



Fitting leaf area data to nonlinear sigmoidal growth curves

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Abstract

Three of the most commonly used sigmoidal growth curves from Richard family which are applied in plant growth simulation modelling are the Logistic, Richard and Gompertz curves. These mathematical functions are suitable to study the sigmoidal pattern of determinate growth. Logistic and Gompertz models have 3 parameters while Richard function has one additional parameter to describe growth kinetics. Both Richard and Gompertz function are flexible enough in describing asymmetrical sigmoidal patterns while logistic function describes symmetrical sigmoidal growth and because of this, all discussed models can be used to predict leaf growth dynamics. Leaf area data was collected from one semi-deciduous species (*Shorea robusta* Gaertn. f.; Family Dipterocarpaceae) and one deciduous species (*Adina cordifolia* Hook. f. ex. Brandis; Family Rubiaceae) growing naturally in terai region at the foot hills of central Kumaon Himalaya to explain the fitting performance of some nonlinear asymptotic models to leaf data. Leaf area expansion was considered a function of time, $y=f(x)$. Growth curves in explaining leaf area dynamics provides insight on the following logical questions which are: length of lag phase, maximum growth rate, when it occurs, the time at which 50% of leaf area growth is completed and finally the upper limit (value) of leaf area growth. For model fitting performance four comparison criteria were used. Coefficient of Determination (R^2), Sum of Squared Error (SSE), Root Mean Square Error (RMSE) and Mean Relative Error (MRE). All the three models fitted well to leaf area data from two species. In both the data sets, Richard curve behaved much more like a logistic curve (δ close to 1), than Gompertz curve. Results indicated that nonlinear sigmoidal fitting is much reliable in explaining leaf growth variations over time as compared to other model forms.

Keywords: Sigmoidal growth curves, Richard family, Logistic model, Richard model, Gompertz model, nonlinear, asymptotic.

Introduction

In plant developmental biology and functional ecology, growth curves are used to model growth of individual plant or plant part over time. Growth characteristics (dependent variables) can be measured as increment in biomass, basal area, volume, diameter, height, leaf area etc. Growth curves can have various growth patterns. In nature plant species have to deal with limited environmental resources and high competition and thus there is always an upper limit of growth for them which proceeds sigmoidally and asymptotically. In the initial phase, growth is rather slow but accelerates afterwards and decreases in the final phase, approaching the upper asymptote (leveling off). This gives a typical sigmoidal pattern of growth whose growth rate is a bell-shaped curve¹. However, a cumulative growth pattern represents a characteristic S-shaped curve. All the equations used in the models denotes the cumulative distribution function. In statistical theory, both S, and bell-shaped growth curves represent a continuous probability distribution. The process of tree/organ growth can be described using this type of growth curves.

Leaf is the most sensitive organ, which reacts instinctively to environmental conditions and affects the growth and development of other organs as well² and so accurate prediction

of leaf area is necessary for precise forecasting of individual plant growth and its organs through dynamic simulation models. Leaf area production in trees is driven by duration of light interception, processing, energy transfer³, rate of biomass accumulation, transpiration and photosynthesis. Leaf area and leaf dry matter which is combined called as leaf size influences a variety of complex processes in plants. Therefore, variations in individual leaf size and its trade-off with total leaf number has important implications for understanding the adjustments made by plants to environmental changes⁴. Neighboring plants generally compete for limiting resources in order to grow and reproduce. Some resources example sun light or water could be monopolized by huge plants and this could lead to asymmetric competition where a plant which is twice as large, grows more than twice as fast. Thus, in order to cover the entire spectrum of different growth phases in plants under limiting conditions, sigmoidal growth curves are used.

Ample studies are available in which growth of population/organisms is described through S-shaped curves. Since the past few decades, there is a growing agreement among plant biologists that traditional approaches such as linear and exponential functions are not fit to describe plant growth. Moreover, in the current scenario gradual availability of large number of statistical software's have made quite easy for

researchers to implement nonlinear models⁵. Thus, working on such dynamic and flexible models are now within the reach of ecologists and plant biologists which was not there earlier. People in the scientific fraternity across the globe have now started fitting sigmoidal functions to almost everything from seed germination, plant growth, growth of mammal, fish, bird and to even bacteria and tumor growth and literature keeps on increasing. Moreover, complex mechanisms as plant-soil interaction; plant-host resistance; plant microbial/environmental interactions and plant defense management system can also be explored using these functions.

As these models have been applied in various fields in many different notions and parameterizations⁶ which makes it a bit difficult to choose the correct model for growth analysis when it comes to plant growth modelling. Hence, in order to fit a dynamic data to such models, it is extremely important that dependent and independent variables along with model parameters should be self-explanatory. Thus, it is necessary that before applying these models to experimental data, they should be reviewed and parameterized/ re-parameterized accordingly.

