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Article

Efficiency in biomass accumulation of diploid potato cultivars (*Solanum tuberosum*, Phureja Group) in contrasting environments at elevation

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ABSTRACT: Phureja Group potato is endemic and important for northern Andean countries such as Colombia, Ecuador and Venezuela, where it is grown over a wide range of elevation. The objective of the study was to compare the biomass accumulation of five potato cultivars in three contrasting environments in elevation from a latent response variable of vector nature, analogous to "heat efficiency index". Destructive samplings were carried to obtain biomass. A biomass accumulation model was proposed using a latent response variable that integrates total biomass per plant with thermal time, analogous to the "heat use efficiency index". The proposed latent response variable allowed measuring the efficiency in biomass accumulation and making comparisons between elevations and cultivars, with a nonparametric longitudinal variance analysis. The middle location was where the highest efficiency in accumulation of total biomass was observed. The accumulation of total biomass was slow at the higher elevation location during the vegetative stage, but it increased considerably after the initiation of the growth of tubers. The study showed a clear genotype-environment interaction, suggesting that biomass accumulation changes with elevation according to the cultivar. The methodology used in this study has the potential to be used in the longitudinal comparison of cultivars and environments, even when variations in elevation or temperature alter the length of growing cycles.

Key words: agrometeorological index, altitude, growth analysis, heat use efficiency, thermal time, longitudinal response variable.

INTRODUCTION

The Phureja Group corresponds to Andean diploid potato genotypes, cultivated on high elevations from central Peru to Ecuador, Colombia, and Venezuela (Berdugo-Cely et al. 2017; Ghislain et al. 2006; Hawkes 1990). For Colombia, the Phureja Group potato presents high importance for its production (Gallón et al. 2019; Seminario et al. 2021), consumption tradition (Cerón-Lasso et al. 2018) and diversity of genotypes, which include thirteen improved cultivars, developed by the Potato Genetic Improvement Program of the "Universidad Nacional de Colombia" (Ñústez 2018). The lack of studies related to the physiological response in contrasting productive environments and its interaction with different cultivars, has generated situations where cultivars are not sown in favorable conditions for best productivity and incorrect management practices have been carried out. In many cases, information relevant to cultivars better known as "Criolla Colombia" or, in other cases tetraploid cultivars, has been used, resulting in situations that limit the productive potential of the new cultivars and lead to discarding them by farmers (Valbuena et al. 2009).

Many weather variables influence growth and productivity of crops; however, temperature is among the most important factor (Jamsheed et al. 2023; Zhang et al. 2022). Temperature regulates the growth rate of multiple organisms including plants (Parthasarathi et al. 2013; Zhang et al. 2022) and in potato its importance in productivity and growth has been described by multiple authors (Navarre and Pavek 2014; Struik 2007b). Temperature has been used as an indicator of the physiological time, and it is considered more accurate than chronological time (Singh and Sing 2014). The thermal time methodology, described as degree days or growing degree days (GDD), allows growth to be related to ambient temperature from the quantification of the heat energy accumulated by a plant during a period (Ahmad et al. 2017; Yin et al. 2016; Zhou and Wang 2018). The use of GDD allows a description of the physiological response of the crop influenced by temperature, permitting comparisons of yield, biomass accumulation and a determination of the performance of a cultivar in different growing regions or planting seasons (Di Benedetto and Tognetti 2016; Zhou and Wang 2018). There are different proposals and models for estimating thermal time; one of the most used to date is the one proposed by Arnold (1959) useful in environments where the environmental temperature does not exceed the thresholds for the development of the crop. However, without the Arnold model, adaptations such as the one proposed by (McMaster and Wilhelm (1997) or more complex models can be used, with better performance for specific areas or non-linear models (Rodríguez et al. 2012; Unigarro et al. 2017; Yin et al. 2016; Zhou and Wang 2018). Biomass or dry mass is a destructive growth variable that provides direct information on fixed carbon and is used directly as total biomass or per organ, or in the construction of indirect measures such as indices (Hunt 1990). When studied longitudinally, incorporating time, these variables allow the development of models used in the analysis of growth that in turn allow us to study the differences in the total growth or distribution of biomass in an organ over time (Di Benedetto and Tognetti 2016). Indices that relate growth variables with environmental variables are called agrometeorological index (Ahmad et al. 2017; Jamsheed et al. 2023). One of them is the heat use efficiency (HUE) index proposed by Rajput (1980)[1]. The HUE typically describes efficiency in the accumulation of biomass (total or per organ) in terms of thermal time, calculated from a ratio between them (Ahmad et al. 2017; Jamsheed et al. 2023; Solanki et al. 2017).

HUE has been used in the description of growth mainly in short-cycle crops, such as the case of corn (*Zea mays* L.) (Jamsheed et al. 2023; Jan et al. 2022), mustard (Islam et al. 2019; Singh and Singh 2014), sesame (Raut and Bankar 2020), rice (Diwan et al. 2017), wheat (Solanki et al. 2017), sorghum (Prakash et al. 2017), millet (*Setaria itálica* L.) (Nandini and Sridhara 2019), peas (Devi et al. 2019) and potato (Darabi 2020; Han et al. 2022; Sakar et al. 2019) in a comparison of cultivars, treatments or production environments. However, in Andigenum potatoes there are no studies that use HUE as a response variable. HUE assessment is usually conducted at a specific time in the crop cycle, typically during harvest, these studies are known as "cross-sectional" present limitations in their conclusions by not considering the temporal dimension (Kesmodel 2018). Some studies have used HUE cross-sectionally at different stages of crop development to understand its dynamics over time (Darabi 2020; Jamsheed et al. 2023; Jan et al. 2022). However, appropriate methodologies for longitudinal data, such, as those described by Noguchi et al. (2012) are required to consider the temporal dimension adequately.

