

Modelling Height-Age Curves in Fast-Growing Deciduous Tree Species from Terai Region of Kumaun Foothills

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ABSTRACT

Modelling tree and stand growth is one of the most significant aspects of forest science and simulation modelling. Such analysis helps in understanding forest dynamics in terms of growth and yield, survival and mortality patterns, biomass partitioning and carbon sequestration capacity of forest stands. In this study, a 3-parametric Chapman-Richards function was applied to evaluate cumulative, absolute and relative height growth curves in three fast growing tree species from Fabaceae family viz. *Dalbergia sissoo*, *Delonix regia* and *Acacia catechu*. Relative growth rates (RGRs) were calculated both as a function of “age” and “size” i.e., time and size dependent RGR. Cumulative, absolute and relative growth rate functions fitted quite well to all three species. Upper asymptotic values for total tree height were found to be maximum in *D. sissoo* (5.61 m), followed by *A. catechu* (4.97 m) and *D. regia* (3.34 m). Size-standardized RGR analysis showed that due to low rate of decline, *D. sissoo* had a superior RGR throughout most of its height development, despite its initial RGR being much less than those of other two species. Residual analysis of the cumulative datasets displayed absence of outliers, and the data were found to be normally distributed. Model parameters for all three species were statistically significant ($P < 0.005$). The study thus investigates function-derived growth rates in plant growth modelling.

Keywords : Absolute growth, adaptive ecology, cumulative growth, relative growth, size-dependent RGR

INTRODUCTION

Growth is a complex phenomenon, and nonlinear-asymptotic mathematical models help in explaining the biological process underlying individual tree- and stand-level growth. In plant growth modelling, it is often required to quantify dynamics of growth, validating

daily growth rates to get integrated and describe expected ultimate growth at the end of growing cycle (Read *et al.*, 2002). A simple function is, therefore, recommended to model and characterize the duration and upper limit of growth process. Within the life cycle of a plant or an organ, cumulative growth can



be separated into three sub-phases: an early accelerating or exponential phase, a middle linear phase and a saturation phase for ripening (Goudriaan & van Laar, 1994). Therefore, the growth pattern typically follows a sigmoid curve whose absolute growth rate is a bell-shaped curve. However, RGR curve is negative exponential or reverse sigmoidal in nature as RGR decreases with increasing age and plant-size. Ample studies are available in which growth of an individual organism/organ or population is described through S-shaped curves. People in the scientific fraternity across the globe have successfully fitted sigmoidal functions to model a wide range of biological processes, from seed germination (Tipton, 1984; Ukalska & Jastrzebowski, 2019) and tree growth (Podor *et al.*, 2014) to the growth of mammals (Zullinger *et al.*, 1984), fish (Hopkins, 1992), birds, even bacteria (Zwietering *et al.*, 1990) and tumor (Sohrabi-Haghighat & Deris, 2020). The literature on these applications continues to grow. All these models define sigmoid curves in which the rate of growth initially increases as size increases from low values, reaches a maximum at a point of inflection, and then gradually decreases towards zero at an upper asymptote, so that they look like the central part of a rotated S (Ratkowsky, 1983).

The model parameters in growth equations have distinct biological meaning. There is an upper asymptote,

a scale parameter, a shape parameter and inflection point which moves up and down along with curve shape and eventually a time constant. Upper asymptote describes the maximum stable value of the response variable and scale parameter determines the scale or statistical dispersion of the probability distribution. The shape or rate parameter determines the rate at which growth initially accelerates and influences the overall curve's shape. The time constant determines the time at which the function has a specific value between its minimum and maximum, or when growth rate is maximum (Pienaar & Turnbull, 1973).

Relative growth rate can be explained as the rate of accumulation of new dry mass per unit of existing dry mass and resembles plant competitiveness (Kishore *et al.*, 2021). It is considered as a central parameter determining a species growth strategy (Grim & Hunt, 1975) and is viewed as an expression of plant vigor. It can further be interpreted as a measure of efficiency of plant material to produce new material (Hunt, 1978) and is an indirect measurement of the rate of resource allocation by plants. Classical methods measured log transformed values of biomass at two successive time intervals (harvests) to get RGR values (Hoffmann & Poorter, 2002).

