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Public potato breeding progress for the Nordic Region of Europe: evidence from multisite testing of selected breeding clones and available released cultivars

Fredrik Reslow[a], Ulrika Carlson-Nilsson[a,b], José Crossa [c,d], Jaime Cuevas[e] and Rodomiro Ortiz [a]

[a]Department of Plant Breeding, Swedish University of Agricultural Sciences (SLU), Lomma, Sweden; [b]Nordic Genetic Resources Center (NordGen), Alnarp, Sweden; [c]International Maize and Wheat Improvement Center (CIMMYT), Texcoco, Mexico; [d]Colegio de Postgraduados, Montecillos, México; [e]Universidad de Quintana Roo, Chetumal, México

ABSTRACT
The breeding of new cultivars is a powerful approach to increase both the quantity and quality of potato harvest per land unit. The aim of this research was to determine using multi-site testing the progress made by the genetic enhancement of potato in Sweden in the last 1.5 decades by comparing advanced breeding clones (T_4 upwards) bred in Sweden (Svensk potatisförädling hereafter) *versus* available released cultivars in Europe and grown in its Nordic Region. The multi-site testing results show that potato breeding based in Scandinavia offers to the growers of the Nordic Region of Europe cultivars for prevailing farming environments and end-user needs rather than relying, as happens today in the market, on foreign cultivars. These cultivars bred elsewhere are not always very suitable for the challenging Nordic agroecosystems, as shown by the results of the multi-site testing herein. Such an approach on relying on foreign cultivars may be advocated for not funding potato breeding in, and for Fennoscandia by those ignoring the results shown by this research.

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Introduction

Potato (*Solanum tuberosum* L.) is, after rice and wheat, the third most important food crop of the world on a consumption per capita per year base, thus contributing to human diets as well as the economy of the producing country. This tuber crop is less influenced by varying food prices than cereals, thus making it well adapted to both subsistence farming as well as for income generation (Andrivon 2017). For example, the potato market value (crisp, fast-food restaurants, industry, table) ranges between 5–6 billion SEK per year in Sweden. Such market depends on a stable supply of high-quality potato with diverse quality traits.

This polyploid crop ($2n = 4x = 48$ chromosomes) shows susceptibility to several pests and pathogens that affect its productivity, as measured by tuber yield. Often, pesticides are used extensively to obtain bumpy harvests. Late blight, caused by the oomycete *Phytophthora infestans* Mont. de Bary, remains the major pest of potato worldwide. This pathogen infects the entire plant (Fry 2008), may cause at least a tuber yield loss of 16% (Haverkort et al. 2009), and whose economic value has been estimated at about US$ 5 billion annually (Duncan 1999; Tsedaley 2014; Lal et al. 2018). The potato crop is sprayed with the largest amounts of fungicides per hectare in Sweden, although its total acreage accounts only for ca. 1% (about 25,000 ha) of the total land agricultural area of the country (SCB 2012).

Potato breeding for host plant resistance shows a great high gross return to investments (Eriksson et al. 2016), as well as for sustainably intensifying agriculture due to its delivery of productivity gains under the same land use, while avoiding risks for human and environmental health due to pesticide use. The main breeding strategy for this crop has been phenotypic recurrent selection (Slater et al. 2017). A typical potato crossbreeding programme refers to developing new cultivars after crossing and selecting after several generations (T_is) of testing among breeding clones (Jansky and Spooner 2018). It remains today as the main force for introducing in potato farming new phenotypes triggered by new genes (Brown 2011). Potato crossbreeding begins with bi-parental crossings using available released cultivars or advanced breeding clones. After germinating the hybrid seed, the resulting seedlings are grown to get at least one tuber of each in the T_1 generation, which will be field grown in single hill (plant)

CONTACT Rodomiro Ortiz rodomiro.ortiz@slu.se Department of Plant Breeding, Swedish University of Agricultural Sciences (SLU), P.O. Box 190, SE 234 36 Lomma, Sweden
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plots. Very strict selection occurs at this stage, thus leading to discarding about 90% or more single hills according to tuber appearance. Thereafter, it will take at least 12–15 years to select promising breeding clones in each T_i generation in plots varying from 10 to 40 plants in the breeding site(s), and to further release it as a new potato cultivar after replicated multi-site trials in the target population of environments. As vegetative propagation continues for most promising breeding clones in each T_i, their number decreases while the number of their testing plots increases.

