



# Dormancy and Physiological Age of Seed Tubers from a Diverse Set of Potato Cultivars Grown at Different Altitudes and in Different Seasons in Kenya

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## Abstract

The study was conducted to determine the dormancy and physiological age characteristics of diverse potato genotypes as influenced by growing altitudes and seasons for future breeding strategies and optimal patterns of use. Dormancy and sprouting characteristics have an impact on tuber production, storability and seed quality for planting and ware for consumption and the market. This study presents the results of dormancy and physiological age measurements conducted on 47 potato genotypes grown at three altitudes with three replications at each location and in two contrasting growing seasons. The seed tubers were evaluated at low altitude under darkness on moist sand storage conditions to assess their dormancy release, number of sprouts, sprout weight, sprout length and percentage tuber weight loss. Results showed significant ( $p < 0.001$ ) differences among genotypes, locations and seasons, and significant interactions between these factors for days to dormancy release, number of sprouts per tuber at dormancy release and at 45 days after dormancy release, length of longest sprout, weight loss percentage of unsprouted and sprouted tubers at dormancy release and at 45 days after dormancy release, respectively. There was a wide variation in time to dormancy release (54 to 136 days); most genotypes showed medium to long dormancy. Seed tubers grown at low altitude showed longer dormancy than those grown at higher altitudes, while genotypic differences in dormancy were very consistent across environments. Genotypes strongly differed in sprouting characteristics and weight loss. There were highly significant interactions between altitude and season for all variables assessed, except for the number of sprouts 45 days after dormancy release and the weight loss after sprouting. Generally, the genotypic effects were larger than those of altitude, season and the interaction effects for all variables evaluated. This paper will allow variety selection to optimize seed quality at planting and minimize storage losses while providing new targets for breeders.

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**Keywords** Altitude · Dormancy · Genotype × environment interaction · Physiological age · Potato genotypes · Season

## Introduction

Potato (*Solanum tuberosum* L.) is grown mainly for its modified underground swollen stem, the tuber, which is either produced for consumption, feed, industrial use or as starting material for the next crop. As the potato crop develops, stolons and tubers are initiated and following a sequence of physiological stages, including stolonization, tuber induction and initiation, tuberization, and bulking, until the tubers finally mature (Struik and Wiersema 1999). During the period between dehauling or harvesting and planting of seed or use as ware, the tubers are dormant for a certain period of time after which they sprout. Dormancy is a physiological phenomenon and varietal characteristic in potato, which sets in soon after tuber initiation (van Ittersum 1992; Struik and Wiersema 1999; Claasens and Vreugdenhil 2000; Aksenova et al. 2013). When planted in its dormant stage, a tuber will not produce an emerging plant readily even when conditions are favorable (van Ittersum 1992; Haverkort 2018). Also, when stored a dormant tuber will maintain good storability until it sprouts. However, since it is difficult to establish when the dormancy period starts, post-tuber bulking dormancy is used for practical purposes and defined as the period from haulm killing (cutting back or destruction of the haulm) to the time 80% of tubers show one or more sprouts of at least 2 mm long (van Ittersum and Scholte 1992; Carli et al. 2016). Dormancy duration is primarily dependent on the cultivar (genotype), and the growing and storage conditions (Eshel and Teper-Bamnlker 2012; Aksenova et al. 2013; Mustefa et al. 2017), with longer dormancy providing the opportunity for an extended storage period (Haverkort 2018). Dormancy is greatly influenced by geographic location and growing season (Struik and Wiersema 1999; van Ittersum 1992; Caldiz et al. 2001; Caldiz 2009; Carli et al. 2016) and its duration is determined by environmental, physiological, and hormonal control mechanisms (Mani et al. 2014) alongside management factors (van Ittersum 1992; Caldiz et al. 2001; Caldiz 2009; Mani et al. 2014) in the field and after harvest (Struik and Wiersema 1999). A wide range in the duration (long, medium, or short) of the dormancy period has been observed in cultivated potato and its wild relative species (Muthoni et al. 2014).

Duration of potato tuber dormancy and the beginning of sprouting have significant economic importance (Aksenova et al. 2012) for seed and ware potatoes. Following dehauling or haulm killing, the seed tuber becomes physiologically independent from its mother plant and shows its own physiological development as influenced by the existing environmental conditions (Struik and Wiersema 1999). The earliest observable stage of sprouting is characterized by visible small white buds, often termed “pipping” or “peeping” (Daniels-Lake and Prangel 2007) or mini-chitting (Struik and Wiersema 1999), which is influenced by physiological age (Eshel and Teper-Bamnlker 2012; Haider et al. 2021). Tuber sprouting is the major visible milestone in determining physiological age (Mani et al. 2014), while at the same time it

leads to major quality losses of stored potato tubers (Mani and Hannachi 2015). Physiological age is defined as the stage of development of a tuber or the process of sprout development, which is modified progressively by increasing chronological age, depending on growth history and storage conditions (Wiersema 1985; Struik and Wiersema 1999; Struik 2007) and length of storage period (Haverkort 2018) and the genotype (Caldiz 2009). Physiological aging stages progress through dormancy break, apical dominance, multiple sprouting, branching, senility, and eventually little tubers, which may form on the sprouts. Caldiz (2009) defined physiological age as the physiological status of a seed tuber at any time, determined by genotype, chronological age, and environmental conditions from tuber initiation until new plant emergence. The physiological age of the tuber is genetically determined (Haverkort 2018) but influenced by the growing and post-harvest environment (Caldiz 2009) and has a great effect on the pattern of sprout growth (Carli et al. 2010) and subsequent crop growth (Struik and Wiersema 1999).

In Kenya, potato can be grown in different growing seasons, i.e., in the long rainy season (from March/April to July/August) and in the short rainy season (from August/September to November/December). Moreover, ware potato is grown at different altitudes and therefore conditions during seed potato production may differ greatly which may affect storability. Generally, potato is grown in the mid- to high-altitude areas, which provide a cool environment for potato growth and production. On the other hand, seed potato is produced in specific potato growing zones and used across the wider potato growing regions with little regard to the effect of its growing environment or altitude on dormancy. Knowledge on seed potato growing environment would be critical in situations where seed is acquired prior to dormancy release or where ware storage is required. Altitude is critical in influencing temperature and other weather factors which affect potato establishment, growth, productivity and physiological aging in Kenya and other Sub Saharan agro-ecologies. An understanding of the behavior of seed tubers of different cultivars grown at different altitudes in relation to dormancy and physiological age (or growth vigor) is necessary to utilize their respective potential in different seasons and environments, for both seed and ware production including storage. In the last few years, there has been an increase in the number of released and candidate varieties in Kenya. However, these varieties have not been widely grown and for most of them their seed dormancy and sprouting behavior have not been studied under local conditions.

This study was conducted to understand and quantify the effects of genotype (variety), growing location (altitude) and season on dormancy and physiological age under “conventional storage” and is the first investigation of this kind in north-western Kenya. Greater understanding of the dormancy needs for a particular environment also allows breeders to select adapted varieties with the correct dormancy profile to balance ware storage and optimal seed physiological age. In situations such as staggered planting and harvesting, growing different varieties with different dormancy periods may also be necessary. Forty-seven diverse genotypes were evaluated during two successive seasons in three replications from a larger study on adaptation trials carried out at three different altitudes. The tubers were evaluated at one location under darkness and semi-ambient (on moist sand) storage conditions to study their dormancy release and physiological age characteristics such as number of sprouts, sprout weight, sprout length, and tuber weight loss percentage.