Recent advances in plant growth modelling apply nonlinear growth models to evaluate and compare growth



rates among plant species. Calculating function-derived growth rates has the attractive property of capturing both age and size dependent growth (Lamont *et al.*, 2023) and is therefore much more suitable than traditional approaches. In this connection, applications of relative growth rate functions include the study of primary characteristics of plants viz. leaf area, basal area, biomass, volume, tree height and diameter at breast height (DBH). Thus, function-derived relative growth rates have become a new tool to investigate competitive adaptiveness of the species in different habitat, soil and environmental conditions (Pommerening & Muszta, 2015; Pommerening & Muszta, 2016).

As RGR is closely related to plant mortality (Gillner *et al.*, 2013) i.e., low relative growth rates for extended periods of time are good indicators of imminent death, hence RGR concept could be applied to investigate survival and mortality trends in different species as well. RGRs are also pre-requisites for quantifying and modelling allometric relationships in plants (Gayon, 2000). Moreover, calculating RGR by applying function-derived growth rates is useful as conventional calculations confound RGR with initial size and fail to capture the temporal dynamics of growth (Rees *et al.*, 2010). In addition, close links between nutrient uptake rates and relative growth rates have also been established (Ingestad, 1982). This study investigates cumulative, absolute and relative growth functions

applied to height vs age data of three fast growing species belonging to the Fabaceae family to evaluate their growth performance and adaptive nature.

MATERIAL AND METHODS

Study site and climatic conditions

The three species viz. *Dalbergia sissoo*, *Delonix regia* and *Acacia catechu*. were raised in experimental nurseries of Uttarakhand Forest Research Institute located at Haldwani (30.3438°N, 77.9996°E) and Lalkuan (29.0676°N, 79.5182°E). The age-height data for three species are provided in Table 1. The soils of the two nurseries were analyzed for various physio-chemical properties as depicted in Table 2. The first two species were raised in Haldwani nursery, and the last one was raised in Lalkuan nursery. These two nurseries were located quite close to each other. The Terai region of Kumaun Himalayas (where the two nurseries are located) enjoys a typical monsoon climate with rich humidity from July to mid-September. Nearly 70% of the annual rainfall is during monsoon (July to September). Mean maximum temperature is 45.3°C (June) and mean minimum temperature is 9.5°C (January). The annual average quantum input (irradiance) is approx. 27.81 mol-2 day-1. The Terai region, a part of central Kumaun Himalaya, is a water-logged alluvial plain with southeast slope. It has deep and fertile loamy



Table 1: Summary statistics of age versus height for three species (mean \pm standard error)

Age (years)	Total height (m)		
	<i>D. sissoo</i>	<i>D. regia</i>	<i>A. catechu</i>
1	0.3 \pm 0.13	0.1 \pm 0.09	0.2 \pm 0.14
2	0.9 \pm 0.17	0.3 \pm 0.13	0.6 \pm 0.23
3	1.5 \pm 0.15	0.7 \pm 0.34	1.3 \pm 0.17
4	2.1 \pm 0.21	1.2 \pm 0.23	1.9 \pm 0.28
5	2.7 \pm 0.19	1.6 \pm 0.37	2.5 \pm 0.39
6	3.1 \pm 0.14	2 \pm 0.21	3 \pm 0.48
7	3.5 \pm 0.23	2.3 \pm 0.15	3.4 \pm 0.37
8	3.9 \pm 0.11	2.5 \pm 0.26	3.8 \pm 0.41
9	4.2 \pm 0.17	2.7 \pm 0.31	4 \pm 0.34
10	4.4 \pm 0.26	2.9 \pm 0.27	4.3 \pm 0.27
11	4.6 \pm 0.16	3 \pm 0.35	4.4 \pm 0.35
12	5.1 \pm 0.29	3.2 \pm 0.18	4.6 \pm 0.43

soil that forms marshy land, free from gravels and boulders. Due to its alluvial plain, the region is quite fertile and dominated by tropical and subtropical vegetation including: *Shorea robusta*, *Adina cordifolia*, *Dalbergia sissoo*, *Acacia catechu* and *Albizia lebbeck*.

