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Understanding Genotype × Environment Interactions in Potato Production to Guide Variety Adoption and Future Breeding Strategies

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Abstract

Potato (*Solanum tuberosum* L.) is a versatile crop given its adaptation, production capacity and utilization, and therefore valuable in many different countries. In Kenya, potato is mainly grown by smallholder farmers for food and cash. Access to quality seed of adapted and acceptable varieties was limited. This led to public–private partnerships with European seed companies working independently or with their Kenyan counterparts in introducing high-quality seed of new varieties. Some of these showed improved yield, quality and disease resistance. However, some European varieties were less adapted to the short photoperiods prevailing in Kenya than the late blight-resistant elite clones from South America, introduced by the International Potato Center (CIP). Traits that influence genotype adaptation can aid breeding cultivars or support their recommendation for certain production areas, but such traits have not been studied in detail for Kenya. This study sought to understand the adaptation of 50 contrasting genotypes from Europe, CIP and Kenya and the traits driving adaptation to four seasons and three altitudes. Genotypes showed a wide range of yields in all environments studied. The factor genotype explained most of the variance for total tuber yield (71.2%), plant height (49.3%) and area under the disease progress curve (25.1%) based on the Wald statistic, followed by season and the genotype by altitude interaction. Other traits studied hardly contributed to the understanding of the responses to the twelve testing environments. However, the largest proportions of variances for days to 50% emergence, days to maturity and canopy cover were accounted for by altitude.

Keywords Adaptation · Altitude · Canopy cover · Disease resistance · North-western Kenya · Season

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Introduction

In Kenya, potato (*Solanum tuberosum* L.) is mainly grown by smallholder farmers for food and cash (Gildemacher et al. 2011; Kwambai et al. 2023a), in two seasons: the short rainy season (from August to November/December) and the long rainy season (from April to August/September). Generally, both processing and table potato is grown by Kenyan farmers. The crop plays a significant role in addressing food security in Kenya because of its high productivity per unit area, the short maturity period when compared to common cereal crops, rising demand particularly in urban areas, and its adaptation to varied farming systems and agro-ecological zones (Fintrac 2015). Potato provides an earlier source of food and income compared to maize, Kenya's main staple, which takes twice or three times as long to mature (Durr and Lorenzl 1980, Fintrac 2015). In north-western Kenya, potato is mainly grown on the slopes of Mt. Elgon, and in the Cherangani hills and higher altitude zones of Uasin Gishu and Elgeyo Marakwet (above 2000 m above sea level). However, the mid-altitude zones (1500 to 2000 m above sea level) also provide potential areas of production yet to be exploited (first authors' personal observation). In order to achieve high and stable tuber yields, selection in the target growing environments is important (Muthoni and Shimelis 2018), which in Kenya cover over 13 counties with diverse conditions (Machangi et al. 2016). This requires extensive multi-locational testing of varieties for adequate representation of environments for better adaptation and high yields. Inadequate testing of imported genotypes across major growing environments prior to release affects the identification or selection of suitable varieties for certain conditions due to large genotype by environment interaction and hence further affects adoption by farmers.

Generally, potato productivity is low, with yields less than 10 t ha^{-1} compared to a potential of 40 t ha^{-1} (NPCK 2018). Despite the low yields, potato is the second most important food security crop after maize (Kaguongo et al. 2008; Fintrac 2015; Muthoni and Shimelis 2018). Numerous factors limit the production and productivity of potato in Kenya, which include limited access to quality seed of adapted, stable and acceptable varieties (Gildemacher et al. 2011; Muthoni et al. 2014; Atieno et al. 2023; Kwambai et al. 2023b). Moreover, pest and disease management practices and other agronomic practices are generally poor, which are associated with less competitive market strategies (Angweni et al. 2020). Also, potato prices are inconsistently influenced by the seasonality of supply and are particularly low during harvesting time (Fintrac 2015).

The Kenyan government increased the attention to potato, resulting in public–private partnerships with European seed companies working individually or with their Kenyan counterparts in introducing high seed quality of new varieties. New European varieties show desirable traits, such as improved yield and resistance to late blight or potato cyst nematodes, and have diverse uses (table, chips, crisps). However, some varieties were less adapted to the short photoperiods prevailing in Kenya than the late-blight resistant types from the International Potato Center (CIP), which seem well adapted and high yielding. While most European varieties are *S. tuberosum*, most of the CIP genotypes released in Africa are a mix of *S. demissum*, *S. tuberosum* (50%) and *S. andigena* (30%) and to a lesser extent *S. acaule*, *S.*

bulbocastanum and *S. phureja* (Mendes T, CIP, personal communication). Moreover, many European varieties require intensive agronomic management (Komen et al. 2017). There is limited knowledge on the adaptation of these new varieties and elite clones from CIP to diverse growing environments (in terms of altitude and season), particularly those in north-western Kenya, and on the traits driving adaptation and the mechanisms of adaptation to the diverse production environments. Phenotyping adaptive traits is important for improving environmental adaptation in crops under global change (Lasky et al. 2015). The phenotype of a plant is determined by its genetic composition (genotype) and the growing environment (Steyn et al. 1993). A genotype is considered to be adapted to a target population of environments (wide adaptation) or specific environments (narrow adaptation) if its yield is better than a reference genotype (Bustos-Korts et al. 2018). As Kenya provides a diversity of highland environments for potato growing, only few genotypes show good yield performance at all sites and in both seasons. Therefore, our goal was to identify phenotypic traits that influenced adaptation of different potato genotypes (from European, CIP and "Kenyan" gene pools) to growing environments (seasons and altitudes) and their associations for enhanced production and efficient breeding.

Fifty genotypes from different sources were evaluated at three altitudes during four seasons. Morphological and physiological traits and their associations were assessed in twelve field trials. The findings will inform breeding efforts to combat challenges of genotype-by-environment interactions under Kenyan conditions and will support early-stage selections and knowledge of traits and factors to consider in developing varieties for specific regions.

Materials and Methods

Environments

The field trials were conducted in three different agro-ecologies: KALRO Kitale at 1837 to 1855 m above sea level (asl), Saboti at medium altitude (2145 to 2234 m asl) in Trans Nzoia County and Lelan at high altitude (2915 to 2935 m asl) in Elgeyo Marakwet county (Supplementary Materials 1–3). The trials were conducted during four consecutive seasons (short rainy seasons of August–November/December in 2019 and 2020 and long rainy seasons of April–August/September in 2020 and 2021), constituting a total of twelve (3 locations × 4 seasons) environments. These twelve environments are described in Supplementary Materials 1, 2 and 3).

Research Materials and Seed Bulking

The potato genotypes were obtained from CIP, IPM Potato Group Ltd./Kirinyaga Seeds Ltd., HZPC Ltd./Kisima Farm Ltd., Agrico East Africa Ltd., DANESPO Ltd. and Kenya Agricultural and Livestock Research Organization (KALRO) Tigoni. They represent varieties from three main gene pools: European (Irish, Dutch, Hungarian), CIP and "Kenyan", with the latter having cultivars' origin from either of the other two gene pools. The genotypes used were selected based on their current and previous popularity or value (released or under testing). They include released varieties and advanced/elite clones from CIP and IPM Potato Group/Teagasc. In this study, elite clones refers to clones with high potential to be released as varieties based on their agronomic and other special attributes. In order to build sufficient seed for three trial sites in a season and sustained seed for subsequent trials, the seed was multiplied for two consecutive seasons: May–August 2018 at St. Patrick's Iten High School farm, Elgeyo Marakwet county and November 2018–February 2019 at Uswo Farm in Uasin Gishu county with the latter supported by supplemental irrigation since it was planted towards the end of the short rainy season. The genotypes tested were Arka, Alibaba, Antarctica, Asante, Bikini, Buffalo, Challenger, CIP392617.54, CIP392797.22, CIP393077.159, CIP393079.4, CIP393280.64, CIP393371.58, CIP394611.112, CIP395112.6, CIP396018.241, CIP398190.200, CIP399072.21, CIP399075.22, Commando, Desiree, Destiny, Dutch Robijn, Fandango, Gravity, Imagine, Infinity, Java, Kenya Karibu, Kenya Mpya, Kerr's Pink, Konjo, Manitou, Markies, Maverik, Mayan Gold, Meru, Panamera, Roslin Tana, Royal, Sagitta, Sarpo Mira, Shangi, Sherekea, Spunta, Tigoni, Tornado, Unica, Vanilla and Voyager. Some CIP genotypes included in the set were later found to be duplicates: Kenya Mpya was the same as CIP393371.58, Konjo was the same as CIP393077.159 and Unica was the same as CIP392797.22; however, in this paper, they are treated as "different" genotypes and reported separately.