## Materials and Methods

### Genotypes Tested, Bulking of Starting Material, and Seed Tuber Production Sites

The 47 potato genotypes used in the study included released varieties and non-released genotypes in Kenya obtained from different seed companies and research institutions (Table 1). Three genotypes (Shangi, Dutch Robijn, and Tigoni) were considered as local checks based on their current or previous popularity in the study areas. The Kenya Agricultural and Livestock Research Organization (KALRO) improved varieties included those that resulted from collaborative work with the International Potato Center (CIP) and other partners. Starting seed lots were obtained as mini-tubers or first-generation seed tubers which were multiplied by the first author for two or three seasons to obtain physiologically uniform seed lots before commencing the short rainy season 2019 and the long rainy season 2020 adaptation field trials at three altitudes. The trial locations were Lelan (2915 to 2930 m above sea level), Saboti (2161 to 2178 m) and KALRO-Kitale (1850 to 1853 m). All genotypes were harvested at the same time at each site, either after natural senescence (early maturing types) or after dehauling by cutting back the tops (medium or late maturing types). Table 2 shows details of the environments where trials were conducted and the timing of relevant field operations. Weather data for Lelan was not available; however, Chebet et al. (2017) working at Kapyego near Lelan created a dummy weather station by extrapolation of temperature data from neighboring weather stations over several years using the lapse temperature method of Minder et al. (2010), which provided synthetic temperature data with the lowest average of 12 °C, which suggests cool conditions at high altitude.

**Table 1** Genotypes studied, their sources and origin

Genotypes	Source*	Origin
CIP392617.54, CIP392797.22, CIP393077.159, CIP393079.4, CIP393280.64, CIP393371.58, CIP394611.112, CIP395112.6, CIP396018.241, CIP398190.200, CIP399072.21, CIP399075.22	CIP, Nairobi	CIP, Peru
Alibaba, Antarctica, Bikini, Buffalo, Commando, Fandango, Gravity, Imagine, Infinity, Java, Maverick, Tornado, Vanilla	IPM Potato Group Ltd / Kirinyaga Seeds Ltd	Ireland
Dutch Robijn		Netherlands
Challenger, Panamera, Sagitta, Voyager	HZPC Ltd	Netherlands
Destiny, Manitou, Markies	Agrico E.A. Ltd	Netherlands
Spunta	KALRO Tigoni	Netherlands
Asante, Kenya Karibu, Kenya Mpya, Konjo, Meru, Tigoni, Unica	KALRO Tigoni	CIP
Shangi	KALRO Tigoni	Unknown
Kerr's Pink, Roslin Tana	KALRO Tigoni	UK
Arka	KALRO Tigoni	Germany
Royal, Sarpo Mira	DANESPO Ltd	Denmark

\*Source is in reference to the immediate supplier of the seed material used and not necessarily the breeder

**Table 2** Growing environments and timing of planting, dehauling, and harvesting of the field trials from which the experimental material was sourced, as well as the start and end of dormancy/physiological age experiments

Location of field trials	Altitude (m.a.s.l.)	Season	Rainfall (mm)	Average temperature (°C)	Planting date	Dehauling date	Dehauling to storage (days)	Harvesting date	Start of lab storage date	End of lab storage date
KALRO Kitale	1853	Short rains 2019	837	19.4	16/08/2019	29/11/2019	32	14/12/2019	31/12/2019	28/05/2020
		Long rains 2020	1181	19.6	22/04/2020	28/07/2020	35	11/08/2020	03/09/2020	03/02/2021
Saboti	2161	Short rains 2019	874	18.0	20/08/2019	03/12/2019	28	17/12/2019	31/12/2019	01/06/2020
		Long rains 2020	894	17.7	22/04/2020	03/12/2019	28	21/12/2019	10/09/2020	01/02/2021
Lelan*	2915	Short rains 2019	-	-	26/08/2020	21/12/2019	31	16/01/2020	21/01/2020	15/06/2020
		Long rains 2020	-	-	24/04/2020	29/08/2020	39	18/09/2020	07/10/2020	08/02/2021

*m.a.s.l.* meters above sea level

\* Weather data were not available for Lelan

## Experimental Design and Setup

From harvesting to commencement of storage experiments, the tubers were stored at KALRO-FCRI Kitale under ambient conditions for some days that differed between locations but with only small variations at each location except for Lelan where wet weather conditions delayed harvesting in the long rainy season 2020 (Table 2). The assessments were conducted at KALRO Kitale in a laboratory modified using plywood on the outside of the wall and newspapers on the inside to create a dark environment, while ventilation was ensured by use of 5-cm waste pipes with bends along the wall. Aluminum paint was applied on the external side of the plywood to act as a heat reflector and to enhance darkness. Inside, green bulbs were used when light was required for operations and measurements. Temperature and relative humidity (RH%) in the storage room were recorded throughout each experimentation period at intervals of 15 min, using a Hobo Data Logger (HOBO U23-001 Temp/RH, Producer, City) with the launching program: HOBOWare-3.7.16\_1108\_1030\_windows. The set-up of the storage environment was to mimic conventional storage. The temperature and relative humidity during storage ranged from 17.2–23.9 °C (average 20.6 °C) and 51–90% (average 70.5%) RH, and 18.3–23.9 (average 21.1) °C and 34–88% (average 61%) RH in the 2019 short and 2020 long rainy seasons, respectively (Supplementary Material Figs. 1 and 2). The experiment was conducted following CIP procedures for standard evaluation and management of advanced clones (Carli et al. 2016) with a minor modification of placing the tubers on moist but not wet sand to provide moisture necessary for sprouting. A randomized complete block design (RCBD) with three replications was used consistent with the design of the parent field trials.

## Data Collected

Fifteen (15) tubers per plot were selected at random weighing 26–123 (average 67) g and 45–123 (average 86) g each in 2019 and 2020, respectively to mimic farmers' practice because standard tuber size selection was not always practical. The weight variation represented the possible seed tuber sizes planted by farmers. For each treatment the tubers were placed partially on the surface of moist sand in a partially sand-filled bowl. The sand was moistened prior to seed placement by injecting 60 ml clean water into the sand at the center and four other evenly spaced spots equally using a 60 ml syringe and thoroughly mixing to ensure uniformity. The tubers in each bowl (experimental unit) were marked 1 to 15 for identification using a permanent marker. Tubers were observed after 10 days of storage and then every 10 days for monitoring and recording of data. When the sand in the bowl tended to dry up 60 ml clean water was carefully injected as above without mixing the sand but allowing the water to seep through the sand slowly, avoiding wetting of the tubers.

