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The Use of Thermal Time to Describe and Predict the Growth and Nutritive Value of *Lolium perenne* L. and *Bromus valdivianus* Phil

Iván Calvache [1,2], Oscar Balocchi [1], Rodrigo Arias [1] and Máximo Alonso [1,*]

[1] Animal Production Institute, Faculty of Agriculture and Food Science, Austral University of Chile, P.O. Box 567, Valdivia 5090000, Chile; ivan.calvache@uach.cl (I.C.); obalocch@uach.cl (O.B.); rodrigo.arias@uach.cl (R.A.)

[2] Graduate School, Faculty of Agriculture and Food Science, Austral University of Chile, P.O. Box 567, Valdivia 5090000, Chile

* Correspondence: maximo.alonso@uach.cl; Tel.: +56-63-222-1242

Abstract: The thermal time, expressed in accumulated growing degree-days (AGDD), was used as a predictor to describe and simulate the independent growth of two pasture crops, *Lolium perenne* L. and *Bromus valdivianus* Phil. Two sinusoidal models (four-parameter Logistic and Gompertz) were applied to the growth variables (total leaf blade length per tiller—LBL, and accumulated herbage mass—AHM). The nutritive value of pastures was predicted and modeled using regression equations (linear and quadratic), depending on each nutrient. Data for modeling were collected from a two-year study, in which LBL, AHM, and nutritive value variables for *L. perenne* and *B. valdivianus* pastures were measured at three-day intervals. Defoliation was determined according to the AGDD, such that the swards were defoliated at 90, 180, 270, 360, and 450 AGDD. The Logistic and Gompertz models presented similar values for the growth rate (GR) parameters, superior asymptote (A_{sup}), inferior asymptote (A_{inf}), and point of maximum growth (P_{max}). In both species, the maximum growth was 260 AGDD. The GR was similar for both species in different seasons of the year, but the maximum AHM varied, with *B. valdivianus* presenting a higher value (+1500 kg DM ha^{-1}) than *L. perenne* during the spring. The regressions accurately described the nutritive value, demonstrating a positive linear relationship between the AGDD and concentrations of neutral and acid detergent fiber (NDF, ADF), an inverse linear relationship with crude protein (CP), and a quadratic relationship with metabolizable energy (ME) and water-soluble carbohydrate (WSC) concentration.

Keywords: accumulated growing degree-days; mathematical models; accumulated herbage mass

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1. Introduction

Temperature is one of the most important and influential factors for grass growth cycles, from planting through harvest. It is usually expressed in thermal time (TT) as accumulated growing degree-days (AGDD) [1] and is frequently used to determine the seasonal growth of a wide variety of forage species and crops [2,3]. With a few exceptions in some seasons, AGDD values are usually positive. However, on certain occasions, the values are negative or zero, in which case the AGDD value is considered as zero [4].

In addition to temperature, factors such as soil moisture, solar radiation, fertilization, and pasture management affect growth cycles. Thus, growth can be mathematically described using different modeling tools [5]. It has been suggested that regression models are useful tools to describe and simulate grass growth [6]. In addition, they allow for the attainment of parameters based on different climatic conditions, providing a simple way to obtain the information necessary to make decisions about defoliation frequency (DF). Models that consider temperature as the predictor variable for grass growth can be classified as those where TT is expressed either as AGDD or hydrothermal time (HT).

Thermal time is determined by subtracting the plant's base growth temperature from the average air temperature, while HT is calculated by combining the ambient temperature and thermal water time over the potential water base and integrating that value with the additional factor of temperature to describe growth [6,7]. These models are focused on the base and maximum temperatures for optimal growth. Thus, when the maximum temperature for a particular species is surpassed or when its base temperature is not met, its growth will slow or even stop [8]. The aforementioned conditions generally occur in seasons with extreme temperatures, such as summer and winter where growth rates can slow or stop over the course of the day.

Traditionally, TT has been integrated into nonlinear growth curves to describe and model the growth patterns and the physiological variables of grasses [9]. For example, linear models, such as the absolute growth rate (AGR) model, assume that grass growth is constant and limitless, while exponential models, such as the relative growth rate (RGR) model, assume an asymptote where the slope equals zero. The parameters for each model are estimated for specific situations and locations. Thus, the widespread use of these models is not always feasible. In most of the grass modeling research, the fit of the growth curve depends on information gathered in the field. This information is usually scarce and therefore restricts an accurate estimation of the accumulated herbage mass (AHM) or leaf growth at a predetermined time [10,11]. The RGR is usually calculated as ($\ln W_2 - \ln W_1)/(t_2$-t_1), where W_1 and W_2 correspond to the AHM (expressed in kg DM ha^{-1}) at times t_1 and t_2 [12]. The variable t can be expressed as circadian TT or AGDD, depending on the function of the data. Growth rate (GR) values are often found using the logarithm of the slope in a linear regression between AHM and time. The two important components of pasture growth are the AHM and change in nutritive value over time. The latter influences the biological and economic value of pastures. Most mathematical models are oriented toward the study of pasture development and predict the daily growth as a function of AHM based on atmospheric factors [3] but fail to integrate the effect of growth on the nutritive value over time.