All seed materials were planted each time at a specific site under the same management to standardize starting material. Harvesting was done at the same time but relatively early with some compromise between early and late maturing types to achieve acceptable seed tuber sizes and non-extreme physiological age at harvesting. The seed tubers for planting were harvested after dehaulming and transported to KALRO Njoro (1st multiplication cycle) and KALRO Tigoni (2nd, 3rd and 4th multiplication cycles) for cold storage, respectively. The 1st cold storage at KALRO Njoro was done for 15 days at 4 °C to create a shock in the seed material to accelerate dormancy breaking for the short rains 2019 planting. All other seeds harvested were held at the same temperature in cold storage for different and longer periods between seasons before planting the 2020 long rains, 2020 short rains and 2021 long rains trialling periods. Part of the seed stock used to plant the long rainy season 2020 trials was held for seven months at 4 °C to plant the short rainy season 2020 trials. The seeds were planted without de-sprouting each time to simulate farmers' practices.

Field Trials

The experiments were laid out in a randomized complete block design with three replicates at each location with a plot of twenty plants in two 3-m-long rows per cultivar spaced at 0.75 m × 0.30 m and surrounded by one border (guard) row of the variety Dutch Robijn on each side (Supplementary Material 4). Seed tubers were planted in furrows approximately 15 cm deep on flat ground, and ridging was done later during weeding. Recommended agronomic practices were carried out at each site to minimize influences other than genotype and environment. All management operations were carried out manually including two times a hand weeding with a hoe plus hand pulling of weeds as necessary. Fertilizers used were 500 kg/ha diammonium phosphate, DAP (18:46); 230 kg/ha P_2O_5/98.9 kg/ha P; 90 kg/ha N at planting and 300 kg/ha calcium ammonium nitrate (26%); 78 kg/ha N, as top dress. Potassium and most other nutrients were adequate in the soil except for excess or deficiencies of calcium, magnesium and zinc at some sites and seasons (Supplementary Material 2), but deficiencies were not corrected, in line with local farmers' practices. Occurrence of insect pests and late and early blight were monitored and controlled with appropriate pesticides when necessary, using a knapsack sprayer. The insecticides used were lambda-cyhalothrin and alpha-cypermethrin against common insect pests (cutworm, aphids, whiteflies, thrips). Fungicides against late and early blight were alternated, involving Mancozeb, Ridomil, Trinity Gold 452 WP, Twigalaxyl 720 WP, Mistress and Infinito (see Supplementary Material 5). The study was not a late blight resistance trial, but an adaptation trial of genotypes under recommended crop management practices including late blight control. The area under the disease progress curve (AUDPC) was used as a measure to understand the response of the genotypes to late blight pressure under disease management and trial conditions and to assess their potential resistance. The experiments at each site were harvested on one day after complete senescence or de-haulming depending on the days to physiological maturity of the late maturing variety(ies).

Data Collection and Processing

Data collected included days to 50% emergence, days to maturity, plant height (highest of four or five plants; cm) at 7-day intervals, non-marketable tuber yield and total tuber yield. Days to maturity refers to the days from emergence to physiological maturity as shown by the foliage colour change from green to yellow. At harvest, all the potato plants in the two central rows were harvested, and the tubers separated into marketable (approximately $\geq$ 28-mm diameter) and non-marketable (chats $<$ 28-mm diameter, diseased, defected tubers), which were weighed to provide marketable and non-marketable tuber yields per plot, then converted into tuber yield per hectare. In order to accommodate the wide diversity in growth and maturity stages among the genotypes tested (Supplementary Material 6A), the canopy cover dynamics were captured using a square grid (Supplementary Material 6B) early during the build-up growth phase only as opposed to the commonly used three growth phases: build-up, maximum canopy cover and decline phases (Nieto 2016; Khan et al. 2019). The canopy cover was converted into area under canopy cover progress curve (AUCCPC) using IdeTo, an Excel-based calculator that calculates AUDPC (Simko 2021), with the unit %.d. Late blight disease severity percent was scored using a late blight severity assessment score protocol developed by Cox and Large (1960). These data were later converted into AUDPC, according to Simko and Piepho (2012), with the unit %.d. Differences in late blight severity were attributed to the delay in time of disease management and the less effective fungicides used in the first trial period (short rainy season 2019), with more severe infestation at KALRO Kitale because of the warm-humid conditions prevailing at that site. The relative area under the disease progress curve (rAUDPC), often used to assess genetic differences across seasons, is relatively easy to calculate from the absolute values.

The data collected were analyzed using mixed model analysis in GenStat 19th Edition VNSI computer package (VSN International 2017) for genotype, season, location and their interactions. Also, mixed model analyses were done on the same data for trialling period, location and their interactions to understand the phenotypic behaviour of genotypes during each trial period and at each location. The trialling period refers to the individual period a trial was conducted in the four rainy seasons (short rainy 2019, long rainy season 2020, short rainy season 2020 and long rainy season 2021). Two linear mixed models without random values were designed as below:

(i) Entry Name + Season + Location + Entry Name.Season + Entry Name.Location + Season.Location + Entry Name.Season.Location + Bloc
(ii) Season year + Location + Season year.Location + Bloc

Mean and average variance of the difference were used as statistic measures (Tables 3, 4, 5, 6). Correlation and regression analyses were computed to provide an understanding of the relationships among parameters and their possible contributions to the variances observed.

Results

Statistical Analysis

Genotype, Season, Location (Altitude) and Trialling Period Main Effects

The *F* test in the linear mixed model (LMM) for the three-factorial analysis showed significant ($p < 0.001$) main effects of genotype (G), season (S) and location (L) for the traits days to 50% emergence, days to maturity, AUCCPC, AUDPC, non-marketable tuber yield and total tuber yield and their interactions (Table 1). The popular variety Shangi was often among the top performers for these traits. Main effects of genotype and location were also significant for plant height, but the season effect was not ($p > 0.05$). Detailed mixed model analyses for the different measured traits are shown in the Supplementary Materials 7 – 13. Also, the results showed significant ($p < 0.001$) effects of trialling period (TP), location (L) and their interaction for the same traits (Table 2). The genotype means are shown in Table 3.

Crop Parameters (traits)

Days to 50% Emergence The highly significant differences among genotypes for days to 50% emergence explained 9.6% of the variance (Table 1) with mean ranges of 16.9 to 21.7 days to 50% emergence (Table 3). The genotypes CIP395112.6, Manitou, Desiree and Maverick took the longest time to emerge while CIP392797.22, Imagine,

Table 1 Mixed model analysis showing percent variance of mean Wald statistics significance test (probability of *F* value; *F* pr) for potato genotype, season, location and their interactions for days to 50% emergence, days to maturity, plant height, area under canopy cover progress curve (AUCCPC), area under the disease progress curve (AUDPC), non-marketable tuber yield and total tuber yield in four seasons and at three different locations in north-western Kenya

Fixed term	n.d.f.	Days to 50% emergence		Days to maturity		Plant height		AUCCPC		AUDPC		Non-marketable tuber yield		Total tuber yield	
		Wald statistics	Percent of variance	Wald statistics	Percent of variance	Wald statistics	Percent of variance	Wald statistics	Percent of variance	Wald statistics	Percent of variance	Wald statistics	Percent of variance	Wald statistics	Percent of variance
Genotype	49	1031.04***	9.6	229.66***	7.1	1306.01***	49.3	913.92***	26.7	374.63***	25.1	661.89***	75.1	1586.98***	71.2
Season	1	58.94***	0.5	693.02***	21.5	1.50 ns	0.1	26.77***	0.8	230.01***	15.4	76.9***	5.0	216.58***	9.7
Location	2	8959.15***	83.3	1955.56***	60.7	998.49***	37.7	2144.93***	62.7	112.82***	7.5	65.0***	5.7	26.15***	1.2
G×S	49	225.88***	2.1	42.78 ns	1.3	39.87 ns	1.5	87.61***	2.6	173.98***	11.6	102.59***	5.3	62.37 ns	2.8
G×L	98	353.08***	3.3	31.11 ns	1.0	112.32 ns	4.2	119.95 ns	3.5	197.42***	13.2	136.06**	5.2	201.36***	9.0
S×L	2	13.86***	0.1	236.16***	7.3	125.82**	4.8	69.13***	2.0	128.4***	8.6	41.92***	0.3	38.38***	1.7
G×S×L	98	97.76 ns	0.9	34.87 ns	1.1	59.82 ns	2.3	57.64 ns	1.7	277.04***	18.5	111.13 ns	3.3	91.40 ns	4.1
Replication	2	13.10 ns	0.1	0.06 ns	0.0	4.44 ns	0.2	1.20 ns	0.0	0.03 ns	0.0	4.89 ns	0.1	5.20 ns	0.2
Total	899	10,752.81	100.0	3223.22	100.0	2648.27	100.0	3421.15	100.0	1494.33	100.0	1200.38	100.0	2228.42	100.0

n.d.f. number of degrees of freedom, *G* genotype, *S* season, *L* location, *AUCCPC* area under canopy cover progress curve, *AUDPC* area under the disease progress curve, *G*×*S* genotype by season interaction, *G*×*L* genotype by location interaction, *S*×*L* season by location interaction, *G*×*S*×*L* genotype by season by location interaction, *, ** and *** = significant at 5%, 1% and 0.1% level of probability, respectively. *ns* non-significant at a 5% probability level. The results were averaged for two seasons (short and long rainy seasons) across two years (2019 and 2020 for the short rainy season and 2020 and 2021 for the long rainy season)