The flexible dynamics curve used to model leaf area increment over time in this case revealed the entire process of leaf area growth: i. How much time is needed to initiate the process of leaf area synthesis, i.e. how extended will be the lag time? Or at what time the leaf area growth will accelerate? ii. What will be the maximum growth rate (slope of inflection)? iii. when this will occur (time of inflection)? iv. At what time will 50% of leaf area will be synthesized?, v. What shall be the final leaf area growth value (i.e. upper asymptote value also called as carrying capacity).

Solver, which is an add-in function of Microsoft Excel was used for nonlinear curve fitting of leaf data. Several algorithms are used in nonlinear regression including the Marquardt-Levenberg, Nelder-Mead and Gauss-Newton methods⁷. Solver, which is designed on the powerful and reliable generalized reduced gradient (GRG) method, can be utilized as an easy iteration method to tackle nonlinear and asymptotic models. A detailed discussion about Solver function can be found in literature⁸. Like other algorithms it has similar properties which requires to put initial parameter values and use these values to get a better estimation of the parameters used in iterative process. In this context, the purpose of study was to present growth curves from the Richards family, with particular regard to those forms that are useful for modeling plant/organ growth. The proposed models are applied to study the dynamics of leaf growth in two tree species namely *Shorea robusta Gaertn. f. (Sal)* and *Adina cordifolia Hook. f. ex. Brandis (Haldu)* growing naturally in terai region of central Kumaon Himalaya.

Material and methods

Site details and climatic conditions: The study was conducted in Lalkuan forest (29° 04 N, 079° 30 E and 230.2m amsl) which comes under Nainital Forest Division. The area falls under terai

region which is at the foothills of central Kumaon Himalaya. Soil is alluvial which is highly fertile in nature. The region is extremely moist and thickly forested.

Terai region is water logged alluvial plain with gentle south-east slope, deep and fertile moist loamy soil which is free from boulders and gravels⁹. Area has a mixed vegetation and is dominated by *Sal* and other associated species including *Haldu*. The region is full of floral diversity and represents tropical and sub-tropical forest type.

Mean maximum temperature is 22.5°C (January) and 45.3°C (June) and mean minimum temperature is 9.5°C (January) and 33°C (June) respectively. Average rainfall in winter is 32-33.1 mm, average rainfall in summer is 84.6-87.0mm and average annual rainfall during warm-rainy season is 477.2-527.8mm. Site enjoys typical monsoon climate with rich humidity during July to mid September. Nearly 70% of the annual rainfall is monsoonal during July-September.

Experimental Design: Important leaf transition phases (leaf bud burst/leaf flush, leaf area expansion and leaf maturation) were captured using 12 data points. To observe leaf phenology six (6) average sized matured trees (CBH > 97.77cm) were selected within 666.7m² circular permanent plot of radius 14.56m¹⁰. Leaf area measurement was undertaken after interval of seven (7) days each. Total Six (6) random trees of *Shorea robusta* and *Adina cordifolia* were permanently marked in Lalkuan forest (3 from each specie; n=3) and tagged them as *SR₁*, *SR₂*, *SR₃*, *AC₁*, *AC₂*, *AC₃*. Sample of three trees each were taken to generate the mean leaf area data (Table-1). Twenty (20) vegetative shoot buds per tree were marked in spring season. For *Shorea robusta*, tagging of shoot buds was completed in the month of February, 2020 leaf bud initiation started from mid of March and leaf area measurement began from April 08 and ended in June 24, 2020 (12 data points). For *Adina cordifolia*, shoot bud tagging was completed by mid-April, leaf flush initiated by May/June and leaf area measurement commenced from July 01 and ended in September 27, 2020. On an average, single marked bud gave rise to approximately 10-20 shoots and per shoot about 15-25 leaves. Mean leaves were calculated as total number of leaves over total number of shoots. Leaves from each of the trees were collected randomly on each of the sampling date (at weekly intervals from bud break to full leaf expansion) from the marked twigs. All collected leaves from individual species were sketched on graph paper to measure the leaf area.

Nonlinear asymptotic growth models: Eventually, all three asymptotic nonlinear models were tested and compared to predict the fitted-y. For model comparison, four criteria were used namely: Coefficient of Determination (R²), Sum of Squared Error (SSE) which accounted for the unexplained variations in the model Root Mean Square Error (RMSE) and Mean Relative Error (MRE). All statistical analysis was done in Microsoft Excel, 2019. Nonlinear curve fitting was performed in “Solver” which is an inbuilt add-in function in Excel, 2019

itself. Solver assists in fitting nonlinear regression functions via an iterative algorithm¹¹ which minimizes the sum of squared error (SSE) between experimental and predicted data. Thus, model obtains maximum likelihood when the SSE is minimized. Hundred (100) iterations each were performed for every model with maximum time of hundred (100) seconds at 0.000001 precision level.