The first models developed to estimate grass growth were empirical, examining the genetic potential of plants and field measurements of growth [13]. The first nonlinear equations to express general grass growth were similar to those used in animal growth modeling. These equations considered the type of growth and its maximum growth rate along with genetic and environmental factors of the species [14]. More recent models are based on the efficient use of abiotic factors, such as ambient temperature, precipitation, light, fertilization, and pasture management [15,16]. These models provide a more precise description of grass growth dynamics over the course of a year. However, the dynamics and spatial−temporal pasture development respond to complex processes that are also dynamic in time. Therefore, a novel model must consider different temporal and spatial scales and must be validated under the same conditions as its development. Therefore, the objectives of this study were: (1) To utilize TT, expressed in AGDD, as a predictive variable for the growth of two grasses (*Lolium perenne* L. and *Bromus valdivianus* Phil.) by using a sinusoidal curve fit adjusted for ambient temperature, (2) to calculate and compare growth parameters between the two species under different environmental conditions, and (3) to use linear and nonlinear regressions to predict the nutrient composition of both pastures over time.

2. Materials and Methods

2.1. Site Description and Experimental Design

The data for this study were obtained from a research project designed to compare both grasses and were previously reported by Calvache et al. [17]. All the experiments were conducted between the spring of 2015 and autumn of 2017 at the Universidad Austral de Chile's Agricultural Research Station (AARS) (39 460 S, 73 130 W, 12 m above sea level) in Valdivia, southern Chile. The study site has a temperate climate with an average annual temperature of 12.5 °C and a total annual rainfall of 1284 mm. A total of thirty experimental plots of 15 m^2 each (3 × 5 m) were used in a completely randomized block design (three blocks). Each block comprised 10 plots with three observational units corresponding to a tiller in each plot. Therefore, each plot had one replicate (the average of the 3 tillers). In each block, there were five plots sown with 30 kg ha^{-1} of *L. perenne* cv. Alto and five plots with 45 kg ha^{-1} of the *B. valdivianus* Phil. native seed collected in the region. Plots were sown in the autumn of 2015, and the first defoliation was in the spring of 2015. The sampling interval or DF for both species in all plots was 90 AGDD, such that samples were taken every 90 AGDD until reaching 450 AGDD (DF1 = 90, DF2 = 180, DF3 = 270, DF4 = 360, and DF5 = 450 AGDD).

2.2. Climatic Information

Climatic data were obtained from a weather station located 5 m from the field experiment site (available online at http//www.agromet.inia, accessed on 1 April 2021). Maximum and minimum temperatures were used to estimate the AGDD. Grass growing data were collected from the experimental plots between the spring of 2015 and autumn of 2017. This dataset was used to calculate the equation of best fit for each season during the growth period of the pastures from 0 to 450 AGDD. The TT model was calculated based on the concept of AGDD [18], according to the following equation:

$$\text{AGDD} = \sum[(T_{max} + T_{min})/2] - T_{base} \quad (1)$$

where T_{max} is the maximum daily air temperature at 1.5 m above ground level, T_{min} is the minimum daily air temperature, and T_{base} is the temperature at which cellular activity stops [19]. The base growth temperature (T_{base}) for forage species in this study was 5 °C, as determined by previous studies performed under similar conditions [17,20].

2.3. Yield Components

Three tillers per plot were marked at the base with different-colored clips to identify them individually. The total leaf blade length (LBL) per tiller was recorded at three-day intervals and the AHM was recorded at each defoliation point. The first sampling was conducted in the spring of 2015.

2.4. Nutritive Value

Nutritive value data were obtained at each defoliation event using near-infrared spectroscopy (NIRS) with a FOSS-NIRSystems MODEL 6500 (FOSS NIRSystem Inc. in North America, Silver Spring, MD). The data collected included the concentration of crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), metabolizable energy (ME), water-soluble carbohydrates (WSC), and dry matter (DM) using the prediction equations developed based on the wet chemistry results developed by the Animal Nutrition Laboratory of the Universidad Austral de Chile. The standard errors and the R^2 values (which are listed in parentheses) of the cross-validation used were 0.78 (0.98), 1.92 (0.93), 1.19 (0.93), 0.30 (0.84), and 6.99 (0.96) for CP, NDF, ADF, ME, and WSC, respectively.

2.5. Statistical Analysis and Model Selection

The dataset was analyzed using SAS (SAS Institute, V11.0, 2014). Descriptive statistics were used to estimate and classify the coefficient of variation (CV) as high (CV > 30%), medium (CV = 10–30%), and low (CV < 10%) [21]. In addition, each variable in the dataset was tested for normality (Shapiro–Wilks) and homoscedasticity (Levene). When parametric assumptions were not met, data were transformed using either natural logarithms or square roots. Data points outside of ±2 standard deviations of the average were considered as outliers [22] and were removed from the analysis. The models were estimated by using the average of defoliation by season within each species.

Four-parameter Logistic and Gompertz models were selected because they are the most commonly used models for grass growth modeling [10,11] and they also allow for the equalization of the error level during validation. Model selection was performed based on the Akaike information criterion (AIC) and Bayesian information criterion (BIC). The AIC is a technique based on the in-sample fit to estimate the likelihood of a model to predict/estimate the future values, while BIC is another criterion for model selection that measures the trade-off between the model fit and complexity of the model [23]. Moreover, the coefficient of determination (R^2) and correlation (r) were used to further examine the goodness-of-fit of the model.

$$\mathrm{AIC} = 2k - 2\,x\ln(L) \tag{2}$$

where k is the total number of parameters in the model, including the intercept and σ^2, and L is the maximum likelihood or least squares.

$$\mathrm{BIC} = -2\ln(L) + K\log(n) \tag{3}$$

where L is the maximum value of the likelihood function of the model, and n is the number of data or observations.

$$\mathrm{RMSE} = \sqrt{\frac{\sum_{i=1}^{n}[(y_i) - y_i]2}{n}} \tag{4}$$

where $E(y_i)$ and y_i are the responses between the observed and predicted values for the value i, respectively, and n is the sample size (n = 1080 in this study).