Experimental design

The species were planted in 2011, and the total tree height data were collected at one year interval till 2023. The experiment was laid out in Randomized Complete Block Design (RCBD) with three replications. Trees were planted at a spacing of 2 m x 2 m and examined for 12 consecutive years. For developing height- age curves, total height (m) of the trees were measured using marked poles.

Model function used and biological interpretation of model parameters

A 3-parametric Chapman-Richards function (Richards, 1959) was applied to model age-height relationships for three fast growing species. The function is quite flexible and accurate and can be explained as a generalization of Bertalanffy's growth function for animal growth. The function is often used to model individual trees and stands. In a cumulative growth function, model parameters a , b and $c > 0$, " a " is the tree height (H) final value (upper asymptotic value), " b " is related to growth rate and " c " denotes absolute curve shape and inflection point. Details of growth function are provided in Table 3.



Table 2: Soil physio-chemical characteristics at two experimental sites (0-15 cm depth) (mean ± standard error)

Parameters	Nursery 1 (Haldwani)	Nursery 2 (Lalkuan)
Sand (%)	43.06 ± 0.57	38.08 ± 1.17
Silt (%)	28.57 ± 0.51	20.95 ± 1.89
Clay (%)	34.98 ± 0.69	39.37 ± 0.82
Bulk Density (g/cm ³)	1.37 ± 0.05	1.39 ± 0.02
Porosity (%)	49.27 ± 0.77	45.97 ± 0.45
Moisture (%)	5.55 ± 0.08	12.95 ± 0.09
Water Holding Capacity (%)	61.82 ± 0.75	55.47 ± 0.59
Temperature (°C)	22.25 ± 0.02	21.21 ± 0.01
pH	7.2 ± 0.00	7.1 ± 0.00
C (%)	0.91 ± 0.07	0.97 ± 0.05
N (%)	0.25 ± 0.01	0.31 ± 0.03
P (%)	0.013 ± 0.02	0.019 ± 0.01
Soil Organic Matter	1.57 ± 0.01	1.78 ± 0.07

Modelling height growth

Tree height was selected as a primary plant characteristic for growth modelling. The next step was to regress the tree height values with tree-age using a cumulative function (Figure 1a). Further, AGR (the measurement of total growth per unit time) was calculated with the help of model parameters from fitted cumulative data, applying an AGR-function (Figure

1b). Then, RGR was calculated from AGR by dividing AGR with observed tree heights. These observed RGR values were eventually compared with estimated RGR values by using a relative growth function. The estimated RGR values were expressed both as a function of time (time-dependent RGR) (Figure 1c) and predicted heights (size-dependent RGR) (Figure 1d) applying an RGR function.

Table 3: Functions of cumulative, absolute and relative growth rates. *a*, *b* and *c* are model parameters, *H* is the total tree height, “*t*” denotes “tree age” and *e* is exponential

Function Name	Chapman- Richards
Growth Function	$H = a(1 - e^{-bt})^c$
Absolute Growth Rate	$abce^{-bt}(1 - e^{-bt})^{c-1}$
Relative Growth Rate	$bc(1 - e^{-bt})^{-1}$
Source	Richards, (1959)



Model fitting and evaluation

Nonlinear model fitting was performed with Excel Solver which is an add-in function in Microsoft Excel, 2021. Excel solver has emerged as an important statistical tool for convenient nonlinear model fitting of such equations to observations. It is an add-in function in Microsoft Excel and was used for nonlinear model fitting of the tree height-age data. It is designed on the powerful and reliable generalized reduced gradient (GRG) method and can be utilized as an easy iteration method to tackle nonlinear and asymptotic models. It operates by fitting nonlinear regression models via an iterative algorithm (Bowen & Jerman, 1995) which minimizes the sum of squared error (SSE) between observed and predicted datasets. Thus, the model obtained maximum likelihood when SSE is minimized. More details of solver function can be accessed through literature (Smith & Lasdon, 1992). Like other algorithms it has similar properties which require initial parameter values and use these values to get a better estimate of the parameters used in the iteration process. For data fitting, the number of iterations was set at one thousand (1000) with a precision of 0.000001. The convergence criterion for accepting the values of parameter estimates was taken as 0.001. Adjusted coefficient of determination (R^2 adj.) (Lebedev & Kuzmichev, 2020), residual standard error (RSE) (Chenge, 2021) and Bayesian information criterion (BIC) (Schwarz, 1978) were used for model evaluation. Models with maximum R^2 adj. and minimum RSE and BIC values were considered to perform the best.