Following mathematical functions were used to describe leaf growth:

$$\text{Logistic Model}^{12}: Y(t) = \frac{\alpha}{[1 + \exp\{-k(t - T_i)\}]}$$

Re- parameterisation¹³ to calculate lag phase (Tλ)

$$Y(t) = \frac{\alpha}{[1 + \exp\{-k(t - T\lambda) + 2\}]}$$

$$\text{Richard Model}^{14}: Y(t) = \frac{\alpha}{[1 + \delta \exp\{-k(t - T_i)\}]^{\frac{1}{\delta}}}$$

Re- parameterisation¹³ to calculate lag phase (Tλ)

$$Y(t) = \frac{\alpha}{[1 + \delta \exp(1 + \delta) \exp\{-k(t - T\lambda)\}]^{\frac{1}{\delta}}}$$

$$\text{Gompertz Model}^{15}: Y(t) = \alpha \exp[-\exp\{-k(t - T_i)\}]$$

Re- parameterisation¹³ to calculate lag phase (Tλ)

$$Y(t) = \alpha \exp[-\exp\{-k(t - T\lambda) + 1\}]$$

***Abbreviations:** Y(t)= expected cumulative leaf area growth at time “t”; α= upper asymptote (theoretical maximum for Y(t)); k= growth rate coefficient which is a shape parameter; T_i= time at an inflection i.e. time at which maximum growth rate is achieved; Tλ = lag time.

$$\text{Model validation: } R^2 = 1 - \left(\frac{SSE}{SST}\right)$$

$$SSE = \sum (\hat{Y} - Y)^2$$

$$SST = \sum (Y - Y_i)^2$$

$$RMSE = \sqrt{\left(\frac{SSE}{n}\right)}$$

$$MRE = \left(\frac{1}{n}\right) * \frac{\sum (Y - \hat{Y})}{Y_{\max} - Y_{\min}}$$

***Abbreviations:** R²= Coefficient of Determination; SSE = Sum of Squared Error; SST= Sum Squared Total; \hat{Y} = predicted/ fitted Y value; Y= experimental/observed values; Y_i= observed mean; n= number of observations or data points; Y_{max}= maximum experimental value; Y_{min}= minimum experimental value; RMSE = Root Mean Square Error; MRE= Mean Relative Error.

RGR_{max} (η_i) and AGR_{max} (μ_i) for logistic model was calculated as: η_i = $\frac{k}{4}$; μ_i = $\frac{\alpha k 16}{4}$, for Richard model, η_i = $\frac{k}{1 + \delta}$; μ_i = $\frac{k \alpha}{(1 + \delta)^{1 + \frac{1}{\delta}}}$, and for Gompertz model, η_i = $\frac{k}{e}$; μ_i = $\frac{\alpha k 16}{e}$ respectively.

Asymptotic standard error needed to be calculated for model validation for which more complex and time-consuming computer programs were required¹⁷. To avoid this, an alternative approach was adopted in this investigation where the standard error of the data around the prediction curve was calculated by dividing sum of squared error (SSE) by degree of freedom (DOF) to get the variance of experimental data (Y). The square root of variance gave the standard error of the Y (Residuals) which was further used to calculate the Confidence Intervals (CI).

The CI is a sign of probability that the true experimental data lie within the range specified by the probability formula¹⁸. It commonly uses 95% CI, which means that there is a 95% probability that the experimental value lies within the interval. Lower CI values indicate high precision or accuracy level of data. In order to calculate CI, the *critical-t* value was calculated which depended upon probability and its associated DOF¹⁹.

Microsoft Excel, 2019 has a built-in function (TINV) which allowed calculations of the critical t-value, thus bypassing the need to look up t-value tables. Once the critical t-value was obtained, it was multiplied by standard error of the residuals to get the CI. The lower the CI, the better the model accuracy. DOF for each model was calculated as number of data points (Y) minus number of parameters in function.

Results and discussion

Leaf area prediction using three nonlinear mathematical models has been described for *Sal* and *Haldu* trees growing naturally in Lalkuan Forest in Uttarakhand. Measured leaf area is shown in Table-1. Leaf area ranged from 170.868cm² in *Shorearobusta* to 221.032cm² in *Adina cordifolia* at the final harvest. Growth pattern of leaf area resembled an S-shaped curve. Parameters for every model of leaf growth has been depicted in Table-2.

The R², SSE, RMSE and MRE were evaluated for every model and all models reasonably fit the leaf area data for two species. Confidence Intervals (CI) were also calculated for each model which further assisted in model validation. In *Shorearobusta*, the best fit model based on comparison criteria was Logistic>Richard>Gompertz while in *Adina cordifolia* it was Gompertz>Logistic>Richard. In *Adina cordifolia* data, the Mean Relative Error (MRE) displayed a negative value which was ignored (minus sign was ignored). This happens, when the fitted or predicted values is greater than the experimental or actual values.