[Equation (5)] Four-parameter Logistic regression

$$Y = c + \frac{(d-c)}{\left(1+10^{(a.(b-x))}\right)} \tag{5}$$

where Y is the random variable to evaluate, a is the GR, b is the maximum growth point, c is the inferior asymptote, d is the superior asymptote, and x is the independent variable.

Four-parameter Gompertz

$$Y = a + (\,b - a)Exp(-Exp(-c(x-d))) \tag{6}$$

where Y is the random variable to evaluate, a is the inferior asymptote, b is the superior asymptote, c is the GR for a given time x, d is the inflection point, and x is the independent variable.

The nutritive value of plants is best represented by a simple linear or quadratic regression [24]. A simple linear regression was used for CP, NDF, ADF, WSC, and DM data, while quadratic regression was used for ME and some WSC data.

Simple linear regression model

$$Yt = \beta_0 + \beta_{1\times 1} + \beta_{2\times 2} + \ldots + \beta_p X_p + \varepsilon \tag{7}$$

Quadratic linear regression model

$$Yt = \beta_0 + \beta_1 X + \beta_{2\times 2} + \beta_{3\times 3} \ldots + \beta_p X_p + \varepsilon \tag{8}$$

where Y_t is the dependent variable, X_1, X_2 … , Xp are independent variables, and β_0, β_1, β_2, … , β_p are parameters of the independent variable. β_o is the "constant" intercept, β_i ($i > 0$) are the parameters with respect to each independent variable, and p is the number of independent parameters in the regression.

2.6. Model Validation

Models were validated according to accuracy, measured as the average distance between each observed data point and the equivalent predicted line.

$$Af = 10^{\sum[\log(\frac{x_p}{x_b})]/n} \tag{9}$$

where x_p is the value of the specific maximum predictive growth rate (°C^{-1}), x_b is the value of the maximum specific observed growth rate (°C^{-1}), n is the number of observations, and Af is the accuracy value in the prediction.

The dataset used for validation of the models was obtained from samples collected in the same experimental plots (n = 300). This dataset was not used in the model development. Thus, models were cross-validated by evaluating the percent variation of data that could be explained by the model [25,26]. The percent variation was considered the coefficient of determination (R^2) and was associated with the coefficient of correlation, which was developed using minimum squares [27].

3. Results

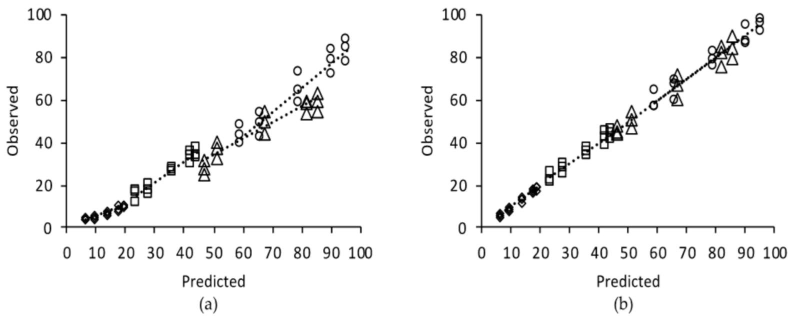
3.1. Grass Growth

A summary of the selection criteria for both models and species for both LBL and AHM is presented Table 1. The Gompertz model presented the highest AIC values in the spring for both species (*L. perenne* and *B. valdivianus*) with 0.52 for LBL, whereas the Logistic model showed the lowest AIC value in the spring for both species with 0.48. The Gompertz model only had a lower BIC value in the spring when compared to the Logistic model. The R^2 and RMSE were similar between seasons and species (Figures 1–4).

Table 1. Selection criteria values to evaluate the Logistic and Gompertz models to predict the leaf blade length and accumulated herbage mass production as a function of the accumulated growing degree-days.

Species	Season	Model	Leaf Blade Length (cm)				Accumulated Herbage Mass (kg DM ha^{-1})			
			AIC	BIC	RMSE	R^2	AIC	BIC	RMSE	R^2
L. perenne	Summer	Logistic	0.55	43.19	0.76	0.93	0.54	194.23	116.65	0.97
		Gompertz	0.45	43.61	0.77	0.93	0.46	194.57	117.96	0.97
	Autumn	Logistic	0.51	92.75	3.96	0.92	0.56	189.51	99.65	0.92
		Gompertz	0.49	92.84	3.97	0.92	0.44	189.98	101.23	0.92
	Winter	Logistic	0.51	78.66	2.48	0.93	0.57	174.03	59.50	0.97
		Gompertz	0.49	78.76	2.48	0.93	0.43	174.57	60.57	0.97
	Spring	Logistic	0.48	102.78	5.53	0.92	0.52	210.33	199.50	0.94
		Gompertz	0.52	102.61	5.50	0.92	0.48	210.52	200.77	0.94
B. valdivianus	Summer	Logistic	0.53	54.56	1.11	0.96	0.49	209.90	196.68	0.94
		Gompertz	0.47	54.83	1.12	0.96	0.51	209.79	195.95	0.94
	Autumn	Logistic	0.57	95.51	4.34	0.95	0.42	192.09	108.63	0.95
		Gompertz	0.43	96.06	4.42	0.94	0.58	191.46	106.36	0.95
	Winter	Logistic	0.54	78.46	2.46	0.94	0.61	190.77	103.95	0.93
		Gompertz	0.46	78.76	2.48	0.93	0.39	191.67	107.09	0.92
	Spring	Logistic	0.48	93.66	4.08	0.94	0.53	215.24	234.95	0.94
		Gompertz	0.52	93.51	4.06	0.94	0.47	215.48	236.88	0.94