Statistical significance and cross validation of model parameters

Statistical significance (cross validation) of model parameters was determined through Jack- Knife resampling technique (Harris, 1998). Model parameters were statistically tested to estimate uncertainties in their behaviour (Table 4). Jack- Knife technique is basically a resampling method which involved a leave-one-out strategy of the estimation of parameters in a dataset of “N” observations. To elaborate, if there are a total of “N” numbers in a dataset, the predictor is trained on N-1 training examples and tested on remaining one data point, i.e., leave-one-out cross validation technique was implemented. Then, process was repeated “N” times and eventually predicted values of each sample was calculated.

Residual analysis

The Shapiro-Wilk test was conducted to check for residual normality. In addition, residual (Figure 2) and Q-Q plots (Figure 3) were also established for all three species to test for residual symmetry. Statistical analysis was all implemented in Microsoft Excel 2021 using Real Statistics Resource Pack.

RESULTS AND DISCUSSION

Table 1 demonstrates the summary statistics of tree height versus age for *Dalbergia sissoo*, *Delonix regia* and *Acacia catechu*, all fast-growing deciduous species belonging to family Fabaceae. Chapman-Richard’s model



was applied to evaluate height-growth rates (cumulative, absolute and relative) of three species in question (Figure 1). Results confirmed strong correlations between tree age and total tree height ($R^2_{adj.}$ ranging from 0.99996-0.99997) in all three species. $R^2_{adj.}$ is a direct measurement of strength of association between two variables. The higher the $R^2_{adj.}$ value, the stronger the association. Upper asymptotic values for total tree height were found to be maximum in *D. sissoo* (5.61 m), which was followed by *A. catechu* (4.97 m) and *D. regia* (3.34 m). Tree height displayed extremely good-fit ($R^2_{adj.} \geq 0.99996$) when regressed with tree age. This meant that tree age explained $\geq 99.996\%$ of the variation in tree height growth. To test the normality of residual, Shapiro-Wilk test was used. The p-value was found to be greater than 0.05 ($p > 0.05$) for all species indicating that residuals do not violate the assumption of normal random error. Moreover, residual (Figure 2) and Q-Q plots (Figure 3) also suggested normal distribution. Residual analysis of the cumulative datasets displayed no outliers, and the residuals were found to be normally distributed. Model parameters were statically significant ($p < 0.05$).

Results demonstrated that, AGR peak for *D. sissoo* and *A. catechu* exceeded that of *D. regia* and was 17.3% and 21.1% more in magnitude than *D. regia* (Figure 1b). When compared in the 2nd year of tree growth, *A. catechu* had a greater AGR than that of *D. sissoo*,

but by the 12th year, *D. sissoo*'s AGR was significantly greater than that of *A. catechu*.

Time-dependent RGR suggested that RGR for all three species declined throughout growth and appeared to have quite similar growth pattern (Figure 1c), which is often the case with trees of the same functional group and growing under similar environmental conditions. In the middle of growth, time-dependent data depicted that *D. regia* had a 4.5% greater RGR than *D. sissoo* and 2.7% greater RGR than *A. catechu* (Figure 1c). The curves almost formed parallel lines in the order, *D. regia* > *A. catechu* > *D. sissoo*, i.e., *D. regia* had the highest RGR throughout its lifetime and *D. sissoo* had the lowest (Figure 1c). Analysing RGR on size basis corrects for variation in the initial size so that species can be compared at a common size. The replacement of "age" with a "primary growth characteristic" of a plant (tree heights in this case) allowed depicting size- standardized RGR. In this case, size-dependent RGR gives a completely different picture altogether and *D. sissoo* exhibited a growth pattern different from that of *D. regia* and *A. catechu*. *D. sissoo* growth starts with a comparatively low rate but finishes with a rate markedly higher than those of other species (Figure 1d). Thus, height-standardization data suggested that *D. sissoo* had a significantly greater RGR than *D. regia* and *A. catechu* do. Here, at a common height of 1 m, *D. sissoo* had a greater RGR than *D. regia* and *A. catechu* (Figure 1d).



