

# A statistical model to predict titratable acidity of pineapple during fruit developing period responding to climatic variables



Elodie Dorey<sup>a,b,\*</sup>, Patrick Fournier<sup>a</sup>, Mathieu Léchaudel<sup>c</sup>, Philippe Tixier<sup>d,e</sup>

<sup>a</sup> CIRAD, UPR 26, Station de Bassin plat, 97455 Saint Pierre Cedex, La Réunion, France

<sup>b</sup> Réunion Fruits et Légumes, Pierrefonds, 97410 Saint Pierre, La Réunion, France

<sup>c</sup> CIRAD, UPR HortSys, Station de Bassin plat, 97455 Saint Pierre Cedex, La Réunion, France

<sup>d</sup> CATIE, Departamento de Agricultura y Agroforestería, 7170, Cartago, Turrialba, 30501, Costa Rica

<sup>e</sup> CIRAD, UPR 26, CAEC, Quartier Petit Morne, BP 214 – 97285 Lamentin Cedex 2, Martinique, France

## ARTICLE INFO

### Article history:

Received 22 March 2016

Received in revised form 11 July 2016

Accepted 12 July 2016

### Keywords:

*Ananas comosus* (L.) Merr.

Statistical model

Fruit quality

Temperature

Total radiation

Rainfall

## ABSTRACT

Acidity greatly affects the nutritional properties and organoleptic properties of fruits. Pineapple acidity is strongly affected by climatic factors during fruit growth but there is a lack of knowledge about their period of influence. A statistical model was developed to: (i) identify the periods (referred to as “integration periods”) during the flowering–harvest interval during which climatic variables (rainfall, global radiation and temperature) affect titratable acid content (TA) of pineapple fruit at harvest; and (ii) to predict TA at harvest on Reunion Island. The model was developed in two steps. In Step 1, those integration periods that were best correlated with TA were identified for each climatic variable. In Step 2, a complete linearized mixed-effect model (GLM) was built to predict TA based on all candidate variables. Temperature greatly affected TA in early growth periods, whereas total radiation had a considerable effect in late growth periods. Rainfall greatly affected TA in both early and late growth periods. In the complete GLM, the climatic variables and the interaction between temperature and rainfall were significantly correlated with TA at harvest and explained 60% of the variance. Comparison of model predictions and observations from 14 pineapple fields indicated that the model accurately predicted TA (RRMSE = 0.08). This model should help farmers to select the planting date and flowering induction date in order to optimize TA in pineapple fruit on Reunion Island.

© 2016 Elsevier B.V. All rights reserved.

## 1. Introduction

Acidity greatly affects the nutritional properties (Silva et al., 2004; Zampini et al., 2008) and organoleptic properties (Bai and Lindhout, 2007; Lobit et al., 2002) of fruits. In the case of pineapple, the harvest index is determined by the sugar/acid ratio (Paull and Chen, 2003) which can be altered according to high and low acid clones studied (Saradhulhat and Paull, 2007). Citric and malic acids are the two dominant organic acids in most types of fruit (Lobit et al., 2003) and represent 60% and 36%, respectively, of the organic acids in pineapple fruit at harvest (Chan Jr. et al., 1973). Variation in acidity during fruit growth mainly results from variations in citric acid content, whereas malic acid content is relatively constant (Singleton and Gortner, 1965). During pineapple fruit growth, acidity increases until the exterior of the fruit becomes

yellow (for those pineapple cultivars whose fruit surfaces change color during ripening) and then decreases until harvest (Singleton and Gortner, 1965; Smith, 1988; Teisson and Pineau, 1982). Acidity is the result of complex physiological processes in which respiration plays an important role, i.e., acids are used as metabolites for respiration during pineapple growth and maturation (Wills et al., 1986). This is especially true for pineapple because pineapple uses CAM photosynthesis in which CO<sub>2</sub> is stored as malate (a four-carbon acid) during the night and then used for photosynthesis during the day (Cote, 1988).

Disentangling the effect of climatic variables on acidity is difficult because the variables may affect plant physiological processes at different periods of fruit growth (Marsh et al., 1999). However, there is an increasing demand for predictive models to predict fruit quality attributes (Tijskens et al., 2010; Unuk et al., 2012). Some studies have attempted to link a single climatic variable to fruit acidity, e.g., temperature was linked to grape acidity (Etienne et al., 2013; Sweetman et al., 2014), and rainfall was linked to nectarine acidity (Thakur and Singh, 2012). The failure to consider multiple

\* Corresponding author at: CIRAD, UPR 26, Station de Bassin plat, 97455 Saint Pierre Cedex, La Réunion, France.

E-mail address: [elodie.dorey@cirad.fr](mailto:elodie.dorey@cirad.fr) (E. Dorey).

variables (e.g., temperature, rainfall and radiation) limits the usefulness of these studies. In addition, the timing and duration of the period during which the climate variable must be considered are poorly understood. A model that predicts the effect of multiple climatic variables on acidity is unavailable but would help farmers to adjust their periods of production to optimize fruit quality.

