 5 d after bloom (DAB) to low fruit numbers to produce low yields (about 15 t ha^{-1} at harvest). Other trees were thinned to higher fruit numbers to produce normal crop levels (40–50 t ha^{-1}). The growing season had adequate rainfall, and average temperatures and solar radiation. The trees were healthy, and there were no indications of significant stress. The data sets consisted of the means of 25–30 fruits per treatment monitored at 10–12 dates during the season by measuring maximum fruit diameters with electronic calipers. At each date fruits of a range of sizes were collected from adjacent trees with similar crop levels to determine the relation of fruit diameter to fruit weight. The regressions were used to estimate the fresh weights of the monitored fruits at each date.

Fruit growth data were also gathered in related thinning experiments on 'Empire' in the same orchard in 1987 and 1988. The treatments consisted of thinning by hand between bloom and 40 DAB to give high and low crop levels. Data was also gathered from treatments with early (5 DAB) and late (30 DAB) thinning of individual spurs on each tree to a single king fruit on trees with high or low crop loads. To assess a second cultivar at a different location, the model was fitted to data on fruit growth from hand thinned 10 year old slender–spindle trained 'Golden Delicious' trees on M.27 rootstock in six–row beds (8889 trees per ha) yielding 74 t ha^{-1} in 1991 in the experimental orchards of the University of Bologna, Italy. In this season, there was a very early bloom followed by an extended cold period of about 60 d before normal weather.

Fitting the expolinear model

The Goudriaan–Monteith expolinear equation is:

$$W = (Cm/Rm)\ln\{1 + \exp[R_m(t - \text{tb})]\}$$

where W = plant (or fruit) weight, C_m = maximum absolute growth rate (in weight gain
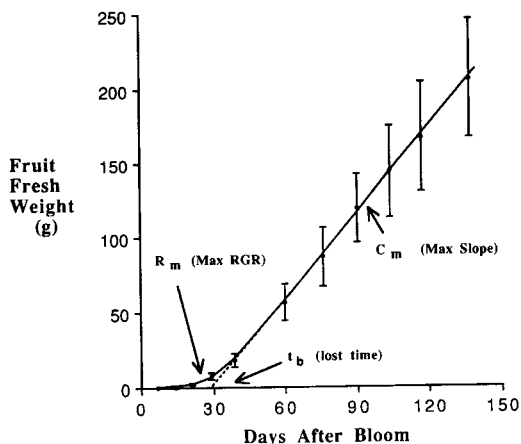
FIG. 1.

Seasonal increase in fruit fresh weight of 'Empire' apple on lightly–cropped trees with early thinning to single fruits in 1987. Error bars represent the standard deviation of the same 28 fruits at each date. The line is the fitted expolinear model. Regression parameter estimates were: $C_m = 1.95$ g day^{-1}, $R_m = 0.167$ g g^{-1} day^{-1}, $t_b = 30$ days.
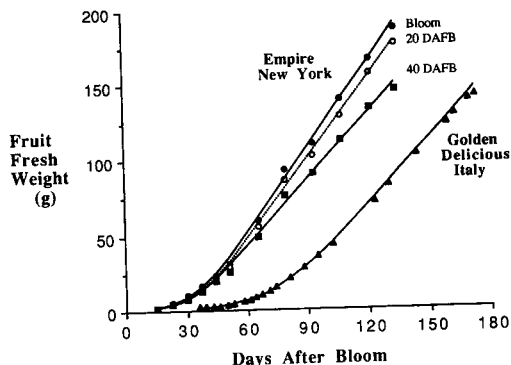

FIG. 2.

Seasonal curves and fitted expolinear models for 'Empire' apple fresh weight increases in Geneva, New York in 1988 as affected by the time of hand thinning (at bloom or at 20 or 40 d after full bloom) to a moderate crop level, and for 'Golden Delicious' apple growing in Bologna, Italy in 1990. The early period after bloom in Bologna was very cold.

per day reached in the linear phase), R_m = maximum relative growth rate (in weight gain per unit weight per day), t = time in days, t_b = x axis intercept of the linear growth phase (termed the "lost time") (Figure 1).