Each tuber used was weighed (g) at the onset of the storage period as initial tuber weight (ITW), at dormancy release (when 80% of the tubers had at least one sprout longer than 2 mm) (intermediate tuber weight, INTW) and at 45 days after dormancy release (final

tuber weight, FTW) using an electronic weighing scale (Shimadzu ELB6000S; Max 6000 g; d=1 g; Min 20 g; Producer, City). The tubers were de-sprouted (removal of sprouts) before recording the final tuber weight. Other variables assessed were number of eyes per tuber, days to dormancy release (DR) (i.e., day number of DR minus day number of dehauling, the dehauling day being the same for all genotypes within one location and season). In order to understand physiological age attributes, data were collected on (i) initial number of sprouts per tuber (when 50% of the tubers had shown sprouting (piping/peeping; mini-chitting) or initial number of sprouts), (ii) number of sprouts at dormancy release (when 80% tubers had at least one sprout longer than 2 mm), and (iii) number of sprouts at 45 days after dormancy release. Also, at 45 days after dormancy release data collected were number of sprouts per gram tuber, length (mm) of the longest sprout, weight (g) of sprouts per seed tuber (using an electronic weighing scale; FisherScientific XD-2200; sensitivity 0.01 g; Producer, City), weight loss percentage of sprouted tubers, and weight of unsprouted tubers at dormancy release. Also collected were data on sprouting pattern [apical dominance (1), multiple sprouting (2), and branching (3)].

From the tuber weights collected, percentage tuber weight losses (PW) of unsprouted tubers (USPT) at dormancy release when the weight loss is basically through the periderm and lenticels and of sprouted tubers (SPT) 45 days after dormancy release when the weight loss is mainly due to number of sprouts and sprout growth, were determined using the formulae:

$$(i) \quad PW_{USPT} = (ITW - INTW/ITW) \times 100 \quad (1)$$

$$(ii) \quad PW_{SPT} = (ITW - FTW/ITW) \times 100 \quad (2)$$

Data were analyzed using GenStat 19<sup>th</sup> Edition VNSI computer package (VSN International 2017).

The statistical analysis was done using linear mixed model analysis, linear regression, and correlation analysis.

The linear mixed models used were:

$$(iii) \quad \textit{Genotype} * \textit{Season} * \textit{Location} + \textit{Replication} \quad (3)$$

$$(iv) \quad \textit{Season} - \textit{Year} * \textit{location} + \textit{Replication} \quad (4)$$

The regression analysis equation used was:

$$(v) \quad Y = a + bx \quad (5)$$

where  $Y$ =dependent variable,  $a$ =intercept,  $b$ =slope, and  $x$ =independent (explanatory) variable.

However, for better visual comparison of the widely varying data points and distributions of observations, descriptive statistics were done using pirate plots in R

(Philips 2017). A pirate plot shows raw data as individual points of each observation, descriptive statistics (mean, median) by a line, and inferential statistics by a band for prediction of accuracy in place of error bars all in one plot (Philips 2017) from which inferential comparisons can be made with confidence. The pirate plot shows the individual observations and the density of the distribution with the average, which allows comparison of different groups of data.

## Results

The results of the significance test (probability of  $F$  value;  $F$  pr) for fixed effects of selected variables measured are shown in Table 3. The means of nine variables as influenced by genotype across three locations and seasons are summarized in Supplementary Material Table 1 and means of selected variables as influenced by  $G \times E$  in Supplementary Material Tables 2, 3 and 4. The analysis of variance table for fixed model analysis and percentage of variation contributed by genotype, location, season, and their interaction based on Wald statistic are shown in Table 3.

### Dormancy Release

Results on days to dormancy release showed a significant ( $p < 0.001$ ) effect for genotype by location by season ( $G \times L \times S$ ) interaction (Table 3). Values ranged from 47 to 173 and from 44 to 145 days in the short and long rainy seasons, respectively, with an overall genotype mean of 87.6 days across environments and seasons (Supplementary Material Table 1). There were large differences among potato genotypes on days to dormancy release, which resulted in five dormancy categories; very short, short, medium, long, and very long across locations (Supplementary Material Table 5). Generally, the genotypic effects were significantly larger than the main effects of location and season and larger than the interaction effects (Table 3).

The two-way interaction between genotype and location on dormancy release showing the consistent genotypic effect is shown in Fig. 1A. Some genotypes (Kerr's Pink, CIP392617.54, Unica, CIP392797.22, Kenya Mpya, CIP393371.58, CIP396018.241 and Vanilla) showed genotypic stability in dormancy release across locations. However, a few; Markies, Antarctica and CIP 394,611.112 showed variations between locations (Fig. 1A), while Destiny, Dutch Robijn and CIP393280.64 varied between seasons compared with other genotypes (Fig. 1B). Generally, seed tubers of all varieties from Lelan, which had the highest altitude, exhibited the shortest dormancy. The interaction between genotype and location was significant and some small changes in variety ranking occurred between the Kitale and Saboti sites with Kitale generally expressing the longest dormancy while also being the lowest altitude site.

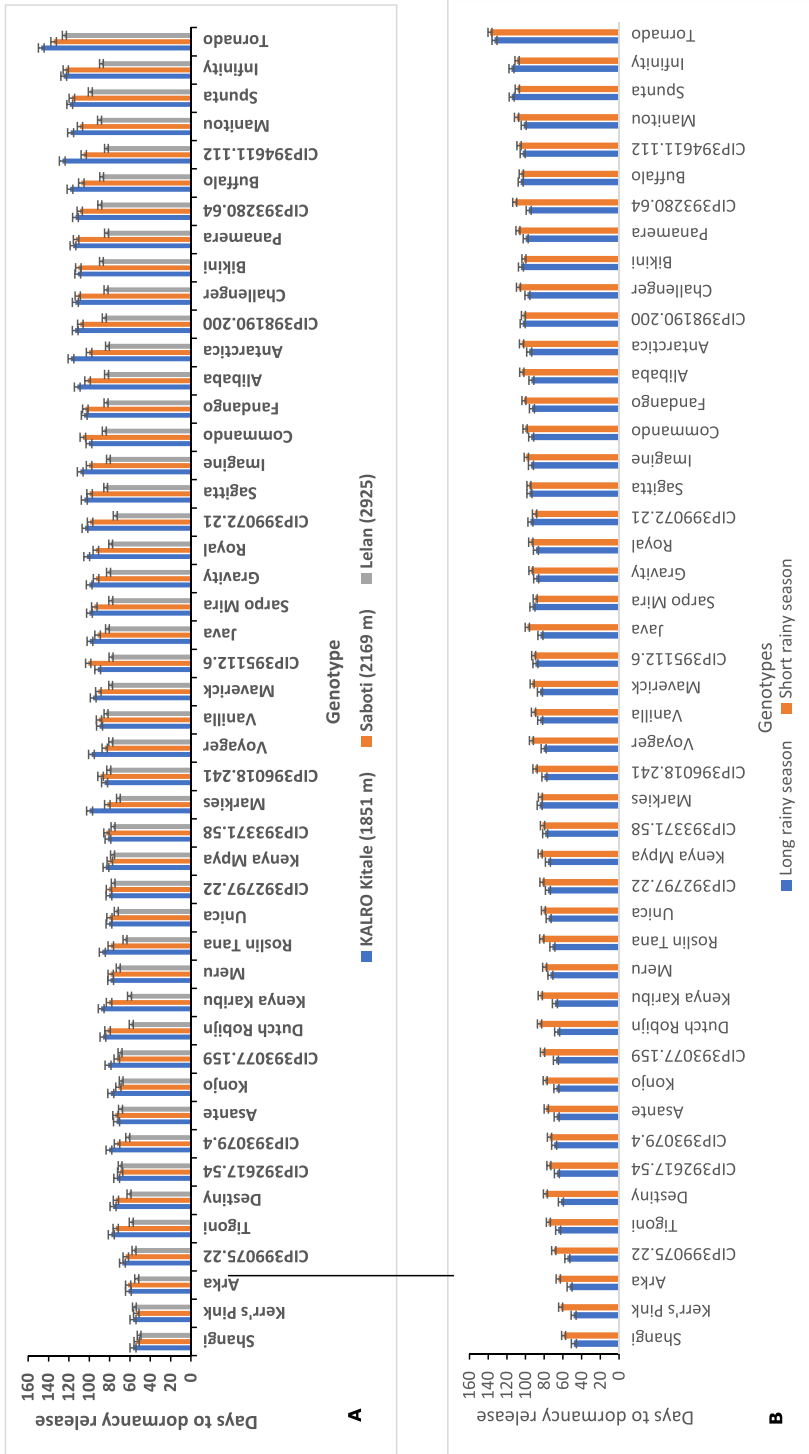
The trend of significant genotype by season effect on dormancy is shown in Fig. 1B where the short rainy season consistently showed longer dormancy for most genotypes. Genotypes Shanghi and Tornado remained at the extremes for short and long dormancy, respectively (Fig. 1B). The average days to dormancy release among