Initial investigations revealed that maximum leaf area in *Shorearobusta* was formed between 6th and 7th harvest (53.134 cm²) and in *Adina cordifolia* was synthesized between 4th and 5th harvest (64.244cm²). Analyzing the model parameters for both data sets it can be said that in *Shorearobusta* lag time (Tλ) for Logistic and Richard’ function was nearly mid of 3rd harvest and for Gompertz function it is approximately third harvest which means that the growth rate was slow till Tλ and after that it accelerated, reached its maximum value at Ti, afterwards the growth rate gradually decreased and reached nearly zero when experimental y value reached upper asymptote, α (Table-2). This gives a perfectly bell-shaped growth rate curve. *Adina cordifolia* leaf area data suggested that lag time for Logistic function and Richard’s function is nearly 2nd harvest while for Gompertz function it is 1st harvest. Time at inflection (Ti) i.e. time at which growth rate reaches its maximum value also varied between tree species and models as well. Growth rate in Gompertz curve peaked earlier (α/e) than logistic and Richard curve. Richard curve in both the data sets behaved much like a logistic curve (δ=1) than Gompertz curve. For *Shorearobusta* data, Confidence Interval (CI) of Logistic, Richard and Gompertz curve came out to be 18.527, 20.032 and 21.328 respectively while for that of *Adina cordifolia* the values were calculated as 36.874, 39.869 and 31.996 respectively.

Comparison: Comparing the three growth functions are fellows
Logistic function: Here, time at which the leaf area growth reached maximum rate of Ti was provided directly in the function. Model described that Ti is a location parameter which horizontally shifted the growth curve without changing its shape. The logistic function relates with a cumulative normal distribution which is symmetrical about the point of inflection (Ti) whose coordinates are (Ti, α/2) which means that Ti indicated the time at which 50% of leaf area was synthesized. Model showed that growth rate coefficient is always a positive value and larger value suggested a speedy rise from zero to upper asymptote (α). A new parameterization was used in the logistic model in which the inflection time (Ti) was replaced by lag-time (Tλ) to understand the leaf-are a dynamics at an early stage of growth. Lag time described low period of leaf growth (lag period) after which growth rate considerably increased. The lag time for leaf growth occurred for t=Tλ, when, $Y(t) = \frac{\alpha}{1+e^2}$ i.e. it always felled at 11.92% of the upper asymptote.

Richard function: Also known as generalized logistic curve and was used to deal with asymmetric growth. Here, an additional parameter (δ) was introduced to the logistic function which managed which asymptote was nearest to the inflection point (Ti). When testing leaf growth patterns δ always had a positive value. In the Richard model, Ti was floating and could be given as a proportion of upper asymptote (α). Parameter δ determined this proportion which felled at $\frac{\alpha}{(1+\delta)^{\delta}}$. The

parameter δ had following interpretations. If δ<1, less than half of leaf area would be synthesized before Ti (as in Gompertz

curve); if δ=1, half of leaf area would be synthesized before Ti and half afterwards (as in logistic curve); but when δ>1, more than half of leaf area would be synthesized before Ti. Also, α/2

$$\text{leaf area would be synthesized until time: } t = k Ti - \frac{\log\left[\frac{2^{\delta}-1}{\delta}\right]}{k}$$

In both the data sets, Richard’s curve behaved much more like a logistic curve (δ=1), than Gompertz curve.

Table-1: Leaf variations of two species (n = 3) evaluated with different time (cm²) ±SE.

Time	Mean Leaf Area SR	Mean Leaf Area AC
1	7.083 ±0.891	9.351 ± 1.036
2	10.167 ±1.733	21.502 ± 1.090
3	19.070 ± 1.513	45.083 ± 2.100
4	36.918 ± 2.632	51.006 ± 1.650
5	41.163 ± 3.583	115.250 ± 1.750
6	46.035 ± 2.428	137.667 ± 2.963
7	99.169 ± 3.182	141.252 ± 1.650
8	105.150 ± 2.902	150.083 ± 2.598
9	136.819 ± 1.938	166.013 ± 2.126
10	150.765 ± 4.051	172.917 ± 1.977
11	157.883.25 ± 2.732	201.252 ± 2.115
12	170.868 ± 3.848	221.032 ± 4.504

Gompertz function: Gompertz curve was initially used to predict mortality of human population but the function that was used was a probability distribution function. Much later, the famous cumulative form of this model was used²⁰. Here also, the meaning of different parameters is same as in other models but it is a double exponential function. Curve shape is changed by curve parameters (k and α) but did not alter the value of location parameter (Ti). The parameter Ti controlled the time at which the inflection occurred. Gompertz curve is also asymmetrical about the point of inflection having coordinates (Ti, α/e), which meant that by the time Ti, approximately 36.8% of leaf area would be synthesized while α/2 synthesis will take place until time t= Ti-log (log (2))/k.