The objective of this research was to evaluate the biomass accumulation efficiency of diploid potato cultivars from Phureja Group in environments with variations in elevation. To achieve this, a form for estimating a latent response variable analogous to the HUE was proposed, which addressed the problems of overdispersion in the original data and allowed longitudinal comparison between cultivars in environments where the length of the growing season varied due to elevation.

MATERIALS AND METHODS

Plant material

Five improved diploid potato cultivars (*Solanum tuberosum*, Phureja Group) were evaluated. Table 1 descript information related to its adaptation range in elevation in Colombia, department of origin and year of release for each cultivar.

[1] Rajput, R. P. (1980). Response of soybean crop to climate and soil environments. Indian Agricultural Research Institute. Rajput RP. Response of Soybean crop to climatic and soil environments. Ph.D. Thesis, 1980; IARI, New Delhi, India.

Table 1. Cultivar name, adaptation range and year of release to the market for the potato (*Solanum tuberosum*, Phureja Group) cultivars evaluated.

Cultivar	Elevation (masl)	Department (Colombia)	Release year
Criolla Dorada	2500 – 3200	Nariño	2015
Criolla Ocarina	2500 – 3200	Nariño	2015
Paola	2400 – 2800	Antioquia	2015
Violeta	2400 – 2800	Antioquia	2015
Criolla Colombia	2400 – 3200	Antioquia, Cundinamarca, Boyacá and Nariño	2005

Source: Elaborated by the authors using data from cultivar registration report (GIP, 2020; Ñústez 2011)

The experimental plots were established in March 2018 in three locations in Cundinamarca (Colombia) from two municipalities contrasting in elevation and geographically close (Table 2) characterized by an average annual precipitation of 745±143mm (IDEAM 2018)[2]. The localities were selected because they are traditional zones to produce potatoes from Phureja Group in Colombia of the province of "Sumapaz" (Ñústez-López and Rodríguez-Molano 2020), and they had maintained a pasture crop in the previous year. The high elevation (3200 masl) was an intervened area where tuber potatoes are generally produced for asexual seed, while the locations of middle (2700 masl) and low elevation (2300 masl) corresponded to traditionally production areas for fresh consumption.

Table 2. Location and characteristics of experimental localities.

Elevation (masl)	Municipality	Geographic location	Tave* (°C)	Tmin* (°C)	Tmax* (°C)	ARH* (%)	Zone life Holdridge (1971)
High (3200)	Sibaté	4°25'33.43"N 74°15'31.56"W	10.1	7.0	15.6	87.5	Montane moist forest
Middle (2700)	Sibaté	4°28'27.77"N 74°17'01.95"W	12.5	9.1	17.3	90.7	Lower montane dry forest
Low (2320)	Granada	4°30'02.88"N 74°22'23.74"W	15.4	13.1	18.4	95.0	Lower montane dry forest

Tave: Average temperature; Tmin: Minimum temperature; Tmax: Maximum temperature; ARH: Average relative humidity. *Data obtained with data-loggers established in each location (ELMA DT-171, Elma instruments, Ryttermarken-Denmark). Source: Elaborated by the authors.

At each location, three plots of 90 m^2 were established per cultivar and distributed at random. A density of 33,333 planting sites per hectare was used (1 m between the rows and 0.3 m between the planting sites) that was traditionally used by local farmers and similar to other authors (Lagos-Burbano and Betancourt-Andrade 2021; Ñústez-López and Rodríguez-Molano 2020; Saldaña-Villota and Cotes-Torres 2020). Tubers were used a seed, which were sown once by planting site. The tuber seeds were free of diseases or physiopathies, they presented a multiple sprouting stage and had a homogeneous size (20-25 g). Management practices were generally the same in all locations, including phytosanitary management, cultural practices, soil management and fertilization. For the soil management a dolomite lime (1 $t{\cdot}ha^{-1}$) was applied and incorporated at all localities one month before owing.

The crops were fertilized for major elements using 20 g of granulated fertilizer of grade 15-15-15 equivalent to an application of 100 $kg{\cdot}ha^{-1}$ of each of the major elements (nitrogen, phosphorus, and potassium) accord to Ñústez-López and Rodríguez-Molano (2020) and minor elements were applied with commercial products via foliar applications.