Table 3 (Continued)

G×S	46	118.27***	6.9	335.05***	7.0	242.76***	7.5	158.59***	4.8	116.96***	11.7
L×S	2	16.15 ns	0.9	399.76***	8.3	0.86 ns	0.0	65.21***	2.0	60.81***	6.1
G×L×S	92	94.90 ns	5.5	144.79***	3.0	177.75***	5.5	162.72***	4.9	149.83***	15.0
R	2	5.06 ns	0.3	4.79 ns	0.1	3.70 ns	0.1	10.65**	0.3	2.14 ns	0.2
R×L				26.79***	0.6	10.44*	0.3	5.63 ns	0.2		
SE		0.03		0.08		0.13		0.09			0.03

n.d.f.=number of degrees of freedom, Dormancy=average days from dehauling or haulm killing to dormancy release, NoISpr=initial average number of sprouts per tuber when 50% of the tubers had shown sprouting (pipping/peeping; mini-chitting), NoSpr0=average number of sprouts per tuber at dormancy release, NoSpr45=average number of sprouts per tuber at 45 days after dormancy release, LLSpr45=average length of longest sprout per tuber (mm) at 45 days after dormancy release, WSpr=average weight of sprouts per gram of tuber at 45 days after dormancy release, %WLUST=average weight loss percentage of unsprouted tubers at dormancy release, %WLST45=average weight loss percentage of sprouted tubers at 45 days after dormancy release, NoEyes=average number of eyes per tuber, SPG=sprout pattern growth, G×L=genotype by location, G×S=genotype by season, L×S=location by season, G×L×S=genotype by location by season. \*, \*\*, \*\*\* = Significant at  $p < 0.05$ ,  $p < 0.01$  and  $p < 0.001$ .



**Fig. 1** Average days to dormancy release of 47 varieties grown at three locations, representing different altitudes across the long and short rainy seasons (A) and two different seasons across the three altitudes (B) in order ranked by overall mean value for variety in north-western Kenya

genotypes across locations and seasons were 95.6, 90.7, and 76.7 days for Kitale, Saboti, and Lelan (Table 4). The average for the two seasons was 84.1 and 91.2 days for the short and long rains, respectively. These gave a difference of 19 and 7 days overall between the highest and lowest altitudes and long and short rainy seasons, respectively (Table 4). The mean number of days from haulm killing to dormancy release alongside the raw data points and inferential statistics/confidence interval, and smoothed densities (Philips 2017) for genotype, location, and season is illustrated in the pirate plots (Fig. 2). The expression of the genotypic variation was different among the different location  $\times$  season combinations. The location by season interaction was also highly significant for days to dormancy release (Table 3). Lelan and KALRO Kitale showed the shortest and longest days to dormancy release during both seasons, respectively (significant at  $p < 0.001$ ; Fig. 2). Lelan showed distinct subgroups on dormancy release in each season and low mean days to dormancy release compared to the other locations. There was no significant season effect at KALRO Kitale, whereas at Saboti and (especially) Lelan, the short rainy season had significantly longer dormancy than the short rainy season and the  $S \times L$  interaction showed greater variation in the long rainy season for these two locations.

Table 5 shows the Pearson correlations coefficient between the different parameters measured. Dormancy release showed a significant ( $p < 0.05$ ) moderate negative correlation ( $R = -0.395$ ) with altitude. Also, dormancy release showed a weak negative correlation with most variables measured except with average percentage weight loss of unsprouted tubers, and of sprouted tubers and average weight of sprouts per tuber where dormancy showed moderate and weak, positive correlations with  $R$  values 0.489, 0.185, and 0.156, respectively.

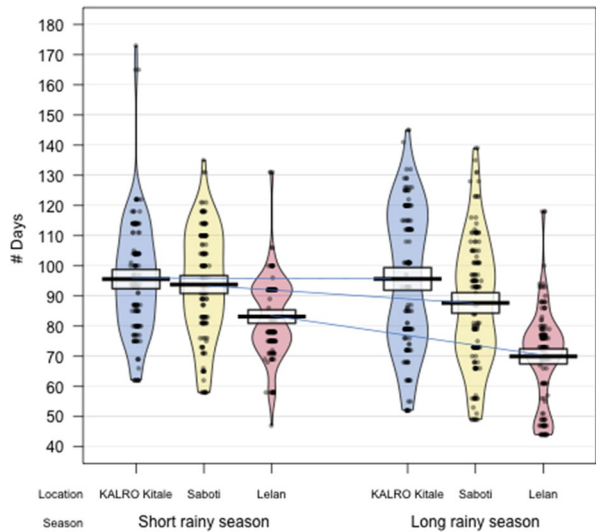
### Number of Sprouts per Tuber

The number of eyes per tuber and sprouts per tuber at initial sprouting and at dormancy release showed significant ( $p < 0.001$ )  $G \times L \times S$  interaction effects (Table 3), while the interaction effect on number of sprouts per tuber at 45 days after dormancy release was less clear ( $p < 0.038$ ; Table 3). Values of the average number of sprouts at initial sprouting (peeping) ranged from 0.3 to 3.3 (mean 1.00), at dormancy release from 0.8 to 5.8 (mean 1.8) and at 45 days after dormancy release from 1.0 to 11.5 (mean 4.4) (Supplementary Material Table 1). The means for number of sprouts as influenced by location and season are

**Table 4** Mean number of days from haulm killing to dormancy release under ambient laboratory storage conditions of different potato cultivars grown at three locations during two seasons in north-western Kenya

Season	Location			Mean
	KALRO Kitale (1850–1855 m.a.s.l.)	Saboti (2161– 2178 m.a.s.l.)	Lelan (2915– 2937 m.a.s.l.)	
Long rainy season	95.4	87.2	69.6	84.1
Short rainy season	95.7	94.1	83.7	91.2
Mean	95.6	90.7	76.7	87.6