Moreover, lag phase parameterization was also done for Gompertz model where Ti was replaced by Tλ. Here, Tλ felled when y(t)= α * EXP(-e) i.e. a lag time always occurred at 6.6% of the upper asymptote, α.

Models	Tree species	α	δ	k	Ti	T λ	η_i	μ_i
Logistic	<i>S. robusta</i>	183.265	NA	0.535	7.221	3.482	0.134	24.508
	<i>A. cordifolia</i>	205.521	NA	0.528	5.377	1.591	0.132	27.144
Richard	<i>S. robusta</i>	177.691	0.969	0.536	7.287	3.324	0.272	24.029
	<i>A. cordifolia</i>	209.436	1.019	0.528	5.340	2.187	0.262	27.505
Gompertz	<i>S. robusta</i>	226.080	NA	0.257	6.811	2.923	0.95	21.468
	<i>A. cordifolia</i>	225.080	NA	0.315	4.517	1.339	0.116	26.060

Table-3: Model validation.

Models	Tree species	R ²	SSE	RMSE	MRE
Logistic	<i>S. robusta</i>	0.99	603.710	7.0929	0.00167
	<i>A. cordifolia</i>	0.96	2391.367	14.1167	0.00478
Richard	<i>S. robusta</i>	0.99	603.710	7.0929	0.00167
	<i>A. cordifolia</i>	0.96	2391.367	14.1167	0.00476
Gompertz	<i>S. robusta</i>	0.98	799.988	8.1649	0.00407
	<i>A. cordifolia</i>	0.97	1800.451	12.2490	0.00150

