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Bertalanffy-Pütter Models for the Growth of Tropical Trees and Stands

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Abstract

The Bertalanffy-Pütter (BP) five-parameter growth model provides a versatile framework for the modeling of growth. Using data from a growth experiment in literature about the average size-at-age of 24 species of tropical trees over ten years in the same area, we identified their best-fit BP-model parameters. While different species had different best-fit exponent-pairs, there was a model with a good fit to 21 (87.5%) of the data ("Good fit" means a normalized root-mean-squared-error *NRMSE* below 2.5%. This threshold was the 95% quantile of the lognormal distribution that was fitted to the *NRMSE* values for the best-fit models for the data). In view of the sigmoidal character of this model despite the early stand we discuss whether the setting of the growth experiment may have impeded growth.

Keywords

Bertalanffy-Pütter (BP) Differential Equation, Growth Model, Normalized Root-Mean-Squared-Error (*NRMSE*), Simulated Annealing

1. Introduction

There are multiple factors that influence the growth of trees and forest stands [1] and therefore also a variety of growth equations used in forest science [2] [3] [4] and [5]. Practitioners often use simple three-parameter models, e.g. of Brody [6], Gompertz [7], or Verhulst [8], as these are numerically tractable. The four-parameter Chapman-Richards growth function [9] is popular, too (110,000 hits in Google Scholar). However, the use of many different growth models makes the comparison of the outcomes difficult. Therefore, here we consider the five-parameter Bertalanffy-Pütter (BP) model, as it generalizes these models and provides a more unified approach using growth curves with better fits to the data.

We ask, if a further unification is possible, provided that the environment is the same: Is there a three-parameter BP-model that fits well to most growth data (with different optimal parameters for each data), provided that the growth conditions for all trees are the same? We illustrate this question for growth data from Devaranavadgi [10] about the average heights of 24 species of tropical trees that were grown on dry and shallow soil. **Table 1** provides the data. The data represent the first 11 years of an early forest stand with final mean heights for the species between 2.56 and 9.60 m. We therefore assume that for each species

Table 1. Species and data.

No.	Name		Max[1] in m	height at age data (height in cm, rounded to 0 decimals; year at bottom)[2]										
	common	Species		h_1	h_2	h_3	h_4	h_5	h_6	h_7	h_8	h_9	h_{10}	h_{11}
T01	ear-pod wattle	*Acacia auriculiformis*	15 - 30	52	81	141	241	319	370	450	532	590	640	680
T02	black cutch	*Acacia catechu*	15	46	61	123	185	251	292	349	391	416	421	430
T03	gum-arabica tree	*Acacia nilotica*	20 - 25	48	68	123	175	271	324	383	440	470	522	544
T04	river tamarind	*Leucaena leucocephala*	2 - 10	38	63	166	272	381	491	572	761	864	920	960
T05	Indian siris	*Albizzia lebbeck*	18 - 30	15	83	181	281	372	469	530	572	601	644	663
T06	neem	*Azadirachta indica*	15 - 20	34	83	126	189	253	329	388	421	456	497	521
T07	orchid tree	*Bahunia purpurea*	5	64	83	149	201	251	321	376	419	455	471	489
T08	bastard teak	*Buteo monosperma*	6 - 12	11	29	69	101	150	184	211	231	249	259	269
T09	beach oak	*Casuarina equisitefolia*	6 - 35	95	114	134	178	230	281	312	350	372	390	404
T10	ironwood	*Senna siamea*	18	69	91	138	181	223	275	337	372	419	457	481
T11	Indian rosewood	*Dalbergia sissoo*	10 - 15	52	85	149	201	265	313	351	399	431	442	451
T12	red flame-tree	*Delonix regia*	12 - 17	16	31	69	121	163	193	231	252	273	281	302
T13	Indian goose-berry	*Emblica officianalis*	8 - 23	83	135	188	279	343	406	511	568	603	612	624
T14	lemon-scented eucalyptus	*Eucalyptus citriodara*	30	79	176	283	373	465	589	641	742	812	864	885
T15	some eucalyptus	*Eucalyptus hybrid*	-	82	123	184	282	341	494	529	572	589	621	649
T16	anjan tree	*Hardwickia binata*	25 - 30	31	73	146	209	259	311	355	478	539	562	591
T17	axle-wood	*Anogeissus latifolia*	20	38	62	124	182	239	331	388	446	486	519	591
T18	sweet inga	*Pithecellobium dulce*	5 - 20	81	123	179	221	279	334	386	429	461	499	519
T19	yellow flame-tree	*Peltoferrum ferrugeneum*	15 - 25	22	31	172	317	395	463	472	457	481	508	529
T20	Indian beech	*Millettia pinnata*	15 - 25	13	49	109	182	234	289	356	406	442	477	496
T21	mesquite	*Prosopsis juliflora*	12	96	135	197	262	311	362	399	441	471	492	503
T22	raintree	*Samanea saman*	15 - 25	68	101	159	206	266	313	354	391	423	454	468
T23	black plum	*Syzygium cumini*	6 - 20	58	72	98	136	165	172	192	209	233	246	256
T24	tamarind	*Tamarindus indica*	30	37	49	89	129	178	209	237	270	296	313	321
	year			‘90	‘91	‘92	‘93	‘94	‘95	‘96	‘97	‘98	‘99	‘00
	mean annual temperature (˚C)[3]			26.5	27.1	27.6	27.5	27.4	27.8	28.2	28.1	28.2	27.9	27.6