Pineapple ('Queen Victoria' cultivar) is produced on Reunion Island, an island located in the Indian Ocean, east of Madagascar. Pineapple is the major fruit to be commercially produced on the island. It is grown under a wide range of conditions on Reunion Island where the elevation ranges from 50 m to 900 m a.s.l. and annual rainfall ranges from 500 mm to 5000 mm. The final content of acid in pineapple at harvest is thus strongly influenced by climatic factors (Bartholomew and Paull, 1986; Singleton and Gortner, 1965). The diversity of conditions under a relatively homogeneous management makes this production area particularly suitable to study the effect of climatic conditions on titratable acid (TA) content. Furthermore, pineapple pests are nearly absent on this island, reducing the possibility of confusing the effects of climatic variables on TA are confounded with the effects of pests on plant growth and health. An unusual feature of pineapple production on Reunion Island is that the fruit may be harvested every month of the year because floral induction is controlled by the farmer. This makes it possible for the farmer to control the timing of fruit production in order to optimize acidity and other properties of fruit quality. This flexibility in fruit production time also facilitates research on the effect of climatic variables on TA.

In this paper, we use a dataset that includes 1448 measurements of TA from pineapples grown in different regions of Reunion Island to: (i) identify the periods in the flowering-harvest interval during which climatic variables may affect TA; and (ii) establish a statistical model to predict TA at harvest. This model enabled us to determine the periods in which rainfall, total radiation and temperature have the greatest impact on TA at harvest. The integration of the selected climatic variables into a linear model constitutes a useful tool for predicting TA at harvest.

## 2. Materials and methods

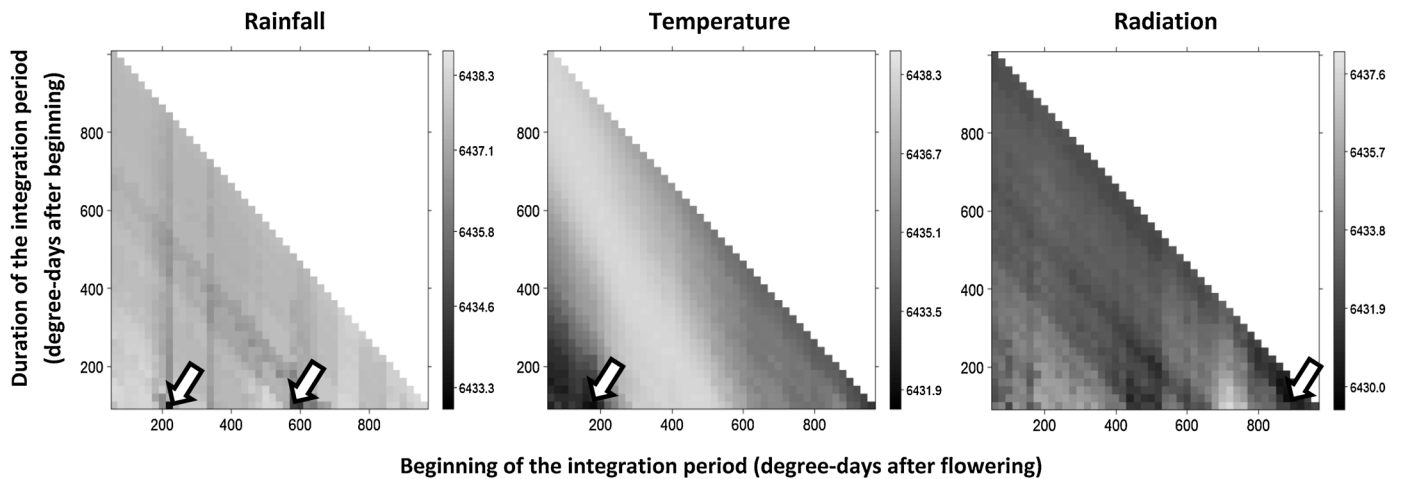
### 2.1. Field sites

We measured the TA content, which is a common measure of fruit acidity (Lobit et al., 2002), for 1448 pineapple fruit in 14 independent experiments performed between 2007 and 2012 at three different sites on Reunion Island: Bérive (55°31'10.59"E,21°17'10.21"S); CIRAD's Bassin Plat Research Station (55°29'20.64"E,21°19'21.62"S); and Saint Benoit (55°42'12.86"E,21°05'53.85"S), all planted with the 'Queen Victoria' cultivar (Table 1). Flowering was induced in all of the fields by application of ethephon (Ethrel; Bayer SA) at 3 L ha<sup>-1</sup> when the plants reached a weight of 1.2 kg. In irrigated fields, drip irrigation was applied under a plastic mulch during vegetative growth, and the soil water status was regularly checked with Watermark sensors (Irrrometer Company, Riverside, CA, USA). The other fields (on the east side of the island) were not irrigated and received only rainfall. Except for irrigation and fertilization, the fields were managed identically and according to the local, recommended cultural practices. Suckers (250 ± 25 g) were planted through polyethylene mulch, and all fields except fields 6 and 7 were fertilized with 300 kg ha<sup>-1</sup> of nitrogen (650 kg of urea) and 450 kg ha<sup>-1</sup> of potassium (900 kg of sulfate) or with 150 kg ha<sup>-1</sup> of nitrogen (325 kg of urea) and 225 kg ha<sup>-1</sup> of potassium (450 kg of sulfate), as indicated in Table 1. Fields 6 and 7 received 150 kg ha<sup>-1</sup> of nitrogen (325 kg of urea) and 225 kg ha<sup>-1</sup> of potassium (450 kg

**Table 1**  
Description of experiments used to establish a relationship between climatic variables and pineapple TA content at harvest of 'Queen Victoria' cultivar on Reunion Island.