Table 2 Mixed model analysis showing percent variance of mean Wald statistics significance test (probability of *F* value; *F* pr) for trialling period (TP), location and their interactions for days to 50% emergence, days to maturity, plant height, area under canopy cover progress curve (AUCCPC), area under disease progress curve (AUDPC) and total tuber yield at three different locations and four seasons in north-western Kenya

Fixed term	n.d.f.	Days to 50% emergence		Days to maturity		Plant height		AUCCPC		AUDPC		Total non-marketable tuber yield		Total tuber yield	
		Wald statistics	Percent of variance	Wald statistics	Percent of variance	Wald statistics	Percent of variance	Wald statistics	Percent of variance	Wald statistics	Percent of variance	Wald statistics	Percent of variance	Wald statistics	Percent of variance
TP	3	136.36***	2.5	7774.3**	48.0	571.5***	32.3	378.8***	13.8	619.7***	63.0	114.6***	35.9	534.2***	75.6
Location	2	5249.59***	96.9	7405.4**	45.7	860.8***	48.6	1969.3***	71.6	104.2***	10.6	43.5***	13.6	17.2***	2.4
TP×L	6	23.34***	0.4	1011.7**	6.2	335.2***	18.9	400.6***	14.6	259.2***	26.4	156.6***	49.0	152.0***	21.5
Replication	2	7.59*	0.1	0.3 ns	0.0	3.8 ns	0.2	1.1 ns	0.0	0.0 ns	0.0	4.7 ns	1.5	3.4 ns	0.5
Total	35	5416.88	100.0	16,191.7	100.0	1771.3	100.0	2749.8	100.0	983.2	100.0	280.9	100.0	706.7	100.0

n.d.f. number of degrees of freedom, *TP* trialling period of two short rainy seasons (2019 and 2020) and two long rainy seasons (2020 and 2021), *L* location, *TP×L* trialling period×location interaction, *, ** and ***=significant at 5%, 1% and 0.1% level of probability, respectively. *ns* non-significant at a 5% probability level. The results were averaged across genotypes

Table 3 Means of days to 50% emergence, days to maturity, plant height, AUCCPC, AUDPC, non-marketable tuber yield and total tuber yield of 50 potato genotypes averaged across three locations and four trialling seasons in north-western Kenya

	Days to 50% emergence	Days to maturity	Plant height (cm)	AUCCPC (%.d)	AUDPC (%.d)	Non-marketable tuber yield (t ha^{-1})	Total tuber yield (t ha^{-1})
Alibaba	19.6	92.8	47.6	830.3	189.1	2.4	34.0
Antarctica	20.0	90.2	44.1	918.1	273.9	3.3	26.5
Arka	20.8	88.5	38.8	651.5	231.4	5.5	13.9
Asante	17.4	92.9	59.3	1050.7	63.0	2.9	39.6
Bikini	19.7	87.7	38.1	614.8	461.4	2.8	19.7
Buffalo	18.7	88.8	45.3	906.0	268.5	2.5	38.4
Challenger	20.4	90.8	44.5	727.4	314.6	2.2	26.9
CIP392617.54	17.4	96.1	69.4	811.9	18.3	2.2	42.9
CIP392797.22	16.9	93.0	60.7	1214.1	58.2	2.4	57.9
CIP393077.159	18.9	95.9	63.9	1019.7	64.4	1.8	44.4
CIP393079.4	18.3	87.4	51.0	1020.4	261.6	2.3	35.5
CIP393280.64	20.1	97.8	73.9	815.7	12.6	2.1	41.7
CIP393371.58	21.0	96.9	66.7	1052.3	10.7	2.8	50.3
CIP394611.112	17.9	98.0	63.9	1033.3	18.3	4.4	45.6
CIP395112.6	21.7	103.9	71.8	776.5	13.4	2.3	53.5
CIP396018.241	19.7	95.7	53.5	628.3	46.2	3.0	24.0
CIP398190.200	18.5	95.9	60.9	888.6	57.8	2.5	48.2
CIP399072.21	19.6	96.3	79.6	839.0	30.0	4.5	40.6
CIP399075.22	19.9	98.7	61.5	788.0	24.9	5.2	33.1
Commando	18.6	91.9	50.7	766.3	310.4	2.4	31.3
Desiree	21.6	96.1	48.8	766.0	37.4	2.3	28.9
Destiny	19.8	92.9	46.1	942.8	258.5	2.8	30.9
Dutch Robijn	18.6	92.3	62.0	983.5	171.3	4.8	32.6
Fandango	18.8	91.2	53.0	808.3	310.1	2.8	30.7

Table 3 (continued)

	Days to 50% emergence	Days to maturity	Plant height (cm)	AUCCPC (%.d)	AUDPC (%.d)	Non-marketable tuber yield (t ha^{-1})	Total tuber yield (t ha^{-1})
Gravity	19.9	90.9	35.9	615.9	488.9	2.6	19.3
Imagine	17.0	84.1	47.9	1006.2	520.4	3.2	32.5
Infinity	19.7	93.8	49.9	630.2	194.5	1.6	25.5
Java	20.6	92.9	50.4	919.4	12.5	2.8	44.8
Kenya Karibu	18.7	97.8	67.2	996.7	77.8	3.4	39.3
Kenya Mpya	21.1	95.9	65.5	924.4	14.3	2.7	40.2
Kerr's Pink	17.5	88.4	39.7	847.5	365.9	5.4	21.7
Konjo	18.0	96.2	67.2	1040.0	24.2	1.8	49.9
Manitou	21.6	95.0	51.0	826.8	157.5	1.6	38.2
Markies	19.4	91.8	50.8	900.5	195.9	2.6	34.7
Maverick	21.5	89.1	53.8	789.5	194.6	1.7	31.2
Mayan Gold	17.5	93.6	54.0	745.5	55.2	3.1	23.0
Meru	20.4	96.1	64.8	944.2	2.5	3.1	43.1
Panamera	19.7	91.5	59.0	806.9	150.9	1.7	39.2
Roslin Tana	17.4	93.6	59.4	958.2	33.2	3.0	41.9
Royal	18.3	84.4	43.6	896.2	230.5	2.3	27.6
Sagitta	20.3	89.5	41.5	633.0	294.8	1.6	20.1
Sarpo Mira	20.7	92.8	44.1	949.0	9.3	2.7	44.4
Shangi	**17.1**	**93.2**	**71.8**	**1102.0**	**121.3**	**3.8**	**39.9**
Sherekea	18.1	102.2	64.8	922.6	2.9	5.3	34.0
Spunta	19.1	90.1	53.7	802.4	119.5	1.6	26.9
Tigoni	18.4	95.8	58.2	783.7	36.6	5.2	28.7
Tornado	18.6	90.2	39.6	856.9	305.8	2.1	30.8

Table 3 (continued)

	Days to 50% emergence	Days to maturity	Plant height (cm)	AUCCPC (%.d)	AUDPC (%.d)	Non-marketable tuber yield (t ha^{-1})	Total tuber yield (t ha^{-1})
Unica	17.2	92.4	61.5	1185.3	67.6	2.4	56.5
Vanilla	19.5	94.2	43.7	759.9	303.5	3.0	23.8
Voyager	19.8	87.3	51.1	864.4	121.6	2.4	33.6
Mean	19.2	93.1	54.9	871.2	152.2	2.9	35.2
Minimum	16.9	84.1	35.9	614.8	2.5	1.6	13.9
Maximum	21.7	103.9	79.6	1214.1	520.4	5.5	57.9
Av. var. of the difference	0.17	6.31	8.75	2236	4705	0.17	6.39

AUCCPC area under the canopy cover progress curve, *AUDPC* area under the disease progress curve. Values in bold represent the local check variety, *Av. var.* average variance

Table 4 Mean main effects of trialling period on days to 50% emergence, days to maturity, plant height, AUCCPC, AUDPC, non-marketable tuber yield and total tuber yield of 50 potato genotypes across three trial sites

Trialling period	Days to 50% emergence	Days to maturity	Plant height (cm)	AUCCPC (%.d)	AUDPC (%.d)	Non-marketable tuber yield (t ha^{-1})	Total tuber yield (t ha^{-1})
Short rains 2019	19.6	74.8	55.7	978.5	460.0	2.8	37.5
Long rains 2020	19.2	93.8	65.7	889.1	49.1	2.5	45.3
Short rains 2020	18.2	97.8	53.5	718.6	53.5	3.7	25.9
Long rains 2021	19.9	105.5	44.6	898.6	45.8	2.6	32.5
Mean	19.2	93.0	54.9	871.2	152.1	2.9	35.3
Av. var. of the difference	-	0.39	0.80	574.10	401.30	-	0.76

