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Prediction of potato sprouting during storage

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ABSTRACT

Potato sprouting during storage occurs after a break in dormancy, leading to a decrease in quality and consequently economic losses. We used 3379 records from multi-year and multi-environment trials of 537 potato varieties to identify the main factors driving potato dormancy and to develop predictive models for an efficient sprouting forecast. The variety explained the majority of the dormancy variability (60.3%), followed by the year (13.9%) and the location (5.4%). About 250 predictors were considered to develop a predictive model of potato dormancy. The selected model had a validation precision of 14.59 days; it used the variety class and the sum of the daily maximum temperatures in the air during the period from planting to harvest as predictors. The predictions of the selected model were supported by results of the *in vivo* trial using dormancy measurements from potato varieties grown under different temperature regimes in greenhouse conditions. With the growing impact of climate change on crop production, predictive models as developed here can provide an efficient and cost-effective tool to optimize the control of potato sprouting during storage.

1. Introduction

After harvest, the potato value chain requires long-term storage to supply high-quality potatoes for year-long processing to satisfy market requirements. The evolution of physiological age leads to the breaking of dormancy and thus to the sprouting of potatoes during storage (Delaplace et al., 2008). Sprouting alters potato quality by causing shrinkage, weight loss, and a decrease in turgidity (Alexandre et al., 2015; Sonnewald and Sonnewald, 2014; Teper-Bamnolker et al., 2010) and therefore must be controlled.

Various approaches are used to control potato sprouting, such as decreasing storage temperature (Blauer et al., 2013; Magdalena and Dariusz, 2018; Muthoni et al., 2014), using chemicals to delay sprouting (Corsini et al., 1979; Mahajan et al., 2008; Paul et al., 2016b), or using the dormancy length of potato varieties to manage storage (Magdalena and Dariusz, 2018). The first approach may not be adequate for the storage of potatoes dedicated to processing, as most varieties are susceptible to sweetening when stored at low temperatures. This phenomenon of sweetening due to the accumulation of reducing sugars is also called "cold-induced sweetening" (CIS) (Hou et al., 2017; Sowokinos, 2001). High sugar levels induce browning of the potato after frying and produce toxic compounds such as acrylamide that may raise concerns for human health (Paul et al., 2016a; Wiberley-Bradford and Bethke, 2017). The advantage of using anti-sprouting products is their broad effectiveness for any variety at any temperature. However, some products are associated with a risk of toxicity for the consumer, and there is an increasing demand from consumers and national agencies for food free of chemical products. Indeed, chlorpropham (CIPC) has been used for decades to control sprouting in potatoes, but the European Union recently decided to not renew the approval of this molecule due to concerns raised for consumers regarding this active substance and its metabolite 3-chloroaniline, and due to the identification of data gaps preventing to perform a final consumer risk assessment (European Commission, 2019; European Food Safety Authority (EFSA) et al.,

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2017). The metabolites of CIPC, such as aniline, have further increased concerns for consumers since those molecules have been detected in the potato's skin (Orejuela and Silva Poma, 2005; Paul et al., 2014; Smith and Bucher, 2012). Molecules that pose fewer health risks have been recently commercialized, and they seem promising as replacements for CIPC, but their costs remain high; some require several applications to be effective during the entire storage season, which is time-consuming (Curty, Personal communication), and it is unclear whether consumers and authorities will accept them in the future. Therefore, using potato varieties with a long dormancy period could be a sustainable solution to avoid or delay the sprouting of potatoes, thus avoiding or eliminating the use of anti-sprouting products and consequently increasing the benefits for human health and the environment. However, the dormancy of potato varieties is not known for all varieties, or information found about dormancy is sparse and conflicting (Agriculture and Horticulture Development Board (AHDB), 2019). Therefore, in this context, predicting potato dormancy is of great interest for the management of storage. For instance, the capacity to predict potato dormancy may allow the processing of priority batches of short-dormancy varieties, thus minimizing or avoiding the use of chemicals and optimizing the management of stocks.

Potato sprouting appears during storage after a break in the dormancy period (Coleman, 1987; Daniels-Lake and Prange, 2007), but the definition of dormancy is subject to discussion. Reust (1982) described dormancy as the "period between tuber initiation and the development of the first sprouts". Emilsson (1949) mentioned a "rest period" where the potatoes are unable to sprout and a "dormancy period" where the tuber is maintained without sprouting under optimal conditions. Three periods were also defined: endodormancy regulated by physiological factors internal to the meristem, paradormancy regulated by external physiological factors, and ecodormancy. During this last period, dormancy can be maintained under specific environmental conditions (Delaplace, 2007; Lang et al., 1987). It is necessary to take into consideration that the length of this period depends on complex mechanisms to predict potato dormancy. In the literature, authors have reported that varieties display differential responses in dormancy length (Aksenova et al., 2013; Burton, 1978; Danieli et al., 2018; Daniels-Lake and Prange, 2007; Magdalena and Dariusz, 2018; Muthoni et al., 2014; Suffle et al., 2016). However, dormancy is also influenced by phytohormones, metabolites, and environmental conditions during both the growing season and storage (Aksenova et al., 2013; Delaplace, 2007; Delaplace et al., 2009; Muthoni et al., 2014; Reust, 1982; Sonnewald and Sonnewald, 2014). Factors related to the growing season that influence dormancy include the temperature (Levy and Veilleux, 2007; Magdalena and Dariusz, 2018; Muthoni et al., 2014; Reust, 1982; Zommick et al., 2014), the water supply (Czerko and Grudzińska, 2014; Muthoni et al., 2014), the soil humidity (Firman et al., 1992), the soil fertility (Muthoni et al., 2014), and the photoperiod (Fernie and Willmitzer, 2001; Muthoni et al., 2014). Firman et al. (1992) studied the importance of soil moisture and physiological age on the emergence of seed tuber sprouts in the field. They showed that temperature influenced the growth rate of sprouts and demonstrated that the growth rate is different in dry soil compared to wet soil. After harvest, the temperature and the atmosphere composition during storage also play important roles in dormancy duration (Aksenova et al., 2013; Burton, 1958; Caldiz, 2009; Celis-Gamboa et al., 2003; Czerko and Grudzińska, 2014; Daniels-Lake and Prange, 2007; Magdalena and Dariusz, 2018; Muthoni et al., 2014; Reust, 1982; Reust et al., 2001; Struik, 2007a, 2007b; Struik et al., 2006; Suttle, 2007).