Note: [1]typical maximal heights (from diverse sources); [2]data from Devaranavadgi [10], [3]data from Belgaum airport (VABM weather station, 200 km SW of Vijaya Pura) and retrieved using Mathematica 12.1 for “Bijapur, Karnataka, India”.

the data represent the initial growth phase of the trees, whence BP-models are suitable. Note that all mentioned models have none or one inflection point; in the latter case the growth curves are sigmoidal (S-shaped). The growth curve of a tree may display several inflection points, each representing another sigmoidal growth phase, c.f. [11] and [12], whence a single sigmoidal growth curve is capable of modeling only one of these phases.

For each species we identify the best-fit parameters for the BP-model, from which we compute additional parameters with a silvicultural relevance, such as the location of the inflection point (maximal yearly growth) and asymptotic height (final expected size of the first growth phase). As to the above-mentioned research question, we speculate that the experimental setup of the growth study, from which we have taken the data, may have impeded the growth of most trees. For, the analysis of the inflection points indicates an early slowing down of growth (unexpected at this early phase) and we identified a single three-parameter model that had a "good fit" (defined later) to most data.

As for another application, we use these models to check if temperature has affected tree growth. For, in temperate climate, higher temperatures enhance growth, while in tropical climate growth slows down [13] [14].

2. Materials and Methods

2.1. Data

We used the literature data of **Table 1** (see also **Figure 5**) from Devaranavadgi [10]: An unspecified number of trees from 24 species was planted in 1990 and tree heights were measured annually till 2000 (11 data per species). The table informs about the species T01 - T24 and reports their average-height-at-age data (The source paper provides additional information, such as soil composition. There is no information about the standard deviation of the heights). The data are of additional interest, as often tree size is measured by other parameters [15]. **Table 1** also informs about the annual mean temperatures (for 1990, …, 1999) for the larger region around Vijaya Pura. We used Mathematica to retrieve them from the Wolfram Alpha database.

The growth data were obtained during a study at the Regional Agricultural Research Station of Vijaya Pura (district Bijapur, Karnataka, India), located in the Deccan plateau. **Figure 1** pinpoints the study site. It has a semi-arid climate with temperatures ranging from 15˚C to 42˚C and average annual rainfall of 594 mm with 39 rainy days. The region suffers from deforestation owing to poor management practices, low fertility of soil, and a harsh climate [16]. The study therefore searched for species with added economic or ecological value that were suitable for re-forestation. Note that some of the species that the study considered may become invasive in more humid areas (e.g. mesquite).

2.2. Growth Model

The Bertalanffy-Pütter (BP) model describes tree growth by means of the differential

Figure 1. Plot of India and of Karnataka state (shades of beige), and in red the study site Vijaya Pura, the airport at Belaum, and of the state capital Bengaluru (Bangalore). Plot using Mathematica 12.1, based on Open Street Map (the plotted boundaries are neither endorsed by the authors nor may they be correct).

Equation (1) of Pütter [17] for the tree height $h(t)$ at time t. The differential equation can be solved analytically, though in general not by means of elementary functions [18].

$$h'(t) = p \cdot h(t)^a - q \cdot h(t)^b \tag{1}$$

Tree growth models for temperate climates often use difference equations, *i.e.* the derivative $h'(t)$ in Equation (1) is replaced by the difference $h(t+1) - h(t)$. In temperate climates this assumption is warranted, as the sharp seasonal changes are apparent from the growth rings. We use the differential equation, as we consider tropical trees. Further, the yearly growth data showed random fluctuations, while the height-at-age data used for the fitting of model (1) were comparably smooth.