Experiments	Location	N Fertilization (kg N ha <sup>-1</sup> )	Irrigation	Elevation	Flowering date	Harvest mdate	Annual rainfall (mm)	Average annual temperature (°C)	Average annual global radiation (MJ m <sup>-2</sup> )	Mean of fruit weight at harvest (g)	Mean of TA at harvest	Number of fruits
1	Bérive	150	no	550	25-07-2010	26-11-2010	877	20.7	17.8	597	11.85	123
2	Bérive	300	no	550	25-07-2010	27-11-2010	877	20.7	17.8	606	13.98	121
3	Bassin Plat	300	no	150	17-08-2012	24-11-2012	556	23.1	20.2	492	11.92	34
4	Bassin Plat	150	yes	150	21-08-2012	26-11-2012	556	23.1	20.2	674	11.24	24
5	Bassin Plat	150	yes	150	16-04-2012	30-07-2012	556	23.2	19.6	696	21.41	120
6	Bassin Plat	150 <sup>a</sup>	yes	150	08-08-2011	20-11-2011	537	23.5	20.6	601	11.81	63
7	Bassin Plat	150 <sup>a</sup>	yes	150	17-05-2010	12-09-2010	766	24.1	19.4	767	13.38	159
8	Bassin Plat	300	yes	150	17-05-2010	13-09-2010	766	24.1	19.4	810	15.84	130
9	Bassin Plat	300	yes	150	19-08-2012	23-11-2012	556	23.1	20.2	618	10.93	57
10	Bassin Plat	300	yes	150	14-07-2012	26-10-2012	424	24.5	20.3	663	18.43	323
11	Bassin Plat	300	yes	150	14-08-2007	27-11-2007	1050	23.0	23.5	562	11.92	30
12	Saint Benoit	300	no	290	07-09-2009	19-01-2010	3616	22.7	18.1	560	12.75	72
13	Saint Benoit	300	no	340	26-04-2010	04-09-2010	4005	21.1	15.2	936	15.63	89
14	Saint Benoit	150	no	340	26-04-2010	07-09-2010	4005	21.1	15.2	882	13.38	103

<sup>a</sup> A legume cover crop was disked into the soil before planting.



**Fig. 1.** Plot of AIC values as a function of the beginning and duration of the integration period for each climatic variable (rainfall, temperature and global radiation). As indicated by the scale to the right of each panel, a darker color indicates a lower AIC value. The arrows represent the integration period with the lowest values of AIC selected as potentially meaningful variables (see Table 2 for details). As indicated, rainfall has two integration periods, and temperature and radiation each have one.

of sulfate), and a legume cover crop was disked into the soil before planting as an organic fertilizer.

## 2.2. Measurement of climatic variables

In all fields, the weather station consisted of a Campbell Scientific (Logan UT) CR500 datalogger that recorded temperature and precipitation (WXT 520 weather sensor, °C and mm, respectively), and global radiation (CS300 silicon pyranometer,  $W m^{-2}$ ) at 1-min intervals and that was located next to the field and 1 m above the soil surface.

## 2.3. Fruit sampling

The harvest stage was selected on the basis of the peel color of fruit. Fruit were harvested at coloration C2, defined as a half basal yellow coloration, which occurred approximately 1318 degree days (DDs) after flowering, with  $9.24^{\circ}C$  as the basal temperature for determining DDs (Lechaudel et al., 2010). A field was considered to be in the flowering stage when at least one corolla was visible to 50% of the inflorescences. After harvest, the fresh mass of every fruit was determined (Table 1). Each fruit was then peeled, and pulp tissues were sub-sampled. A sample of pulp was mixed in a Grindomix blender (Retsch, Haan, Germany) to obtain the volume of pineapple juice needed to measure TA.

## 2.4. TA measurement

TA was determined for each of the 1448 harvested fruit. TA of the juice sample, expressed as milliequivalents of acid per 100 mL of pineapple juice, was measured by titration with a 0.1 N NaOH

solution up to a pH 8.1 endpoint; an automated titrimeter was used (Schott, Mainz, Germany).

## 2.5. Statistical analysis

The relationship between climatic variables and TA was investigated in two steps. First, we studied the trend of correlations between TA and temperature, rainfall and radiation. To do this, we constructed a matrix that contained all possible combinations of climatic variables at all possible times between flowering and harvesting for each field and each date of harvest. We refer to these in-between times as “integration periods”. To compare fields at different elevations, we measured time in terms of DDs. All combinations of climatic variables and integration periods were thus defined by a given number of DDs after flowering and by a given duration in DDs (cases in which the end of the period exceeded the harvest date were eliminated). We established this matrix with a 20-DD step, leading to 666 possible integration periods for each climatic variable (Table S1). For each integration period, we calculated the mean value of each climatic variable with the exception of rainfall, which was cumulative. We then used a linearized mixed-effect model and the lmer function from the lme4 package (Bates et al., 2012) to calculate Akaike’s Information Criterion (AIC) (Akaike, 1973) to assess the effect of each integration period of each climatic variable on fruit TA content; the field was included as a random term in the model. The graphical representation of AIC values as a function of the beginning and duration (with a minimum value of 100-DD) of the integration period allowed us to determine which integration periods (one or two periods depending on the variable) best predicted fruit TA content, i.e., which periods resulted in the lowest AIC values. This procedure was accomplished with a computerized algorithm. All statistical analyses were performed with R software (R Development Core Team, 2014). At the end of this first step, a list of candidate variables was defined (each candidate variable represented a specific integration period for a climatic variable).