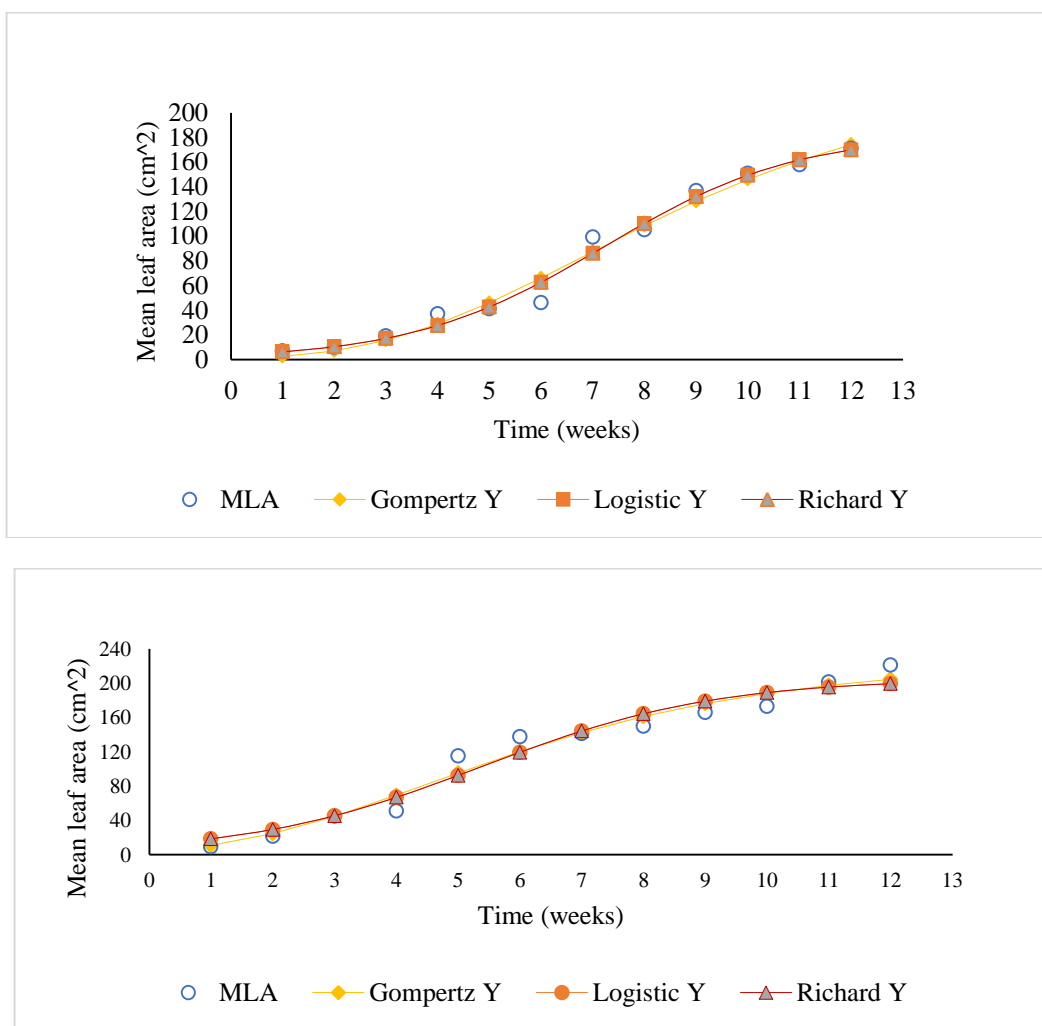


Figure-1: Fitted growth curves from the Richard’s family to experimental data describing the dynamics of cumulative leaf area growth of *Shorearobusta* and *Adina cordifolia*.

The nonlinear modelling of growth process has not only advantages in mathematically explaining growth but it also acts as an effective tool in estimating the relationship among plant organs as well. Furthermore, nonlinear estimation techniques may contribute to determination of the economic information in plant growth mechanisms.

Leaf area is an important plant characteristic which plays a significant role in performing plant photosynthesis. Leaf area growth also assists in understanding complex mechanisms of biomass synthesis and its allocation to different plant parts. Such holistic studies give insight on the adaptability patterns and performance of plants in different environmental conditions.

Therefore, accurate measurement of leaf area is essential to analyze the interaction between tree/organ growth and environment.

Logistic, Richard and Gompertz models have successfully proved their robustness by effectively describing a wide range

of combinations of individual plant groups or plant parts with their respective environments. Different tree species varies in maturity, environmental adaptations and growth vigor.

Environment includes availability of water, sunlight, soil nutrients and other growing conditions. Mathematical models to describe leaf area growth are an important components of computer simulation growth modelling. In both tree species, the S- shape curve followed a different pattern. This occurred due to difference in the phenotypes of the two trees in question and their different levels of adaptability.

To evaluate any growth data, care should be taken to select a suitable growth curve whose parameters should be able to be interpreted biologically²¹.

To conclude, all these proposed models were found to be suitable for describing leaf area data in both species and sigmoid curves should be given priority over other model forms to investigate growth and development in plants over time.

Table-4(a): Comparison of statistical parameters of models before solver calculation.

Models	Species	SSE	df	SE of Y	R ²	Critical-t	CI
Logistic	SR	2980.381	9	18.198	0.93	2.26216	41.166
	AC	2875.452	9	17.874	0.95	2.26216	40.435
Richard	SR	2980.381	8	19.301	0.93	2.09302	40.398
	AC	2875.452	8	18.959	0.95	2.30600	43.719
Gompertz	SR	1734.399	9	13.882	0.96	2.16037	29.990
	AC	13233.221	9	38.345	0.76	2.26216	86.743

Table-4(b): Comparison of statistical parameters after solver calculation.

Models	Species	SSE	df	SE of Y	R ²	Critical-t	CI
Logistic	SR	603.710	9	8.190	0.99	2.26216	18.527
	AC	2391.367	9	16.301	0.96	2.126216	36.874
Richard	SR	603.710	8	8.687	0.99	2.30600	20.032
	AC	2391.367	8	17.289	0.96	2.30600	39.869
Gompertz	SR	799.988	9	9.428	0.98	2.26160	21.328
	AC	1800.451	9	14.144	0.97	2.26216	31.996