Table 4: Chapman-Richard's parameter estimates and evaluation statistics of cumulative height growth and relative height growth in three species ($\pm SE$)

Model	Model Parameters	<i>D. sissoo</i>	<i>D. regia</i>	<i>A. catechu</i>
Chapman- Richard's (Cumulative Growth)				
	a	5.612 \pm 0.07	3.339 \pm 0.28	4.97 \pm 0.17
	b	0.204 \pm 0.13	0.297 \pm 0.01	0.279 \pm 0.13
	c	1.679 \pm 0.08	2.861 \pm 0.03	2.409 \pm 0.06
	R ² adj.	0.99996	0.99997	0.99996
	RSE	0.008	0.005	0.008
	BIC	-105.03	-116.22	-104.31
(Relative Growth)				
	b	-0.215 \pm 0.05	-0.245 \pm 0.07	-0.266 \pm 0.11
	c	1.728 \pm 0.15	2.544 \pm 0.09	2.354 \pm 0.03
	R ² adj.	0.9999	0.9979	0.9998
	RSE	0.003	0.024	0.007
	BIC	-133.63	-82.09	-111.06

Thus, it can be stated that *D. sissoo* curve, due to low rate of decline, had a superior RGR throughout most of its height development, despite the fact that its initial RGR was lower than that of *D. regia* and *A. catechu*. A smooth decline in RGR function relates to low mortality and vice versa. Ordering of species was interestingly reversed in contrast to age-dependent RGR. *D. regia* was the species with smallest final height and sharpest RGR decline during the study span of 12 years (Figure 1d). The universal decrease in RGR resulted from a combination of a variety of factors including an accumulation of non-photosynthetic biomass in the form of stems and root, self-shading of leaves and decrease in local concentration of soil nutrients (Philipson *et al.*, 2012). In addition, the continuous decrease in RGR with age and size has also been associated with changes in

physiological processes in relation to tree size and decline in photosynthetic activity as a result of increased water stress in leaves of larger trees (Ryan *et al.*, 2006). Moreover, increased respiratory losses also led to decline in RGR as taller trees experience greater metabolic costs (Binkley, 2021).

In this study, initial values of RGR were high for all three species. Instantaneous RGR can initially manifest very large values if early growth before the inflection point is exponential and typically decreases with increasing time and size. The curve of RGR declined throughout as the tree height increased. Recent advances in plant growth modelling have allowed a deeper understanding of the ecological processes that was not possible with traditional approaches. The application of function- derived growth rates in the



recent past have been used to evaluate relationship between seed size and growth rates (Turnbull *et al.*, 2008); to quantify the costs of investment in chemical defence (Paul-Victor *et al.*, 2010); to document trade-offs between growth and survival (Rose *et al.*, 2009), to study the effect of hemi-parasitic plants on their hosts (Hautier *et al.*, 2010) and partitioning the components of relative growth rates (Rees *et al.*, 2010).

In addition, ecological significance of high RGR (initial values > 1) in all the three fast growing species (Figure 1c, d) could be due to a high rate of

accumulation of resources or a rapid completion of life cycle (Grime, 1979). High RGR leads to a rapid increase in plant size which ends up occupying a larger space, both above and below ground. Consequently, such plants have the opportunity to acquire a larger share in limiting resources like water, nutrients and light in contrast to slow growers. Fast growing species may also profit from a high RGR, as they mostly occur in disturbed habitats, and therefore must complete their life cycle over a short and uncertain period. The completion may be facilitated by a fast vegetative growth phase (Poorter, 1989).