The dormancy of the different potato varieties is subject to change depending on the above-mentioned factors. Most of these environmental parameters will be affected in the future by climate change; therefore, it is of interest to identify and quantify the main variables influencing dormancy duration. This would allow the building of a robust predictive model of dormancy parameterized with predictors that are easy to record in the field. The limitations of previous studies conducted on the same topic include the small sizes of the datasets used and the use of only a few varieties, or only a few years of trials. In the present study, we took advantage of an unprecedented large dataset containing dormancy observations obtained from field trials managed under contrasted environmental conditions by Agroscope (Nyon, Switzerland) over a period of 25 years.

Given the increasing climate variability, dormancy models can enable the improvement of potato storage management and reduce losses caused by sprouting.

2. Materials and methods

2.1. Data collection and preparation

2.1.1. Field trials

Field trials have been conducted during 25 growing seasons (from 1990 to 2014) by Agroscope, the Swiss agricultural research center, in five experimental sites located at different altitudes in Switzerland, namely "La Frêtaz" (elevation of 1200 m asl), "Les Mottes" (elevation of 455 m asl), "Grangeneuve" (elevation of 680 m asl), "Goumoëns" (elevation of 609 m asl), and "Changins" (elevation of 420 m asl). A total of 537 varieties were tested, and each was included in at least three different experiments, allowing the acquisition of 3379 records. All varieties tested were varieties registered in the official European variety catalog. They are listed in the Supplementary Material 1. Potatoes were planted from March to June and harvested from August to September, depending on the year and location. The soils were fertilized when necessary following the usual agricultural practices. Before potato emergence, a herbicide was applied according to the best management recommendations each year. Haulm destruction was implemented with a combination of chemicals (various products) and mechanical treatments (the EnviMaxX machine from Rema environmental machinery B. V., the Netherlands). Potatoes were treated to prevent late blight (*Phytophtora infestans*) approximately once a week from emergence to haulm killing, using various fungicides. After harvest, potatoes were stored at room temperature (around 15 °C) for two weeks in the dark to promote healing. Then, the potato tubers were calibrated, weighed, and stored in wooden crates ($0.6 \times 0.4 \times 0.18$ m) at a rate of 10 kg per crate for each variety, trial, and location. The tuber diameter used for the post-harvest trials ranged from 42.5 mm to 70 mm. The temperature was gently decreased from 15 °C to 8 °C at a rate of 3 °C every 48 h, and potatoes were kept at 8 °C and 85% relative humidity (RH).

During the 25 studied growing seasons, the following weather data were collected from Agrometeo (https://www.agrometeo.ch/, accessed 2017) and from MeteoSwiss (Federal Office of Meteorology and Climatology MeteoSwiss, Switzerland): the daily average temperature (°C) in the air at two meters above the soil; the daily minimum temperature (°C) in the air at two meters above the soil; the daily maximum temperature (°C) in the air at two meters above the soil; the daily average temperature (°C) at the level of the soil (i.e., at five cm above the soil); the daily average soil temperature (°C) at a depth of 10 cm; the daily average relative humidity (%); the daily precipitation (mm); the daily maximum precipitation intensity (= maximum precipitation per hour registered in the day) (mm/h); and the daily average insolation (= solar irradiance) (MJ m^{-2}). Plots were only irrigated for a few growing seasons and only at the "Changins" location. Irrigation data were handled by adding the water amounts per day to the daily precipitation data. The tuber initiation date was recorded for one location (Goumoëns), eight years and 67 varieties, which allowed the acquisition of 126 records. To fill this data gap, we set 16 days after the emergence as the date of theoretical tuber initiation for all locations in the dataset where this information was missing. This value was obtained by averaging the period from emergence to tuber initiation date from the tuber initiation recorded for the 67 tested varieties (average = 16.37 days). The standard deviation of tuber initiation was 4.05 days, representing less than 5% (3.04%) of the entire growing period (from planting to harvest), which was on average equal to 132.94 days in the dataset. The date of the main physiological stages of the crop (i.e., planting, emergence, tuber initiation, and maturity) and the dates of crop management operations (e.g. haulm killing and harvest) were also recorded and used to define the following periods: from planting to emergence, from planting to tuber initiation, from planting to haulm killing, from planting to harvest, from emergence to haulm killing, from emergence to harvest, from tuber initiation to haulm killing, from tuber initiation to harvest, and from haulm killing to harvest. For all these periods, the above-mentioned weather data (e.g., temperature, precipitation, or relative humidity) were summed and/or averaged for each period and recorded in the database (list in the Supplementary Material 2). During storage, potatoes were considered sprouted when 80% of tubers in the crate had visible sprouts of a minimum length of three mm, according to the definition of the end of dormancy established by Reust (1982, 1986). The sprouting date was recorded at the time that the tubers first displayed the characteristics described the abovementioned definition. In this study, we will consider the dormancy period as follows: the period between the harvest and the sprouting date during storage.

2.1.2. *Greenhouse trial*

A greenhouse trial was conducted in which seed tubers of the Bintje variety were placed at 18 °C and under light for 18 days to stimulate germination before planting. A total of 42 tubers were planted in square pots of 10 liters following good practices for greenhouse trial management. A standard soil was used (Swiss mixture from the company RICOTER Erdaufbereitung AG, mixture for organic gardening, Switzerland; composition: 30% white peat 0–30 mm; 30% country soil sterile and 40% Coco-Peat) and mixed with substrate for plant cultivation (Gerbr. Brill Substrate GmbH & Co. KG, Typ 4, Germany) (ratio 2:1). Ammonium nitrate fertilizer was added and mixed into the soil mixture; about 30 g of fertilizer were mixed with 100 liters of soil mixture (ammonium nitrate fertilizer composition: total N = 27% + total Mg = 2.5% and Ca = 9%, LANDOR fenaco Genossenschaft, Switzerland). Plants were kept in the same room at ambient temperature for 10 days, corresponding to 99% emergence (average temperature of 17 °C). The 42 plants were divided into seven greenhouse chambers and grown at two different temperatures (15 or 20 °C), with four chambers at 15 °C (four replicates) and three chambers at 20 °C (three replicates). Data loggers (LogTag® temperature recorder, model: TRIX-8, Amatempérature Sàrl, Switzerland) were placed close to the plants from planting to harvest to measure the air temperature for each replicate (one record per hour). Plants were irrigated manually two or three times a week, and a photoperiod of 12 h of light and 12 h of dark was applied. To prevent infestation by thrips (*Thrips tabaci, Frankliniella occidentalis*), we placed *Amblyseius cucumeris* auxiliaries in each plant (Andermatt Biocontrol Suisse AG). Potatoes were haulm killed 67 days after emergence and harvested 34 days after haulm killing to allow proper skin set. The harvested tubers were calibrated for each plant to identify the proportion of tubers (number and weight) smaller and larger than 32 mm. The average weight per tuber of each caliber and from each plant was calculated by dividing the total weight of tubers per plant by the number of tubers per plant. The tubers were then stored in a storage chamber at 12 °C and 85% RH for one week to stimulate healing, and then the temperature was lowered to 8 °C at a rate of 2 °C every four days. Sprouting assessment was performed every two weeks. The length of the biggest sprout of each tuber and from each plant was measured.