In the second step, we built a complete linearized mixed-effect model based on all candidate variables in order to predict TA content; field was a random term in the model. We used a backward model selection process to find the optimal model by eliminating non-significant variables and their interactions (Zuur, 2009) using the lme4 package (Bates et al., 2012). We verified the normality of residues of the models (Fig. S1). A pseudo-correlation coefficient was calculated to determine the percentage of the variance

**Table 2**

The combinations of integration periods and climatic data (rainfall, temperature and radiation) that were most closely correlated to the TA content of pineapple fruit at harvest. An integration period refers to that period when the data were used in the model. Integration periods were defined by their beginning, i.e., by the number of degree-days (DD) after flowering, and by their duration.

Variable code	Variable	Beginning (DD)	Duration (DD)
R220	Rainfall220	220	100
R600	Rainfall600	600	120
T180	Temperature180	180	100
Rg880	Radiation880	880	120

**Table 3**

Summary of the analysis of variance (ANOVA) performed on the complete model  
 $TA = T180 + R220 + R600 + Rg880 + T180:R600 + (1|field)$ .

Model	Df	AIC	logLik	deviance	Pr > ChiSq
Complete	8	6420.5	-3202.2	6404.5	
-T180	7	6434.8	3210.4	6420.8	5.0 e-05
-R220	7	6425.6	-3205.8	6411.6	7.4 e-04
-R600	7	6432.9	3209.5	6418.9	1.0 e-05
-Rg880	7	6436.9	3211.4	6422.9	1.8 e-05
-T180:R600	7	6433.3	3209.6	6419.3	1.1 e-05
NULL	3	6436.3	-3215.2	6430.3	9.5 e-05

R220, R600, T180 and Rg880 are defined in Table 2.

Df = Degrees of freedom; AIC = Akaike's Information Criterion; logLik = log-likelihood value; Pr > ChiSq = P > P value of Chi-squared test.

in TA content that was explained by the model (West et al., 2003). The final model was used to predict the effect of climatic variables (in the range observed in our experiments) on TA content. Predictions were carried out with the predictSEmer function in the AICcmodavg package (Mazerolle, 2006). The goodness of fit of the model was evaluated based on the relative root mean squared error (RRMSE) (Kobayashi and Salam, 2000), which is commonly used to quantify the mean difference between simulations and measurements. RRMSE was calculated as follows:

$$RRMSE = \frac{\sqrt{\frac{1}{N} \sum_{i=1}^N (y_i - \hat{y}_i)^2}}{\bar{y}}$$

where  $y_i$  is the observed value,  $\hat{y}_i$  is the corresponding simulated value, N is the number of observed values, and  $\bar{y} = \sum_{i=1}^N \frac{y_i}{N}$  is the mean of observed values.

### 3. Results

In the plots of the duration of the integration period on the beginning of the interruption period (Fig. 1), the zones with the lowest AIC values indicated those integration periods for each climatic variable that most affected TA content. As indicated in Table 2, the following combinations of variables and integration periods generated the lowest AIC values: temperature beginning at 180 DD after flowering and continuing for 100 DD (Temperature180); rainfall beginning at 220 DD after flowering and continuing for 100 DD (Rainfall220); rainfall beginning at 600 DD after flowering and continuing for 120 DD (Rainfall600); and total radiation at 880 DD after flowering and continuing for 120 DD (Radiation880).

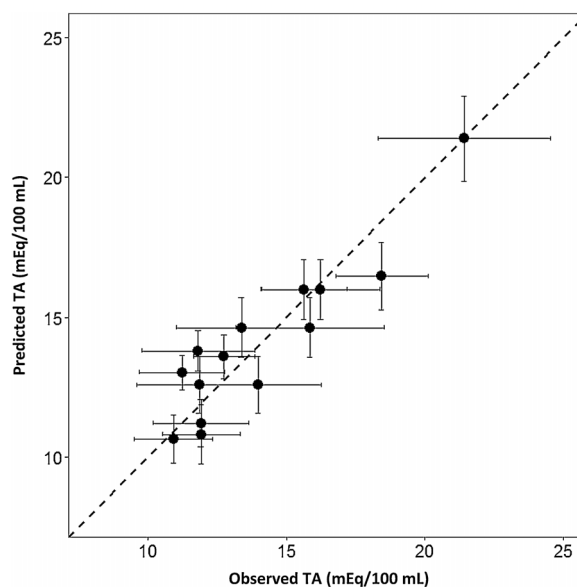
All four of the selected climatic variables were significantly correlated with TA in the complete GLM (Tables 3 and 4). The complete GLM with the four significant variables and the interaction (T180 × R600, Table 3) explained 60% of the variance of TA at harvest (estimated with the pseudo-correlation coefficient). Comparison of observed and predicted data for the 14 fields demonstrated that the model accurately simulated TA content at harvest (RRMSE=0.08) (Fig. 2). Temperature180 and Rainfall600 had a

**Table 4**

Results of the linear mixed-model:  $TA = T180 + R220 + R600 + Rg880 + T180:R600 + (1|field)$ .