The model parameters of Equation (1) have no meaning a priori. They are to be determined from fitting the model to height-at-age data: Four parameters are displayed in the equation, namely the exponent-pair $a < b$ and the scaling constants p and q. An additional parameter is the initial value at age 1, meaning $h(1) = c > 0$. While in forestry literature also negative exponents were considered ($a < 0$, $b = 1$), as thereby a growth model of Schnute [19] would fit into the

BP-framework [20], this paper assumes non-negative exponents.

In this form, the BP-model was popularized by Bertalanffy [21] [22] [23] as a model of ontogenetic growth. According to Bertalanffy, the growth of animals, plants and biomass would be governed by certain biophysical principles, which in their most general form would be embodied by Equation (1). Specifically, the growth of trees would be based on an allometric relation between living biomass and photosynthetic area [24], whereby the exponent-pair (a, b) would be related to plant metabolism.

Each exponent-pair (a, b) defines a unique three-parameter model BP(a, b), using the parameters p, q, c. For comparison, **Figure 2** plots the exponent-pairs of well-known models and compares them with the exponent-pairs that this paper scanned in an initial search for the optimal model parameters.

Common named three-parameter models are the Brody [6] (monomolecular) model BP(0, 1) of bounded exponential growth, the Verhulst [7] model of logistic growth BP(1, 2), the model BP(2/3, 1) of von Bertalanffy [21], or the model BP(3/4, 1) of West [25]. Four-parameter models that are special cases of equation (1) are the generalized Bertalanffy model ($b = 1$, $a < 1$) and the Richards [9] model ($a = 1$, $b > 1$). The Gompertz [7] model is the limit case BP(1, 1) with a different differential equation, where b converges to $a = 1$ from above [26]; similarly for the generalized Gompertz model (model class $a = b$) with Equation (2):

$$h'(t) = p \cdot h(t)^a - q \cdot \ln(h(t)) \cdot h(t)^a \tag{2}$$

Note that BP(1, 1) is attractive amongst botanists, as the same model (with different parameters c, p, q) is capable of describing different dimensions of plant-growth (e.g. height, basal area, volume), provided that there exists an allometric relation between these dimensions. The other models do not have this property (*i.e.* different exponent-pairs are needed for different dimensions).

Alternative parametrizations of the model use empirically meaningful parameters, such as the asymptotic height h_{max} (limit of the height at infinite time) or

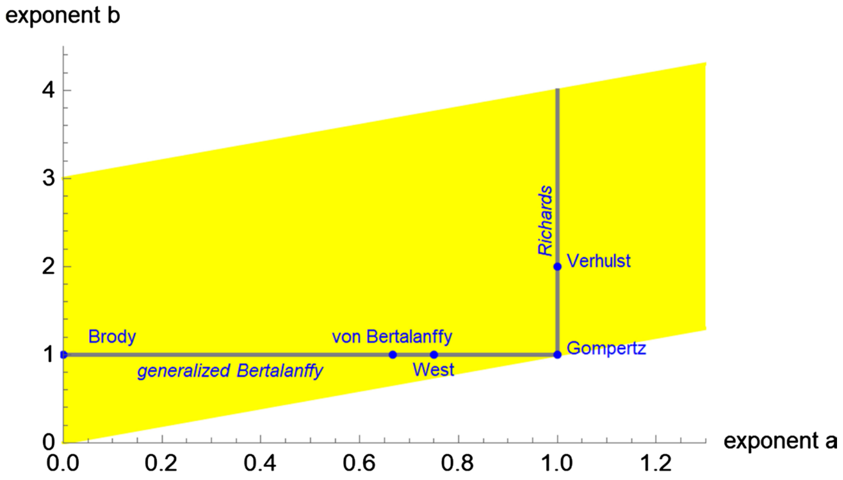

Figure 2. Special models (blue dots), model classes (grey lines), and the initial search grid (yellow). Plot using Mathematica 12.1.