2.2. *Data analysis*

The R software version 3.6.3 (R Core Team, 2019) was used for data preparation and statistical analysis.

2.2.1. *Field trails*

An analysis of variance (ANOVA) was conducted to confirm the effect of the factors variety, location, and year on the potato dormancy duration. In this analysis, the 25 years of trials were considered, as well as the five locations and the 537 tested varieties. A given variety for a given year was considered as the experimental unit, and the dormancy duration from harvest until sprouting date was accessed for each experimental unit. This allowed the acquisition of 3379 records (see Section 2.1.1.). The percentage of the variability explained by each factor was calculated by the ratio of the sum of squares for the considered effect to the total sum of squares.

As some varieties were only tested three times during the 25 years of testing, the prediction of the dormancy for those varieties could be less reliable due to a lack of sufficient reference dormancy values. Therefore, the regression coefficients estimated by the ANOVA model for each variety as a dummy variable were used to define an additional explanatory variable called “variety class”. Based on these estimates, varieties tested fewer than ten times during the 25 years of testing were placed in the same variety class as the varieties closest in dormancy that were tested more frequently. However, all varieties that were tested at least 10 times were kept to limit the bias that could come from the effect of combination with other varieties less tested. Finally, 143 different variety classes were identified: 85 classes containing grouped varieties and 58 classes containing individual varieties (i.e., tested at least 10 times).

A validation was performed using one third of the records (randomly selected) for each variety class (N = 1102) to assess the accuracy of the developed prediction model. The remaining samples were used to calibrate the model (N = 2277). Validation and calibration sets were independent. This splitting was done using the CARET package version 6.0–86 in R (Kuhn, 2020) that ensures the presence of all varieties in both the validation and calibration sets. The predictors used in the regression were previously mentioned in the data section; however, variety class was used instead of variety. Moreover, the location and the year of testing were not retained in the prediction model because they were characterized by the weather predictors. Consequently, 247 predictors were considered to develop the model predicting potato dormancy. All predictors were not available for all records. The completeness of the calibration set varied from 44.1% (N = 1005) to 100% (N = 2277) as follows: 94 predictors had a completeness of at least 75%, 131 predictors had a completeness ranging from 50% to less than 75%, and 22 predictors had a completeness of less than 50% (Supplementary Material 2).

The predictive model was built using a forward selection approach for the predictors. So, the predictors were added to a linear model one by one. First, 247 univariate regressions were performed. For each model, the following statistical parameters were calculated: the coefficient of determination (R^2c), the root mean square error (RMSEc) of the calibration, the RMSE (RMSEv), and the R^2 of the validation (R^2v). The predictor included in the univariate model with the highest R^2v was kept. Then, bivariate regressions were developed by fixing the first retained predictor and testing the remaining 246 variables as the second predictor. Again, the second predictor was selected based on the model that gave the highest R^2v. This procedure was repeated until the inclusion of an additional predictor in the model explained less than 1% of the additional variability in dormancy. This allowed us to avoid the potential problem of overfitting. Finally, all regression coefficients of the prediction model were studied to determine whether the model generated an expected weight for all selected predictors.

The qualitative effect of variety was studied using the regression coefficients estimated by the selected model for each variety class dummy variable. Therefore, in our model, the effect of variety is represented by 142 regression coefficients. By default, R software fixed the regression coefficient for the first variety class dummy variable to zero. The result is that the coefficient of regression represents the averaged dormancy between the considered variety class and the one taken as reference. To better understand these data, the regression coefficients were re-scaled after calculation using the Bintje variety as reference since it was the most widely tested variety in our dataset. To re-scale the data, the regression coefficient estimated for each variety class dummy variable was subtracted by the one estimated for the Bintje variety. Finally, differences in averaged dormancies between varieties were plotted.

2.2.2. *Greenhouse trial*

The sum of daily maximum temperatures in the air from planting to harvest for each replicate (3 replicates for plants grown at 20 °C and 4 replicates for plants grown at 15 °C from emergence to harvest) was calculated using the maximum temperature recorded per day (one record per hour).

Data for all measured variables of the six plants per greenhouse chamber were averaged before the analysis. Our experiment was conducted using a nested design. We used a one-way linear mixed model with the temperature of growth as a fixed effect (15 and 20 °C) to evaluate the number of small and large tubers and the average weight of small or large tubers after harvesting. The length of sprouts was fitted to a two-way linear mixed model that included temperature (two levels: 15 and 20 °C) and the period of observation (days after harvest = DAH, four levels) as fixed effects. Models were adjusted using the lme4 R package version 1.1–23 (Bates et al., 2015). The data for the length of the sprouts were transformed using "$\log_e (x + 1)$" to ensure the homogeneity of the variance and normality. The greenhouse chambers were considered a random factor for all the models. The effect of the greenhouse chambers was removed to improve the model when this effect was not significant. We performed significance tests for the fixed effects for the measured variables (with a confidence interval of 95%) using a Chi-square test or an F-test in cases where the effect of the random factor was not significant. Calculations were performed using the "car" R package (Fox and Weisberg, 2019). The marginal post hoc Tukey test (emmeans method) using the "emmeans" R package (Lenth, 2020) was used to compute the multiple comparison post hoc tests to identify mean differences within factors and interactions. For data summary and graphics, we used various R packages ("ggplot2", "plyr", "Rmisc", "lattice", and "cowplot" packages) (Hope, 2013; Sarkar, 2008; Wickham, 2011, 2016; Wilke, 2019).