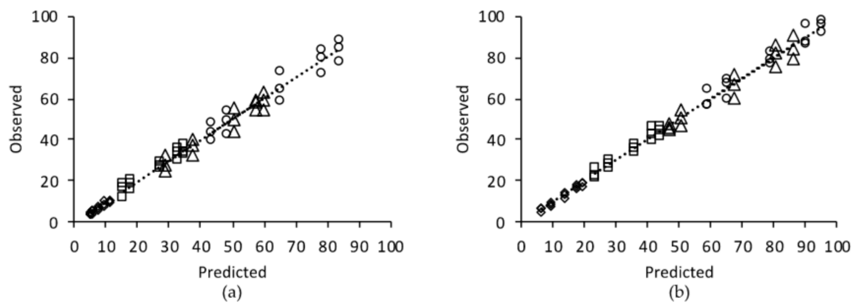
L. perenne: *Lolium perenne* L., *B. valdivianus*: *Bromus valdivianus* Phil., AIC: Akaike information criterion, BIC: Bayesian information criterion, RMSE: Root-mean-square error, and R^2: Determination coefficient.



Summer (◊): $p < 0.0001$ $R^2 = 0.96$ RMSE = 1.02
Autumn (Δ): $p < 0.0001$ $R^2 = 0.94$ RMSE = 4.00
Winter (□): $p < 0.0001$ $R^2 = 0.94$ RMSE = 2.26
Spring (○): $p < 0.0001$ $R^2 = 0.94$ RMSE = 3.76

Summer (◊): $p < 0.0001$ $R^2 = 0.96$ RMSE = 1.02
Autumn (Δ): $p < 0.0001$ $R^2 = 0.94$ RMSE = 4.00
Winter (□): $p < 0.0001$ $R^2 = 0.93$ RMSE = 2.38
Spring (○): $p < 0.0001$ $R^2 = 0.93$ RMSE = 3.88

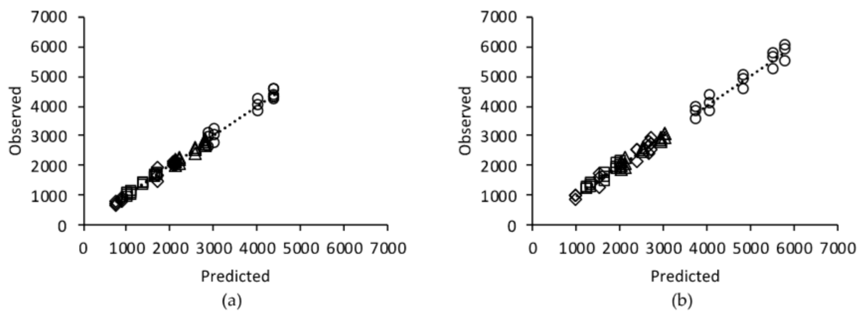
Figure 1. Observed v. predicted data for leaf blade length as calculated by the four-parameter Logistic model for *Lolium perenne* L. (**a**) and *Bromus valdivianus* Phil (**b**). R^2 = Determination coefficient.; RMSE = Root mean square error.



Summer (◊): $p < 0.0001$ $R^2 = 0.93$ RMSE = 0.71
Autumn (Δ): $p < 0.0001$ $R^2 = 0.93$ RMSE = 3.65
Winter (□): $p < 0.0001$ $R^2 = 0.93$ RMSE = 2.29
Spring (○): $p < 0.0001$ $R^2 = 0.92$ RMSE = 5.06

Summer (◊): $p < 0.0001$ $R^2 = 0.96$ RMSE = 1.02
Autumn (Δ): $p < 0.0001$ $R^2 = 0.94$ RMSE = 4.00
Winter (□): $p < 0.0001$ $R^2 = 0.93$ RMSE = 2.38
Spring (○): $p < 0.0001$ $R^2 = 0.93$ RMSE = 3.88

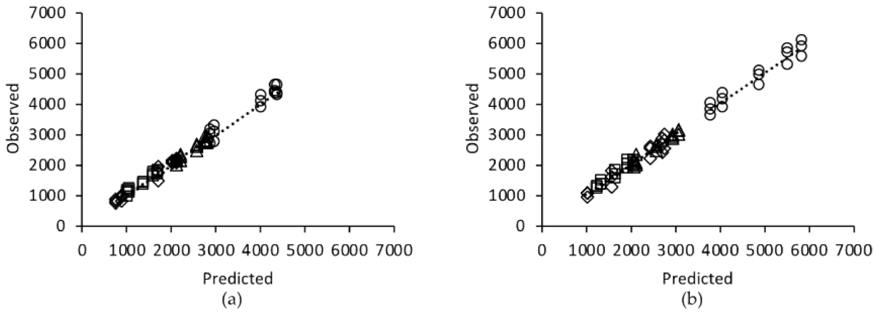
Figure 2. Observed v. predicted data for leaf blade length as calculated by the four-parameter Gompertz model for *Lolium perenne* L. (**a**) and *Bromus valdivianus* Phil (**b**). R^2 = Determination coefficient.; RMSE = Root mean square error.



Summer (◊): $p < 0.0001$ $R^2 = 0.97$ RMSE = 107.3
Autumn (Δ): $p < 0.0001$ $R^2 = 0.92$ RMSE = 91.67
Winter (□): $p < 0.0001$ $R^2 = 0.97$ RMSE = 54.73
Spring (○): $p < 0.0001$ $R^2 = 0.94$ RMSE = 183.5

Summer (◊): $p < 0.0001$ $R^2 = 0.94$ RMSE = 180.9
Autumn (Δ): $p < 0.0001$ $R^2 = 0.95$ RMSE = 99.93
Winter (□): $p < 0.0001$ $R^2 = 0.93$ RMSE = 95.62
Spring (○): $p < 0.0001$ $R^2 = 0.94$ RMSE = 216.1

Figure 3. Observed v. predicted data for accumulated herbage mass production according to the four-parameter Logistic model for *Lolium perenne* L. (**a**) and *Bromus valdivianus* Phil (**b**). R^2 = Determination coefficient.; RMSE = Root mean square error.