the inflection point (height h_{infl} reached at age t_{infl}). Asymptotic height is an important silvicultural measure, as it allows to assess the ultimate yield. It depends both on the species and on the environment, where the tree was planted. The inflection point informs when growth was fastest. The maximal annual growth rate is important for plant biology, as it informs about the basal metabolic rate [27]. These parameters are computed from the parameters of Equation (1) as follows; for t_{infl} numerical equation solving is used. Growth is unbounded, if $q = 0$ and it is not sigmoidal, if $a = 0$.

$$h_{max} = \left(\frac{p}{q}\right)^{\frac{1}{b-a}} \quad \text{and} \quad h_{infl} = \left(\frac{a}{b}\right)^{\frac{1}{b-a}} \cdot h_{max} \tag{3}$$

Some authors [28] were concerned that asymptotic length would be unreliable if it exceeded the maximal observed length substantially. We therefore compared h_{max} with typical tree heights.

2.3. Goodness of Fit and Method of Calibration

We sought for parameters that minimized *SSE*, the sum of squared errors for fitting the BP-growth function to height-at-age-data. If $h(t)$ is a solution of Equation (1), using certain exponents $a < b$ and parameters p, q, c, and if h_i are the $n = 11$ average weights, then *SSE* is defined by Equation (4):

$$SSE = \sum_{i=1}^{11} \left(h_i - h(i)\right)^2 \tag{4}$$

The data-fitting exercise for the BP-model is more challenging than for the Richards model, where standard optimization routines may run into difficulties [29]. In recent papers a method of data-fitting was developed for the BP-model [30] [31] [32] and [33]. This method was based on a grid-search, whereby we searched the best-fitting exponent-pairs (a, b) on a grid with step size 0.01 in both directions (**Figure 1**). For each grid point we identified the best fitting model parameters (p, q, c) that minimized *SSE* using a custom-made variant of the method of simulated annealing [34]. Simulated annealing alone could be used to optimize for all five parameters (a, b, p, q, c) at once, but often the so computed parameters achieved a suboptimal fit. Note that we optimized also for the initial values c, whence in **Table 2** the best-fit values for c slightly differed from the observed initial heights h_1 in **Table 1**.

For each time series, the best-fit parameters (a_{min}, b_{min}, p_{min}, q_{min}, c_{min}) achieved the least value of *SSE*, namely SSE_{min}. Thereby, for the exponents we aimed at an accuracy of 0.01 (defined from the grid), while the other parameters were identified with a higher accuracy.

Our method of obtaining the five best-fit parameters of the BP-model requires for each dataset the consideration of many three-parameter models whereby for all these models the best-fit parameters need to be computed. We utilize the surplus information from this approach and ask, if one three-parameter model would fit for all (or for most) species, if the notion of "fit" was somewhat relaxed; *i.e.*

Table 2. Parameters of the best-fit models and measures for the goodness of fit (rounded to 3 decimals).

No.	Best-fit parameters[1]					Derived parameters[2]			Goodness of fit[3]		
	a	b	c	P	q	h_{max}	h_{infl}	t_{infl}	*SSE*	*RMSE*	*NRMSE*
T01	0.83	1.02	0.435	1.720	1.137	8.839	2.987	4.909	0.101	0.096	1.4%
T02	1.09	1.51	0.399	1.066	0.568	4.477	2.060	4.393	0.048	0.066	1.5%
T03	1.04	1.15	0.387	2.824	2.312	6.165	2.472	4.888	0.069	0.079	1.5%
T04	0.30	11.12	0.242	0.756	0+	9.601	6.876	7.594	0.309	0.167	1.7%
T05	0.48	1.35	0.153	1.119	0.203	7.095	2.161	3.352	0.032	0.054	0.8%
T06	0.94	1.17	0.381	1.585	1.056	5.831	2.251	4.500	0.037	0.058	1.1%
T07	0.60	3.18	0.590	0.429	0.007	5.060	2.651	5.126	0.031	0.053	1.1%
T08	0.87	1.10	0.097	1.969	1.549	2.843	1.025	3.915	0.007	0.025	0.9%
T09	1.70	2.17	0.893	0.476	0.245	4.128	2.455	5.413	0.026	0.049	1.2%
T10	0.69	2.50	0.667	0.358	0.016	5.566	2.733	5.915	0.017	0.040	0.8%
T11	0.39	2.81	0.485	0.509	0.012	4.773	2.110	4.158	0.027	0.05	1.1%
T12	0.80	1.02	0.100	1.943	1.499	3.251	1.078	3.800	0.018	0.040	1.3%
T13	0.32	10.25	0.813	0.527	0+	6.200	4.373	6.203	0.062	0.075	1.2%
T14	0.00	6.90	0.805	0.980	0+	9.238	NA	NA	0.095	0.093	1.0%
T15	1.25	1.85	0.789	0.662	0.216	6.444	3.353	4.641	0.271	0.157	2.4%
T16	0.21	16.74	0.352	0.524	0+	5.876	4.509	7.880	0.235	0.146	2.5%
T17	0.86	1.03	0.326	1.845	1.313	7.393	2.558	5.081	0.109	0.099	1.7%
T18	0.34	3.26	0.813	0.434	0.003	5.769	2.660	4.748	0.010	0.030	0.6%
T19	0.68	1.31	0.003	2.095	0.761	4.992	1.763	3.031	0.314	0.169	3.2%
T20	0.22	2.88	0.102	0.586	0.006	5.499	2.091	4.589	0.024	0.047	0.9%
T21	0.94	1.33	0.929	0.927	0.476	5.515	2.265	3.503	0.015	0.037	0.7%
T22	0.99	1.12	0.653	2.268	1.824	5.342	2.068	3.966	0.011	0.031	0.7%
T23	0.69	0.87	0.531	1.357	1.096	3.273	0.903	2.452	0.034	0.056	2.2%
T24	1.05	1.21	0.313	2.120	1.732	3.528	1.454	4.391	0.020	0.043	1.3%