3. Results

3.1. *Main factors influencing potato dormancy*

In this study, we considered dormancy as the period between the harvest and the sprouting date during storage. This definition is generally used in practice by the potato sector. The dormancy period varied from 27 days to 179 days, with an average of 96.29 days in the dataset (all varieties, years, and locations taken together). The variety effect explained 60.3% of the dormancy variability ($p < 0.001$). Among the 537 studied varieties, the dormancy period of the varieties varied on average from 50 (Lucera [N = 3]) to 158 days (Taurus [N = 3]). Several popular varieties had short dormancies (e.g. Agata, Annabelle, Nicola, or Amandine, which displayed an average dormancy of 57 days [N = 22], 57 days [N = 16], 72 days [N = 25], and 75 days [N = 20], respectively), while other popular varieties had long dormancies (e.g. Agria, Panda, Lady Claire, or Verdi, which displayed an average dormancy of 131 days [N = 96], 130 days [N = 24], 120 days [N = 68], and 120 days [N = 10], respectively) (Fig. 1).

The year effect explained 13.9% of the dormancy variability ($p < 0.001$). For instance, during the 25 years of testing for the Bintje variety, the observed dormancy ranged from 67 days (N = 7) to 125 days (N = 9) (Fig. 2).

The location effect was less important than the two above-mentioned effects and explained 5.4% of the dormancy variability ($p < 0.001$). The average dormancy observed in the location "Changins" was 93 days (N = 2138), while in the "La Frêtaz" (N = 576), "Goumoëns" (N = 219), "Grangeneuve" (N = 330), and "Les Mottes" (N = 116) locations, the average dormancies were 110, 100, 92, and 88 days, respectively.

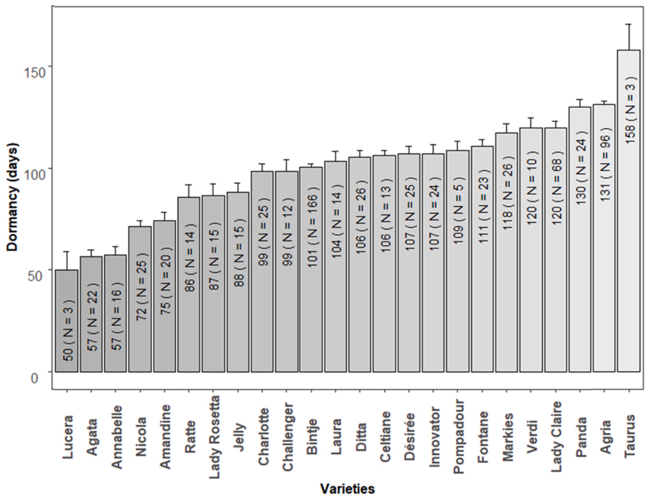

Fig. 1. Average days of dormancy with their standard errors observed for popular tested varieties. The number of records (N) available for each variety is indicated on the bars.

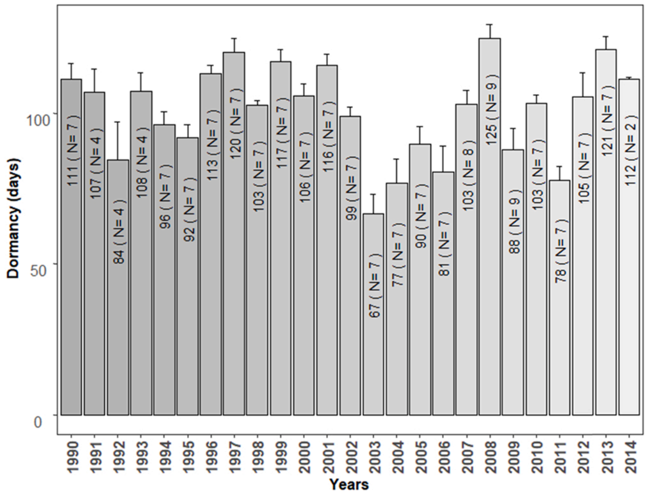

Fig. 2. Average days of dormancy (days) with their standard errors observed for the Bintje variety during the 25 years of tests. The number of records (N) available for each year is indicated on the bars.

3.2. *Prediction model of potato dormancy*

A total of 247 univariate linear regressions were initially performed using the calibration set and then applied to the validation set. R^2v ranged from 0.00 to 0.52, and RMSEv varied between 18.49 and 27.53 days. For the sake of conciseness, all models are not shown; only the five models with the best values for goodness of fit are presented (Table 1). The model explaining the majority of the dormancy variability included the variety class as a fixed effect. The corresponding R^2v was 0.52, which is well ahead of all other models (Table 1). The R^2c was close to R^2v (0.58 and 0.52), suggesting good model robustness. The RMSEv was 18.49 days. The univariate model including the sum of the daily maximum temperatures from tuber initiation to harvest had the highest R^2v after the model that included the variety class (Table 1). The different sample sizes used in the calibration and validation set between the predictors are related to data availability, which may vary for the predictors used. The 247 predictors and the corresponding number of records for each predictor are listed in the Supplementary Material 2.

For the second step in the development of the predictive model, bivariate models that always included the variety class plus one of the

Table 1

Calibration and validation prediction performance of the five univariate models predicting potato dormancy with best values for goodness of fit.

Dormancy ~ predictor	Calibration			Validation		
	N	R^2	RMSE (days)	N	R^2	RMSE (days)
Variety class	2277	0.58	17.90	1102	0.52	18.49
Sum of the daily maximum temperatures in the air for the period from tuber initiation to harvest	1754	0.17	23.98	839	0.16	24.24
Sum of the daily average temperatures in the air for the period from tuber initiation to harvest	1746	0.16	24.12	835	0.16	24.25
Sum of the daily maximum temperatures in the air for the period from emergence to harvest	1730	0.16	24.06	822	0.16	24.23
Sum of the daily average temperatures in the air for the period from emergence to harvest	1722	0.15	24.23	818	0.15	24.27

N = number of samples, R^2 = coefficient of determination, RMSE = Root mean squared error.