Brown (2011) indicated that one named cultivar was released by the US Northwest Tri-State Potato Breeding Consortium after testing and selecting on average 60,000 T_1s in the first year, while practice tells that a cultivar may be registered after planting 10,000 T_1 seedlings per year if crossbreeding within the cultigen pool, and 100,000 T_1 seedlings per year when crossing with wild species (Eriksson et al. 2016). Potato breeding for Sweden began in 1903 at a semi-public institute in Svalöv, and since the mid-2000s is a small enterprise at the Swedish University of Agricultural Sciences (SLU) in Skåne and Umeå (Ortiz et al. 2020). Every year SLU's potato breeding programme makes about 35 bi-parental family offspring to obtain ca. 10,000 breeding clones in the first cycle of selection (T_1), which is based on tuber characteristics including quality and host-plant resistance to *Phytophthora infestans*. Tuber quality traits are cooking and frying quality, flesh colour, and specific gravity. Graminor does potato breeding for Norway from Bjørke Research Station, near the city of Hamar. This programme develops potato cultivars aiming high and stable production of good quality, high host plant resistance to pathogens (late blight, scab), and consumer preferences. Danespo (Give, Denmark) is the largest potato breeding company in northern Europe and releases potato cultivars to meet demands from growers, consumers and the industry for host plant resistance, tuber quality and profitability. The aim of this research was to determine using multi-site testing the progress made by the genetic enhancement of potato in Sweden in the last 1.5 decades by comparing advanced breeding clones (T_4 upwards) bred in Sweden (Svensk potatisförädling hereafter) *versus* available released cultivars in Europe and grown in its Nordic Region.

Materials and methods

Multi-site trials comprised 169 potato breeding clones and cultivars in Helgegården, and 256 breeding clones and cultivars in both Mosslunda and Umeå (although one cultivar did not grow at all in last site likely due to the poor quality of its planting tubers). A list indicating country of origin and year of release (when available) of these breeding clones and released cultivars is given in Supplementary Table 1. The reference cultivars or checks for the multi-site trials were the late blight susceptible 'Bintje', the high yielding 'Connect', 'Carolus', the most preferred table potato in Sweden 'King Edward', and the early maturing 'Solist'. The breeding clones were in their fourth generation (T_4) of selection in Sweden (Ortiz et al. 2020), while the cultivars those released and grown in Europe during the last 200 years. A few old Nordic cultivars kept by the Nordic Genetic Resource Center (NordGen) were also included. The testing sites were Helgegården and Mosslunda – which are nearby the city of Kristianstad (56°01′46″N 14°09′24″E, Skåne, southern Sweden)– and Umeå (63° 49′30″N 20°15′50″E), which is a city in northern Sweden. The cropping season for potato was about 3.5–4 months in Skåne (end of May – early September 2020), while only 90 days in Umeå (early June – end of August 2020). The average daily temperatures during respective growing seasons vary between 12 and 18°C in the southern sites, and 12.5–16°C in Umeå. The average monthly precipitation amounts to 42–64 mm nearby Kristianstad, and 48–75 mm in Umeå. The day-lengths range between 11.5 h (around harvest) and 17.5 h (mid-growing season) in Skåne, and 14.5 (harvest)–ca. 21 h (early cropping season) in Umeå.

The field layouts were incomplete blocks with two replications of 10 plants each, which is the plot size for standard evaluation trials of advanced breeding clones (CIP 2007). Plant spacing was 0.3 m between plants within the rows and 0.7–0.75 m between rows. The experimental designs for the field trials were a 13×13 simple lattice in Helgegården, and a 16×16 simple lattice in both Mosslunda and Umeå. Fungicide treatments were only used in Helgegården to control late blight throughout the growing season, which facilitated estimating tuber yield potential. Crop husbandry practices were those used for potato farming in each site.