Temperature and degree-day determination

Environmental temperature in each location was recorded using ELMA DT–171 dataloggers (Elma instruments, Ryttermarken-Denmark) with hourly recording frequency. The emergence of the crop was established when the plot reached 80% for this

[2] [IDEAM] - Instituto de Hidrología, Meteorología y Estudios Ambientales. (2018). Datos climáticos históricos promediados por mes periodo 1981 a 2010. http://www.ideam.gov.co/web/tiempo-y-clima/clima%0A

attribute, from the moment the temperature was considered for the calculation of the GDD. The GDDs were estimated using the Eq. 1 proposed by Arnold (1959), using daily values of the i-th maximum temperature (${}_{max}T_i$), the i-th minimum temperature (${}_{max}T_i$), with $i = 1,2,\ldots, n$, where n represented the number of days. And finally, a constant for base temperature (T_b), taken as 2 °C and upper limit of 29 °C (Marulanda-Zapata et al, 2023; Saldaña-Villota and Cotes-Torres 2020; Soto et al. 2018).

$$GDD = \frac{1}{2}\sum_{i=1}^{n}(maxT_i + minT_i) - T_b \tag{1}$$

Biomass accumulation

Using a functional adjustment approach (Di Benedetto and Tognetti 2016; Hunt 1990), 10 samplings dates were carried out by location at the same time and were distributed throughout the crop cycle, (Table 2). For each sampling date, six plants per cultivar were used. The plants were collected randomly, but it was guaranteed not to take contiguous plants or plants from the edge of the plot. The plants were collected the same day and processed in the plant physiology laboratory of the Universidad Nacional de Colombia in Bogotá. The plants were dried in ovens at 75 °C (Thelco Model 16, Precision Scientific Company, Chicago, USA) by six days, but when the plants already showed tubercles, it was necessary to increase the number of days when they reached constant weight. The weight of each plant was recorded to estimate the total biomass per plant (BTo) equivalent to grams of dry mass.

Latent response variable - Heat use efficiency for Phureja Group potatoes

Biomass accumulation per locality and per crop was carried out using BTo values as the response variable and GDD as the explanatory variable. This relationship has usually been posited with nonlinear models as shown by Zhou and Wang (2018). For this study the relationship between BTo and GDD was established from the 27 regression models of the Statgraphics Centurion XVI statistical software (Statpoint Technologies INC 2013)[3], typically used in growth analysis, from which the 10 with the best fit were selected. The model with the best fit was selected from the less root mean square error (RMSE). Using the best fit model to describe biomass accumulation, a latent response variable was proposed, namely the heat efficiency index (HUE), which relates the BTo to the GDD, from a quotient between these variables. Considering that proposal it was a specific HUE for Phureja Group potatoes where the BTo is normalized with GDD, it was called "HUE_w".

Experimental design

To compare between cultivars and localities over time using HUE_w, the taxonomy of the experimental design with a nonparametric approach of Brunner et al. (2002) was used. An *F2LDF1 design* was established, where the acronym LD represents the longitudinal nature of the study, F1 is the within subject's factor associated with sampling times, and F2 the bifactorial structure associated with genotypes and environments. The first factor corresponded to cultivars (five levels: Criolla Colombia, Criolla Ocarina, Criolla Dorada, Paola and Violeta) and the second to evaluation locations (three levels: 2300, 2700 and 3200 masl).

Statistical analysis

A nonparametric longitudinal analysis of variance was performed for the *F2LDF1* design. The comparison between groups was based on the construction of confidence intervals with the longitudinal nonparametric approach developed by Brunner et al. (2002). For the interpretation and discussion of the intervals, the criterion of the confidence intervals described by

[3] Statpoint Technologies INC. (2013). Statgraphics Centurion XVI V16.2.04 (16.2.04).

Cumming et al. (2007) was used. The variable associated with the evaluation time involved the ten sampling points. These ranges by the nonparametric approach used, are monotonous in growth such as the GDD in each locality and even better, with the chronological time range associated with the days after emergency (DAE). By having chronological dates for sampling points, any metric could be used, such as the class mark of that range of variation in sampling times. The option finally used was the range of DAE, however a class mark would have generated the same result in the analysis of variance if the monotonous growth pattern exists. The analysis was carried out with the "nparLD" library with ANOVA Type statistics (Noguchi et al. 2012), and the plots with the "ggplot2" library (Wickham 2016) of the R statistical software (R Core team 2023).

RESULTS AND DISCUSSION

The GDD of each temporal sampling was estimated as the mean of the GDD of the three locations (Table 3). The sampling column omits the chronological times because they are different for each locality, however, the time range associated with emergency days (DAE) is presented. This is precisely the difficulty of comparing biomass accumulation in contrasting environments since development cycles are usually inherent in each elevation of the experimental locality. The GDD solves this limitation and allows the comparison of biomass accumulated normalized precisely by the thermal time for the different cultivars in the considered elevations.

Table 3. Growing degree-days (GDD) in each of the samplings for the three localities.

Sampling	Low elevation (2300 masl)		Middle elevation (2700 masl)		High elevation (3200 masl)		Mean
	DAE	GDD	DAE	GDD	DAE	GDD	GDD
1	9	152	10	118	12	111	127
2	18	245	19	221	24	214	227
3	24	344	30	345	34	300	330
4	32	441	38	435	45	429	435
5	38	523	48	541	56	539	534
6	48	661	56	637	68	658	652
7	54	760	64	735	80	758	751
8	62	873	75	858	93	868	866
9	69	965	87	975	108	1,002	980
10	76	1,125	94	1,109	114	1,105	1,113

DAE: days after emergence; GDD: Growing degree-days.Source: Elaborated by the authors.