Initially the model was fitted to data of fruit growth on low crop trees using the nonlinear regression procedure (NLIN) of the SAS statistics program (SAS Institute, Cary, NC) for estimating the model parameters. The model was also fitted to the higher crop load data and the data for 'Golden Delicious' to examine how different crop loads, cultivars and seasonal climates affected the growth patterns and model parameters.

RESULTS

The model appears to fit well the growth data of 'Empire' apples thinned early to a light crop as shown by the graphic analysis (Figure 1) and the statistical analysis of fit (Table I). To compare the model parameters for data on fruit growth in different thinning treatments, data were fitted from three treatments that all had low to moderate final crop levels established after bloom, but which differed by the time of thinning (at bloom, 20 and 40 DAB). The later thinning times allowed some early season competition that reduced fruit growth rates in the latter part of the cell–division period before thinning. In all three cases for 'Empire' apples in New York the seasonal growth pattern appeared to be described well by the expolinear model (Figure 2). Similarly, data from Bologna Italy on 'Golden Delicious' were fitted well even though the pattern over time was strongly shifted due to very low temperatures for several weeks after bloom (Figure 2). The expolinear regression parameters showed that the three treatments on 'Empire' had similar maximum relative growth rates, R_m, and "lost times", t_b, but the linear growth rates, C_m differed in proportion to the final sizes (Table II). The 'Golden Delicious'

TABLE I

Analysis of variance of the expolinear fit of 'Empire' seasonal apple fruit fresh weight growth (see Figure 1)

Source	Degrees of freedom	Sum of squares	Mean squares	F	p
Regression	3	3273559	1091186		
Residual	305	134628	441		
Lack of fit	8	603	75	0.17	n.s.
Pure error	297	134026	451		

TABLE II
Expolinear parameter estimates for three 'Empire' and one 'Golden Delicious' apple fruit growth curves shown in Figure 2

Treatment	R_m g g^{-1} day^{-1}	C_m g day^{-1}	t_b days	Final fruit weight (g)
Empire-Bloom	0.115	1.89	34	187
Empire-10 DAB	0.108	1.79	33	181
Empire-40 DAB	0.126	1.47	32	146
G. Delicious	0.072	1.47	74	142

TABLE III
Estimated cortical cell numbers and linear phase growth rates per cell in 'Empire' apple from a range of thinning treatments that induced differences in final fruit size (data from treatments shown in Figures 1 and 2)

Thinning treatment	Final fruit fresh wt (g)	Estimated cortical cell no. (millions)	Estimated linear cell growth rate ng FW cell^{-1} day^{-1}
Bloom 1987	207	59.6	33
Bloom 1988	190	55.0	34
10 DAB 1988	179	51.6	35
40 DAB 1988	151	43.0	34

fruits, however, had much lower R_m and much longer "lost time" due to the cold early season. The linear growth rates, though, were very similar to the 40 DAB 'Empire' fruit and both cases gave similar final fruit sizes.

Research on apple thinning and anatomy in coordinated studies within the same 'Empire' orchards has shown that the effects of several different timings of thinning led to differences in final fruit size that were most closely associated with differences in cell numbers in the cortex (Goffinet *et al.*, 1995). Since the apple fruit grows by cell division early in the season and by cell expansion after the first 3–5 weeks, the growth rate during the linear phase, C_m, may then be a reflection of numbers of cells and not of differences in growth per cell. This was examined by estimating the numbers of fruit cortical cells from regressions of fruit weight versus numbers of cortical cells developed by Goffinet *et al.* (1995) from fruit samples from the same trees used in this

study. Assuming that the great majority of the weight of the fruit is contained in the cortex, the growth rate per average cell per day was estimated by dividing the linear growth rate (C_m) by the cortical cell numbers. The estimated growth rate per cell was close to constant at 33–35 ng cell^{-1} day^{-1} even though the final fruit sizes varied from 151 to 207 grams and the linear growth rates varied from 1.47 to 1.95 g day^{-1} (Table III). The possibility that after cell division, apple cortex cells grow at a maximum rate of about 35 ng cell^{-1} day^{-1} under non–limiting conditions suggests an upper limit on fruit growth rates after cell division ceases and an upper limit on final fruit size. This question needs further examination under a range of conditions.