Fixed effects	Estimate	Standard error	t value
Intercept	-0.40	11.04	0.04
T180 (°C)	2.70	0.64	4.22
R220 (mm)	-0.10	0.04	-2.31
R600 (mm)	2.54	0.66	3.82
Rg880 (MJ m <sup>-2</sup> )	-1.75	0.38	-4.67
T180:R600 (°C mm)	-0.12	0.03	-3.89

R220, R600, T180 and Rg880 are defined in Table 2.



**Fig. 2.** Observed and simulated TA content of 'Queen Victoria' pineapple at harvest on Reunion Island. Horizontal and vertical error bars show the standard errors of observations and of predictions, respectively. The dotted line is the 1:1 line.

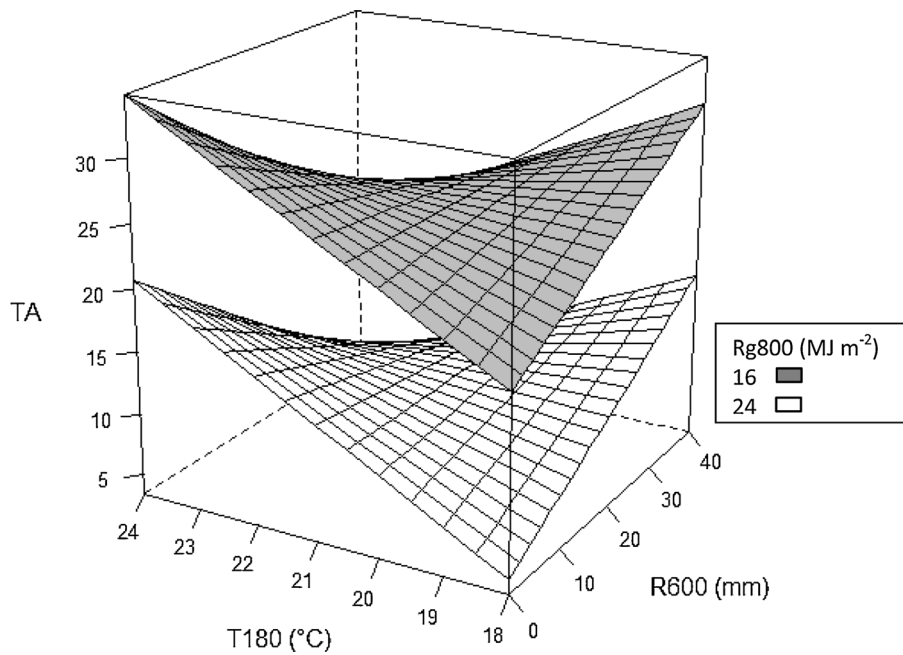
strong positive effect on TA (slopes were 2.70 and 2.54, respectively). The other variables in the model had a moderate negative effect on TA, except for Radiation880, which had a strong negative effect with a slope of -1.75. Predictions with the complete model within the range of climate data on Réunion Island showed the relative effects of Rainfall220, Rainfall600, Temperature180, and Radiation880 on TA (Fig. 3).

Among the four significant variables identified in this research, two involve the early growth of pineapple fruit: Temperature180 and Rainfall220. We found that rainfall affects TA at two distinct periods, one beginning at 220 DD and the other beginning at 600 DD after flowering. The global radiation beginning at 880 DD after flowering and continuing for 120 DD (Radiation880) was significantly correlated with TA content (Table 2).

Fields 5, 7, 8, 10, 13, and 14 had the heaviest fruit and had a growth period in winter, when temperatures were relatively low, leading to high TA values. Conversely, high temperatures during the period of cell division in fields 3, 4, 6, and 9 resulted in small fruit and low TA values. Our results indicate that fruit harvested from November to February, which is characterized by sunny days, had the lowest TA values (Table 1).

### 4. Discussion

The method used to select climate variables (in this case: Temperature180, Rainfall220, Rainfall600, and Radiation880) is novel because it did not depend on the limited information available concerning the period of influence of each variable. Although the climate just before harvest is known to affect pineapple fruit growth and TA content at harvest (Zhang et al., 2011), we showed that conditions during other stages of pineapple growth could also affect TA content at harvest. Because all of the possible combinations of integration periods and climatic variables were expressed in DD after flowering, these combinations could be associated with a period of pineapple fruit growth. The aim of the first step of the method used here was not to define precisely the effect of climatic variables but rather to identify critical periods when each climatic variable most affects TA content at harvest. For each variable, those integration periods with the lowest AIC values were considered the most useful for predicting TA content at harvest. To our knowledge, this method



**Fig. 3.** Predictions of pineapple TA content (mEq/100 mL) at harvest from the complete model (Table 3) as explained by the four explicative variables (Table 2). R600 and T180 variables were considered among their variation ranges as observed in the dataset. R220 was fixed to its mean value (R220 = 20 mm) and Rg800 was fixed to its first and third quantiles, observed among its variations.

has not been previously used to assess the relationship between climatic variables and fruit quality. We believe that this method can be used in many other contexts to link climatic variables to agricultural and food characteristics.