**Fig. 2** Pirate plots (the individual points show the raw data observed, the blue, yellow and pink areas show the distributions) and  $L \times S$  interaction (blue lines) for mean number of days from dehauling or haulm killing to dormancy release of 47 potato cultivars grown at three locations (KALRO Kitale (1850–1855), Saboti (2161–2178), and (2915–2937 m above sea level) during the short and long rainy seasons in north-western Kenya



illustrated in pirate plots (Figs. 3 and 4) and that of  $G \times L$  and  $G \times S$  in Supplementary Table 3 and 4. Lelan stood out as it produced more genotypes with higher numbers of sprouts than the other locations, in both seasons and for both dates of observations. The  $L \times S$  interaction was also highly significant for number of sprouts at dormancy release, with much higher values for the short rainy season than in the long rainy season for the location at the highest altitude but with the opposite trend for the location at the intermediate altitude. Figure 3 shows pirate plots for the number of sprouts at dormancy release and the  $G \times E$  interaction effect between location and season on number of sprouts per tuber dormancy release but all the genotypes responded to the environment factors at slight, but significant, variations. Negligible  $G \times E$  interaction effect between location and season on the average number of sprouts at 45 days after dormancy release (DADR) was observed (Fig. 4). Lelan gave the highest significant ( $p < 0.001$ ) number of sprouts and Saboti the least during both seasons but the ranking of genotypes remained constant (Table 3; Figs. 3 and 4). However, Saboti and KALRO Kitale showed near similar effect but with some tendency of interaction between them.

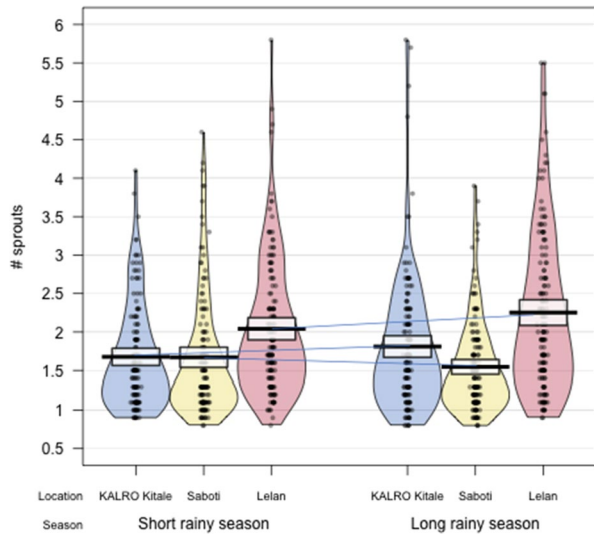
There were significant ( $p < 0.01$ ) moderate positive correlations ( $R = 0.409$ ) between average number of eyes and average number of sprouts at dormancy release and at 45 DADR (Table 5). Also observed were strong and moderate positive correlations between average number of initial sprouts and average number of sprouts at dormancy release ( $R = 0.608$ ) and at 45 DADR ( $R = 0.360$ ), respectively. There were moderate and weak, positive correlations between altitude and average number of sprouts at dormancy release ( $R = 0.327$ ) and at 45 DADR ( $R = 0.239$ ), respectively. There were strong negative correlations between number of sprouts per gram tuber and average final tuber weight ( $R = -0.617$ ) and average initial tuber weight ( $R = -0.598$ ), respectively.

**Table 5** Pearson correlations between parameters measured

	AFTW	AITW	LLSpr45	Altitude	NoEyes	NoISpr	NoSpr45	NoSpr0	NoSpr45/g	%WLUST	%WLST45	WSpr	Dormancy
AFTW	-												
AITW	<b>0.993</b>	-											
LLSpr45	-0.253	-0.211	-										
Altitude	0.166	0.145	-0.146	-									
NoEyes	0.135	0.134	0.041	0.069	-								
NoISpr	-0.143	-0.107	0.210	0.052	0.146	-							
NoSpr45	-0.167	-0.145	0.120	0.327	0.409	0.360	-						
NoSpr0	-0.038	-0.013	0.118	0.239	0.312	<b>0.608</b>	<b>0.510</b>	-					
NoSpr45/g	- <b>0.617</b>	- <b>0.598</b>	0.246	0.081	0.223	0.366	<b>0.808</b>	0.386	-				
%WLUST	- <b>0.463</b>	-0.393	0.307	- <b>0.513</b>	-0.156	0.154	0.020	0.011	0.289	-			
%WLST45	-0.366	-0.278	<b>0.500</b>	-0.028	0.071	0.386	0.366	0.309	0.455	0.428	-		
WSpr	-0.038	0.031	<b>0.506</b>	-0.014	0.171	0.391	0.271	0.300	0.217	0.236	<b>0.689</b>	-	
Dormancy	-0.119	-0.080	0.293	-0.395	-0.136	-0.220	-0.165	-0.164	-0.062	<b>0.489</b>	0.185	0.156	-

AFTW = average final tuber weight (g) at 45 days after dormancy release, AITW = average initial tuber weight (g), LLSpr45 = average length of longest sprout per tuber (mm) at 45 days after dormancy release, Altitude, NoEyes = average number of eyes per tuber, NoISpr = number of sprouts (initial) when 50% of the tubers had shown sprouting (pipping/peeping; mini-chitting) (initial number of sprouts), NoSpr45 = average number of sprouts per tuber at 45 days after dormancy release, NoSpr0 = average number of sprouts per tuber at dormancy release, NoSpr45/g = average number of sprouts per gram of tuber at 45 days after dormancy release, %WLUST = average weight loss percentage of unsprouted tubers at dormancy release, %WLST45 = average weight loss percentage of sprouted tubers at 45 days after dormancy release, WSpr = average weight of sprouts per tuber (g) at 45 days after dormancy release, Dormancy = days from dehauling to dormancy release. Critical levels for |r| at n = 47 are 0.2876 for p = 0.05; 0.3721 for p = 0.01 and 0.4647 for p = 0.001. Correlations that are significant at p ≤ 0.001 are in bold

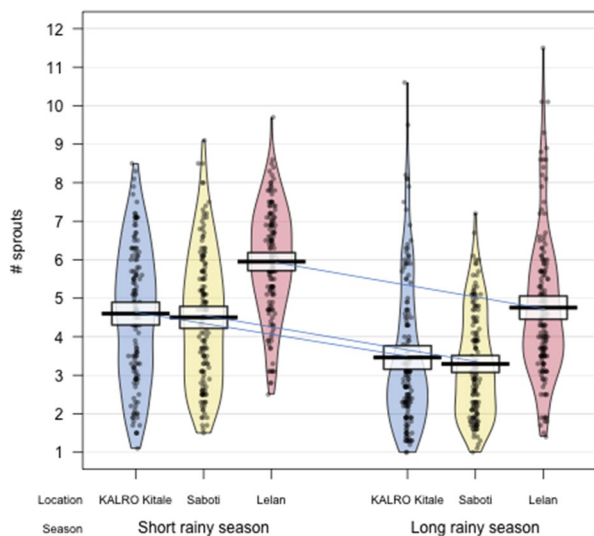
**Fig. 3** Pirate plots (the individual points show the raw data observed, the blue, yellow and pink areas show the distributions) and L×S interaction (blue lines) for average number of sprouts per tuber at dormancy release for 47 potato genotypes produced at three different locations (KALRO Kitale (1850–1855), Saboti (2161–2178), and Lelan (2915–2937 m above sea level) during the short and long rainy seasons in north-western Kenya