Table 3 shows the samplings performed and the GDD for each one of them. It was observed that although the days vary between locations due to elevation, the GDD between locations remain within a range and are similar. Because the methodology of Noguchi et al. (2012) works with full factorial experiments, it requires the same levels over time and for this reason the estimation of a mean value of GDD for each of the samplings was performed to implement the analysis of variance in repeated measures. This does not mean that an improvement or correction in the response variable that considers the distances between sampling points and the distances between GDD and DAE cannot be carried out in subsequent studies.

Modeling of biomass accumulation as a function of thermal time

The response variable BTo was used to describe growth in terms of accumulated biomass. The thermal time in GDD was considered the explanatory variable of the physiological time. The direct relationship between plant growth and temperature was considered (Parthasarathi et al. 2013; Zhou and Wang 2018), as well as its monotonous increasing behavior with which it was possible to obtain different statistical models that allowed studying the relationship between the variables (Table 4).

Table 4. Main models selected with greater adjustment to the ratio of total biomass variables per plant and thermal time in accumulated degree-days.

Model	Equation	RMSE
1	$\widehat{BTo} = e^{(-1.87641 + 0.227493 * \sqrt{GDD})}$	0.531
2	$\widehat{BTo} = e^{(-11.0816 + 2.34191 * Ln(GDD))}$	0.559
3	$\widehat{BTo} = e^{(0.520769 + 0.00492015 * GDD)}$	0.607
4	$\widehat{BTo} = e^{(1.81629 + 0.00000362598 * GDD^2)}$	0.835
5	$\widehat{BTo} = e^{(5.17528 - (\frac{662.477}{GDD}))}$	0.864
6	$\widehat{BTo} = (-1.49175 + 0.0151605 * GDD)^2$	2.221
7	$\widehat{BTo} = (2.16387 + 0{,}0000119061 * (GDD)^2)^2$	2.336
8	$\widehat{BTo} = (-8.22446 + 0.673206 * \sqrt{GDD})^2$	2.430
9	$\widehat{BTo} = (-33.5476 + 6.62187 * Ln(GDD))^2$	2.830
10 (Linear)	$\widehat{BTo} = (-68.8671 + 0.256509 * GDD)$	58.800

$\widehat{BTo}$: Total estimated biomass per plant (g); GDD: Accumulated degree-days; RMSE: root mean square error. Source: Elaborated by the authors.

Of the series of models tested, only the two with better fit are presented, using as a selection criterion the RSME (Burnham and Anderson 1998). The functional form of the first model was selected in the list, as it presented the best fit by grouping the information of all cultivars in the evaluation environments, as well as for each cultivars independently. The functional form of the statistical model is described as:

$$y_i = exp(a + bx_i^{0.5}) + \varepsilon_i \tag{2}$$

where y_i was associated with the *i–th* response value (BTo), x_i represented the *i–th* value of the explanatory variable associated with the GDD, with a and b as model parameters and finally with ε_i as the residual errors. The models adjusted for each cultivar using the functional form in (2) showed a greater adjustment in the case of the "Criolla Colombia" cultivar (Table 5).

Table 5. Models adjusted by cultivating using out functional reference

Cultivar	Equation	RMSE
Criolla Colombia	$\widehat{BTo} = e^{(-1.93601 + 0.232237 * \sqrt{GDD})}$	0.466
Criolla Ocarina	$\widehat{BTo} = e^{(-1.80173 + 0.220568 * \sqrt{GDD})}$	0.472
Criolla Dorada	$\widehat{BTo} = e^{(-2.34741 + 0.238095 * \sqrt{GDD})}$	0.524
Paola	$\widehat{BTo} = e^{(-1.79297 + 0.228564 * \sqrt{GDD})}$	0.546
Violeta	$\widehat{Bto} = e^{(-1.50461 + 0.218048 * \sqrt{GDD})}$	0.541

Source: Elaborated by the authors.

All the evaluated cultivars showed a similar growth trend, however, the contrasting elevation between localities, modified the duration in days of the cultivation cycles, limiting the comparison between cultivars using chronological time. This condition limits the applicability of the methodology of Brunner et al. (2002); Noguchi et al. (2012), as it requires a defined sampling point and absence of covariates. In this sense, the consideration of thermal time as an alternative allows us to describe the physiological time of the crop although we have a differentiated development between localities. It seems logical to weight or standardize the BTo by the magnitude of the thermal time expressed in accumulated degree days (GDD) in such a way that the values at each sampling point are comparable, so a functional form such as in eq. 2 was used in principle to discover the relationship between BTo and GDD. This strategy allowed to standardize the accumulation of biomass by the GDD variable and thus generate the proposal that was finally used as a response variable in the longitudinal variance analysis to study the effect of the factors involved in the model.

The biomass accumulation model in eq. 2 is characteristic when the total biomass accumulation of some semi-annual crops is studied (Di Benedetto and Tognetti 2016). The biomass increase observed until the end of GC for diploid cultivars of the Phureja Group is attributable to tuberization, which extends from approximately 330 GDD to the end of GC.