Two significant variables identified in this research (Temperature180 and Rainfall220) involve the early growth of pineapple fruit. The initial fruit size, which is generally related to cell division, is highly correlated to fruit weight at harvest (Lechaudel et al., 2005) as demonstrated by Hall et al. (2006) who studied that kiwifruit weight at 50 days after anthesis explained 75% of the size variations of ripe kiwifruit. Early stages of fruit growth are generally sensitive to water supply, carbon supply, and temperature (Génard et al., 2010). Thus, Temperature180 and Rainfall220 probably affect the establishment of fruit cells during cell division and their significance in the complete model was more related to fruit growth than to TA at harvest. In tomato, a low temperature during early fruit growth induced a longer period of cell division, leading to an increase in cell number (Bertin et al., 2006).

In current study, TA values were high for the heaviest fruit with a growth period in winter whereas high temperatures during the period of cell division resulted in small fruit and low TA values. TA values can be high for pineapple ripening in winter (Collins, 1960; Joomwong, 2006) because low temperatures and a long period of fruit development lead to an accumulation of compounds in fruit (Zhang et al., 2011). At low temperatures, the rate at which organic acids are synthesized exceeds their rate of consumption as substrates for respiration (Huet and Tisseau, 1959). In future studies, it would be interesting to separate night and day temperature since it can affect differently the CAM metabolism (Holtum and Winter, 2014).

TA at harvest was affected by rainfall at two distinct periods, one beginning at 220 DD and the other beginning at 600 DD after flowering. Few studies have considered the effect of rainfall on pineapple TA at harvest. However, the relationship between TA and deficit irrigation was largely studied in others fruits. Py and Tisseau (1965) demonstrated that TA of pineapple increases with excessive water supply. The same trend was observed on nectarines (Thakur and Singh, 2012) and on some vine cultivars (Trigo-Cordoba et al.,

2015; Rubio et al., 2004). But some authors reported a negative relationship between water supply and TA in ripe fruits (De la Hera-Orts et al., 2005; des Gachons et al., 2004; Hockema and Etxeberria, 2001).

In our study, fruit harvested in summer with high values for global radiation had the lowest TA values. Variation in fruit acidity has often been related to the harvest period, and several authors demonstrated that pineapple acidity can be low when global radiation increased (Combres, 1983; Malézieux, 1991; Malézieux and Lacoëuilhe, 1991). In Ivory Coast, a 66% decrease in global radiation increased the TA content of pineapple (Combres, 1979). The positive effect of radiation reduction on TA was also observed for apple (Schrader et al., 2011), grapevine (Uhlig, 1998), and tomato (Wada et al., 2006) in partial shade experiments. The strong effect of global radiation on pineapple acidity is not a new finding (Combres, 1979; Malézieux, 1988; Malézieux and Lacoëuilhe, 1991) but the method used in the current study better defines when the exposure to global radiation strongly affected final acidity.

Testing the model with external data would be useful for confirming its validity and for extending its utility over a broader range of climatic conditions. The 14 fields used to build the model, however, included a broad range of seasons and locations where pineapple is grown on Réunion Island. Our model will help farmers select the date of planting and date of flowering induction in order to optimize TA and pineapple quality on Réunion Island. Another interesting perspective will be to study and to model the effect of the thermal time between flowering and harvest. We believe that including thermal time between flowering and harvest would allow testing different harvest strategies. While it required much more data, it may be valuable to include this additional factor in the model.

#### Acknowledgements

The authors thank B. Abufera and G. Tullus (CIRAD, UR 26, Reunion Island) for technical assistance during the field experiments, and M. Darnaudery (CIRAD, UR HortSys, Reunion Island) and J. Minier (CIRAD, UMR Qualisud, Reunion Island) for assistance

with biochemical analysis. Elodie Dorey received funding from the Association Nationale de la Recherche et de la Technologie (ANRT) through a doctoral grant from the Convention Industrielle de Formation par la Recherche (CIFRE).

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.scienta.2016.07.014>.