The tuber traits evaluated across all sites were total yield per plot (kg), and by size (<40 mm, 40–50 mm, 50–60 mm, >60 mm; kg), as well as starch in the flesh, which was determined as percentage according to the specific gravity after harvest. However, some cultivars (incl. 'King Edward') did not yield enough tubers for specific gravity tests in Mosslunda. The area under disease progress curve (AUDPC) was used to measure host plant resistance to late blight in Mosslunda because it is a very useful quantitative assessment of disease intensity over time, for comparison over years or across sites, or plant health management. The trapezoidal method is the most used for estimating the

AUDPC as the average disease intensity between time points. AUPDC was estimated for each breeding clone or cultivar following the scoring of late blight severity in each plot (Fry 1978) every 7 days. The late blight susceptible cultivar 'Bintje' was planted as a 'spreader row' in both sides of each incomplete block to ensure a continuous source of inoculum.

The reducing sugar content in the tuber flesh was determined after harvest in Umeå using a potato glucose strip test. Tubers were cut in half lengthwise and the knife wiped between cuts. The strip was put flat to the length of the cut tuber and each half pressed against the other to ensure total moisturising of the whole strip. The strip was removed and after waiting for 1 min it was compared against a colour chart. If the strip was darker that 1/10% colour, the chips are likely to get a dark colour after frying.

Data analysis

Single-environment trial linear mixed model for data analysis. The potato cultivar denotes as y_{irb} represents the trait response of the ith ($i = 1, \ldots, I$) potato cultivar (C_i) in the rth replicate ($r = 1,2, \ldots, R$) (REP_r), at the bth incomplete block nested within the rth replicate ($b = 1,2, \ldots, B$) [$InBl(REP)_{b(r)}$] of an specific environments. This response is defined by the following linear mixed model:

$$y_{irb} = \mu + C_i + REP_r + InBl(REP)_{b(r)} + e_{irb}, \quad (1)$$

with the summation of μ, overall mean, the random potato cultivar main effect $\left[C_i \overset{iid}{\sim} N(0, \sigma^2_C)\right]$, the random replicate effect $\left[REP_r \overset{iid}{\sim} N(0, \sigma^2_{REP})\right]$, the random effect of the incomplete block nested within replicate $\left[InBl(REP)_{b(r)} \overset{iid}{\sim} N(0, \sigma^2_{InBl(REP)})\right]$ and a random error term $\left[e_{irb} \overset{iid}{\sim} N(0, \sigma^2_e)\right]$. From this linear model, $N(.,.)$ denotes a normal random variable, *iid* stands for independent and identically distributed responses and σ^2_C, σ^2_{REP}, $\sigma^2_{InBl(REP)}$, and σ^2_e are the variances for potato cultivar, the replicate, the incomplete block within replicate and the residual, respectively. As indicated, this single-environment model does not allow borrowing of information among genotypes because they are treated as random outcomes that are independent with equal variance (*idd*). An uncontrolled environmental and or cultivar effect that were not possible to be controlled *a priori* can be introduced in Equation (1) as fixed effects regression covariable. The main output of these analyses for each environment produces the Best Linear Unbiased Predictor (BLUP). As noted by Bernardo (2020), 'best' refers that the sampling variance of what is being predicted is minimised, while 'unbiased' indicates that it has an expectation of zero.

Multi-environment trials linear mixed model for data analysis. For the multi-environment trial linear mixed model some components of Equation (1) remain the same and others change. Here, the environment main effect (E_j) and the cultivar × environment interaction (CE_{ij}), generally represented as G×E, are considered. Also, the design factors change accordingly. Therefore, the potato cultivar denotes as y_{ijrb} represents the trait response of the ith ($i = 1, \ldots, I$) potato cultivar (C_i) in the jth environment (location or location-year combination) ($j = 1,2, \ldots S$) for the rth replicate ($r = 1,2, \ldots, R$) nested within the jth environment ($REP_{r(j)}$), in the bth incomplete block within the rth replicate and the jth environment ($b = 1,2, \ldots, B$) [$InBl(REP\ E)_{b(rj)}$] and the interaction of the cultivar × environment interaction (CE_{ij}), represented by the following linear model:

$$y_{ijrb} = \mu + C_i + E_j + REP(E)_{r(j)} + InBl(REP,\ E)_{b(rj)} + CE_{ij} + e_{irb}, \quad (2)$$