Efficiency in the use of heat in Phureja Group potatoes

From the model represented by eq. 2, a latent variable was proposed to integrate the variables BTo and GDD. In this case the GDD that initially acted as an explanatory variable, now acted as a weight for the response variable BTo to create a new response variable (with justified integration based on its statistical relationship). The proposed latent variable was called Phureja Group potatoes heat use efficiency (HUEw) because of its relationship with the traditionally used HUE. However, this new variable is specific to the Grupo Phureja potatoes cultivars evaluated and its use in other crop species requires its estimation and evaluation, and it is not considered a replacement for the traditional HUE. The integration was based on the simplified non-linear model (without intercept) that was adjusted in each cultivar using the best fitted model in Table 4. The functional form used was:

$$y = exp(bx^{0.5}) \tag{3}$$

or $Lny = bx^{0.5}$ once the logarithm operator has been applied. Let y the vector of BTo and x the vector of GDD considered as fixed although its nature is random (Gujarati and Porter 2010). The Ln and $\sqrt{x}$ operators acted on each element of the vector, so that when doing an element–wise division (Cichocki et al. 2009), a vector associated with the parameter b and not a scalar was obtained, and such as usually operated. In this way b represented a vector with the same length as the response variable; so this response latent variable was labelled as HUE_w.

$$HUE_w = \frac{Ln(BTo_j)}{{GDD_j}^{1/2}} \tag{4}$$

with j=1,2,...,n; where n is the number of BTo or GDD records (with GDD>0). Recognizing that negative values can be obtained by applying the logarithmic function when $BTo_j<1$, it is recommended using a uniform scale homothetic transformation of all the data of the variable BTo so that the j-th Ln(BTo)≥0 (800 g instead of 0.8 kg in the particular measure of BTo).

The BTo (Fig. 1a.), like the HUE traditionally used (Fig. 1b.), have a greater dispersion when the thermal time is greater. The use of HUE_w achieved a residual variance approximately 100 times lower than the HUE (0.2829/0.0029), remaining relatively constant over time; this was obtained by fitting the model without elevation discrimination. This possibility of reducing variability is a desirable property in crop modeling, since it is usually part of one of the necessary assumptions in a large group of statistical analyses, especially those with a parametric approach. Another aspect that should be highlighted is that the HUEw is more intuitive since it is reasonable that the higher the GDD required to accumulate a certain amount of biomass, the lower the efficiency and not higher than the usual HUE, that is, the greater the need for degree days then less should be the measure of efficiency. It is precisely what this proposal achieves, which allows a direct and clear interpretation.