246 remaining explanatory predictors were evaluated. R^2v ranged from 0.41 to 0.70. RMSEv varied between 14.59 and 20.94 days. The five bivariate models with the best values for goodness of fit are presented in Table 2. It is important to note that the five predictors represent temperature parameters. The differences in prediction performance between models (Table 2) were less important than those observed between variety class and other tested predictors in the univariate models (Table 1). These low differences in prediction performance between bivariate models might be due to collinearity between predictors. The model with the highest goodness of fit for validation (R^2v and RMSEv) relied on data with few missing records. This model included the sum of the daily maximum temperatures in the air during the period from planting to harvest as a second predictor (Table 2) and explained 70% of the variability in dormancy (R^2v = 0.70). The RMSEv was 14.59 days. By subtracting the part of the variability explained by the univariate model including only the variety class, we can conclude that this second predictor explained an additional 18% of dormancy variability. Based on the regression coefficient (−0.02), the sum of the daily maximum temperatures in the air during the period from planting to harvest had a negative influence on potato dormancy.

Table 2

Calibration and validation prediction performance of the five bivariate models predicting potato dormancy with best values for goodness of fit.

Dormancy ~ variety class + predictor	Calibration			Validation		
	N	R^2	RMSE (days)	N	R^2	RMSE (days)
Sum of the daily maximum temperatures in the air for the period from planting to harvest	2175	0.72	14.32	1048	0.70	14.59
Sum of the daily maximum temperatures in the air for the period from tuber initiation to harvest	1753	0.73	14.31	839	0.69	14.75
Sum of the daily maximum temperatures in the air for the period from emergence to harvest	1729	0.73	14.25	822	0.69	14.70
Sum of the daily average temperatures in the air for the period from planting to harvest	2167	0.72	14.50	1044	0.69	14.75
Sum of the daily average temperatures in the air for the period from tuber initiation to harvest	1745	0.72	14.42	835	0.69	14.83

N = number of samples, R^2 = coefficient of determination, RMSE = Root mean squared error.

A second validation analysis was performed to assess the robustness of the above-mentioned bivariate model. The bivariate models were run with a smaller set of data used for the validation containing the same amount of data for all the tested variables (N = 454 instead of N = 1048) (Supplementary Material 3). We observed that the bivariate model with the highest goodness of fit for validation is the same for both dataset (RMSEv = 14.92 and RMSEv = 14.59) (Table 2 and Supplementary Material 3). This validation analysis confirms the robustness of the selected bivariate model with the sum of the daily maximum temperatures in the air during the period from planting to harvest as second predictor.

The third step in the development of the predictive model consisted of developing 245 models including three explanatory variables. The first and second predictors were the ones selected from the univariate and bivariate models, respectively. For the third step, the remaining predictors were evaluated. R^2v and RMSEv for the 245 developed models ranged from 0.66 to 0.71 and between 14.33 and 15.83 days, respectively. Table 3 summarizes the five three-trait models with best values for goodness of fit.

As already observed with the bivariate models, the differences in goodness of fit between the best candidate models were small. The model showing the highest R^2v included the average of the daily average insolation data for the period from emergence to tuber initiation as the third explanatory variable. This combination of variables explained 71% of the dormancy variability.

This corresponds to an increase of only 1.20% of R^2v compared to the bivariate model (Table 4). Therefore, the prediction accuracy of a model including three predictors was not highly improved compared to the

Table 3

Calibration and validation prediction performance of the five models predicting potato dormancy using three predictors with best values for goodness of fit.

Dormancy ~ variety class + sum of the daily maximum temperatures in the air for the period from planting to harvest + predictor	Calibration			Validation		
	N	R^2	RMSE (days)	N	R^2	RMSE (days)
Average of the daily average insolation data for the period from emergence to tuber initiation	1546	0.75	13.80	736	0.71	14.33
Average of the daily maximum temperatures in the air for the period from planting to harvest	2175	0.73	14.09	1048	0.70	14.46
Average of the daily average insolation data for the period from haulm killing to harvest	1901	0.74	14.17	919	0.70	14.60
Period from planting to harvest	2175	0.73	14.18	1048	0.70	14.51
Average of the daily average temperatures in the air for the period from planting to harvest	2167	0.73	14.12	1044	0.70	14.50

N = number of samples, R^2 = coefficient of determination RMSE = Root mean squared error.

Table 4
Performance of the models including one to five predictors within the forward selection.

Number of predictors	Variable added to the model	Validation R^2	% of variability explained by the added predictor	RMSEv (days)
1	Variety	0.52	51.82	18.49
2	Sum of the daily maximum temperatures in the air for the period from planting to harvest	0.70	17.82	14.59
3	Average of the daily average insolation data for the period from emergence to tuber initiation	0.71	1.20	14.33
4	Average of the daily maximum temperatures in the air for the period from emergence to tuber initiation	0.73	1.75	13.90
5	Sum of the daily average soil temperatures at a depth of 10 cm for the period from maturity to harvest	0.74	1.30	14.01
6	Average of the daily maximum temperatures in the air for the period from planting to emergence	0.75	0.72	13.82

R^2 = coefficient of determination, RMSEv = validation root mean squared error.

selected bivariate model. Moreover, the average of the daily average insolation data for the period from emergence to tuber initiation that was included as the third explanatory variable in the model is not easy to collect in the field.

Models with four, five, and six predictors were also tested, and we found R^2v values of 0.73, 0.74, and 0.75, respectively. Their respective RMSE values were 13.90 days, 14.01 days, and 13.82 days (Table 4). We did not go further than six predictors because the additional predictor explained less than 1% of the dormancy variability (Table 4). As observed for the models including three predictors, the models with four, five, and six predictors had only a marginal increase in R^2v and improvement of prediction accuracy compared to the selected bivariate model (Table 4). Thus, since the most robust model is always the most parsimonious, the model with best values for goodness of fit is the one including two explanatory variables (Table 2). Moreover, this model had the advantage of including variables that are easy to record in the field.

3.3. *Varietal differences in dormancy*

The effect of variety was modeled as a categorical variable, and it was studied using the selected bivariate model. The regression coefficients for the main 58 individual varieties tested in our dataset and rescaled based on the Bintje variety are presented in Fig. 3. Several varieties had regression coefficients close to the one estimated for the Bintje variety (i.e., fixed at zero), meaning that the dormancy of these varieties is close to the dormancy of Bintje. For instance, the dormancy of the varieties “Charlotte” (regression coefficient = −2.26 days), “Gourmandine” (regression coefficient = 0.64 days), “Granola” (regression coefficient = 4.25 days), “Challenger” (regression coefficient = - 2.87 days), “Erika” (regression coefficient = 2.50 days), or “Juliette” (regression coefficient = 3.47 days) were similar to the reference dormancy of the Bintje variety. In contrast, the variety “Agata” had a shorter dormancy of 42.57 fewer days compared to the Bintje variety. For the variety “Agria”, dormancy was 30.09 days longer than the dormancy of the Bintje variety (Fig. 3).