Summer (◊): $p < 0.0001$ $R^2 = 0.97$ RMSE = 108.5
Autumn (Δ): $p < 0.0001$ $R^2 = 0.92$ RMSE = 93.12
Winter (□): $p < 0.0001$ $R^2 = 0.97$ RMSE = 55.72
Spring (○): $p < 0.0001$ $R^2 = 0.94$ RMSE = 184.7

Summer (◊): $p < 0.0001$ $R^2 = 0.94$ RMSE = 180.3
Autumn (Δ): $p < 0.0001$ $R^2 = 0.95$ RMSE = 97.84
Winter (□): $p < 0.0001$ $R^2 = 0.92$ RMSE = 98.51
Spring (○): $p < 0.0001$ $R^2 = 0.94$ RMSE = 217.9

Figure 4. Observed v. predicted data for accumulated herbage mass production according to the four-parameter Gompertz model for *Lolium perenne* L. (**a**) and *Bromus valdivianus* Phil (**b**). R^2 = Determination coefficient.; RMSE = Root mean square error.

Table 2 presents the parameterization of both models for LBL and AHM. The Gompertz model exhibited the greatest values (between 0.008 and 0.01) for the slope of the tangent line to the inflection point across all seasons for LBL. The lowest slope value for GR was found with the Logistic model during the summer for *L. perenne* and *B. valdivianus.* This indicates a low GR for grass during this season, compared to those of autumn and spring. The slope values reported refer to the linear period of the exponential growth curve. The AHM exhibited the same pattern as LBL did, but with different values, varying from 0.007 to 0.021 (Table 2). The highest values for LBL and AHM were observed in the Gompertz model during the spring (99 cm and 6.025 kg DM ha^{-1}, respectively). The lowest values were found in the winter for both species in the Logistic model. The parameterization produced coordinates of AGDD X between 201.8 in the autumn and 303.9 in the summer for LBL. For AHM, the derivative varied between 188.1 and 267 AGDD, which was the maximum growth point at which the slope began to change (Table 2).

Table 2. Model parameterization of the four-parameter Logistic and Gompertz models for *Lolium perenne* L. and *Bromus valdivianus* Phil. during the four seasons of the year.

Species	Season	Model	Leaf Blade Length (cm)				Accumulated Herbage Mass (kg DM ha^{-1})			
			a-GR	b-P_{max}	c-A_{Inf}	d-A_{Sup}	a-GR	b-P_{max}	c-A_{Inf}	d-A_{Sup}
L. perenne	Summer	Logistic	0.006 ± 0.003	303.9 ± 28.1	4.25 ± 0.74	11.45 ± 1.25	0.015 ± 0.004	244.9 ± 9.7	764.7 ± 74.3	2106 ± 52.2
		Gompertz	0.008 ± 0.004	288.1 ± 42.7	4.46 ± 0.55	12.67 ± 0.55	0.021 ± 0.004	222.3 ± 10.3	773.3 ± 67.8	2131 ± 62.7
	Autumn	Logistic	0.007 ± 0.003	220.1 ± 26.2	25.56 ± 5.79	60.12 ± 2.81	0.01 ± 0.005	249.1 ± 17.1	2116.9 ± 70.9	2822 ± 51.9
		Gompertz	0.01 ± 0.005	201.8 ± 19.8	28.3 ± 3.00	60.83 ± 3.33	0.02 ± 0.005	225.1 ± 18.2	2126 ± 58.3	2842 ± 66.3
	Winter	Logistic	0.009 ± 0.003	250.3 ± 17.2	14.86 ± 2.00	34.79 ± 1.5	0.009 ± 0.002	265.4 ± 11.9	1002 ± 47.3	1735 ± 44.1
		Gompertz	0.01 ± 0.004	227.5 ± 17.4	15.4 ± 1.45	35.53 ± 1.91	0.01 ± 0.003	242.8 ± 13.0	1023 ± 35.4	1776 ± 61.3
	Spring	Logistic	0.008 ± 0.003	262.5 ± 21.2	41.97 ± 4.87	84.32 ± 4.35	0.01 ± 0.008	242.9 ± 16.0	2912 ± 120.5	4415 ± 84.4
		Gompertz	0.01 ± 0.004	240.6 ± 21.3	43.6 2 ± 3.26	86.44 ± 5.66	0.02 ± 0.008	220.3 ± 16.2	2916 ± 114.6	4429 ± 95.2
B. valdivianus	Summer	Logistic	0.006 ± 0.002	245.4 ± 21.1	4.84 ± 1.91	19.71 ± 1.30	0.01 ± 0.003	204.8 ± 15.4	884.03 ± 197	2736 ± 97.2
		Gompertz	0.009 ± 0.003	224.6 ± 18.7	6.00 ± 1.08	20.44 ± 1.72	0.02 ± 0.005	188.1 ± 11.3	991.4 ± 117	2751 ± 107.2
	Autumn	Logistic	0.009 ± 0.003	264.5 ± 15.2	45.38 ± 3.37	86.0 ± 3.10	0.009 ± 0.003	266.1 ± 13.7	2007 ± 79.7	3067 ± 75.3
		Gompertz	0.01 ± 0.004	241.5 ± 16.7	46.40 ± 2.58	88.27 ± 4.34	0.01 ± 0.004	245.5 ± 14.4	2039 ± 60.4	3118 ± 97
	Winter	Logistic	0.007 ± 0.003	244.67 ± 21.7	22.2 ± 2.9	44.85 ± 2.00	0.008 ± 0.003	267.0 ± 18.6	1221 ± 83	2056 ± 79.3
		Gompertz	0.01 ± 0.004	221.9 ± 20	23.4 ± 1.73	45.78 ± 2.61	0.01 ± 0.004	242.3 ± 21.6	1237 ± 65	2113 ± 120
	Spring	Logistic	0.006 ± 0.002	256.54 ± 22.4	56.6 ± 5.15	97 ± 4.20	0.007 ± 0.003	264.2 ± 19.5	3699 ± 226.8	5891 ± 210.7
		Gompertz	0.01 ± 0.003	235 ± 20.8	59.1 ± 2.86	99 ± 5.33	0.01 ± 0.004	241.4 ± 20.3	3788 ± 151	6025 ± 294.3