## References

- Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N., Csáki, F. (Eds.), 2nd International Symposium on Information Theory. Tsahkadsor, Armenia, USSR, September 2–8, 1971, Budapest: Akadémiai Kiadó, pp. 267–281.
- Bai, Y., Lindhout, P., 2007. Domestication and breeding of tomatoes: what have we gained and what can we gain in the future? *Ann. Bot.* 100 (5), 1085–1094.
- Bartholomew, D.P., Paull, R.E., 1986. Pineapple fruit set and development. In: Monselies, S.P. (Ed.), *Handbook of Fruit Set and Development*. CRC Press, Boca Raton, Florida, USA, pp. 371–388.
- Bates, D., Maechler, M., Bolker, B., 2012. lme4: linear mixed-effects models using Eigen and Eigen++. R package version 0.999375-42.
- Bertin, N., Bussi eres, P., G enard, M., 2006. Ecophysiological models of fruit quality: a challenge for peach and tomato. *Acta Hort.* 718, 633–645.
- Chan Jr., H.T., Chenchin, E., Vonnahme, P., 1973. Nonvolatile acids in pineapple juice. *J. Agric. Food Chem.* 21 (2), 208–211.
- Collins, J.L., 1960. *The Pineapple*. Interscience Publishers inc, New York, 295p.
- Combres, J.C., 1979. Contribution   l' tude de l'action du climat sur les principales composantes de la production. Contribution to the study of the action of climate on main production component. In R union annuelle IRFA doc. interne n  60.
- Combres, J.C., 1983. Bilan  nerg tique et hydrique de l'ananas. Utilisation optimale des potentialit s climatiques. Energy and water balance in pineapple. Optimal use for climatic potential. In *Compte rendu d'activit s*. IRFA.
- Cote, F.X., 1988. Photosynth se et photorespiration d'une plante   m tabolisme crassulac en: *Ananas comosus* (L.) Merr. *Etude des  changes gazeux*. Vol. Ph.D. Universit  Paul Sabatier, Toulouse.
- De la Hera-Orts, M., Martinez-Cutillas, A., Lopez-Roca, J., Gomez-Plaza, E., 2005. Effect of moderate irrigation on grape composition during ripening. *Span. J. Agric. Res.* 3, 352–361.
- des Gachons, C.P., Leeuwen, C.V., Tominaga, T., Soyer, J.P., Gaudill re, J.P., Dubourdieu, D., 2004. Influence of water and nitrogen deficit on fruit ripening and aroma potential of *Vitis vinifera* L cv Sauvignon blanc in field conditions. *J. Sci. Food Agric.* 85, 73–785.
- Etienne, A., Genard, M., Lobit, P., Mbeguie-A-Mbeguie, D., Bugaud, C., 2013. What controls fleshy fruit acidity? A review of malate and citrate accumulation in fruit cells. *J. Exp. Bot.* 64 (6), 1451–1469.
- G enard, M., Bobin, C., Gautier, H., Massot, C., B nard, C., Larbat, R., Bertin, N., Le Bot, J., Adamowicz, S., Bourgaud, F., 2010. Elaboration de la qualit  du fruit: composition en m tabolites primaires et secondaires. *Innov. Agron.* 9, 47–57.
- Hall, A.J., Richardson, A.C., Snelgar, W.P., 2006. Modelling fruit development in 'HAYWARD' kiwifruit. *Acta Hort.* 707, 41–47, <http://dx.doi.org/10.17660/ActaHortic.2006.707.4>.
- Hockema, B.R., Etxeberria, E., 2001. Metabolic contributors to drought-enhanced accumulation of sugars and acids in oranges. *J. Am. Soc. Hortic. Sci.* 126 (5), 599–605.
- Holtum, J.A.M., Winter, K., 2014. Limited photosynthetic plasticity in the leaf-succulent CAM plant *Agave angustifolia* grown at different temperatures. *Funct. Plant Biol.* 41 (8), 843–849.
- Huet, R., Tisseau, M.A., 1959. Observation sur l' volution de l'ananas apr s la coupe. *Fruits* 14 (6), 271–275.
- Joomwong, A., 2006. Impact of cropping season in Northern Thailand on the quality of smooth cayenne pineapple. II Influence on physico-chemical attributes. *Int. J. Agric. Biol.* 8 (3), 330–336.
- Kobayashi, K., Salam, M.U., 2000. Comparing simulated and measured values using mean squared deviation and its components. *Agron. J.* 92 (2), 345–352.
- Lechaudel, M., Genard, M., Lescouret, F., Urban, L., Jannoyer, M., 2005. Modeling effects of weather and source-sink relationships on mango fruit growth. *Tree Physiol.* 25 (5), 583–597.
- Lechaudel, M., Damour, G., Fournier, P., Joas, J., Jahiel, M., 2010. How to predict the harvest date of tropical fruit: from simple methods to complex models. *Acta Hort.* 880, 175–182.
- Lobit, P., Soing, P., G enard, M., Habib, R., 2002. Theoretical analysis of relationships between composition, pH, and titratable acidity of peach fruit. *J. Plant Nutr.* 25 (12), 2775–2792.
- Lobit, P., G enard, M., Wu, B.H., Soing, P., Habib, R., 2003. Modelling citrate metabolism in fruits: responses to growth and temperature. *J. Exp. Bot.* 54 (392), 2489–2501.
- Mal zieux, E., Laco uilhe, J.J., 1991. Analyse de la variabilit  de rendement chez l'ananas (*Ananas comosus* (L.) Merr.). I. Caract risation dans les conditions de C te d'Ivoire, des fluctuations saisonni res du rendement et certains facteurs li s   la qualit  des fruits. *Fruits* 46 (3), 227–239.