Notes: [1]0+ means a positive number rounded to 0; [2]h_{max} is asymptotic height, (t_{infl}, h_{infl}) is the inflection point (NA for $a = 0$); [3]*RMSE* is root-mean-squared-error, $NRMSE = RMSE/h_{11}$.

"good fit" rather than best fit. We thereby identify, for each species, those exponent-pairs, where the corresponding three-parameter growth model has a "good fit", and then we form the intersection of these 24 (or of fewer) sets. Our definition of a "good fit" is based on the normalized root-mean-squared-error *NRMSE*, as it allows to compare the fit across different species of different height. *NRMSE* expresses the root-mean-squared-error (*RMSE*; 11 is the number of data-points) as a percentage of the maximal observed height (h_{11} of the last data-point):

$$RMSE = \sqrt{\frac{SSE}{11}} \quad \text{and} \quad NRMSE = \frac{RMSE}{h_{11}} \tag{5}$$

Further, to define a "good fit" we use a threshold for *NRMSE*, based on a statistical analysis of the distribution of the observed *NRMSE*-values of the best-fit models. We found that a lognormal distribution would fit to these values (Section 3.2) and we therefore use the threshold corresponding to the 95% quantile of this distribution. As explained below, for the present data this threshold is 2.5%.

2.4. Materials

We used Mathematica 12.1 (Wolfram Research) for computer algebra, including optimization and statistical analysis, and to access meteorological data (Wolfram repository). We used nonparametric methods, as not all data were normally distributed: Spearman rho for rank correlation and Spearman rank test for nonzero correlation (using the permutation method with 1000 Monte-Carlo simulation steps). Where we used a parametric distribution (lognormal distribution), we first tested the distribution assumption using the Anderson-Darling statistic [35] and the threshold of $p = 0.05$ (95% confidence).

3. Results

3.1. Best Fit Parameters

The size-at-age data of **Table 1** (c.f. **Figure 5**) inform about 11 annual height measurements. It started in 1990 with average heights h_1 = 11 cm for "bastard teak" T08 to 96 cm for mesquite T21 and it ended in 2000 with h_{11}= 2.56 m for black plum T23 to 9.60 m for river tamarind T04. **Table 2** informs about the growth data, the parameters of the best-fit models, and the goodness of fit.

The best-fit exponent-pairs (*a*, *b*) in **Table 2** identify those three-parameter models BP(*a*, *b*) that achieved the best fit to the data for T01 to T24. **Figure 3**