with the summation of μ, the overall mean, the random potato cultivar main effect $\left[C_i \overset{iid}{\sim} N(0, \sigma^2_C)\right]$, plus the random environment main effect $\left[E_j \overset{iid}{\sim} N(0, \sigma^2_E)\right]$, plus the random replicate effect nested within environments $\left[REP(E)_{r(j)} \overset{iid}{\sim} N(0, \sigma^2_{REP(E)})\right]$, plus the random effect of the incomplete block within replicate and environment $\left[InBl(REP,\ E)_{b(rj)} \overset{iid}{\sim} N(0,\ \sigma^2_{InBl(REP,E)})\right]$, plus the random effect of the incomplete block within replicate and environment $\left[CE_{ij} \overset{iid}{\sim} N(0,\ \sigma^2_{CE})\right]$, and a random error term $\left[e_{ijrb} \overset{iid}{\sim} N(0, \sigma^2_e)\right]$. From this linear model, $N(.,.)$ denotes a normal random variable, *iid* stands for independent and identically distributed responses and σ^2_C, σ^2_E, $\sigma^2_{REP(E)}$, $\sigma^2_{InBl(REP,E)}$, σ^2_{CE}, and σ^2_e and are the variances for the potato cultivar, the environment, the replicate nested within environments, the incomplete block nested within replicate and environments, the cultivar × environment interaction, and the residual variance, respectively. Equation (2) does not allow borrowing of information among cultivar, environments or cultivar × environment interaction because they are treated as random outcomes that are independent with equal variance (*idd*). Similar to single-environment model uncontrolled environmental or cultivar effects that were not possible to be controlled *a priori* can be introduced in Equation (1) as fixed effects regression covariables. The main outputs of these analyses are the BLUPs, which allow comparing breeding clones or released cultivars derived from different populations and evaluated in different environments.

META-R (Alvarado et al. 2020) was used for multi-site analysis of the trials, and to calculate BLUPs for all traits, as well as the least significant difference (LSD), and the coefficient of variation.

Table 1. Mean (± standard error) of best linear unbiased predictors (BLUPs) of potato tuber yield (kg in 10-plant plot using square lattice designs with two reps) and starch content (%, estimated based on specific gravity recording using weight in air and under water) in SLU's Svensk potatisförädling breeding clones and available cultivars for farm planting in Sverige grown at three sites: Helgegården (high yield potential using fungicide treatment), Mosslunda (late blight-prone site) and Umeå (long daylength, short season and relatively low temperature).

			Weight within each tuber size (%) [Y]					Stress lost (%) [X]	
Site	N	Tuber yield (TY)	<40	40–50	50–60	>60	Flesh's starch (FS)	TY	FS
Helgegården	169	10.98 + 0.21	6	26	38	30	15.00 + 0.19		
Mosslunda (late blight)	169 [Z]	7.75 + 0.29	10	31	32	26	12.17 + 0.18	−29.42	−18.67
Umeå (day length)	169	6.92 + 0.12	21	41	26	12	10.27 + 0.17	−36.98	−31.53

Note: [Z] 159 for flesh's starch. [Y] Market tuber size: gourmet cuisine <40, table medium 40–50, table large 50–60, crisp/fry industry >60. [X] Tuber yield or flesh's starch loss due to either late blight in Mosslunda or to day length in Umeå (using as reference the non-stress site at Helgegården).

Results

There were highly significant ($P < 0.001$) differences for all characteristics evaluated among testing sites and genotypes according to the combined analysis of variance (ANOVA) across sites, which also revealed that the genotype × environment interaction (GEI) was highly significant ($P < 0.001$) for all traits. Hence, the analysis of results will be given for each testing site. The lowest coefficient of variation was for tuber flesh starch at harvest (6.04%) and total tuber yield (17.45%). Both tuber yield and flesh's starch losses, on percentage, were about 1/3 for either susceptibility to late blight or sensitivity to long daylength, as measured by comparing the results from the high yield potential site (Helgegården) versus those in Mosslunda and Umeå, respectively (Table 1). These results confirm that abiotic and biotic stress-prone environments negatively affect tuber yield and flesh's starch in potato, being most significant the long daylength stress penalty (>30%) for both characteristics in the short cropping season at Umeå.