AUCCPC area under the canopy cover progress curve, *AUDPC* area under the disease progress curve, *Av. var.* average variance

Table 5 Mean values of days to 50% emergence, days to maturity, plant height, AUCCPC, AUDPC, non-marketable tuber yield and total tuber yield of 50 potato genotypes as influenced by season across three trial sites

Season	Days to 50% emergence	Days to maturity	Plant height (cm)	AUCCPC (%.d)	AUDPC (%.d)	Non-marketable tuber yield (t ha^{-1})	Total tuber yield (t ha^{-1})
Short rainy season	18.9	86.5	54.6	848.6	256.9	3.3	31.6
Long rainy season	19.6	99.7	55.2	893.8	47.5	2.5	38.9
Mean	19.2	93.1	54.9	871.2	152.2	2.9	35.2
Av. var. of the difference	0.34	12.62	17.49	4472.00	9410.00	0.34	6.39

AUCCPC area under the canopy cover progress curve, *AUDPC* area under the disease progress curve, *Av. var.* average variance

Table 6 Mean values of location main effects on days to 50% emergence, days to maturity, plant height, AUCCPC, AUDPC, non-marketable tuber yield and total tuber yield of 50 potato genotypes at KALRO Kitale (1837–1855 m asl), Saboti (2145–2234 m asl) and Lelan (2915–2935 m asl) across four seasons

Location	Days to 50% emergence	Days to maturity	Plant height (cm)	AUCCPC (%.d)	AUDPC (%.d)	Non-marketable tuber yield (t ha^{-1})	Total tuber yield (t ha^{-1})
KALRO Kitale	16.0	83.7	64.3	1060.2	258.0	3.1	37.0
Saboti	16.9	87.0	58.1	986.8	90.8	3.2	33.9
Lelan	24.7	108.5	42.3	566.6	107.6	2.4	34.9
Mean	19.2	93.1	54.9	871.2	152.1	2.9	35.2
Av. var. of the difference	0.52	18.93	26.24	6708.00	282.30	0.77	19.20

m asl metres above sea level, *AUCCPC* area under canopy cover progress curve, *AUDPC* area under disease progress curve, *Av. var.* average variance

Shangi, Unica, Asante, CIP392617.54, Roslin Tana, Kerr's Pink and Mayan Gold took the shortest time to emerge. The long rainy season had significantly ($p < 0.001$) more days to 50% emergence than the short rainy season (Table 4). However, trialling periods differed in days to 50% emergence without consistency with season (Table 5). Location (altitude) had a larger effect, accounting for 83.3% of the variance in days to 50% emergence (Table 1; Supplementary Material 7). Lelan (24.7 days) had the longest period to 50% emergence, followed by Saboti (16.9 days) and KALRO Kitale (16.0 days), effects that were consistent with the altitudes of these sites (Table 6).

Days to Maturity Days to maturity varied significantly ($p < 0.001$) among genotypes, which explained 7.1% of the variance (Table 1) with a mean range of 84.1 to 103.9 days (Table 3). Season and location explained 21.5% and 60.7% of the variance. The short rainy season showed significantly ($p < 0.001$) faster maturity than the long rainy season (Table 4). At Lelan, genotypes took longer to reach maturity during the long rainy season than during the short rainy season. However, at KALRO Kitale and Saboti season did not affect days to maturity (Table 7). The effect of location was significant ($p < 0.001$) with the high-altitude site Lelan taking longer (108.5 days) to maturity than Saboti (87.0 days) and KALRO Kitale (83.7 days), an effect consistent with altitude (Table 7). Trialling period (TP) and location (L) revealed highly significant differences (Tables 2 and 5) with TP and L explaining 48.0% and 45.7% of the variance (Table 2), respectively.

Plant Height Genotypic differences in plant height were highly significant, accounting for 49.3% of the variance (Table 1). The mean plant height ranged from 35.9 to 79.6 cm with CIP genotypes dominating the top tallest 12 genotypes (Table 3). On the other hand, the old and new European genotypes dominated the 20 shortest genotypes. The long rainy season showed taller plants than the short rainy season but season did not have a significant effect across locations (Tables 1 and 4). Location effect on plant height explained 37.7% of the variance, with highest values at KALRO Kitale (64.3 cm) followed by Saboti (58.1 cm) and then Lelan (42.3 cm), consistent with altitude (Table 6). Trialling periods were significantly ($p < 0.001$) different from each other in plant height (Table 5), where TP and L explained 32.3 and 48.6% of the variance, respectively (Table 2).

Area Under Canopy Cover Progress Curve There were significant ($p < 0.001$) differences among genotypes in AUCCPC, with genotype explaining 26.7% of the variance (Table 1). Genotypes showed ranges between 614.8 and 1214.1%.d with an overall mean of 871.2%.d AUCCPC (Table 3). Nine CIP genotypes among the 50 genotypes tested showed the highest AUCCPC (Table 3). The old and new European genotypes were among the top 10 genotypes with the lowest AUCCPC. Also, season showed highly significant differences across experimental sites with higher AUCCPC observed in the long rainy season than in the short rainy season (Table 4). Trialling periods and locations differed significantly ($p < 0.001$) in AUCCPC (Tables 5 and 6), each explaining 13.8 and 71.6% of the variance, respectively (Table 2), with

Table 7 Mean values for days to 50% emergence, days to maturity, plant height (cm), AUCCPC (%.d), AUDPC (%.d), non-marketable tuber yield (t ha^{-1}) and total tuber yield (t ha^{-1}) of 50 potato genotypes as influenced by location and trialling period

Trialling period	KALRO Kitale	Saboti	Lelan	Mean
Days to 50% emergence				
Short rains 2019	17.0	17.2	24.7	19.6
Long rains 2020	16.0	16.9	24.7	19.2
Short rains 2020	14.8	16.1	23.7	18.2
Long rains 2021	16.3	17.7	25.7	19.9
Mean	16.0	16.9	24.7	19.2
Days to maturity				
Short rains 2019	69.9	70.1	84.2	74.8
Long rains 2020	81.6	84.5	115.5	93.8
Short rains 2020	89.3	96.3	107.9	97.8
Long rains 2021	93.8	97.1	125.5	105.5
Mean	83.6	87.0	108.3	93.0
Plant height (cm)				
Short rains 2019	66.9	67.8	32.4	55.7
Long rains 2020	80.2	66.2	50.8	65.7
Short rains 2020	61.5	56.1	42.8	53.5
Long rains 2021	48.6	42.7	42.5	44.6
Mean	64.3	58.2	42.1	54.9
AUCCPC (%.d)				
Short rains 2019	1177.7	1201.7	556.1	978.5
Long rains 2020	1157.8	1029.4	480.0	889.1
Short rains 2020	939.7	792.0	424.1	718.6
Long rains 2021	965.4	924.2	806.1	898.6
Mean	1060.2	986.8	566.6	871.2
AUDPC (%.d)				
Short rains 2019	836.6	271.7	271.7	460.0
Long rains 2020	75.2	33.5	38.7	49.1
Short rains 2020	97.0	46.6	16.9	53.5
Long rains 2021	15.4	8.1	113.8	45.8
Mean	256.1	90.0	110.3	152.1
Non-marketable tuber yield (t ha^{-1})				
Short rains 2019	2.3	3.5	2.5	2.8
Long rains 2020	2.4	2.3	2.8	2.5
Short rains 2020	4.9	3.9	2.3	3.7
Long rains 2021	2.7	2.9	2.1	2.6
Mean	3.1	3.1	2.4	2.9
Total tuber yield (t ha^{-1})				
Short rains 2019	37.9	38.4	36.2	37.5
Long rains 2020	47.0	48.3	40.7	45.3
Short rains 2020	33.2	20.8	23.8	25.9
Long rains 2021	30.0	28.1	39.3	32.5
Mean	37.0	33.9	35.0	35.3

AUCCPC area under canopy cover progress curve, *AUDPC* area under disease progress curve

KALRO Kitale showing the highest AUCCPC and Lelan the lowest ($p < 0.001$), consistent with altitude.