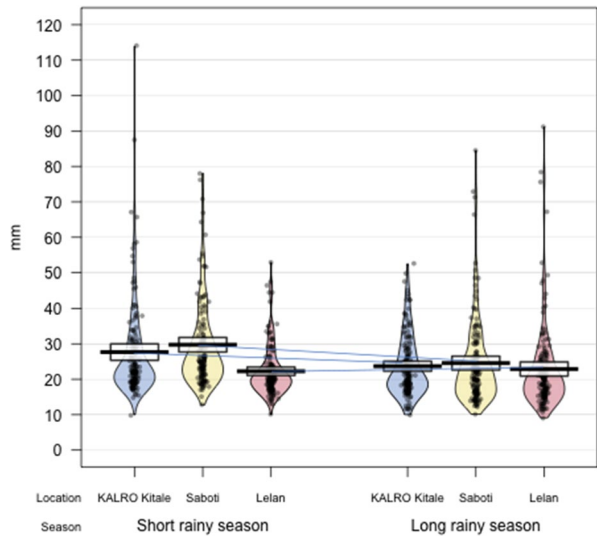
**Length of Longest Sprout**

There were highly significant ( $p < 0.001$ ) effects of the  $G \times L \times S$  interaction on the length of the longest sprout per tuber at 45 days after dormancy release (Table 3), with mean values ranging from 14.5 to 48.4 mm, with an overall mean of 24.7 mm (Supplementary Material Table 1). For the sprout length, the three-way interactions are illustrated in the pirate plot (Fig. 5). The genotypic variation slightly differed among the different location×season combinations but was in general rather small.

**Fig. 4** Pirate plots (the individual points show the raw data observed, the blue, yellow and pink areas show the distributions of means) and L×S interactions (blue lines) for average number of sprouts per tuber at 45 days after dormancy release (DADR) for 47 potato genotypes produced at three different locations (KALRO Kitale (1850–1855), Saboti (2161–2178), and Lelan (2915–2937 m above sea level) during the short and long rainy seasons in north-western Kenya



**Fig. 5** Pirate plots (the individual points show the raw data observed, the blue, yellow and pink areas show the distributions) and  $L \times S$  interactions (blue lines) for average length of longest sprout per tuber at 45 days after dormancy release (DADR) at three different locations (KALRO Kitale (1850–1855), Saboti (2161–2178), and Lelan (2915–2937 m above sea level) during the short and long rainy seasons in north-western Kenya



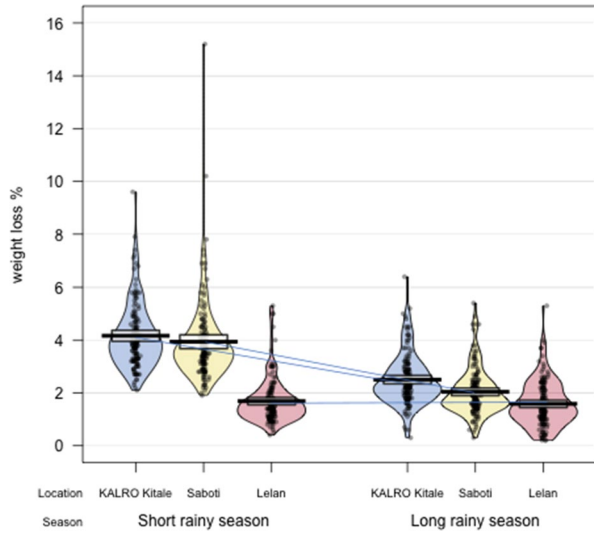
Location by season interaction showed a divergent interaction effect for the different sites for average length of the longest sprout per tuber which was not consistent with altitude (Fig. 5). Lelan had the shortest length of the longest sprout with no difference between the two seasons, whereas Saboti had the longest sprout followed by KALRO Kitale where both were longer in the short rainy season than in the long rainy season.

On sprouting pattern, the genotypes showed apical and multiple sprouting patterns at 45 days after dormancy release (Supplementary Material Table 6). However, branching pattern was observed in some genotypes on the de-sprouted tubers later in storage after 45 days following dormancy release. There was a strong positive correlation ( $R=0.506$ ) between average length of longest sprout per tuber and average weight of sprouts per tuber (Table 5).

### Percentage Weight Loss for Unsprouted and Sprouted Tubers

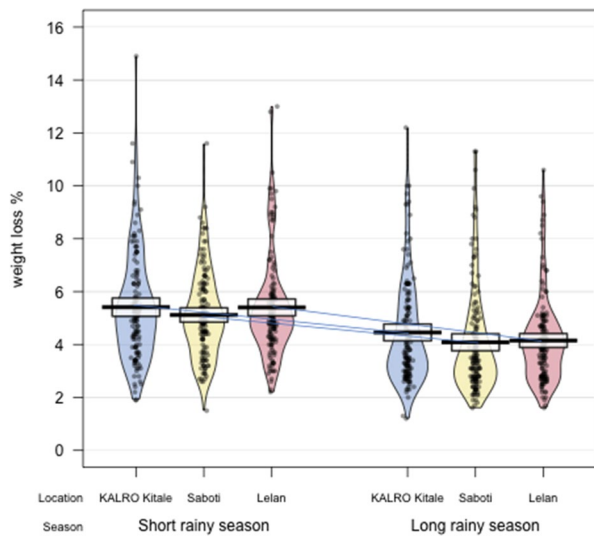
For the percentage weight loss, the effects of  $G \times L \times S$  interaction were highly significant ( $p < 0.001$ ), for both unsprouted tubers at dormancy release and sprouted tubers at 45 days after dormancy release (Table 3). The ranges were 1.5 to 4.8% (mean 2.6%) for unsprouted tubers and 2.7 to 9.1% (mean 4.7%) for sprouted tubers (Supplementary Material Table 1). Figures 6 and 7 show the pirate plots of means and the  $L \times S$  interaction effects of these two variables. There was a significant ( $p < 0.001$ )  $L \times S$  interaction effect on percentage weight loss of unsprouted tubers with KALRO Kitale and Saboti showing consistently significant higher percentage weight loss than Lelan and much larger differences between the two seasons but not at Lelan (Fig. 6). However, for the percentage weight loss of sprouted tubers at 45 days after dormancy release, the  $L \times S$  interactions showed small differences between locations with inconsistency with altitude, but large differences between the seasons (Fig. 7).