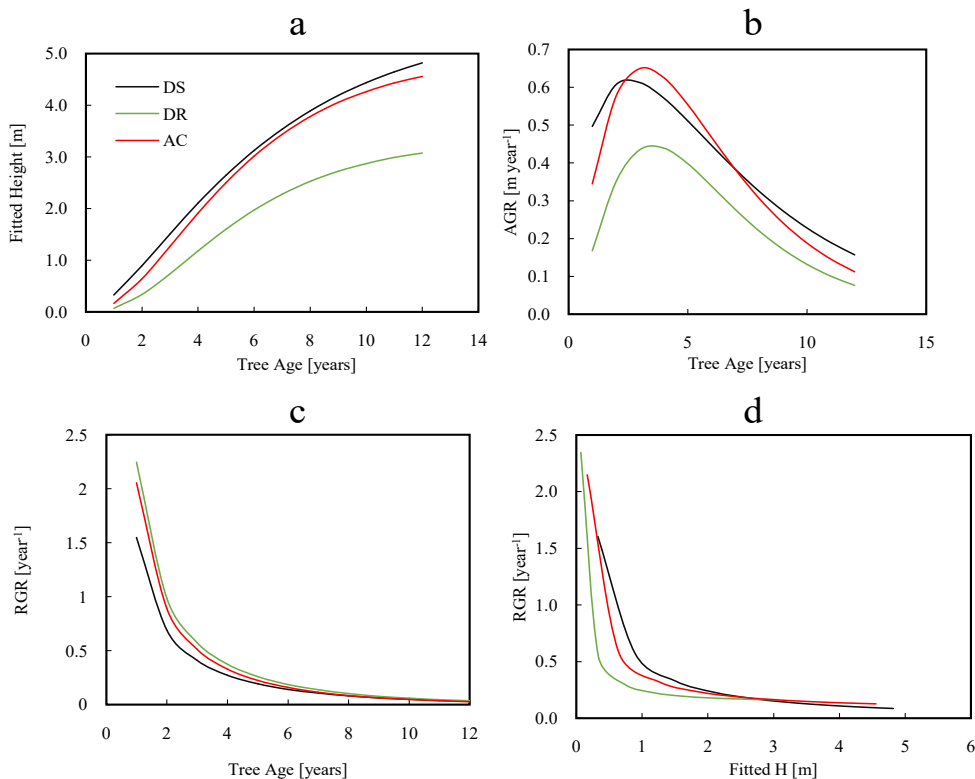


Figure 1: Chapman-Richard's function fitted to mean relative height growth rate of three species viz. *D. sissoo*, *D. regia* and *A. catechu* on (c) time basis and (d) size-basis along with cumulative and absolute growth rate curves (a, b)

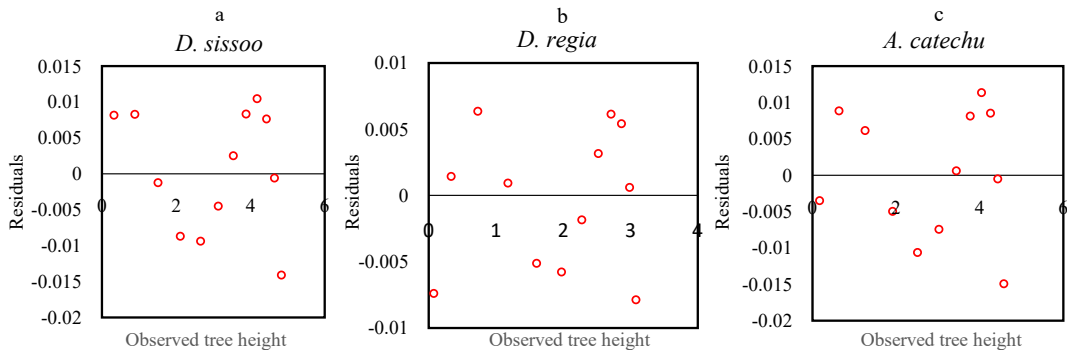


Figure 2: Residual plots of the three species developed from cumulative dataset: a) *Dalbergia sissoo*, b) *D. regia*, c) *Acacia catechu*.

RGR is a complex phenomenon that is governed by differences in physiology, morphology and biomass partitioning (Shipley, 2006) and so much effort has been put into partitioning the components of relative growth rates (Rees *et al.*, 2010). To find the relative contribution of all associated factors, RGR can be split into: $RGR = NAR \times LAR$, where $LAR = SLA \times LMF$. NAR is the Net Assimilation Rate, LAR is the Leaf Area Ratio, SLA is the Specific Leaf Area and LMF is the Leaf Mass Fraction. RGR is defined as the log transformed values of increase in the biomass in unit time and per unit of growing material. NAR gives the information regarding the increase in biomass per unit leaf area and per unit time which also reflects the average photosynthetic efficiency of leaves. SLA is the photosynthesizing leaf area produced per unit of leaf mass and strongly correlates with leaf thickness and biomass distribution pattern of plants.