Area Under the Disease Progress Curve There were highly significant differences among genotypes in AUDPC (range 2.5 to 520.4%.d); genotype explained 25.5% of the variance (Table 1). Thirteen genotypes showed very low AUDPC (2.5 to 2.8%.d), demonstrating late-blight resistance, across altitudes comprising eleven CIP and two European genotypes. Twelve other European varieties including Kerr's Pink had very high AUDPC (268.5 to 520.4%.d), demonstrating susceptibility (Table 3). rAUDPC analysis was also calculated (Supplementary Material 16–20) but due to the large difference between trials, where most had very low late blight severity, it was not considered as informative as the AUDPC analysis. Table 1 shows that season showed highly significant effects across sites with the highest AUCCPC observed during the short rainy season (15.4% of the variance), while location was less important (7.5% of the variance), with the highest mean value at KALRO Kitale and lowest at Saboti (Table 6). However, this was not reflected in the trialling periods where short rains 2019 had the highest AUDPC while long rains 2021 gave the lowest values (Table 5). The trialling period and location explained 63.0 and 10.6% of the variance, respectively (Table 2).

Non-marketable Tuber Yield Genotype showed significant ($p < 0.001$) differences on non-marketable tuber yield, explaining 75.1% of the variance (Table 1) and with a mean range from 1.6 to 5.5 t ha^{-1} (Table 3). Season significantly ($p < 0.001$) affected non-marketable tuber yield, explaining 5.0% of the variance (Table 1) with means of 3.3 t ha^{-1} and 2.5 t ha^{-1} across experimental sites for the short and long rainy seasons, respectively (Table 4). Location main effect explained 5.7% of the variance, with Saboti giving higher values than KALRO Kitale and Lelan (Table 6). Trialling period and location showed highly significant effects, which explained 39.5 and 13.6% of the variance, respectively (Table 2). The trialling period short rains 2020 had the highest non-marketable tuber yield and the long rains 2020 the lowest (Table 5).

Total Tuber Yield Genotypes showed significant ($p < 0.001$) differences in total tuber yield (Table 3), explaining 71.2% of the variance (Table 1), with the mean ranging from 13.9 t ha^{-1} for Arka to 57.9 t ha^{-1} for CIP392797.22 (a copy of Unica with 56.5 t ha^{-1}). Among the top sixteen high-yielding genotypes, which outyielded the standard Shangi (39.9 t ha^{-1}), thirteen were from CIP and three from European gene pools (Table 3). Among the four TPs, the long rainy season 2020 had the highest ($p < 0.001$) total tuber yield followed by short rainy season 2019, long rainy season 2021 and the short rainy season 2020 (Table 4). The TP and L explained 75.6% and 2.4% of the variance, respectively (Table 2). Also, season and location significantly ($p < 0.001$) affected tuber yield, explaining 9.7% and 1.2% of the variance, respectively (Table 1). The long rainy season gave significantly ($p < 0.001$) higher total tuber yields than the short rainy season; a few genotypes showed stable yields across seasons (Table 5; Fig. 1A). The highest significant total tuber yield was obtained at KALRO Kitale, followed by Saboti and Lelan.

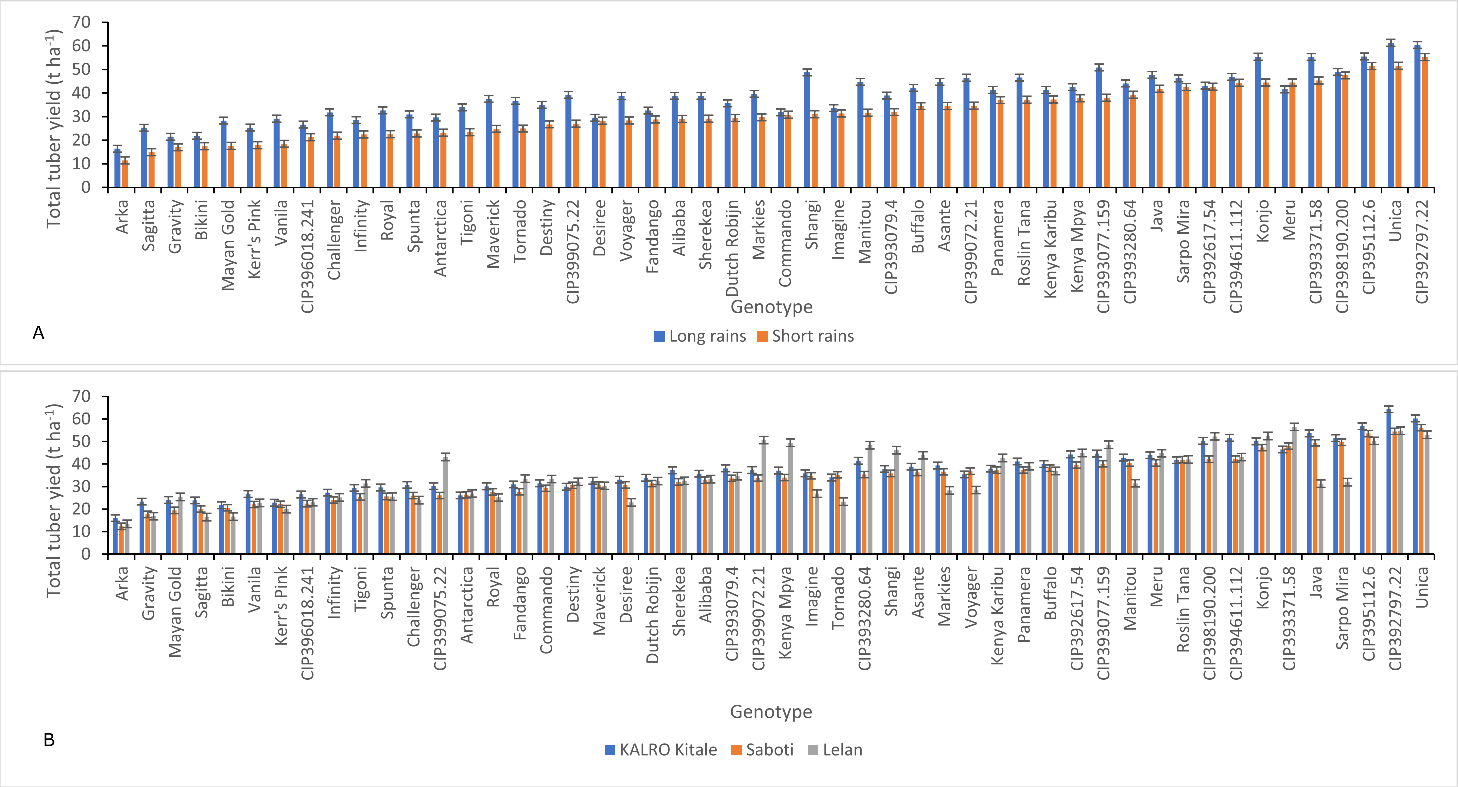

Fig. 1 Mean genotype × season (**A**) and genotype × location (**B**) effects on total tuber yield of 50 potato varieties grown at three locations (altitudes) across four seasons and three locations, respectively, ranked by lowest yielding location (Saboti) and season (short rainy season) in north-western Kenya

Genotype × Environment Interactions (GEI)

Results showed non-significant ($p > 0.05$) genotype × season × location (G × S × L) interactions (GEI) for all crop traits, except AUDPC ($p < 0.001$) (Table 1). G × S × L interaction explained 18.5% of the variance for AUDPC. Genotype × season (G × S) interaction only had significant ($p < 0.001$) effects on days to 50% emergence, AUCCPC, AUDPC and non-marketable tuber yield. Genotype × location (G × L) interaction only showed significant ($p < 0.01$ to < 0.001) effects on days to 50% emergence, AUDPC, non-marketable tuber yield and total tuber yield (t ha^{-1}). Season × location was highly significant for days to 50% emergence, days to maturity, AUCCPC, AUDPC and total tuber yield, and significant ($p < 0.01$) for plant height and non-marketable tuber yield. The variance accounted for by G × E was 17.8%, low compared with the 71.2% accounted for by G. The effects of the S × L interaction on the performance of the genotypes tested are shown in Fig. 2A–G. Days to 50% emergence, days to maturity, AUCCPC, AUDPC, non-marketable and total tuber yields varied significantly ($p < 0.01$ to < 0.001) (Table 1) at each location and season (Fig. 2A, B, D–G); however, plant height, though different, was non-significant ($p < 0.05$) in each season (Fig. 2C). The effects of the trialling period × location (TP × L) interaction were highly significant for all traits (Table 2).

Days to 50% Emergence Genotype × location interactions showed significant ($p < 0.001$) effects on mean days to 50% emergence (Table 1; Supplementary Material 7a). The S × L interaction had a significant ($p < 0.001$) effect on days to 50% emergence, with larger differences between seasons at Lelan than at KALRO Kitale and Saboti, but in absolute terms this interaction effect was very small (Fig. 2A). Also, the effects of TP × L interactions were highly significant (Tables 2 and 7). Although most factors and interactions were significant, variance in days to 50% emergence was mainly explained by location (83.3%) (Table 1) and trialling periods (96.9%) (Table 2).

Days to Maturity There were significant ($p < 0.01$) S × L interactions for days to maturity, which only explained 7.3% of the variance (Table 1). The significant ($p < 0.01$) TP × L interaction explained 6.2% of the variance (Table 2). Season × location interaction showed that the season effect on days to maturity was larger at Lelan than at the other locations (Fig. 2B).