3.4. *In vivo validation of the model*

Based on the composition of the bivariate model, after variety, the sum of the daily maximum temperatures in the air for the period from planting to harvest is the environmental factor that most influences dormancy variability. To test the relevance of this effect, different temperatures were applied under controlled conditions in the greenhouse trial from emergence to harvest. This resulted in obtaining two distinct average sums of daily maximum temperatures in the air from planting to harvest. The average sum of daily maximum temperatures in the air from planting to harvest was 2706 °C ± 122 (mean ± standard error, N = 4) for plants grown at 15 °C and 3223 °C ± 144 for plants grown at 20 °C (mean ± standard error, N = 3).

After harvest, the average number and weight of the large tubers (caliber > 32 mm) were not significantly different between the plants grown at 15 °C (6.8 tubers/plant and 44.7 g) and 20 °C (7.1 tubers/plant and 53.5 g) (P values = 0.75 and 0.16). The average number and weight of the small tubers (caliber < 32 mm) were also not significantly

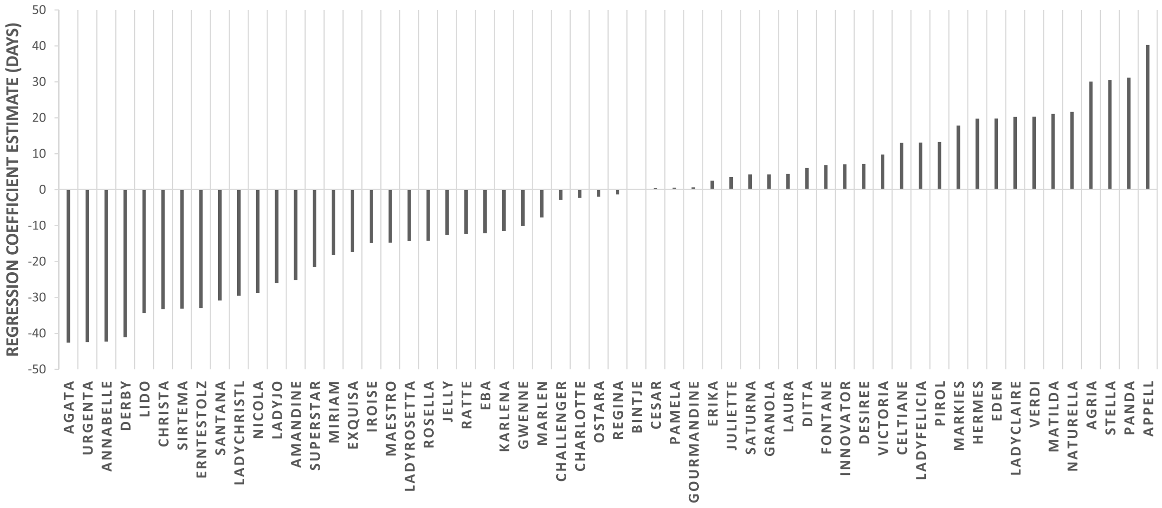

Fig. 3. Regression coefficients for the 58 main tested varieties rescaled based on the Bintje variety estimated from the selected bivariate model. Y-axis is the days of dormancy.

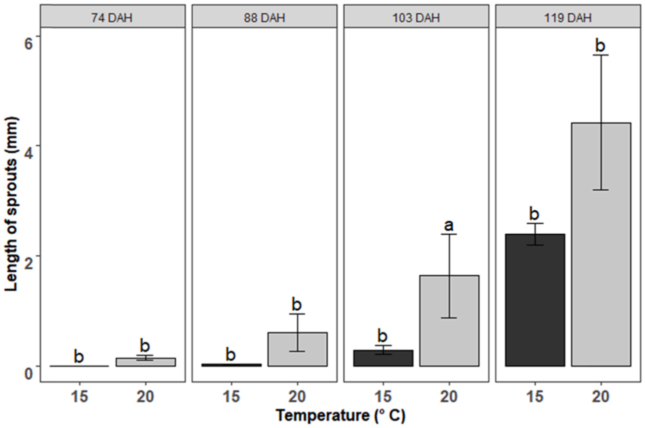

Fig. 4. Average length of the sprouts for the large tubers (caliber > 32 mm) from plants grown at two average sums of daily maximum air temperature from planting to harvest, i.e. 2706 °C ± 122 (plants grown at 15 °C, mean ± standard error, N = 4) and 3223 °C ± 144 (plants grown at 20 °C, mean ± standard error, N = 3) for each observation in days after harvest (= DAH). For a given observation, groups sharing the same letter are not significantly different (Tukey test, confidence level of 95%).

different for plants grown at 15 °C (10.6 tubers/plant and 12.1 g) and at 20 °C (7.1 tubers/plant and 11.1 g) (P values = 0.16 and 0.50). The length of the sprouts during storage was significantly impacted by the temperature during the growing period between emergence and harvest (P value = 0.02) and by the time of observation measured in days after harvest (P value < 0.001). We also observed an interaction between the temperature during the growing season and the time of observation (P value = 0.02). At the beginning of the storage period (74 DAH), sprouting was absent or low, and the length of the sprouts from tubers grown at 20 °C (average of 0.2 mm) was not significantly different from the length of the sprouts of tubers grown at 15 °C (average of 0.0 mm) (P value = 0.52). At 103 days after the harvest, the length of the sprouts of the large tubers was significantly higher for plants grown at 20 °C (average of 1.6 mm of sprouts) when compared to 15 °C (average of 0.3 mm of sprouts) (P value = 0.01). The length of the sprouts of the large tubers at 88 and 119 days after harvest was also higher for plants grown at 20 °C (average of 0.6 and 4.4 mm) compared to 15 °C (average of 0.0 and 2.4 mm). However, it should be noted that the differences for these last two observation periods were not significant, even though the P values were low (0.08 and 0.07) (Fig. 4).