**Fig. 6** Pirate plots (the individual points show the raw data observed, the blue, yellow and pink areas show the distributions) and  $L \times S$  interaction (blue lines) for weight loss percentage of unsprouted tubers at dormancy release for 47 potato genotypes produced at three different locations (KALRO Kitale (1850–1855), Saboti (2161–2178), and Lelan (2915–2937 m above sea level) during the short and long rainy seasons in north-western Kenya



There was a strong positive correlation ( $R=0.993$ ) between average initial tuber weight and average final tuber weight (Table 5). Also, there was a strong negative correlation ( $R=-0.513$ ) between altitude and average percentage weight loss of unsprouted tubers and weak negative correlations with average percentage weight loss of sprouted tubers ( $R=-0.028$ ). A strong negative correlation between average initial tuber weight and average weight of sprouts per gram tuber ( $R=-0.598$ ) and a moderate negative correlation with average percentage weight loss of unsprouted

**Fig. 7** Pirate plots (the individual points show the raw data observed, the blue, yellow and pink areas show the distributions) and  $L \times S$  interaction (blue lines) for weight loss percentage of sprouted tubers at 45 days after dormancy release (DADR) for 47 potato genotypes produced at three different locations (KALRO Kitale (1850–1855), Saboti (2161–2178), and Lelan (2915–2937 m above sea level) during the short and long rainy seasons in north-western Kenya



**Table 6** Results of the linear regression analysis when plotting the results of dormancy and sprouting tests of tubers from the short rainy season (y) against the results of those tests on tubers from the long rainy season (x) for the variables: average days from dehauling to dormancy release (Dormancy), average number of sprouts at dormancy release (NoSpr0), average number of sprouts at 45 days after dormancy release (NoSpr45), average length of longest sprout per tuber at 45 days after dormancy release (LLSpr45), average weight loss in percentage of unsprouted tubers at dormancy release (%WLUST) and average weight loss in percentage of sprouted tubers at 45 days after dormancy release (%WLSST45) of 47 potato genotypes grown at different locations and stored in darkness at KALRO Kitale. We used the average values of three replications per genotype for the regression, i.e.,  $n = 47$  in all cases

Location/variables	Genotype mean	Intercept	Slope	$R^2$	Level of significance of $G \times S$ from mixed model
<b>KALRO Kitale (1850–1855 m.a.s.l.)</b>					
Dormancy	95.6	13.810	1.162	0.822***	<0.001
NoSpr0	1.7	0.471	0.768	0.309***	<0.001
NoSpr45	4.0	0.082	0.747	0.529***	<0.001
LLSpr45	25.5	10.929	0.445	0.518***	<0.001
%WLUST	3.3	0.765	0.418	0.257***	<0.001
%WLSST45	4.9	1.082	0.601	0.411***	<0.001
<b>Saboti (2161–2178 m.a.s.l.)</b>					
Dormancy	90.7	12.653	1.061	0.842***	<0.001
NoSpr0	1.6	1.232	0.179	0.071ns	<0.001
NoSpr45	3.9	0.787	0.533	0.477***	<0.001
LLSpr45	26.7	3.862	0.660	0.575***	0.002
%WLUST	2.9	0.125	1.106	0.470***	<0.001
%WLSST45	4.5	0.351	0.839	0.545***	<0.001
<b>Lelan (2915–2937 m.a.s.l.)</b>					
Dormancy	76.7	17.435	1.040	0.785***	<0.001
NoSpr0†	2.1	1.100	0.554	0.198**	<0.001
NoSpr45	5.4	0.023	0.530	0.290***	0.089
LLSpr45	22.2	8.043	0.695	0.241***	<0.001
%WLUST	2.6	0.446	0.688	0.441***	0.004
%WLSST45	4.7	0.546	0.665	0.554***	<0.001

For  $R^2$  values: ns = not significant; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$

*m.a.s.l.* meters above sea level

tubers ( $R = -0.393$ ) were observed. Also observed were moderate positive correlations between average length of longest sprout per tuber with average percentage weight loss of unsprouted ( $R = 0.307$ ) and sprouted tubers ( $R = 0.500$ ).

### Consistency of Genotype Ranking Across Seasons

Table 6 describes the linear regression equations when plotting the results of the sprouting tests of 47 genotypes for the short rainy season as a function of the results for the long rainy season at each of the three locations. The correlation coefficients

were highest for the number of days to dormancy break and lowest for the number of sprouts at dormancy break. The regression coefficients indicated that the dormancy was systematically longer during the short rainy season than during the long rainy season, as expressed by a much higher intercept, especially at Lelan, with slopes being close to 1. For the other variables, the slopes were usually much smaller than one, indicating that during the short rainy season the genotypic differences were less expressed than during the long rainy season. The only exception was the percentage weight loss of unsprouted tubers 45 days after dormancy break at Saboti.

## Discussion

### Days to Dormancy Release

This study highlighted a wide genotypic variation for dormancy amongst the varieties tested, which revealed that genotype plays a major role in dormancy and the associated characteristics. The genotypic main effect was much greater than effects of location and season with the cultivar ranking remarkably consistent across environments (Fig. 1). However, the expression of shorter dormancy by all genotypes grown at Lelan showed the strong influence of altitude. In general, longer dormancy varieties showed a greater reduction in dormancy period at Lelan which highlights that environment may affect genotypes differently (Won et al. 1999; Baye et al. 2011). However, the effect of season appears to be more exaggerated on shorter dormancy varieties (Fig. 1b). The mean differences in days to dormancy release as influenced by season (7 days) and location (19 days) (Table 4) were small compared with the genotypic variation between the extreme cultivars across environments (85 days) (Supplementary Material Table 1). The wide variation in days to dormancy release allowed genotypes to be grouped in five dormancy categories; very short, short, medium, long, and very long. Acclimatization was considered to have resulted in more days to dormancy release for genotypes harvested at the experimental location.

The effect of higher altitude on shortening dormancy was contrary to expectation because of delay in maturity and lower temperature accumulation. The importance of temperature during the growing season on dormancy has been reported earlier (van Ittersum 1992; Struik and Wiersema 1999; Visse-Mansiaux et al. 2022). These findings partly agree with those of Visse-Mansiaux et al. (2022) where variety explained the majority of the dormancy variability (60.3%) compared with other factors outside the tropics. In the current study, genotype explained 67.9% of the dormancy variation followed by location and  $G \times L \times S$  least (Table 3). Variation in dormancy was explained by high genetic variance: 84.2%, 82.2%, and 78.5% in Saboti, KALRO Kitale, and Lelan, respectively, as explained by the  $R^2$  values (Table 6). While varieties exhibiting short dormancy such as Shanghi are preferred in Kenya they may not be the best for all potato growing agro-ecological zones and needs (Muthoni et al. 2014). Early sprouting varieties may experience pre-mature pipping as a result of stresses (e.g., high temperature or moisture stress) or delayed harvesting

leading to seed and ware quality loss (Murigi 2016). In regions where two or more potato crops are grown consecutively within the same calendar year seed is often partially dormant at planting (Struik and Wiersema 1999) causing delayed crop establishment, with fewer stems and hence tubers due to apical dominance (Caldiz 2009). Thus, dormancy and physiological aging may be limiting factors (Caldiz et al. 2001), which could be managed preferably by exploiting the genetic diversity available provided the other necessary agronomic criteria are met (Machida-Hirano 2015). This could allow selection of varieties targeted for storage or early planting at different altitudes.