- Mal zieux, E., 1988. Croissance et  laboration du rendement de l'ananas (*Ananas comosus* L. Merr.) Vol. Ph.D. INA-PG, Paris, France.
- Mal zieux, E., 1991. Recherche de relations entre biomasse a rienne, la surface foliaire et l'interception du rayonnement solaire chez l'ananas. *Fruits* 46 (5), 523–532.
- Marsh, K.B., Richardson, A.C., Macrae, E.A., 1999. Early- and mid-season temperature effects on the growth and composition of satsuma mandarins. *J. Hort. Sci. Biotechnol.* 74 (4), 443–451.
- Mazerolle, M.J., 2006. Improving data analysis in herpetology: using Akaike's information criterion (AIC) to assess the strength of biological hypotheses. *Amphib. Reptil.* 27 (2), 169–180.
- Paull, R.E., Chen, C.C., 2003. Postharvest physiology, handling and storage of pineapple. *Pineapple: Botany, Production and Uses*, vol. 10. CABI, Wallingford, United Kingdom, pp. 253.
- Py, C., Tisseau, M.A., 1965. *L'ananas. Techniques agricoles et production tropicales*. G.-P. Maisonneuve & Larose, Paris, France.
- R Development Core Team, 2014. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rubio, J.A., Albuquerque, M., Yuste, J., 2004. Influence of water stress and crop load on the physiology and the productivity of Tempranillo under semiarid conditions. In: Reynolds, A.G., Bowen, P. (Eds.), *Viticulture—Living with Limitations*. International Society Horticultural Science, Leuven 1, pp. 99–106.
- Saradhulhat, P., Paull, R.E., 2007. Pineapple organic acid metabolism and accumulation during fruit development. *Sci. Hortic.* 112 (3), 297–303.
- Schrader, L.E., Kahn, C.B., Sun, J., Xu, J., Zhang, J., Felicetti, D.A., 2011. Effects of high temperature and high solar irradiance on sunburn quality, and skin pigments of apple fruit. *Acta Hort.* 903, 1025–1039.
- Silva, B.M., Andrade, P.B., Goncalves, A.C., Seabra, R.M., Oliveira, M.B., Ferreira, M.A., 2004. Influence of jam processing upon the contents of phenolics, organic acids and free amino acids in quince fruit (*Cydonia oblonga* Miller). *Eur. Food Res. Technol.* 218 (4), 385–389.
- Singleton, V.L., Gortner, W.A., 1965. Chemical and physical development of the pineapple fruit. II. Carbohydrate and acid contents. *J. Food Sci.* 30, 19–23.
- Smith, L.G., 1988. Indices of physiological maturity and eating quality in smooth cayenne pineapples. 2. indices of eating quality. *J. Food Sci.* 45, 219–228.
- Sweetman, C., Sadras, V.O., Hancock, R.D., Soole, K.L., Ford, C.M., 2014. Metabolic effects of elevated temperature on organic acid degradation in ripening *Vitis vinifera* fruit. *J. Exp. Bot.* 65 (20), 5975–5988.
- Teisson, C., Pineau, P., 1982. Quelques donn es sur les derni res phases du d veloppement de l'ananas. *Fruits* 37 (3), 741–748.
- Thakur, A., Singh, Z., 2012. Responses of 'Spring Bright' and 'Summer Bright' nectarines to deficit irrigation: fruit growth and concentration of sugars and organic acids. *Sci. Hortic.* 135, 112–119.
- Tijskens, L.M.M., Schouten, R.E., Konopacki, P.J., Hribar, J., Sim i , M., 2010. Modelling the biological variance of the yellow aspect of Granny Smith apple colour. *J. Sci. Food Agric.* 90 (5), 798–805.
- Trigo-Cordoba, E., Bouzas-Cid, Y., Orriols-Fernandez, I., Miras-Avalos, J.M., 2015. Effects of deficit irrigation on the performance of grapevine (*Vitis vinifera* L.) cv. 'Godello' and 'Treixadura' in Ribeiro, NW Spain. *Agric. Water Manage.* 161, 20–30.
- Uhlig, B.A., 1998. Effects of solar radiation on grape (*Vitis vinifera* L.) composition and dried fruit colour. *J. Hort. Sci. Biotechnol.* 73 (1), 111–123.
- Unuk, T., Tijskens, L.M.M., Germ sek, B., Zadravec, P., Vogrin, A., Hribar, J., Sim i , M., Tojnko, S., 2012. Effect of location in the canopy on the colour development of three apple cultivars during growth. *J. Sci. Food Agric.* 92 (12), 2450–2458.
- Wada, T., Ikeda, H., Matsushita, K., Kambara, A., Hirai, H., Abe, K., 2006. Effects of shading in summer on yield and quality of tomatoes grown on a single-truss system. *J. Jpn. Soc. Hortic. Sci.* 75 (1), 51–58.
- West, S.G., Aiken, L.S., Kwok, O., 2003. *Hierarchical and Generalized Linear Models: What Multiple Regression Didn't Tell Us*. American Psychological Association, Toronto, ON, Canada.
- Wills, R.B.H., Lim, J.S.K., Greenfield, H., 1986. Composition of Australian foods 31. Tropical and subtropical fruit. *Food Technol. Aust.* 38 (3), 118–123.
- Zampini, M., Wantling, E., Phillips, N., Spence, C., 2008. Multisensory flavor perception: assessing the influence of fruit acids and color cues on the perception of fruit-flavored beverages. *Food Qual. Preference* 19 (3), 335–343.
- Zhang, X.M., Dou, M.A., Yao, Y.L., Du, L.Q., Sun, G.M., Li, J.G., 2011. Sugar accumulation in 'Smooth Cayenne' pineapple fruits in different harvest seasons. *Acta Hort.* 902, 193–200.
- Zuur, A.F., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York; London.