Average ± standard error of *L. perenne*: *Lolium perenne* L., *B. valdivianus*: *Bromus valdivianus* Phil., GR: Growth rate, P_{max}: Point of maximum growth, A_{Inf}: Inferior asymptote, A_{Sup}: Superior asymptote.

3.2. Nutritive Value

All nutritional variables were fitted to either a simple linear regression or a quadratic regression model. These models were adjusted in the range of 90–450 AGDD. Table 3 summarizes the models that best fitted the data for *L. perenne* and *B. valdivianus* across all seasons. The CP concentrations during the autumn, winter, and spring were best fitted by a linear regression, while the quadratic model was most accurate for summer data (R^2 = 0.87), autumn and spring (R^2 = 0.96). However, the response was similar between species.

Table 3. Regression models for accumulated growing degree-days (X factor) versus nutritive value (Y factor) of *Lolium perenne* L. and *Bromus valdivianus* Phil. The standard error of each coefficient is presented in parentheses.

Variable	Species	Season	Model	R^2	RMSE	$p < \|t\|$
CP (g 100 g^{-1})	*L. Perenne*	Summer	Y = 18.55(1.34) + 0.032(0.01) × AGDD−9.532e − 5(2.06 × 10^{-5}) × AGDD^2	0.87	1.08	0.001
		Autumn	Y = 27.98(0.36) − 0.02(0.001) × AGDD	0.96	0.60	0.001
		Winter	Y = 20.69(0.32) − 0.01(0.001) × AGDD	0.95	0.53	0.001
		Spring	Y = 22.92(0.54) − 0.03(0.001) × AGDD	0.96	0.90	0.001
	B. valdivianus	Summer	Y = 17.83(1.12) + 0.02(0.009) × AGDD − 7.6161 × 10^{-5} (1.73 × 10^{-5}) × AGDD^2	0.85	0.91	0.001
		Autumn	Y = 30.471(0.48) − 0.01(0.001) × AGDD	0.91	0.81	0.001
		Winter	Y = 23.88(0.32) − 0.02(0.001) × AGDD	0.96	0.54	0.001
		Spring	Y = 23.29(0.60) − 0.03(0.002) × AGDD	0.95	1.00	0.001
ME (Mcal kg DM^{-1})	*L. perenne*	Summer	Y = 2.24(0.06) + 0.002(5.1 × 10^{-4}) × AGDD − 6.05 × 10^{-6} (9.2 × 10^{-7}) × AGDD^2	0.81	0.05	0.001
		Autumn	Y = 2.68(0.01) + 0.0003(8.6 × 10^{-5}) × AGDD − 9.70 × 10^{-7} (1.5 × 10^{-7}) × AGDD^2	0.91	0.01	0.001
		Winter	Y = 2.61(3.03) + 2.6 × 10^{-4}(3.6 × 10^{-4}) × AGDD − 1.46 × 10^{-6} (5.5 × 10^{-7}) × AGDD^2	0.86	0.03	0.021
		Spring	Y = 2.59(0.02) + 2.6 × 10^{-4}(2.2 × 10^{-4}) × AGDD − 9.40 × 10^{-7} (4.0 × 10^{-7}) × AGDD^2	0.75	0.02	0.001
	B. valdivianus	Summer	Y = 2.29(0.02) + 7.2 × 10^{-4}(1.7 × 10^{-4})×AGDD − 1.96 × 10^{-6} (3.1 × 10^{-7}) × AGDD^2	0.91	0.02	0.001
		Autumn	Y = 2.57(0.01) + 3.0 × 10^{-4}(1.13 × 10^{-4})×AGDD − 7.64 × 10^{-7}(2.1 × 10^{-7}) × AGDD^2	0.69	0.01	0.004
		Winter	Y = 2.50(0.02) + 7.3 × 10^{-5}(2.2 × 10^{-4}) × AGDD − 9.11 × 10^{-7}(4.1 × 10^{-4}) × AGDD^2	0.87	0.02	0.049
		Spring	Y = 2.50(0.03) + 8.2 ×10^{-4} (2.5 × 10^{-4}) × AGDD − 2.11 × 10^{-6} (4.6 × 10^{-7}) × AGDD^2	0.83	0.02	0.001
NDF (g 100 g^{-1})	*L. perenne*	Summer	Y = 42.37(0.45) + 0.01(0.001) × AGDD	0.78	0.75	0.001
		Autumn	Y = 39.56(0.60) + 0.03(0.002) × AGDD	0.95	1.00	0.001
		Winter	Y = 43.02(0.28) + 0.01(9.6 ×1 0^{-4}) × AGDD	0.94	0.47	0.001
		Spring	Y = 35.08(1.29) + 0.06(0.004) × AGDD	0.93	2.13	0.001
	B. valdivianus	Summer	Y = 50.85(0.42) + 0.01(0.001) × AGDD	0.90	0.71	0.001
		Autumn	Y = 49.36(0.49) + 0.02(0.001) × AGDD	0.92	0.82	0.001
		Winter	Y = 50.10(0.37) + 0.01(0.001) × AGDD	0.91	0.61	0.001
		Spring	Y = 51.78(0.34) + 0.02(0.001) × AGDD	0.98	0.57	0.001
ADF (g 100 g^{-1})	*L. Perenne*	Summer	Y = 19.62(0.55) + 0.02(0.001) × AGDD	0.92	0.92	0.001
		Autumn	Y = 20.34(0.49) + 0.02(0.001) × AGDD	0.93	0.85	0.001
		Winter	Y = 20.90(0.70) + 0.01(0.002) × AGDD	0.93	0.59	0.001
		Spring	Y = 17.80(0.80) + 0.04(0.002) × AGDD	0.94	1.34	0.001
	B. valdivianus	Summer	Y = 28.23(0.47) + 0.01(0.001) × AGDD	0.87	0.78	0.001
		Autumn	Y = 23.70(0.49) + 0.02(0.001) × AGDD	0.92	0.81	0.001
		Winter	Y = 22.81(0.70) + 0.02(0.002) × AGDD	0.89	1.16	0.001
		Spring	Y = 20.51(0.80) + 0.03(0.002) × AGDD	0.94	1.33	0.001