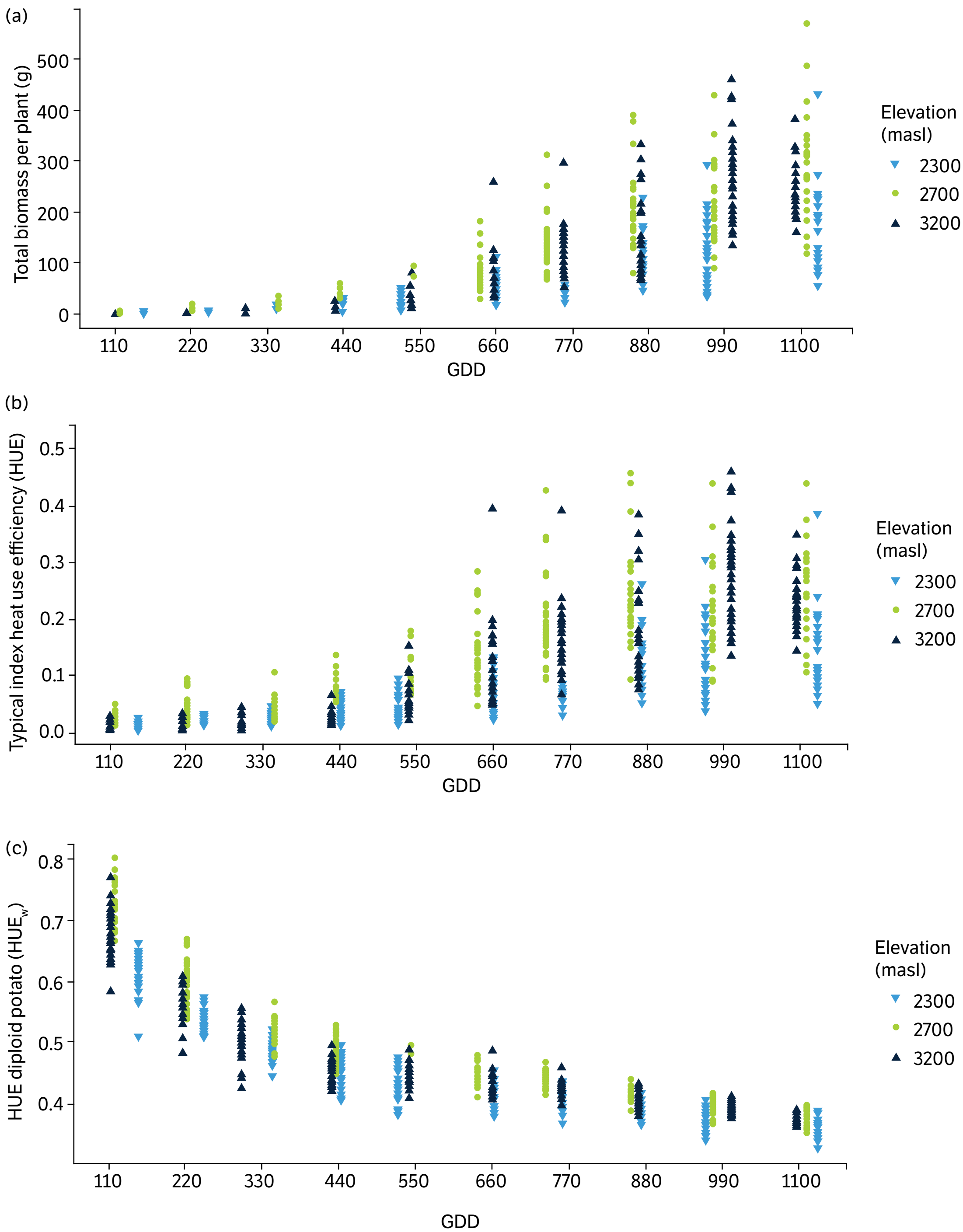

Figure 1. Dispersion over time in degrees days (GDD) of a) total biomass per plant (BTo), b) Typical heat use efficiency index (HUE) and c) latent response variable (HUEw). n = 900.

Source: Elaborated by the authors.

Longitudinal analysis of variance

In the longitudinal variance analysis (Table 6), double statistical interactions were evidenced for the location by time (L×T) and for cultivation by location (C×L), so the p–value of the effects was not interpreted from the main effects (Montgomery 2017). For a better understanding of the interactions, these were described from graphic representations.

Table 6. ANOVA Table using the heat efficiency latent variable (HUEw) by Location (L), Cultivar (C) and Time (T).

Source	L	C	T	L×T	C×T	C×L	L×T×C
p-value	9.69e-50	7.48e-12	2.20e-16	2.51e-12	1.27e-01	1.33e-03	1.83e-01

Source: Elaborated by the authors.

The methodology used in this research proposed by Noguchi et al. (2012) uses the statistical range "relative treatment efficiency" (RTE) as the response variable. The "RTE" is unitless and is interpreted as a probability measure, relative to the effect of a treatment with respect to a reference one (Nardone et al., 2016; Versace et al., 2018). The use of ranges has advantages such as the possibility of extracting information on the empirical distribution functions of the treatments or groups and makes them particularly suitable for studies with non-normal distributions (Noguchi et al. 2019).

For the interaction location by time (Fig. 2), it was found that the plants grown at a lower elevation had a lower HUE_w compared to the other locations and at all sampling points. This indicates that at low elevation the accumulation of biomass was limited in the evaluated cultivars. The intermediate elevation was characterized by generating plants with higher biomass up to approximately 990 GDD that is at the midpoint of the optimal altitudinal range for potatoes from the Phureja Group (2700 masl), an optimal environment for their growth. In initial stages that corresponded to vegetative development only (<330 GDD), the accumulation of biomass was like that of plants of low elevation, however, after 440 GDD, when tuberization began, the higher elevation plants increased their capacity to accumulate biomass to values like those of the average location by 990 GDD and finally exceeded it by 1,100 GDD.

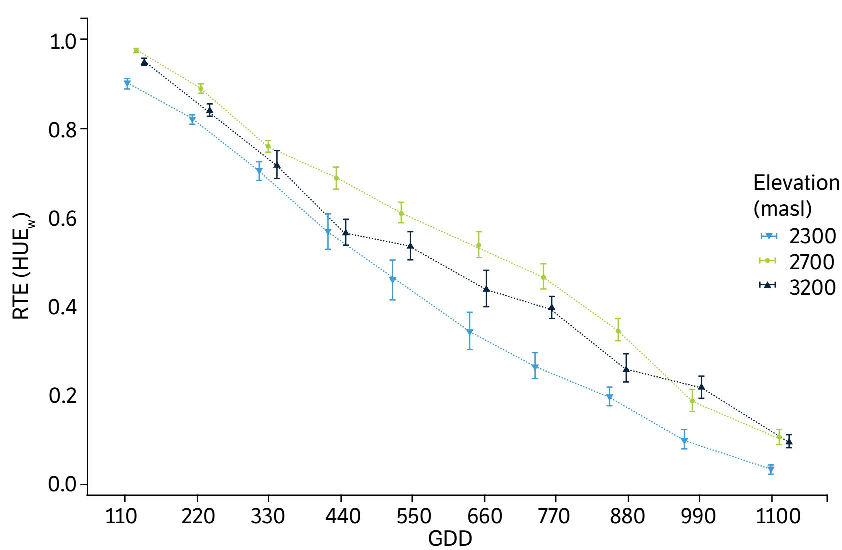

Figure 2. Dynamics over time of the latent response variable HUE_w at three evaluation elevations. The response variable was expressed as RTE.

Source: Elaborated by the authors.

The increase observed in biomass accumulation after tuberization in the upper locality shows that the higher elevation favored this process, which is attributed to differences in the environmental temperature; however, it is important to consider that other environmental factors such as radiation or soil characteristics can influence potato growth (Harris 1978; Jamsheed et al. 2023).