We also observed a faster increase in sprout length during storage for plants grown at 20 °C compared to plants grown at 15 °C. Sprouting from tubers grown at 20 °C started to significantly increase at 103 DAH. The length of the sprouts at 103 DAH was significantly higher (average of 1.6 mm) compared to the length of the sprouts at 74 days and 88 days after harvest (average of 0.2 and 0.6 mm) (P values < 0.001 and 0.01) and continued to significantly increase at 119 DAH (average of 4.4 mm) compared to sprouting at 103 DAH (P value < 0.001). Sprout length at 74 and 88 DAH was not significantly different (P value = 0.11). Sprouting of potatoes grown at 15 °C started to increase later, at 119 DAH. The length of the sprouts was significantly higher at 119 DAH (average of 2.39 mm) compared to the length of the sprouts for the first three observations at 74, 88, and 103 DAH (average of 0.0, 0.0, and 0.3 mm) (P value < 0.001) for which sprouting was low and not significantly different (lowest P value = 0.13).

4. Discussion

With the non-renewal of the most used anti-sprouting product CIPC in Europe (European Commission, 2019), a proper management of potato storage will be vital to avoid economic losses. Anti-sprouting products that are replacing CIPC on the market often require more treatments during the storage season and thus are time-consuming and have a higher cost compared to CIPC (Curty, Personal communication). Therefore, the use of dormancy should be considered to improve potato storage management, and the model built in our study could be an instrumental tool to help farmers in their decisions and to avoid losses during potato storage.

The main factor determining the duration of potato dormancy highlighted by this study was the variety. This explained 60.3% of the variability and was the most critical variable used to predict the duration of dormancy. We observed a range of 108 days between varieties. The lowest dormancy was 50 days for the Lucerna variety; the longest was more than three-fold higher: 158 days for the Taurus variety (see Fig. 1). Our results are in line with Magdalena and Dariusz (2018); they observed dormancy periods ranging from 78 to 155 days, depending on the variety, among six potato varieties tested during three seasons of storage at 8 °C.

The second important factor determining the duration of potato dormancy is related to environmental conditions. Indeed, the year and location together explained almost 20% of the variability in dormancy duration (19.3%), while 13.9% was explained by the year. Thus, year had a higher impact on the duration of dormancy than location. In our trials, the dormancy of the Bintje variety ranged from 67 to 125 days, depending on the year. Magdalena and Dariusz (2018) also observed significant differences in sprouting date between different years of testing and varieties, and underlined that these differences were due to the effect of weather conditions during the growing period of the potato plants. It has been reported in the literature that the water supply (Czerko and Grudzińska, 2014; Muthoni et al., 2014), the temperature (Levy and Veilleux, 2007; Magdalena and Dariusz, 2018; Muthoni et al., 2014; Reust, 1982; Zommick et al., 2014), the soil humidity (Firman et al., 1992), the photoperiod (Fernie and Willmitzer, 2001; Muthoni et al., 2014), or the soil fertility (Muthoni et al., 2014) during the growing season greatly influences the length of the potato dormancy period. These interactions between dormancy and weather conditions were also present in our dataset. The response of the Bintje variety illustrates this; after a growing season with a heatwave (year 2003), the dormancy was only 67 days, while after a colder growing season (year 2008), the dormancy was almost two-fold longer–125 days (Fig. 2). Our results show that effect of both variety and environment drives the length of potato dormancy and underline the effect of climate change on potato dormancy. The expected temperature increase over the next 30–50 years is predicted to be in the range of 2–3 °C (Hatfield and Prueger, 2015; IPCC, 2007). With such an increase in average temperatures during the growing season of potatoes, we can expect a shortening of the dormancy of tubers during storage, with practical consequences for storage management. Among those consequences, we can mention the necessity of early anti sprouting treatments, or the necessity to lower the average temperatures of storage, with consequences for tuber quality with enhanced CIS.

Thanks to our large dataset, we built models to predict the sprouting date of a given potato variety considering its dormancy length and the environmental factors related to its growing season. Within our models, we used weather variables of the different years and locations instead of year and location as categorical factors, which have no predictive power themselves. Of all the models for predicting potato dormancy length tested in our study, the bivariate model including the variety and the sum of daily maximum temperatures during the period from planting to harvest showed a good fit explaining 70% of the variability of the observed dormancy, which is 18% better than the univariate model with only variety as a predictor. This model predicted the dormancy period with a precision of 14.59 days. This level of precision can be considered sufficient in comparison with the average duration of potato storage, which may extend up to eight months (Curty, Personal communication). The robustness of the selected bivariate model was confirmed by a second analysis performed with a smaller set of data used for the validation containing the same amount of records for all variables (N = 454 instead of N = 1048). Other bivariate models with different variables were presenting similar performances in term of prediction (Table 2). The added value of the selected model, in addition to its highest goodness of fit, is that it offers the advantage of using variables that are easy to collect in the field and therefore is easy to use in practice by the growers.

The study of the regression coefficient showed a negative impact of the sum of the daily temperatures from planting to harvest (−0.02). This means that the dormancy length decreases when this temperature increases. This temperature effect was confirmed by our *in vivo* experiment. Indeed, we conducted a greenhouse trial to check the effect of the environmental variable that most influenced the dormancy duration after the variety factor and selected through the models. The Bintje variety was chosen because it was the most represented variety in our trials. We found that at 103 DAH, the length of the sprouts of the large tubers from plants grown at 20 °C was significantly higher (average of 1.6 mm of sprouts) than the ones grown at 15 °C (average sprout length of 0.3 mm). In this greenhouse experiment, we also observed an effect of temperatures during the growing season on the speed of growth of the sprouts during storage. Faster sprouting was observed for tubers from plants grown at 20 °C for which the increase in sprouting significantly began at 103 DAH, compared to tubers harvested from plants grown at 15 °C for which the increase in sprouting was only significant at 119 DAH. These results are consistent with our models as well as with the literature since authors conducted studies on different varieties and showed that high temperatures during the growing season lead to reduced dormancy (Levy and Veilleux, 2007; Magdalena and Dariusz, 2018; Zommick et al., 2014). This impact of temperatures during the growing season on the dormancy length can be explained because high temperatures during the growing season are known to accelerate the physiological aging of the tubers (Caldiz et al., 2001) leading to several physiological and biochemical modifications related to the end of dormancy (Delaplace et al., 2009; Fukuda et al., 2019).