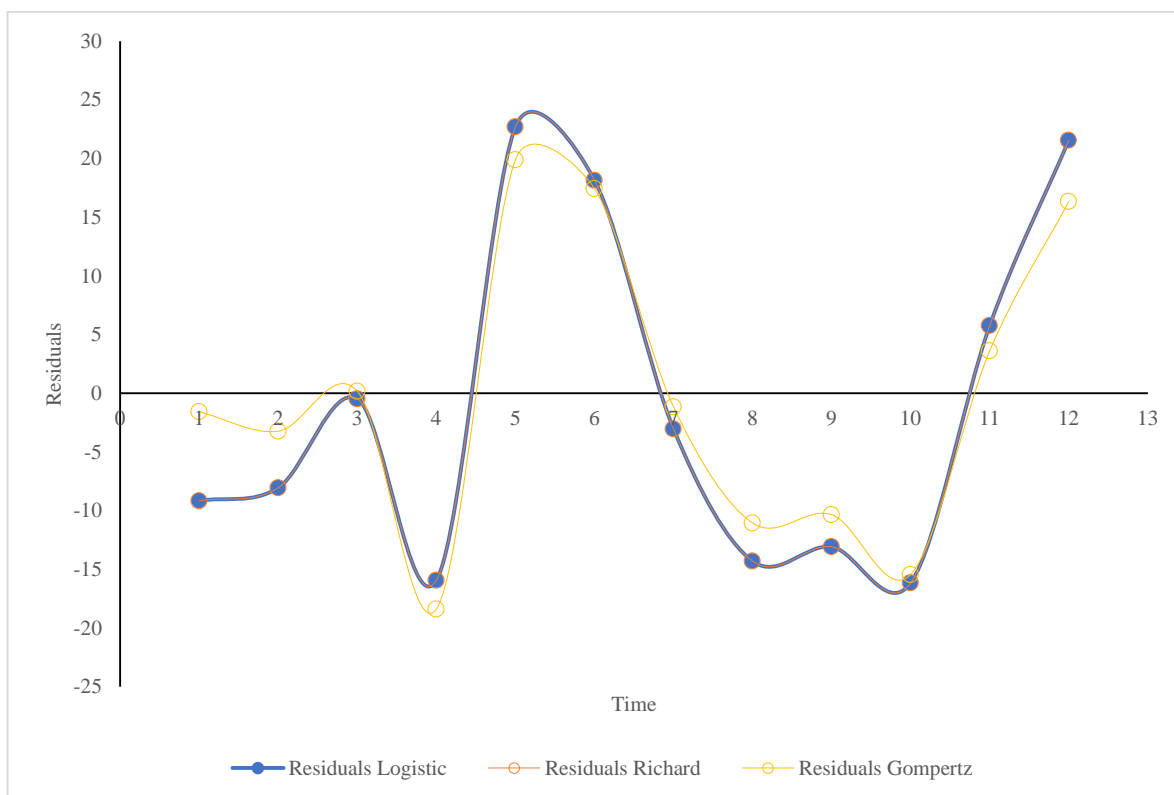
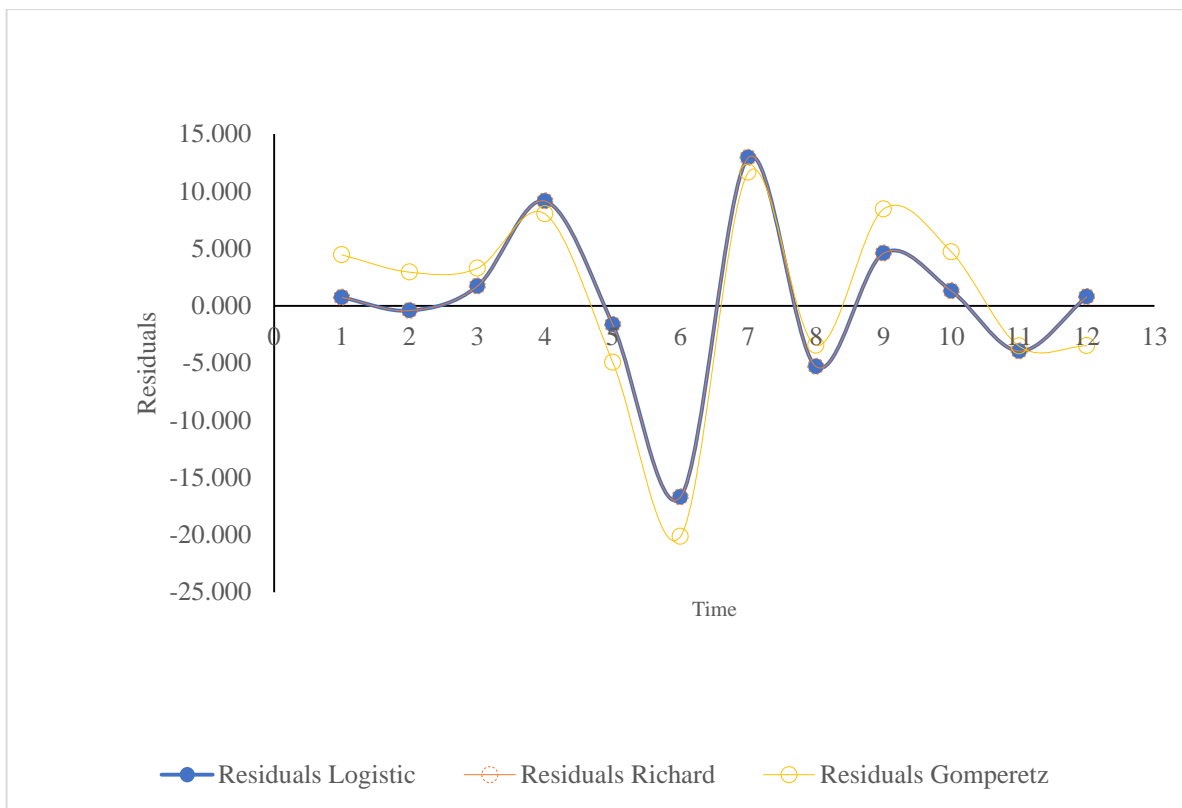


Figure-2: Residuals Vs Time, Logistic, Richard and Gompertz Models for two species.