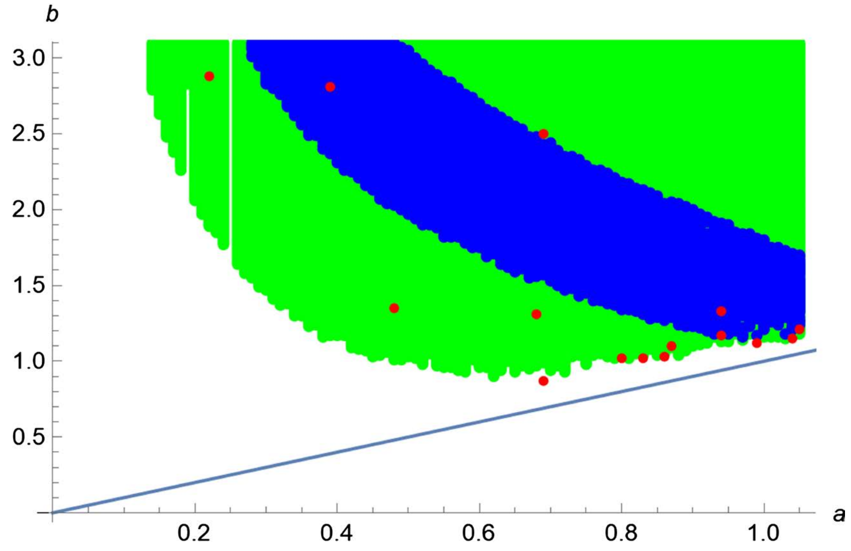

Figure 3. Line $a = b$ (blue) in the region $a < 1.05$, $b < 3$ and best-fit exponent-pairs (red), exponent-pairs with *NRMSE* below 5% for all data (green), and with *NRMSE* below 2.5% for at least 21 data (blue); plot using Mathematica 12.1.

plots those 15 exponent-pairs that were in the region $a \le 1.05$, $b \le 3$ (Not in the plot were three exponent-pairs with $1.05 < a \le 1.7$ and six exponent-pairs with $3 < b \le 16.74$).

As is evident from this picture, none of these exponent-pairs defined a best-fit model for all data, nor did the exponent-pairs concentrate anywhere. Further, the best-fit exponent-pairs differed clearly from those of the named three-parameter models (*i.e.* Brody, Gompertz etc.). The distances of these exponent-pairs were smaller to the lines of exponent-pairs defining the four-parameter models, but none of these models was best-fit, either.

Table 2 informs also about derived parameters, asymptotic height h_{max} and age t_{infl} and size h_{infl} of the inflection point. Three-parameter models have the disadvantage that by Equation (3) there is a fixed ratio between the height at the inflection point and asymptotic height, e.g. 50% ratio t_{infl}/h_{max} for logistic growth. By contrast, for the best-fit models either there was no inflection point for one data (lemon-scented eucalyptus T14) or this ratio varied widely between 27.6% for black plum T23 and 76.7% for anjan tree T16.

When compared with the sample data, asymptotic height of the best-fit model was in the range of 94% - 130% of the maximal observed height h_{11} of **Table 1**. In view of the Anderson-Darling test, for the present data the quotient h_{max}/h_{11} was lognormally distributed (no refutation of this hypothesis: $p = 0.26$). Using the maximum-likelihood estimates for its location and shape parameters (0.082 and 0.079, respectively) we concluded that with 99.5% probability the maximal projected height of any tree was below 133% of h_{11}. However, except for three species (gum-arabica tree T04, orchid tree T07 and sweet inga T18) the usual heights for trees of the considered species (by **Table 1** in most cases 20 m or more) exceeded the asymptotic heights considerably (e.g. by the factor 3 - 5 for rain tree T22).

3.2. Defining the Threshold for a Good Fit

For the best-fit models *NRMSE* varied between 0.6% for sweet inga T18 and 3.2% for yellow flame-tree T19 (**Table 2**). The good fit was also illustrated by **Figure 4**, plotting the BP-model curves for gooseberry T13 and yellow flame tree T19.

Using the Anderson-Darling test, the *NRMSE*-values of **Table 2** followed a lognormal distribution (no refutation owing to $p = 0.93$). We used the maximum-likelihood method to estimate its location and shape parameters (−4.38 and 0.42, respectively). The 95% quantile of this lognormal distribution led to the threshold $NRMSE = 2.5\%$. We used it to define "good fit". In this sense, the fits of anjan tree T16 and yellow flame-tree T19 were not good. For instance, based on the lognormal distribution, yellow flame-tree T19 was an outlier with a probability of only 1.3% for $NRMSE > 3.2\%$. Indeed (**Figure 4**), the growth data for T19 were insofar atypical, as height did not always increase (for average data this can occur if e.g. the largest trees are removed) and as growth finally seemed