LAR is the ratio of the total leaf area to total plant dry weight and provides information about the leaf area constructed per unit biomass. LMF informs about the biomass allocation to leaves in relation to the whole plant. In fast growing deciduous tree species (all three in this case), high RGR values are linked with high values of LAR and SLA (Cornelissen *et al.*, 1998). High SLA signifies small leaves having thin boundaries which results in effective heat transfer on sunny days (Leigh *et al.*, 2017). Thus, SLA has an adaptive value which is in accordance with Poorter's hypothesis (1991) which suggests that RGR is not the target variable for selection, but other variables such as SLA could be more important for conferring advantages in specific habitats. SLA is associated with a number of morphological, physiological and biochemical traits. High SLA resembles relatively low construction cost and high protein concentrations which allows greater efficiency in acquiring the limited



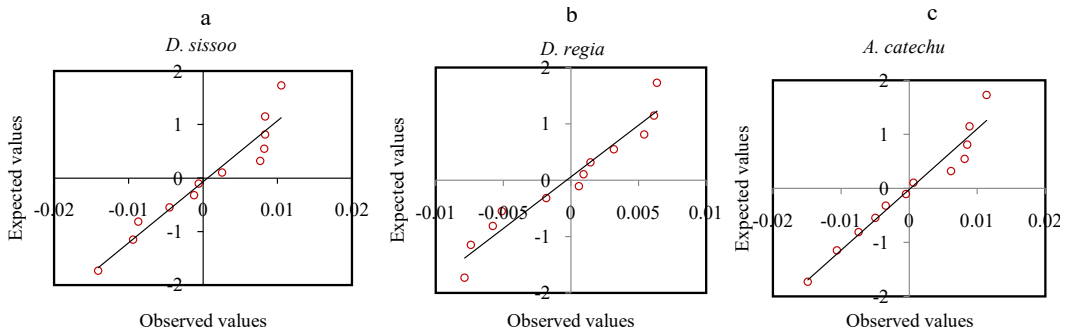


Figure 3: Q-Q plots of three species to check residual normality: a) *Dalbergia sissoo*, b) *D. regia*, c) *Acacia catechu*

resources leading to a better competitive ability in fast growing species (Antunez *et al.*, 2001). A meta-analysis demonstrated that in general, NAR was the best predictor of variations in RGR (Shipley, 2006). However, as the light intensity was reduced, the importance of NAR decreased while that of SLA increased. In other words, the importance of SLA increased on the expense of NAR.

These could be possible interpretations which may provide some insight in understanding the adaptive nature of fast-growing deciduous species in a nutrient rich habitat with relatively high RGR values. This piece of work should encourage fellow researchers to take up the task of investigating the competitive aggression and adaptive ecology of more and more deciduous and evergreen species (two distinct functional groups) of Kumaun Himalaya in terms of cumulative, absolute and particularly relative growth rates. Thus, in my opinion plant growth modelling through function derived growth rates is a much

more realistic approach in assessing the growth performance of plants and in future it can be applied to study interdisciplinary aspects of growth as well.

CONCLUSION

Evaluating tree growth using advance techniques is an important area where growth rates (cumulative, absolute and relative) between different plant functional groups can be analysed and simultaneously compared. Tree growth modelling thus helps a modeler in understanding the mathematical interpretation of a biological growth process, the knowledge of which can be applied to enhance forest yield. In recent years, the easy availability of statistical tools has made this field much more exciting and future growth projections of individual trees and forest stands can be predicted with much less effort. This article thus deals with modelling growth curves generated from height vs age datasets of three fast growing tree species belonging to Fabaceae family. Size- dependent



RGR analysis demonstrated that *D. sissoo* performed better than *D. regia* and *A. catechu*. Key findings of the investigation are high RGR values for all three species which indicated early exponential growth. Initial high values of RGR suggested better acquisition of resources and soil nutrients by all three species in contrast to slow growers. It is recommended that advance growth modelling techniques should be applied to two major functional groups, i.e. fast growing and deciduous trees (competitors or ruderals) and slow growing evergreen trees (stress tolerators) as proposed by Grime (1979) to evaluate their growth performance and competitive aggression in different Himalayan habitats.

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