Plant Height Results showed a non-significant ($p > 0.05$) G × S × L (GE) interaction for plant height (Table 1). However, there was significant ($p < 0.01$) S × L interaction explaining 4.8% of the variance (Table 1), with larger differences between seasons in Lelan and Saboti than in KALRO Kitale. Also, the trialling period × location interaction for plant height was evident (Table 7), explaining 18.9% of the variance (Table 2).

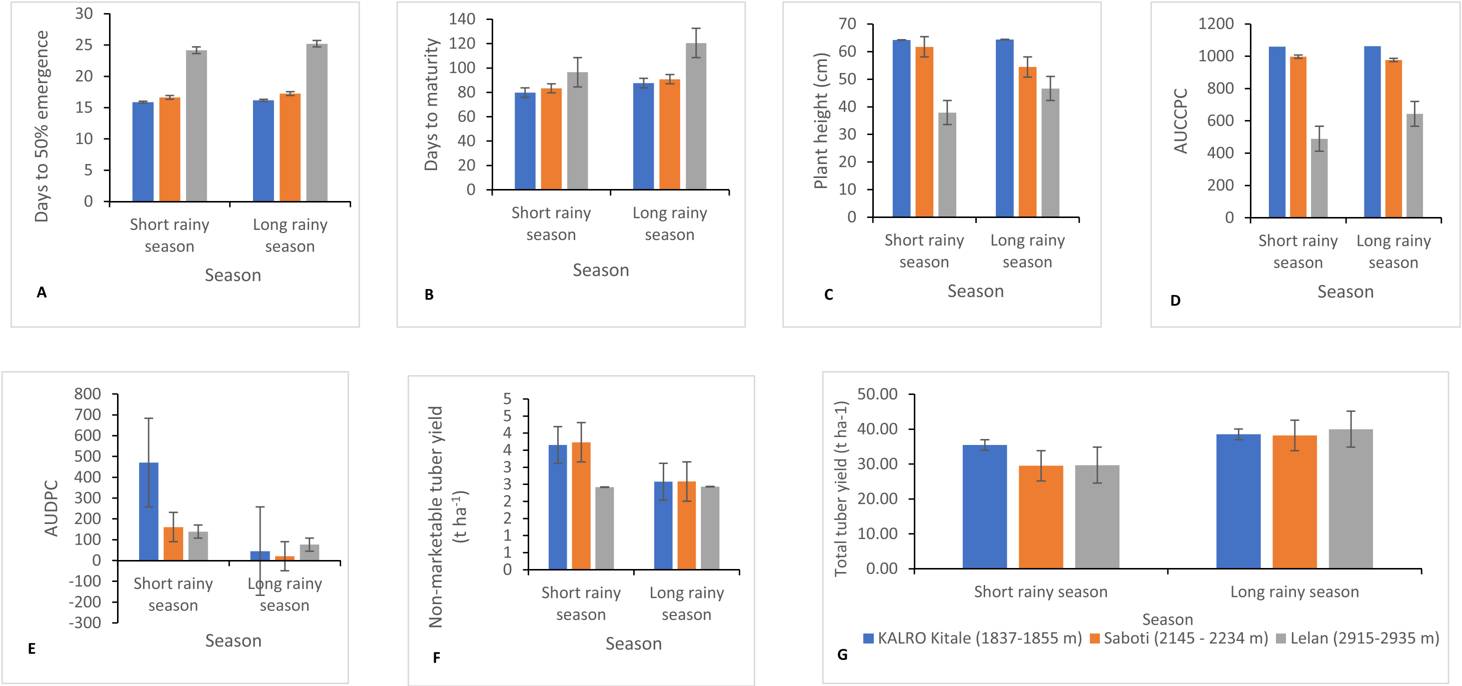

Fig. 2 Effect of season × location (altitude) (G × E) interaction on yield and crop traits; days to 50% emergence (**A**), days to maturity (**B**), plant height (cm) (**C**), AUCCPC (%.d) (**D**), AUDPC (%.d) (**E**), non-marketable tuber yield (t ha^{-1}) (**F**) and total tuber yield (t ha^{-1}) (**G**) in north-western Kenya

Area Under Canopy Cover Progress Curve All interactions contributed relatively little to the percent variance in AUCCPC. The G×S×L and G×L interactions were non-significant for AUCCPC, but the G×S and S×L interaction were significant ($p < 0.001$). As for plant height, the significant S×L interaction showed that the differences between locations were stronger during the short rainy season than during the long rainy season, mainly caused by the low value of AUCCPC at Lelan during the short rainy season (Fig. 2D). However, the trialling period×location interaction accounted for 14.6% of the variance (Table 2), showing that KALRO Kitale had highest values, but smallest differences among seasons compared with Saboti and certainly Lelan (Table 7).

Area Under Disease Progress Curve Unlike all other variables, AUDPC showed a significant ($p < 0.001$) G×S×L interaction accounting for 18.5% of the variance (Table 1). All two-way interactions were also statistically highly significant and relevant (Tables 1 and 7; Fig. 3A and B) but high-performing genotypes showed low AUDPC. The trialling period (and to a lesser extent also the location) had a large effect on the late-blight pressure and therefore very much affected the expression of genetic variation in resistance against the disease, with the short rainy season showing more genetic variation than the long rainy season and KALRO Kitale allowing the expression of genetic variation better than Lelan and Saboti. This was attributed to weather conditions during the trialling period 2019 short rains and the weak fungicides used (not as treatment) compared to subsequent trialling periods, as observed by the first author.

Non-marketable Tuber Yield Non-marketable tuber yield was not much affected by interactions between genotype, season and location. For KALRO Kitale and Saboti, there were higher non-marketable yields during the short rainy season than during the long rainy season, but for Lelan this season effect was absent (Fig. 2F). The interaction between trialling period and location also accounted for a major proportion of the variance (Table 2) as non-marketable tuber yields were high during the short rainy season of 2020 at KALRO Kitale (Table 7).

Total Tuber Yield There was no significant G×S×L interaction for total tuber yield. The local check variety Shangi gave relatively higher tuber yield (but non-significantly so) in the long rainy season compared to other varieties across locations (Fig. 1A). Among the three two-way interactions, the G×L interaction was by far the most important (cf. Table 1; Figs. 1 and 2). The average total tuber yields (33 – 37 t ha^{-1}) realized at each site (Table 6) were relatively close to the attainable yield using national recommended input levels (40 t ha^{-1}), which reveals that crop management was close to optimal allowing yields close to the potential yield. Shangi was outperformed by 21 genotypes at KALRO Kitale, by 20 at Saboti and by 11 at Lelan (Table 3). More of the elite clones from CIP performed relatively well at high altitude (Fig. 1B). The genotypes Antarctica, Roslin Tana, Destiny, Maverick, Kerr's Pink and Dutch Robijn showed stable tuber yields across locations, whereas CIP3999075.22, Kenya Mpya and CIP395112.6