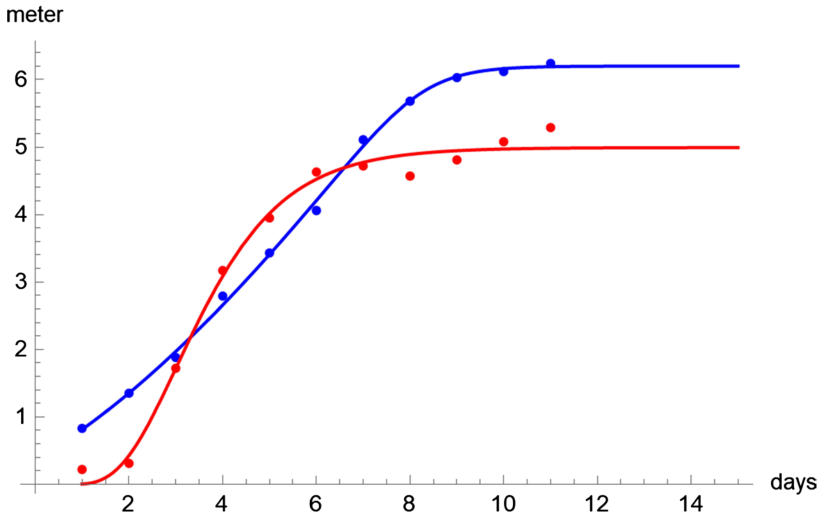

Figure 4. Data and the growth curve for T13 (blue) and T19 (red); plot using Mathematica 12.1.

to accelerate (e.g. more light for the smaller trees, when the largest ones are removed).

There was no exponent-pair (*a*, *b*), where a single model BP(*a*, *b*) could have a good fit to all 24, to 23, or to 22 of our data. The maximal number of data with a common good-fitting model was 21: **Figure 3** (blue region) plots the exponent-pairs corresponding to models with good fits to 21 of our data (whereby for each data different best-fit parameters *c*, *p*, *q* were used). Most of the best-fit exponent-pairs were outside this region (but for their data *NRMSE* in general was below 2.5%). Further, none of the exponent-pairs of the named three-parameter models (e.g. Brody, Gompertz, etc.) was in the blue region of **Figure 3**. However, the West-model had a good fit to 19 models and amongst the named three-parameter models this was the best outcome.

For comparison, we also considered the threshold 5%. Using it there were exponent-pairs whose BP-models could be fitted to all data with $NRMS < 5\%$; the green region in **Figure 3** plots them. The exponent-pairs (1, 2), (2/3, 1), and (3/4, 1) of the Verhulst-model, the von-Bertalanffy-model, and the West-model were in the green area, but the exponent-pairs (0, 1) and (1, 1) of the Brody-model and the Gompertz-model were not.

3.3. Growth and Temperature

In order to explore, to what extent the growth was affected by environmental factors (there was no information to this end in the source paper), we used the annual mean temperatures from **Table 1** (for 1990, …, 1999) and compared them with the relative growth rates per year: $(h_{k+1} - h_k)/h_k$ using h_k from **Table 1** ($k = 1, \cdots, 10$). The Spearman rho was negative for all species with values between −0.879 for axle-wood T17 and −0.514 for black plum T23. This was significant for all except four data (Spearman rank test: $p < 0.05$); the exceptions were ear-pod wattle T01, beach oak T09, anjan tree T16, and black plum T23.

Using the BP-model curves allowed to strengthen this finding, namely that for all species there was a highly significant correlation relating higher temperatures to lower percentual growth h'/h (but with a delay of one year). Spearman rho had the same value for all data, namely −0.842, and it was nonzero with high significance for all growth curves (Spearman rank test: p-value 0.002).

4. Discussion and Speculation

The results of this paper invite two opposite threads for further speculation, namely that perhaps the West model is a universal tree growth model or, alternatively, that perhaps something is wrong with the data.

The former speculation has been forwarded repeatedly in different contexts. For, West [25] [36] [37] [38] [39] developed biophysical arguments in support of the universality of the three-parameter model BP(0.75, 1) for the growth of animals, plants and forests. This claim was often contested as e.g. for trees the biophysical arguments were contingent on additional requirements [40].