The interaction (L×C) made it possible to show that elevation modified the accumulation of biomass in a different way between cultivars (Fig. 3). Criolla Colombia showed higher values of HUE_w at all elevations due to its lower thermal requirement. All cultivars decreased their biomass accumulation at the lowest elevation. In the middle elevation, Criolla Colombia and Paola were characterized by having greater accumulation of biomass. In the highest elevation location, Criolla Colombia was the cultivar with the highest accumulation of biomass, while Criolla Dorada had the lowest value, which may indicate that elevation reduces its growth, as in the other cultivars.

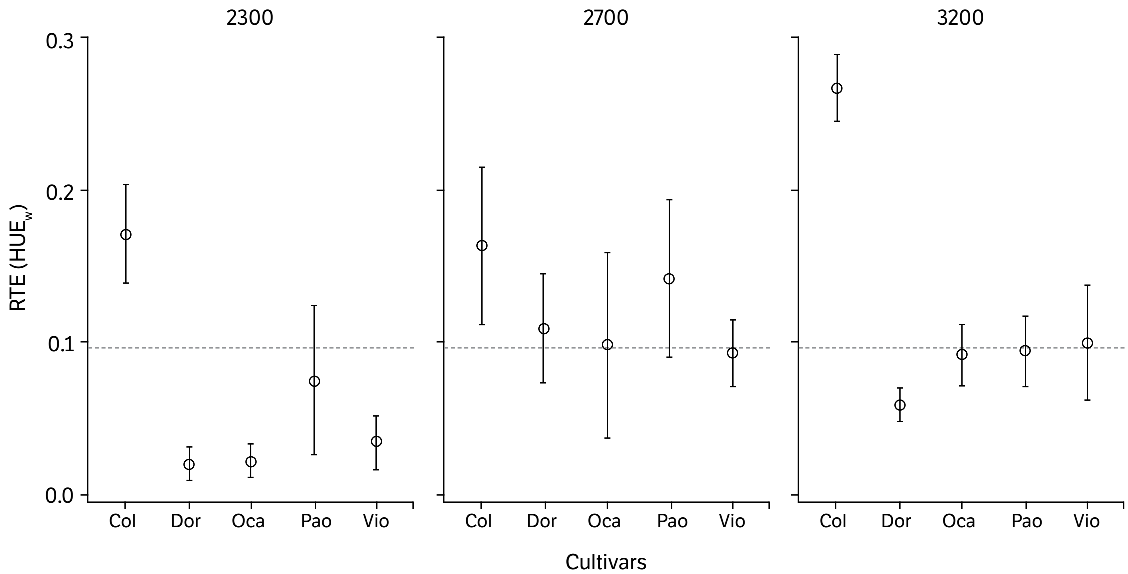

Figure 3. Differences in the latent response variable HUE_w for the final sampling point (1113 GDD) for the interaction between elevations and evaluated cultivars. The horizontal dotted line represents the general average of RTE from HUEw for location. Col: Criolla Colombia; Dor: Criolla Dorada; Oca: Criolla Ocarina; Pao: Paola; Vio: Violeta.

Source: Elaborated by the authors.

The methodology used to calculate the GDD in this study was adequate to describe the physiological time, since there were no low temperatures (<2 °C) that caused negative values for the GDD, or so high that they exceeded the threshold of 29 °C used by Soto et al. (2018) and overestimating the GDD. These characteristics could change at another time of year or study region, especially for low temperatures. The development of a vector latent response variable that integrates a growth variable (BTo) with an estimate of physiological time (GDD) from a nonlinear model had several advantages such as: a) it maintains its monotonous association with the BTo original variable, which is why it is useful to describe growth, b) it reduces and stabilizes the variability of the data, c) allows comparison between sampling points even with differences in the duration of the GC and d) allows a more intuitive interpretation in relation to the efficiency in the accumulation of biomass. In this sense, the use of GDD simplified the description of growth and facilitated the comparison of cultivars in different environments, planting dates (Devi et al. 2019; Diwan et al. 2017; Islam et al. 2019; Nandini and Sridhara 2019; Prakash et al. 2017; Solanki et al. 2017) or elevations as proposed in this research.

At a lower elevation, the evaluated cultivars had lower efficiency in biomass accumulation along the GC compared to the other two elevations. In this environment, Criolla Colombia was the most efficient cultivar. This response may be associated with its native character. The lower response of the other cultivars indicates that their development environment was more limiting to growth. At medium elevation, all cultivars showed a high efficiency in the accumulation of total biomass, which responds to that its elevation was within the production range for diploid potatoes of the Phureja Group. At the highest elevation, the plants showed low efficiency in the accumulation of total biomass during the vegetative phase, which increased in the filling phase of tubers. In this location, Criolla Dorada had the lowest efficiency. This response could be attributed to differences in temperature and radiation. According to Struik (2007a) the average daytime and night temperature ranges influence the respiratory rate. In the diurnal case and in the low elevation the range was 15.5 °C, in the central one was 12.2 °C and 10.1 °C in the upper zone; for the nocturnal case the respective ranges were 2.2 °C, 4.1 °C and 4.0 °C. It is a well-known fact that temperature has a direct effect on the speed of respiratory activity, in fact, the higher the temperature the greater the respiratory activity, which accelerates the maturation process (Torrieri et al. 2010).