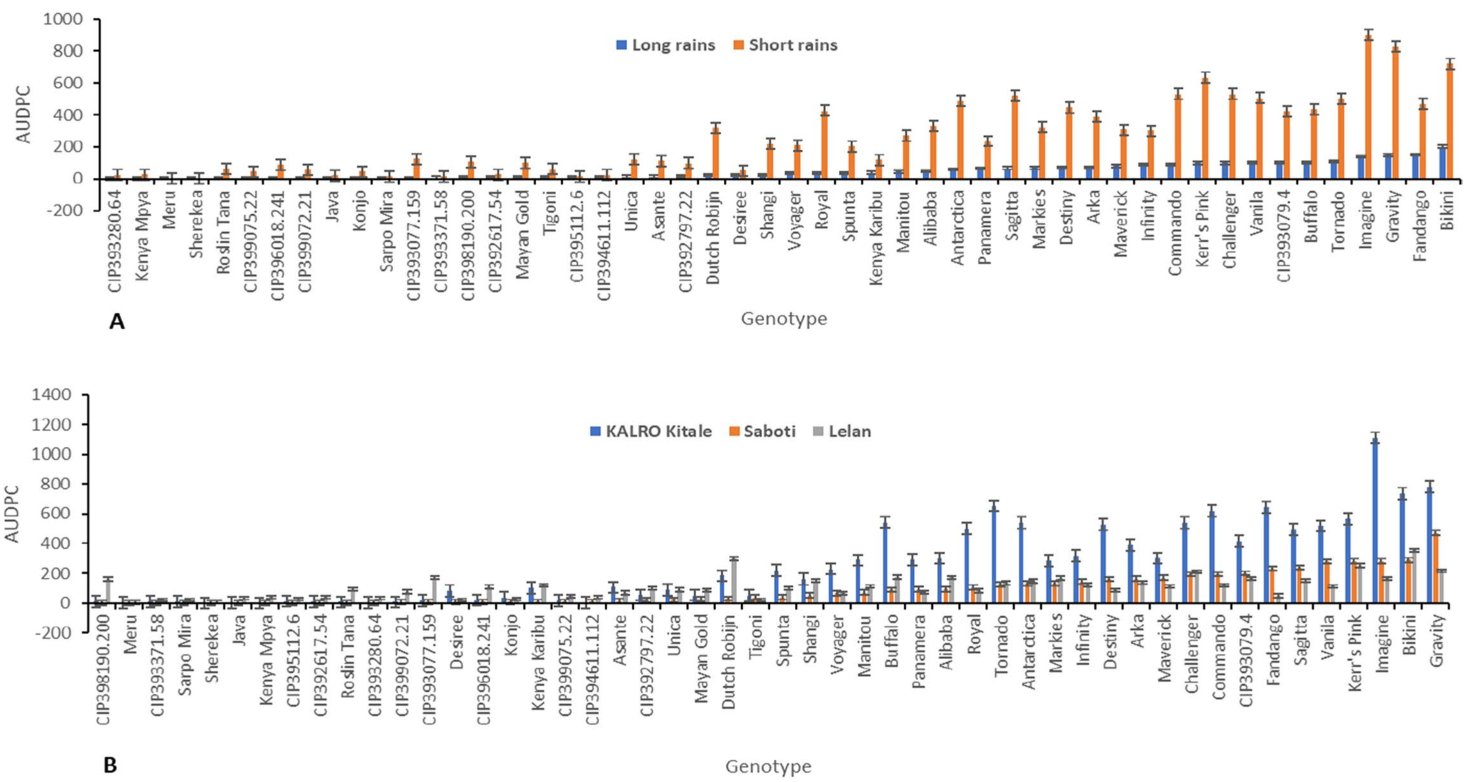

Fig. 3 Late blight severity in the different genotypes as revealed by AUDPC (%.d) in two seasons across three trial sites (**A**) and at KALRO Kitale (1837 to 1855 m asl), Saboti (2145 to 2234 asl) and Lelan (2915 to 2935 m asl) across four seasons (**B**)

Table 8 Table of Pearson correlation coefficients for seven potato traits measured among 50 genotypes based on average values across seasons and locations

Traits measured	Days to 50% emergence	Days to maturity	Plant height (cm)	AUCCPC (%.d)	AUDPC (%.d)	Non-marketable tuber yield (t ha^{-1})	Total tuber yield (t ha^{-1})
Days to 50% emergence	-						
Days to maturity	**0.559*****	-					
Plant height	**−0.467*****	−0.306*	-				
AUCCPC	**−0.501*****	**−0.644*****	**0.555*****	-			
AUDPC	−0.043 ns	−0.367**	−0.041 ns	0.198 ns	-		
Non-marketable tuber yield	−0.222 ns	−0.046 ns	0.093 ns	0.077 ns	−0.039 ns	-	
Total tuber yield	−0.051 ns	−0.040 ns	**0.539*****	**0.451*****	−0.165 ns	−0.048 ns	-

AUCCPC area under canopy cover progress curve, *AUDPC* area under disease progress curve. Critical values for the correlation coefficient $|r|$ at $n=50$ are 0.273 for $p=0.05$; 0.354 for $p=0.01$ and 0.443 for $p=0.001$. Correlations that are significant at $p \leq 0.001$ are in bold. *, ** and *** = significant at 5%, 1% and 0.1% level of probability level, respectively. *ns* non-significant at a 5% probability level were unstable (showing high yields at Lelan), as were Java, Sarpo Mira and Tornado (showing lower yields at Lelan) (Fig. 1B). However, three CIP genotypes (Kenya Mpya/CIP393371.58, Konjo/CIP393077.159 and Unica/CIP392797.22, which were duplicated gave near similar expression on total tuber yields and other traits (Figs. 1A–B and 3A–B) across locations. Although coincidentally the aforementioned genotypes were duplicated, the original data were maintained as the consistencies of the results provide a double check on the reliability of the data in these adaptation trials. There was very little evidence of S × L interaction as yields were similar at all sites within a season except possibly for a higher yield in KALRO Kitale in the short rainy season (Fig. 2G). There was a strong interaction between trialling period and location (Table 7), with different sites performing best in different seasons.

Correlation Between Tuber Yield and Other Variables Measured

The correlation coefficients between total tuber yield and the other measured crop traits averaged across the twelve growing environments are shown in Table 8 ($n = 50$). Days to 50% emergence showed significant moderate negative correlations with plant height ($r = -0.467$) and AUCCPC ($r = -0.501$) and a strong positive correlation with days to maturity ($r = 0.559$). Days to maturity showed strong and moderate negative correlations with AUCCPC ($r = -0.644$), and plant height ($r = -0.306$) and AUDPC ($r = -0.367$), respectively. Both days to 50% emergence and days to maturity showed negative correlation to all traits except days to 50% emergence. Plant height showed significant strong positive correlations with AUCCPC ($r = 0.555$) and total tuber yield ($r = 0.539$). Also, AUCCPC had a significant moderate positive correlation ($r = 0.451$) with total tuber yield. The negative correlations between days to maturity and AUCCPC and plant height were site effects largely influenced by the slow growth combined with a longer growing season during canopy buildup in Lelan due to cooler conditions.

Discussion

The focus of this trial series was to evaluate the performance and suitability of a large set of diverse genotypes at three environments in two seasons under the nationally recommended agronomic practices to determine both genotype performance and genotype by environment interactions. In addition, the trials were analyzed to try and identify which physiological traits would be predictive of yield in these environments to aid breeders in defining phenotypes and effecting selection of genotypes where breeding takes place in very different environments. The size of the trials did not allow additional management factors such as fertilizer rate to be evaluated, which is extremely topical in Kenya as most farmers use considerably lower inputs. Consequently, very high mean tuber yields were realized in this study (Table 6) which highlights the potential of potato in northwestern Kenya under good management, and that high yields are achievable if inputs can be sourced. Typical management practices have been explored in a parallel study (Kwambai et al. 2023a) and the results could be related or compared to the survey results on farmers' practices in our survey work (Kwambai et al. 2023a). In this study, the genotypic effect explained most of the variance for total tuber yield (71.2%), plant height (49.3%) and AUDPC (25.1%) followed by season and then genotype by location interaction.

Genotype

Assessing promising cultivars developed locally or in other regions for yield potential and other important traits at different growing locations is imperative for understanding their yield performance and adaptation to those environments. The large set of diverse genotypes tested, revealed wide variation. More important was the high percent variance attributed to genotypic main effects for total tuber yield, non-marketable tuber yield, plant height and AUDPC. Genetic variation in yield was comparable with earlier reports (e.g. Khan 2012; Bustos-Korts et al. 2018; Raja et al. 2018).

Although the European and some of the old Kenyan genotypes, and few CIP clones showed less adaptability at high altitudes, many performed well at lower altitudes, e.g. several CIP genotypes in addition to Sarpo Mira, which is of Hungarian origin with several major R genes including R8 from the species *Solanum demissum* (Rietman et al. 2012) and Java, which have good processing quality for chips under Kenyan conditions as reported by the NPCK (2021). These two varieties also had high resistance to late blight, which most popular Kenyan varieties lacked. However, Shangi and Unica, which were high yielding with moderate late blight resistance also have good processing qualities for chips. Also, most European genotypes have resistance against potato cyst nematodes (*Globodera rostochiensis*), a new threat in Kenya, and other pests and diseases (Mwangi et al. 2021), while many have superior consumer traits such as good storability and processing qualities (e.g. Markies, Panamera, Manitou), although they are weak in late blight resistance. The use of such cultivars for cultivation in areas they are adapted to and their use as potential parents in breeding programmes could increase yields and advance the Kenyan potato industry.

Significantly strong negative correlations between days to 50% emergence and days to maturity with plant height and AUCCPC across genotypes influenced crop growth, and consequently contributed to total tuber yield performance. The use of morpho-genetic attributes in breeding of cultivars has the potential to guide increased understanding of genotype adaptation early in cultivar development and selection for cultivation (Bustos-Korts et al. 2018). The large number of CIP genotypes which showed higher AUCCPC (canopy cover) confirmed the findings of Cadersa and Govinden (1999) who reported significantly higher canopy cover in tropical potato clones than temperate clones due in part to differences in maturity. Traits such as plant height and AUCCPC or canopy cover, which showed strong association with each other ($R=0.555$) and with total tuber yield ($R=0.539$; $R=0.451$, respectively) (Table 8) could assist breeding of potato cultivars for adaptation to specific or broad growing environments, but also for targeting areas similar to the current study sites. No other traits provided useful insight into understanding the performance of the genotypes for yield. The mean yield of 35.2 t ha^{-1} of genotypes tested was only slightly lower than the yield of Shangi, the most popular variety (Komen et al. 2017; Kwambai et al. 2023a). The difference in yield between the highest and lowest yielding varieties tested was 44 t ha^{-1} indicating the wide difference in yield potential.