However, even using an obviously false universal model may have a rationale, as is illustrated by the practice in fishery science, where the model BP(0, 1), which in general is not the best-fitting model, is used de facto as a universal model for the growth of fish length. A database [41] and [42] collects information about the best-fit parameters for BP(0, 1) for various species of fish in various environments. It has led to new insights, e.g. relating the growth parameters to natural mortality and mean environmental temperature [43]. Because there is no consensus about a common model for the growth of trees, there is no such database yet for the estimated 40,000 species of trees [44]. Considering the present data, the model of West would appear to be suitable for such a database, as it was almost universal in a weak sense: If practitioners consider a trade-off between a slightly lower accuracy of their models and much less effort for data-fitting (compared e.g. to the general BP-model); then for 19 of our 24 data the West-model was a good choice as it had a good fit. The typical heights differed much between the twenty-four species considered in this paper. Could such difference be still compatible with the universality hypothesis?

This question leads to the second speculation mentioned above. One reason for the common growth pattern may be the setting of the growth experiment, as it could have impeded the growth of the trees in about the same way. For, the growth of all trees was sensitive to environmental factors, such as ambient temperature (see above: negative correlation). That the growth may have been impeded is suggested from the fact that for all species, except one. **Table 2** displays an inflection point. This means that from this moment on, for most species within $t_{infl} = 2$ to 6 years, growth began to stagnate. This is atypical for the mean heights that are normally observed for young stands with all trees still in the early growth phase. Further, the typical heights for most species (**Table 1**) clearly indicate much higher trees than reported in **Table 2** as asymptotic heights h_{max}

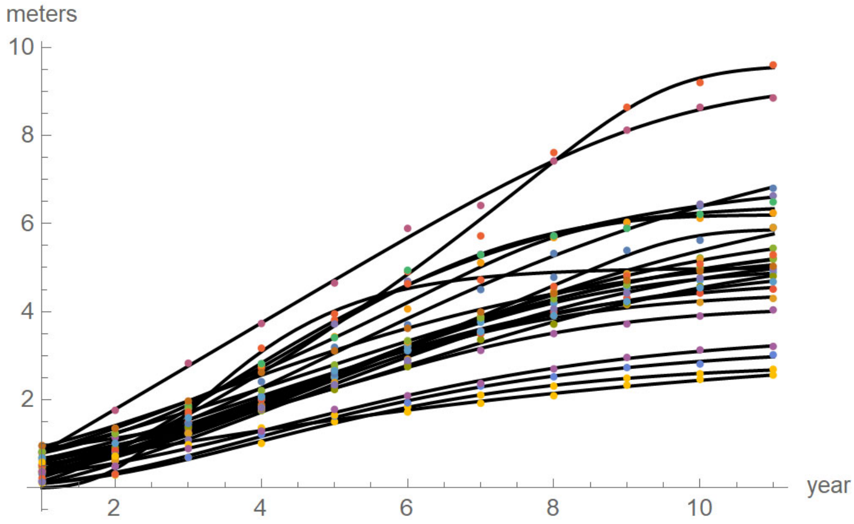

Figure 5. Data and the growth curves for all trees; plot using Mathematica 12.1.

of the 11-year time series. Thus, growth was impeded.

We therefore scrutinized the experimental setting as described in the original data sources [10] [16]. The trees have been planted in 2 m distance from each other on very dry red soil with 30 - 35 cm depth. A main concern was the preservation of soil moisture, which was achieved by the method of planting. Thus, there are two obvious reasons, why the growth of the trees may have beendecayed: Moisture preservation may have failed, or the selected species were not sufficiently adapted to drought. We refute these hypotheses, as such observations would have been reported in the source paper as major findings. Another conceivable explanation is competition between trees for sunlight, which might reduce height growth of suppressed trees at later stages, affecting the mean height. However, 2 m distance between trees below 10 m height usually does not affect height growth much. Thus, in an arid region there remains the explanation of competition belowground. Indeed, soil was shallow and 2 m distance at 30 cm depth result in 4 m^2 per tree and about 1 m^3 soil for its roots, which may not be enough for trees that have the potential to grow to heights and crown diameters of 10 - 30 m. Of course, this proposed "bonsai effect" needs to be tested, but the source paper does not provide sufficient information.

We conclude that BP-models are a useful tool to analyze the height growth of trees and stands. However, the growth curves depend not only on the species but also on the environmental situation. Thereby, as for the present data, the experimental setting may curb the growth to an extent that the same model may fit to many different species.

Finally, we have added **Figure 5** as a graphical summary of the paper, plotting the data in different colors and the best-fitting growth curves.

Acknowledgements and Declarations

The authors declare no competing interests. There occurred no ethical issues, as

the research was based on published data.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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