To verify the relevance of the regression coefficient estimates, we made a comparison of the dormancy information for a few varieties found in the literature. To facilitate the interpretation of these estimates, we have shown those results compared to the Bintje variety (Fig. 3). Bintje is usually described as a variety with medium to long dormancy according to the references (European Cultivated Potato Database, 2020; Le plant de pomme de terre Français, 2020; NIVAP, 2011). Varieties with an estimate in Fig. 3 close to zero also have a medium to long dormancy period (e.g. Gourmandine, Granola or Erika). We noticed that for some varieties, such as Agria, Agata, or Erika, the dormancy length in our model and in the literature were comparable (Agrico, 2020; European Cultivated Potato Database, 2020; Le plant de pomme de terre Français, 2020; NIVAP, 2011), while for other varieties, the dormancy length was slightly different. For instance, the dormancy of the Granola variety is described in the literature as long to very long (European Cultivated Potato Database, 2020; Solana GmbH & Co. KG, 2020), while according to our bivariate model, this variety has a medium to long dormancy (4.25 days longer than Bintje, see Fig. 3). The small differences between the estimate of dormancy given by our model and the dormancy provided by the breeders can be explained by the fact that our estimates are based on a large dataset with multi-environmental trials, while the dormancy provided by the breeders is generally based on trials managed in less contrasted environmental conditions. This highlights the need to collect information related to the weather conditions during the growing season and to harmonize the dormancy characterization of potato varieties.

In addition to its sufficient accuracy, this model was chosen as the most appropriate because it was robust (i.e., calibration and validation results were close) and the predictors included in the model are easy to collect in the field. Indeed, the planting and harvest dates are obviously known, and the daily maximum temperature is readily available from weather stations located in the surrounding area of the field or through simple temperature sensors that can be placed in the field during the growing season. Furthermore, in the context of pesticide reduction, using the dormancy information provided by our model to avoid or delay the use of chemicals to store potatoes is also of great interest.

Several practical storage strategies should be undertaken according to the final use of the potato (processing or fresh market) and depending on the dormancy duration of the varieties (short, medium, or long), as well as the desired storage duration (short-term storage or long-term storage).

The ideal scenario to prevent the use of anti-sprouting products would be to use varieties with long dormancies that can be stored for a long period at 8 °C and that do not require the application of anti-sprouting products for several months. Our model does not allow estimation of the dormancy of a variety for which the variety class of dormancy is unknown or not properly characterized. Therefore, it would be necessary to define the average dormancy of such varieties by testing them in the field and comparing their dormancy period with one of the control varieties for which the variety class is well characterized (e.g. the Bintje variety). This would enable us to integrate those varieties in our model to estimate the date of sprouting for a given storage season.

However, using varieties with long dormancies cannot be the only solution given that market requirements are driving the choice of varieties to be produced (Curty, Personal communication); therefore, it is advisable to also store varieties with medium and short dormancies. For short- and medium-dormant varieties, storage must be carefully planned for each season of storage to avoid food and thus economic losses. Based on the weather during the growing season, our model could be used to predict the dormancy period of these varieties and provide advice on which of the varieties will sprout first and therefore should be sold first, and which varieties will sprout later and can be retained. Another challenge for the adoption of this model by interested stakeholders is the collection of representative data for validation. Indeed, to maximize the accuracy and applicability of a model, it is important to collect large amounts of data using standardized protocols.

Depending on the predicted sprouting date, cold storage could be used to extend the dormancy of potato varieties. However, this is usually not possible for processing varieties because such storage induces sweetening at low temperatures, leading to a risk of production of toxic compounds during potato frying that may raise concerns for human health (Paul et al., 2016a; Wiberley-Bradford and Bethke, 2017). Nevertheless, some varieties that are not sensitive to sweetening can be stored at low temperatures without any problems (Visse-Mansiaux et al., 2019). Since our model was developed based on potatoes stored at 8 °C, it is not appropriate to predict sprouting for potatoes stored at lower temperatures (e.g. 4 °C). Such a prediction would require a revision of the model with new data for dormancy from tubers stored at lower temperatures. A correction coefficient or a new model could then be calculated. Such a corrected model dedicated to cold storage may be effective for the management of the storage of varieties for fresh markets that are usually stored at low temperatures.

Finally, trials are being conducted worldwide in which the potato dormancy date is recorded, and for which weather information is often readily available. This large amount of data from different countries could be collected and would allow for a better characterization of the dormancy of many varieties and a better prediction of the dormancy for a wider range of environmental conditions. This would facilitate the use of the dormancy information for storage management in the future. This tool will help anticipate the consequences of climate change on potato storage losses caused by sprouting and thus improve long-term food security. It could also effectively contribute to the development of a more sustainable agriculture sector by decreasing the use of chemicals through better management of potato storage and consequently answer the demands from consumers to avoid chemicals in food.

In conclusion, our study confirms the important impact of temperatures during the growing season on the dormancy period and shows that a bivariate model can predict with an acceptable level of accuracy the dormancy period for a given variety according to specific weather predictors during the growing season (i.e. sum of daily maximum temperatures during the period from planting to harvest). Our bivariate model has been validated by an *in vivo* experiment and has the advantage of being based on a large dataset, taking into consideration various environments across a wide range of conditions and varieties with many predictors. Consequently, predictive models can improve potato storage management and can help anticipate the consequences of climate change on potato storage.

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CRediT authorship contribution statement

All authors listed have contributed significantly to the work and agree to be in the author list. **Margot Visse-Mansiaux**: Conceptualization, Methodology, Visualization, Investigation, Formal analysis, Writing – original draft, Validation, Writing – review & editing. **Hélène Soyeurt**: Conceptualization, Methodology, Visualization, Investigation, Formal analysis, Validation, Writing – review & editing. **Juan Manuel Herrera**: Formal analysis, Validation, Writing – review & editing. **Jean-Marie Torche**: Investigation. **Hervé Vanderschuren**: Supervision, Project administration, Funding acquisition, Methodology, Investigation, Validation, Writing – review & editing. **Brice Dupuis**: Supervision, Conceptualization, Methodology, Investigation, Project administration, Funding acquisition, Validation, Writing – review & editing.

Author statement

All authors listed contributed to the work and are in agreement with the content of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2021.108396.

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