Season

Wide variations between the long and short rainy seasons for days to maturity, AUDPC and total tuber yield revealed that the two seasons were different in their conduciveness to potato cultivation and had different effects on phenotype, which could provide basis for selection of varieties suitable for specific and across season. However, season had significant but less influence on days to 50% emergence, plant height and AUCCPC as indicated by the lower percentage variance than for genotype and location. Genotypes that showed consistently good and stable performance in tuber yield during both the long and short rainy seasons indicated that they were most suitable for cultivation across seasons (Fig. 1A). The variations in the four trialling periods (each season treated individually) showed that each period was different from the other for all parameters possibly due to changes in seasonal patterns, weather and disease pressure. This suggests that genotypes with broad seasonal adaptations would be beneficial for farmers. The relatively higher tuber yield realized with the local check Shangi in the long rainy season and across locations compared to other varieties indicated that it performed better under cooler and higher rainfall conditions (Fig. 1A, B).

The significant late blight infection encountered during the 2019 short rains trialling period did not provide clear evidence that total tuber yield was significantly affected by the high AUDPC, possibly because the disease set in when the crop had reached an advanced growth stage and the judicious fungicide applications were beneficial to reduce infection before yield was lost. The significant variations in total tuber yield between the trialling periods indicated variable prevailing weather conditions between the same seasons in different years; however, the long rains trialling periods consistently gave higher total tuber yields at Lelan, but inconsistencies were observed at Saboti and KALRO Kitale (Table 7), possibly because of more stable environmental conditions in Lelan. The low AUDPC during the trialling period 2021 long rains could be attributed to the low rainfall, preventing late blight disease development. The aforementioned observations highlight the need for judicious use of fungicides with high efficacy where susceptible cultivars are used but moreover the need for late blight resistance in varieties as farmers traditionally use lower rates of fungicide than recommended practice (Kwambai et al. 2023a).

Location

The high percentage variance and consistent effect of location (Table 1) suggest that altitude had a critical effect on potato phenological traits and consequently crop growth (cf. Minda et al. 2018). The results showed that the higher the altitude the greater the variances among the genotypes for days to 50% emergence, days to maturity, plant height and AUCCPC (Tables 1, 2 and 7), which has implications on crop growth and yield performance. The greater variability among genotypes on total tuber yield at Lelan compared to Saboti and KALRO Kitale showed that most genotypes were more stable at lower altitudes than at higher altitudes possibly because of genotypic sensitivity to low temperatures at high altitude (Fig. 1B). This was more so for the European genotypes, which were selected in warm summer periods in the high latitudes compared to the CIP genotypes, which originated from the high tropical altitudes of South America similar to the high altitudes in Kenya. Tuber yield was similar in Lelan to the other sites probably due to the longer growing season, which compensated for slower emergence, delayed maturity and smaller canopy.

The highest yields at KALRO Kitale could be attributed to favourable weather and good growth vigour associated with high values for plant height and AUCCPC (Table 7). More genotypes showed high and stable total tuber yields at KALRO Kitale, which suggests that the location was a favourable genotype testing site or environment at low to mid-altitude and particularly in the long rainy season. The negative correlation between days to maturity and AUDPC (which was highest at the KALRO Kitale site) is more expected as late blight resistance is often correlated with later maturing varieties. The high yields at the low altitude support the findings of Minda et al. (2019). However, Minda et al. (2018) also observed differences among trialling periods.

Season × Location

The S×L interaction showed that the differences between locations were stronger during the short rainy season than during the long rainy season, mainly caused by short plants and low AUCCPC at Lelan during the short rainy season (Fig. 2C, D). CIP cultivars showed high values for plant height and AUCCPC, characteristics associated with enhanced interception of solar radiation (Haverkort et al. 1991) as a result of the fast canopy cover growth of genotypes (Nieto 2016; Khan et al. 2019), and therefore a high yield potential.

The low total tuber yield across locations and relatively high non-marketable tuber yields recorded during the trialling period 2020 short rains could be attributed to the physiologically and chronologically aged seed used and the relatively low rainfall observed during the same trialling period. The seed planted during the trialling period 2020 short rains was from the same seed lot as the seed planted during the 2020 long rains, and therefore was > 4 months older. Physiologically aged seed contributes to negative effects on seed vigour and productivity (Coleman 2000; Caldiz et al. 2001; Caldiz 2009). Also, the same old seed could have contributed to the early emergence and lowest AUCCPC among the trialling periods, and relatively high non-marketable tuber yield and relatively low total tuber yields due to premature senescence caused by physiologically aged seed (Caldiz 2009). On the other hand, the low yields at KALRO Kitale and Saboti in the long rains 2021 were due to the low rainfall experienced compared to other seasons (Supplementary Material 3) highlighting vulnerability to drought and the need for drought-resistant genotypes.

Genotype by Environment Interaction

This study found that genotype had the greatest influence on total tuber yield compared to other factors and that there were more potentially suitable genotypes than Shangi for the lower altitudes compared to the high altitudes, but Shangi performed much better at high altitude. Genotype yield rank was remarkably consistent at the two lower sites but in general CIP varieties performed better at the high altitude (Lelan), which confirmed their adaptation to lower temperatures. The high yields realized at the low altitude site, KALRO Kitale, where potato is not common, provide new game changing knowledge for an alternative crop to maize and for other similar agro-ecologies.

Genotypic means across environments are suitable indicators of genotypic performance only in absence of G×E interaction (Bustos-Korts et al. 2018). Phenotypes respond differently to different growing environments as a result of the genotype×environment phenomenon, which leads to the measure of adaptability and agronomic stability of a genotype over a number of environments (Zakir 2018). The knowledge of such attributes in genotypes is important in cultivar development, adaptation for cultivation in (a) given environment(s) and recommendation for known cropping conditions (Zakir 2018). The results showed that there were genotypes with specific and broad adaptation to the environments (Figs. 1A, B, and 2G). Although most European cultivars showed poorer yield at high altitude than those from CIP, the low AUDPC shown by some and the relatively good performance at lower altitudes compared with CIP and Kenyan varieties revealed their potential for cultivation in Kenya at low and mid altitudes and for use as breeding parents (Fig. 1B). The temperatures at mid-low altitude are higher comparable to summer in Europe, whereas at 2950 m asl they were much lower than in Europe and comparable to high altitudes in the Andes in South America. The high adaptability of CIP genotypes at high altitudes and across environments could be attributed to their tropical origin of South American highlands, previously mentioned genetic diversity, and clone selection at similar high altitudes (CIP 2014).

It is acknowledged that breeders need access to and use as much genetic diversity as they can get for enhanced response to climate challenges and changing environments (Galluzi et al. 2020). As predicted by Zali et al. (2016), significant fluctuation in yield due to response of genotypes to environmental factors was expressed in this study. Although not investigated, there is a need to understand the effect of both air and soil temperatures on potato establishment and growth to establish the inherent traits or genetic factors associated with adaptation to growing environments, particularly following the extreme slow growth observed on certain genotypes particularly in Lelan. However, although we could not make comparisons in long day regions, the poor performance of some of the European genotypes could be attributed to lack of adaptation to short daylength (Demagante and Vander Zaag 1988).

Conclusion

- The establishment/growth and productivity of the genotypes tested showed wide variations across locations, seasons and trialling periods.
- Predictive traits such as AUCCPC and plant height may assist breeders in selecting candidate varieties when breeding in and for different environments.
- Use of European and CIP genotypes/cultivars endowed with disease resistance in breeding programmes could advance gains in the potato industry by combining favourable traits available.
- Two sites at mid and high altitude would have been sufficient to measure genotype by environment interaction across this altitude transect but a lower altitude site should be considered in the future as potato was equally productive at the lowest site tested.
- European varieties are generally not as suitable at higher altitudes but relatively stable at medium altitude while CIP varieties exhibited consistently high yield performance across all environments.
- Drought and late blight resistance are important in Kenyan conditions for which a good number of the genotypes tested have potential particularly for the latter, while response to drought could further be investigated.
- Different management strategies, which are common among Kenyan farmers, may affect genotype ranking but this study provides useful information on genotype suitability and adaptation.
- High yields can be achieved using the national recommendations.
- The data set obtained provides useful background information on the tested genotypes for the first time and for further in-depth investigations.

Thus, from the current results, Kenya has a collection of superior varieties, which could be promoted in the market and under good agronomic practices for better yields and productivity.

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Data Availability The data that support the findings of this study are available from the corresponding author D.G. upon reasonable request.

Declarations

Conflict of Interest P. C. S. is editor-in-chief of Potato Research; D. G. is editor of Potato Research.

Disclaimer The views expressed in this paper is not of any of the research material providers but solely the responsibility of the authors.

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