Biomass accumulation and the proportion of carbon allocated to tubers decreases with temperature rise above 24 °C. High respiration losses decreased the total gain of carbon at higher temperatures (Timlin et al. 2006). Another aspect to consider is the changing atmospheric composition with elevation. The decrease in temperature at higher elevations also disadvantages the activity of gibberellins in favor of the development of tubers with respect to the aerial part (Navarre and

Pavek 2014; Singh and Kaur, 2016) and explains the efficiency in accumulation of biomass of plants of the highest elevation after the beginning of the tuber filling stage (450 GDD). Other factors favoring tuberization at a lower temperature are the increase in the translocation capacity of assimilates, an increased sink strength (Cai et al. 2012). Criolla Colombia was a cultivar that maintained a relatively stable accumulation of biomass between elevations.

In this sense, although elevation is considered, it is its inherent properties such as atmospheric composition that possibly explain the differences in biomass accumulation and thus in its efficiency measure (Högy and Fangmeier 2009). For this study, the higher elevation generated low efficiency in the accumulation of biomass when the growth was exclusively vegetative (<350 GDD), which can be related by the morphogenetic influence that UV radiation has on plants (Reyes et al. 2004) surveyed from the UVR8 receptor. The atmosphere attenuates UV−B radiation; however, in the tropics where the stratosphere is thinner, UV−B levels are higher and increase more as a function of elevation (Jansen, 2017). The process by which UV−B radiation affects growth is not entirely clear, but it is known that it depends on an antagonistic reaction towards phytohormones such as auxins and gibberellins, causing growth redistribution and limiting vegetative growth (Jansen 2017).

In Colombia some potato crops are established above 3000 masl due to different economic and social factors and the low environmental education in this regard (Minambiente and Fedepapa 2004; Múnera and Piña 2016) and that except for certain genotypes, tuber production is not affected (Lizarazo Peña et al. 2022). Many of the potato crops in páramo areas correspond to seed production, due to the lower incidence of diseases and pests (Ñústez-López and Rodríguez-Molano 2020), although the latter is not necessarily limiting for seed production (Minambiente and Fedepapa 2004). However, the agricultural use of moorland areas has a very important environmental effect, as they provide multiple ecological functions that are difficult to restore, among which its capacity for water regulation, interception and storage stands out (Minambiente and Fedepapa 2004). Climate change has altered the environments for crop production (Yin et al. 2016) and in regions such as the Andes has favored the migration of crops to higher elevations as an adaptive response to growing conditions (Skarbø and VanderMolen 2016), a response that can be more drastic in crops sensitive to high temperatures such as potatoes.

The results found demonstrate that the differences in elevation are important in the regulation of the growth of the Group Phureja. The effects by the interactions show that in a differentiated way by cultivar, the planting elevation modifies the accumulation of biomass of diploid potato cultivars of the Group Phureja. As well as the implications of elevation and temperature on crop growth. Finally, this investigation proposes an alternative way to compare the biomass accumulation of potato cultivars, despite their mismatched timing of development and biomass accumulation. The use of thermal time, and the normalization of biomass accumulation expressed in the latent response (HUE_w) variable facilitated the interpretation of the results intuitively, since it is reasonable to think that if a crop requires a greater amount of GDD to reach a certain biomass, then it is less efficient, so the HUE_w. The can latent response variable (HUE_w) be simple to adopt to and even modify for researchers, according to the model that ends up relating the accumulated biomass with the thermal time.

CONCLUSION

The latent response variable (HUE_w) proposed in this research integrated a growth variable to an environmental variable, analogous to an agrometeorological index "Heat Use Efficiency", but specific for Phureja Group potatoes. The HUE_w allowed the longitudinal comparison of potato genotypes in environments where the duration of the crop cycle was different in days due to elevation. The differences in HUE_w showed that the growth dynamics of potato cultivars is affected by elevation. The results allow inferring the negative effect that low elevations or higher temperatures on growth of potato from Phureja Group, which may indicate the possible effects of climate change on the crop. These variations in growth should be considered in the agronomic management of the crop, especially on the cultivars evaluated and as a reference for the development of new cultivars.

AUTHORS' CONTRIBUTION

Conceptualization: Lizarazo-Peña, P. and Darghan, A.; **Data curation:** Lizarazo-Peña, P.; **Formal analisis:** Lizarazo-Peña, P., Darghan, A. and Nústez-López, C.; **Investigation:** Lizarazo-Peña, P. and Darghan, A. **Methodology:** Lizarazo-Peña, P. and Darghan, A.; **Project administration:** Lizarazo-Peña, P., Darghan, A. and Nústez-López, C.; **Visualization:** Lizarazo-Peña, P. and Darghan, A.; **Writing – review and editing:** Lizarazo-Peña, P., Darghan, A. and Nústez-López, C.; **Resources:** Lizarazo-Peña, P. and Nústez-López, C.; **Supervision:** Darghan, A. and Nústez-López, C.; **Validation:** Darghan, A. and Nústez-López, C.

CONFLICTS OF INTEREST

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data are available in the repository of Pedro Lizarazo and can be found at https://github.com/PEDROLIZARAZO/Biomass-HUEw-diploid-potato.

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