Table 3. *Cont.*

Variable	Species	Season	Model	R^2	RMSE	$p <$ |t|
WSC (g 1000 g^{-1})	*L. Perenne*	Summer	Y = 72.85(3.41) + 0.17(0.02) × AGDD − 1.8 × 10^{-4} (5.2 × 10^{-5}) × AGDD^2	0.93	2.75	0.004
		Autumn	Y = 89.71(4.88) + 0.17(0.04) × AGDD − 1.8 × 10^{-4} (7.5 × 10^{-5}) × AGDD^2	0.87	3.94	0.030
		Winter	Y = 74.46(5.27) + 0.20(0.01) × AGDD	0.90	8.71	0.001
		Spring	Y = 60.97(8.4) + 0.41(0.07) × AGDD − 4.7 × 10^{-4} (1.3e−04) × AGDD^2	0.91	6.80	0.003
	B. valdivianus	Summer	Y = 67.71(3.43) + 0.16(0.02) × AGDD − 1.9 × 10^{-4} (5.2 × 10^{-5}) × AGDD^2	0.90	2.77	0.003
		Autumn	Y = 71.40(3.16) + 0.15(0.03) × AGDD − 1.6 × 10^{-4} (5.56 × 10^{-5}) × AGDD^2	0.91	2.92	0.013
		Winter	Y = 76.43(2.91) + 0.09(0.009) × AGDD	0.88	4.82	0.001
		Spring	Y = 80.56(3.87) + 0.14(0.03) × AGDD − 1.5 × 10^{-4} (5.9 × 10^{-5}) × AGDD^2	0.88	3.13	0.021

CP: Crude protein, ME: Metabolizable energy, NDF: Neutral detergent fiber, ADF: Acid detergent fiber, WSC: Water soluble carbohydrates, *L. perenne*: *Lolium perenne* L., *B. valdivianus*: *Bromus valdivianus* Phil., R^2: Determination coefficient, RMSE: Root-mean-square error, AGDD: Accumulated growing degree-days, Y: Random variable to evaluate.

The energy concentration decreased appreciably with plant maturity, affecting its nutritive value and consequently animal response. This quadratic pattern for the ME concentration can be explained graphically using a Gaussian function. The simple linear regression demonstrated the best fit to predict concentrations of ADF and NDF in both species in all seasons. The R^2 values varied from 0.78 for *L. perenne* in the summer to 0.98 for *B. valdivianus* in the summer and spring. The highest values of the b coefficient in the regression were obtained for *B. valdivianus*, demonstrating that this species has relatively higher ADF and NDF contents than *L. perenne*. The rate of change did not vary greatly between species, and all values were nonzero. The ADF and NDF concentrations increased proportionally with AGDD in both forage species, with 20% greater concentrations in *B. valdivianus*.

Both NDF and CP contents were greater in *B. valdivianus* than in *L. perenne* (Table 3). The AGDD was inversely proportional to the protein concentration, demonstrating that the CP content decreased as the pasture advanced in its growth cycle toward maturity. Thus, for every increase of 10 AGDD, the protein concentration decreased by 0.3 percent.

Both the ME and WSC had better predictions from the quadratic equations (higher R^2). However, this was not true for WSC in the winter, where the linear regression showed a better fit for both species (Table 3). Early growth stages for these species, in which energy is stored, occur during the first 90 to 270 AGDD.

4. Discussion

4.1. Grass Growth

A variety of models can be used to describe and estimate grass growth and nutritive value under different environmental conditions. Complex models use exogenous and inherent grass variables as inputs to obtain precise calculations of the parameters [28,29], but many times, it is difficult for producers to collect all the necessary data. Therefore, a permanent challenge is the use of the minimum number of variables that provide a good estimation of grass growth and the model's ease of use. In this study, TT and season were the only prediction variables used to determine the herbage mass and nutritive value of *L. perenne* and *B. valdivianus*, demonstrating that AGDD is a reliable tool [17]. The R^2 value greater than 0.9 and the low RMSE (Table 1) demonstrate that the Logistic and Gompertz models with TT as the prediction variable are accurate tools in the description and prediction of the LBL and AHM of *L. perenne* and *B. valdivianus* grass.