DISCUSSION

The expolinear form not only fits well the empirical growth data for apple fruit growth, but also has characteristics consistent with the manner in which the apple grows (initial exponential cell division which gradually declines to a linear growth by cell expansion alone). Since there are two distinctly different types of growth with a gradual transition, we feel that the expolinear model of Goudriaan and Monteith (1990) is a better model of fruit growth than the others discussed earlier.

As with any model, there are limitations that must be understood to avoid its inappropriate use. This expolinear model describes the growth pattern of apples under conditions that were as close to optimum as possible to estimate potential growth with little or no crop competition (Figure 1). The effects of early season competition during the cell division phase on season–long growth can be modelled with the expolinear growth function as long as
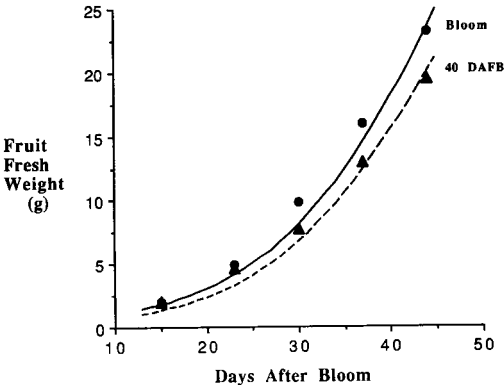

FIG. 3.
Expolinear model fit of fruit fresh weight during early fruit development for 'Empire' apple in New York after hand thinning at bloom or 40 d after bloom. The model was fitted to data over the full season, but only the first 50 d are shown here.

the final crop loads after thinning are low or moderate (Figure 2). This seems to be valid since the linear slope, C_m, appears to be determined by numbers of cells produced in the exponential phase.

The final fruit size was much more closely related to the C_m than to the R_m or T_b. That appears to due to the much longer period of linear growth by cell expansion (15–16 weeks) compared with shorter exponential period (4–5 weeks). Also, the model uses the *maximum* RGR as a key parameter. For apple fruit growth the R_m typically occurs about 7–14 d after bloom (Schecter *et al.*, 1993a and 1993b; unpublished data) while important effects on total cell numbers of thinning treatments can occur in the period of 2–4 weeks after bloom (Figure 3). Consequently, the early season fit may not be as good if a decline in fruit growth occurs due to early competition from other fruits.

The model assumes that there are no major limitations to fruit growth due to non–optimum temperatures. Sigmoidal growth patterns of fruit weight growth can be observed in heavily cropped trees or on lightly cropped trees with low late–season temperatures. However, fitting fruit growth to thermal time with simple linear degree–day calculations (e.g. mean—base temperatures) over the whole season may not be appropriate in all climates, since there does not appear to be a linear response of fruit growth to temperature over the full range of temperatures encountered, especially mid–season high temperatures. A non–linear thermal–time expression would be needed in this case.

The finding that the growth rates per cell during the linear phase appeared to be almost constant suggests that the demand for carbon for fruit growth will be close to constant from the end of cell division to harvest, assuming adequate temperature. This may be useful in the modelling of carbon balances of the apple tree (Lakso and Johnson, 1990; Lakso and Corelli Grappadelli, 1992).

The potential usefulness of this model of the potential growth pattern of the apple is that it provides a baseline measure from which to identify the times at which treatments affect fruit growth. If the inherent growth pattern and the actual growth pattern differ at any time, we may be able to identify more precisely when fruit growth is limited and what the seasonal manifestations of the limitation may be. The model may also be useful for the development of harvest size predictions. Additionally, the model may have promise for other fruits that have a similar growth pattern such as the Asian pear (Caspari *et al.*, 1994).

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