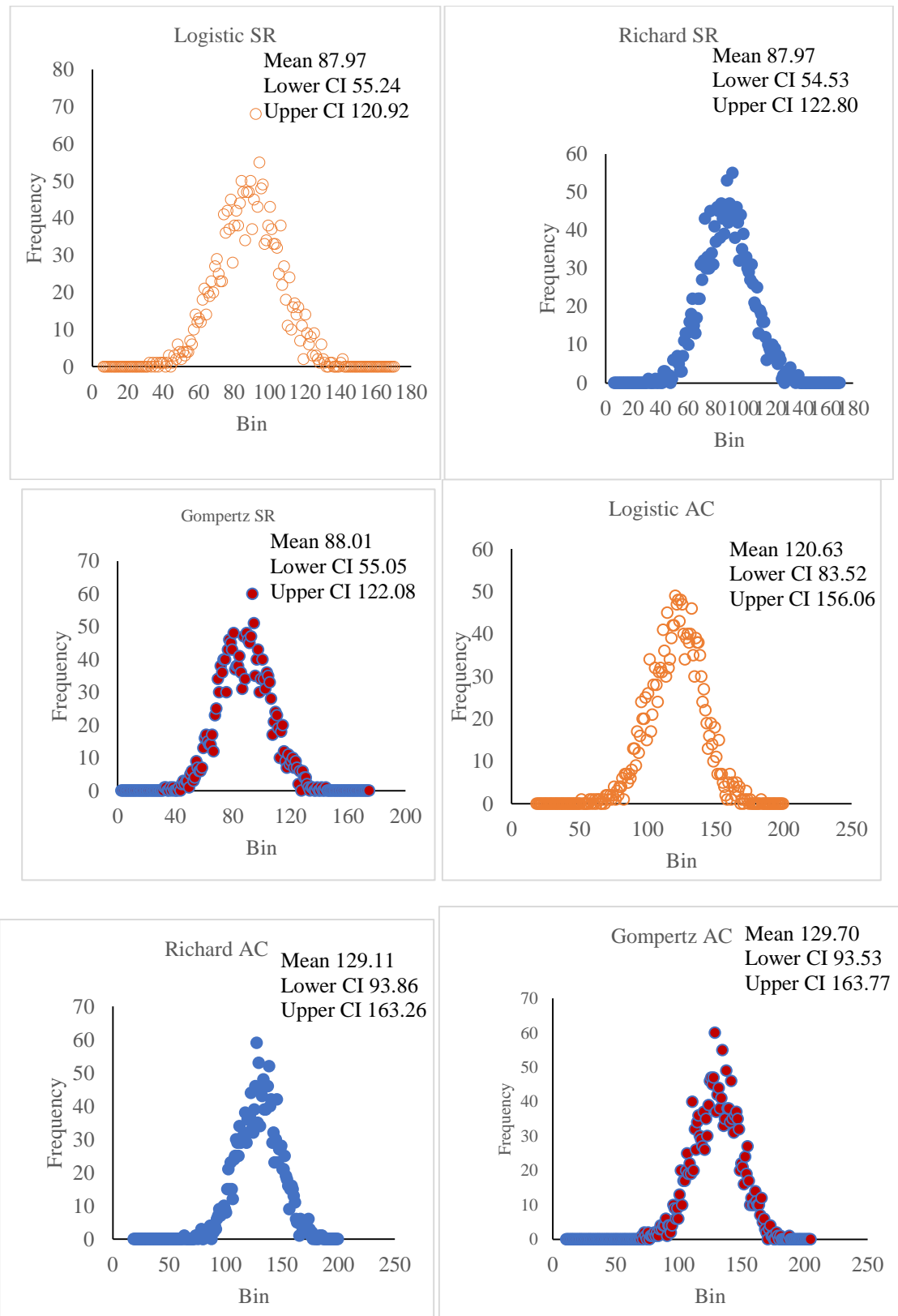


Figure-3: Resampling and frequency distribution of the leaf area data using Bootstrap simulation method with 2000 iterations at $\alpha=0.05$. The curve is a theoretical normal distribution.

Conclusion

To conclude, sigmoidal curves from Richard's family are unique in explaining the growth patterns of trees/organs in different ecological environments. Moreover, deep insight is also provided by such models about the functional adjustments made by plants in order to adapt a wide range of biotic and abiotic stresses. Eventually, all this vital information helps in enhancing the plant performance and conserving species in nature. Thus, it can be clearly stated that nonlinear asymptotic mathematical functions definitely hold an upper edge over linear and exponential functions to investigate plant growth, adaptation and survival.

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