The differences found between seasons for the growth parameters can be primarily explained by the differences in metabolic activity in the grass over the course of the year. In the winter, the metabolic activity of plants can be reduced to 0 [30], and during the summer, the GR is reduced when optimal temperatures are exceeded [31]. During the spring and autumn, when there is an adequate balance between temperature and precipitation, grass metabolic activity can reach 90%, resulting in a greater GR [32]. Therefore, climate is an important factor regulating herbage production and nutritive value [33]. The sigmoid growth reported in this study, explained by both four-parameter models (Logistic and Gompertz) across seasons of the year, accurately described the grass growth, and they have been commonly used in studies that evaluate the growth dynamics of plant communities in different environments [34]. The development of these growth models and their parameters are important when comparing the GR of different species during the year to determine the most adequate DF. Other researchers that have used TT and HT as prediction variables in models to estimate grass growth have arrived at a similar conclusion; the sigmoid curve best describes the growth of a plant community, as it considers distinct developmental phases and is sufficiently robust [13].

The sinusoidal models to predict AHM present some limitations for *L. perenne* in the autumn and for *B. valdivianus* in the winter, resulting in less precise predictions in those seasons. In fact, a P_{max} growth of 40 AGDD was reached earlier than in the other seasons (Table 2). However, the maximum grass growth was estimated at 30 AGDD before what was observed in the field. Pulina et al. [35] suggested that these differences could be attributed to the sensitivity of the models to extreme values during data collection.

The parameters obtained and presented in this study agreed with those obtained by other researchers at different locations using other mathematical tools that integrate distinct climatic and soil variables [28,36]. Likewise, the effect of the AGDD on grass growth is clear and has been widely documented, suggesting that the effect of the AGDD on AHM is a nonlinear response [37].

4.2. Nutritive Value

Environmental conditions not only affect LBL and AHM, but also leaf appearance rate and grass phenology [38,39]. Therefore, it plays an important role in the establishment of grazing frequency, as nutrient concentration varies as a function of TT, season, and other factors [40,41]. The relationships found in the present study between AGDD and nutritive value across the different seasons of the year show a dependency in terms of quality in each species (Table 3). Robbins [42] reported an inverse linear reduction in the CP concentration and a direct linear relationship between the levels of NDF and ADF in grasses that had more AGDD at the defoliation time, which agreed with the current study.

The WSC patterns were similar in *L. perenne* and *B. valdivianus* and were best described by a quadratic model for summer, autumn, and spring. However, a linear model was best for winter, similarly to what was reported by Archontoulis and Miguez [10], as well as Bilge et al. [43]. This implies that in the winter, the herbage accumulated a greater WSC concentration explained by the continuation of photosynthesis and decreased growth, due to the lower temperatures. During the other seasons, grass growth continued at a higher rate than in winter, resulting in the use of the stored WSC [44,45]. Based on the quadratic model, WSC storage begins at 40 AGDD post-defoliation until approximately 270 to 360 AGDD. After that, the grass no longer accumulates WSC linearly, because of the favorable environmental conditions that allow grass growth and tissue renewal, which requires energy consumption. This is also shown by the fact that *L. perenne* and *B. valdivanus* have the highest concentrations of WSC during the winter.

The differences in values for the intercepts in the linear and quadratic regressions for seasons and species were relatively similar for most of the nutritive variables assessed. However, there were differences between seasons for NDF and ADF, with *B. valdivianus* having a greater intercept than *L. perenne,* and with autumn as the season that presented the lowest fiber concentration. Some studies have reported that this occurs because, in the spring, grass growth increases and quickly entering into the reproductive stage. This changes the leaf–stem ratio, and the maturation process requires the quick transport of nutrients to the roots and for seed formation [46,47].

Most models developed to evaluate grass quality have based their results on the NDF and ADF concentration, organic matter digestibility (OMD), CP, nitrogen indigestible in neutral detergent (NIND), and nitrogen indigestible in acid detergent (NIAD) [48–50]. However, few studies have incorporated ME. Some models have estimated their parameters based on the equations for net energy for lactation or maintenance (NE_L or NE_M, respectively) [51,52], and have considered the existing relationship between plant maturity and fiber, as well as CP and OMD. This is because during the plant growth cycle, the ME and CP decrease while the fiber concentration increases [53]. However, in this study, ME concentration was best described by a quadratic equation, because the observed data increased from the start until the asymptote was reached, at which point the slope was equal to 0. After this point, the values fell even lower than those initially observed due to increased plant maturity (Table 3). Other studies have used equations with this kind of pattern to describe similar biological processes in grasses, which supports the results herein presented [54,55].

Finally, the CP and fiber concentrations presented a negative linear relationship with AGDD for all seasons. This demonstrates that at greater AGDD, the protein levels of grasses decrease [56,57]. In general, the CP concentration was well represented by the linear regressions, which reported a variation in the RMSE of 1.08 for *L. perenne* in the summer and up to 0.53 and 0.54 for *L. perenne* and *B. valdivianus*, respectively, in the winter. These values were similar to those reported by other authors [58,59], who developed models using their own logarithms and adjusted these to a nitrogen consumption curve and integrated environmental variables such as precipitation and soil fertility. Regardless of the model used to explain the variations in CP concentration, all arrived at the same conclusion; the protein concentration decreased as the plant's phenological age increased [60].

5. Conclusions

The grass growth of *L. perenne* and *B. valdivianus* over the course of the year in southern Chile can be accurately predicted by using both the four-parameter Logistic and Gompertz models by using AGDD as a predictor variable. Likewise, its nutritive value can be precisely predicted by using linear and quadratic regressions depending of the season of the year evaluated. The sinusoidal models were best suited to predict LBL and AHM, in every season and for both species.

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