### Sprouting Characteristics

The genotypic consistency found in dormancy duration was not found for physiological aging traits after dormancy break. Sprouting behavior was much more sensitive to  $G \times L \times S$  interaction. As with dormancy, an understanding of physiological age of tubers of potato varieties is important since it determines the quality of tubers for storage, processing or subsequent planting. There was significant ( $p=0.038$ )  $G \times L \times S$  interaction effect on the number of sprouts per tuber at 45 days after dormancy release compared with the highly significant ( $p < 0.001$ ) interaction effects on average number of sprouts at initial sprouting and at dormancy release. This was most likely because of the genetic variation in apical dominance among genotypes, which is lost soon after dormancy release. This is supported by the strong positive correlations between initial number of sprouts and the number of sprouts at dormancy release ( $R=0.608$ ) and moderate correlation at 45 DADR ( $R=0.360$ ) (Table 5), when apical dominance started to weaken, which indicated that 60.8% and 36.0% of the variation, respectively were attributed to the initial number of sprouts. Genotypes with strong apical dominance exhibit low plant stem density, which reduces tuber number and hence gives larger tubers and a compromised cultivar yield potential, which may be useful in limited rainfall seasons to maximize tuber size. This is relevant for the short rainy season planted crops. However, following long storage, it may require de-sprouting of seed (Struik and Wiersema 1999) for the long rainy season planting. The high number of sprouts per tuber observed in Lelan at high altitude (low temperatures) compared with Saboti and KALRO Kitale at lower elevations in both seasons, supports the findings of Johansen (2011) who reported more sprouts per tuber when grown at 9 °C than at 15 or 20 °C. This could be attributed to the shortened dormancy break, which weakened the apical dominance (Supplementary Material Table 6). Branching sprouting pattern was observed only on some of the genotypes much later than 45 DADR, which suggested that it occurs when the seed tubers have advanced in physiological age depending on genotype (Carli et al. 2016).

The physiological age of the seed tuber is a component of seed quality and growth vigor, and its effects on crop growth and yield are cultivar-dependent (Hartmans and van Loon 1987; Struik and Wiersema 1999; Struik 2007; Caldiz 2009; Eshel and Teper-Bamnlker 2012). Genotypes with many and/or long, and/or large sprouts were prone to fast physiological aging. The rate at which physiological aging occurs

is partly independent of duration of dormancy (Struik and Wiersema 1999; Struik 2018) which was supported in this study. Both Shangi and Tornado accumulated physiological age rapidly as shown in the results (Supplementary Material Table 1) but were found to have the shortest and longest dormancy period, respectively (Fig. 1A).

Almost all genotypes initially exhibited apical dominance but many transitioned to multiple sprouting patterns at 45 DADR. More genotypes from high altitude attained multiple sprouting (optimal physiological age) earlier followed by those from mid-altitude and then low altitude, which could be explained by the possible shock caused by temperature differences between the growing conditions and storage conditions at the low-altitude experimental location. The warmer conditions during the short rainy season influenced genotypes towards multiple sprouting earlier compared to during the cooler long rainy season. Length of the longest sprout showed significant  $G \times L \times S$  interactions and Lelan at the highest altitude site exhibited the shortest sprout length, which was quite different to Kitale and Saboti. While there was a marked season effect at KALRO Kitale and Saboti, where sprout length was significantly longer in the short rainy season, there were almost no differences between seasons at Lelan. The weak and moderate positive correlations between altitude and average number of sprouts at dormancy release ( $R=0.239$ ) and at 45 DADR ( $R=0.327$ ), respectively, confirmed that with rise in altitude the number of sprouts increases and much more at 45 DADR, which suggests increased influence of altitude on number of sprouts as sprouting advances. The short sprout length at higher altitudes may be influenced by the higher sprout number as suggested by weak positive correlation between sprout length and number of sprouts/gram of tuber 45 DADR ( $R=0.246$ ).

## Weight Loss

Weight loss influenced by number, length of sprouts, and weight of sprouts, determines the longevity of tuber storability and keeping quality (Pande et al. 2007; Mani et al. 2014; Singh and Ezekiel 2003). Some short (e.g., CIP399075.22, Arka) and medium (Java, Antarctica, Sarpo Mira, CIP399072.21) dormancy genotypes which were observed to have smooth skin, had low weight loss of sprouted tubers compared with the extreme short and long dormancy varieties, Shangi and Tornado, respectively (Supplementary Material Tables 1 and 3). Mani et al. (2014) and Embaye et al. (2018) indicated that variations in weight loss among cultivars was attributed to either their periderm characteristics (tuber corky tissues) or their sprouting behavior.

Season had a strong effect on weight loss, which was significantly higher in the short rainy season at all sites when measured at 45 days after dormancy release; however, the effect of season at dormancy release was not noticed at Lelan, possibly due to the effect of cooler growing conditions persisting up to dormancy release. The strong negative correlations between altitude and average percentage weight loss of unsprouted tubers ( $R=-0.513$ ) and lack of correlation for sprouted tubers ( $R=-0.028$ ) suggests that the effect of altitude reduces considerably after dormancy

break (Table 5). The weak positive correlations between dormancy release and length of longest sprout ( $R=0.293$ ) indicates only a weak influence of dormancy on physiological aging, while percentage weight loss of sprouted tubers were weakly negatively correlated (Table 5). Also, the moderate positive correlation between average length of longest sprout per tuber with average percentage weight loss of unsprouted tubers ( $R=0.307$ ) and strong positive correlation with sprouted tubers ( $R=0.500$ ) confirmed that longer sprouts increase weight loss. The consistency of genotype ranking across seasons indicated that genotypes could be selected based on the desired dormancy and sprouting characteristics at each altitude (Figs. 6 and 7).

## Outlook

The current study provides a greater understanding of the effect of genotype, altitude (location), and season on dormancy and physiological age of a wide panel of varieties either being trialled or available in Kenya. Prior to this study little information was available on this topic of relevance to sub-Saharan Africa. The wide genotypic variation identified highlights the availability of varieties that can be selected on the basis of dormancy and physiological age indicators to address agro-ecological and seasonal needs and cropping systems, to help mitigate fluctuation of market prices, enhance potato availability through ware and/or seed storability. Short dormancy varieties would be most suitable for the short period between the long rains harvest and the short rains planting. Medium and long dormancy types have the potential to provide better “quality” seed for the long rainy season crop, while also allowing longer ware storage. Alternate seasonal planting of short and medium to long dormancy varieties within and between the seasons could be used to maximize seed quality and storage of both seed and ware potatoes to meet seasonal and market needs.

Traditionally, higher altitude sites were selected for seed production to limit virus diseases, which are spread by aphids. This study highlights advantages in dormancy break and physiological age characteristics associated with high altitudes. Potatoes produced in the high altitude regions and stored at low altitude breaks dormancy between 1.3 and 43.3 days earlier depending on genotype and dormancy type. This also provides useful management information for tropical regions. The progressive number of sprouts at initial sprouting, dormancy release and 45 days after dormancy release and the length of longest sprout could provide an estimation to farmers to plant seed for optimum crop establishment on the basis of physiological age. The length of the longest sprout and the number of sprouts could provide a simple indicator of seed quality notwithstanding chronological age. The genotypic main effect was greater than environment and season for both dormancy and physiological age traits which highlights their importance for selection in breeding programs although they are complex traits (Slater et al. 2013; Shu et al. 2015). This study in the short term is more likely to guide targeting of current and future varieties for specific production areas and markets based on their dormancy and physiological aging characteristics in conjunction with their agronomical characteristics.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s11540-023-09617-9>.

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**Data Availability** All data are available in the Supplementary material.

## Declarations

**Conflict of Interest** Denis Griffin is Editor of Potato Research; Paul C. Struik is Editor-in-Chief of Potato Research.

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