On average, Svensk potatisförädling clones (32) –particularly those bred for table potato (22) or derived from crop wild relatives (2)– had their tuber yield potential above EU released cultivars available for growing in Sweden (137), though the former had a great percentage of (extra) large tuber sizes (Table 2) in Helgegården. Svensk potatisförädling clones for crisp (8) exhibited, on average, the largest starch content in tuber flesh. The top 10% of high tuber yielding in Helgegården (Table 3) included eight breeding clones of different advanced generations (T_9 [1], T_8 [2], T_6 [3], T_5 [1] and T_4 [1]) and eight cultivars (4 released in The Netherlands, and 1 each released in Great Britain; France, Germany and Ireland). The tuber yields of all of them were larger than those of the reference cultivars or checks except the Dutch high yielding cultivar 'Connect', which was among the top three for tuber yield. The high yielding SLU breeding clones 1402009 [T_5] and SLU 1314015 [T_6] were among the top three for their host plant resistance to late blight in Mosslunda. The former had the highest flesh's starch content among the top yielding germplasm and significantly above all reference cultivars except 'King Edward', which is the most preferred in Sweden.

Svensk potatisförädling breeding clones for table and those derived from crop wild relatives (CWR) were, on average, the highest yielding in a late blight-prone site at Mosslunda (Table 4) due to their host plant resistance to *Phytophthora infestans*. The largest starch content in the flesh at this late blight prone site was noted in the cultivar 'Marius' and thereafter, on average, in the Svenska potatisförädling clones for crisps. Svensk potatisförädling 1415001 (T_5 generation), 2-IV-6 (derived from CWR), 1402009 (T_5) and 1429006 (T_4) along with the Dutch cultivar check 'Connect' were among the top yielding in the late blight prone site at Mosslunda (Table 5). About 8% of Svensk potatisförädling clones had high partial host plant resistance to *Phytophthora infestans* as measured by the AUDPC, and 1402009 and 1314015 (T_6) being the best for this characteristic (Table 6). None of the Svensk potatisförädling clones for crisps were rated as very susceptible, while only 1% of the EU released cultivars had high partial resistance and 18% of them were very susceptible (including the check 'Bintje', which was also used in late blight spreader rows). The Dutch starch cultivar 'Nofy' was the most *Phytophthora infestans* resistant among those potato cultivars bred and released in Europe. None of the Nordic cultivars provided by NordGen had high partial resistance and 1/3 of them were very susceptible, except for the less susceptible the early main crop cultivar 'Marius' (NGB 3100) – grown in Norway for > 100 years due to its relatively high dry matter content and good cooking quality.

On average, Svensk potatisförädling clones for table were the highest yielding under the long daylengths and short season in Umeå, while Svensk potatisförädling clones for crisps were, on average, the best for tuber quality; i.e. flesh's starch and reducing sugars (Table 7). The top performing for tuber yield in this long daylength

Table 2. Mean (± standard error) of best linear unbiased predictors (BLUPs) of potato tuber yield (kg in 10-plant plot using a simple 13 × 13 square lattice design) and starch content (%, estimated based on specific gravity recording using weight in air and under water) in SLU's Svensk potatisförädling clones and available cultivars for farm planting in Sweden at high yield potential site (Helgegården, Skåne, Sweden) under fungicide treatment.

			Weight within each tuber size (%) [V]				
Country/Programme	N [Z]	Tuber yield	<40	40–50	50–60	>60	Flesh's starch
Svensk potatisförädling table	22	13.1 + 0.6	4	19	33	44	14.4 + 0.4
Svensk potatisförädling crisp	8	9.2 + 1.2	5	26	43	26	17.5 + 1.8
Svensk potatisförädling derived from CWR [Y]	2	13.0 + 0.2	9	45	36	11	16.1 + 0.8
Released cultivars available for Sweden	137	10.7 + 0.2	6	27	39	28	14.9 + 0.2
'Blaue Schweden'	1	4.8	10	48	36	6	14
Sweden [X]	3	10.0 + 1.4	13	38	35	14	16 + 1.4
Austria [W]	3	11.4 + 1.4	7	32	41	20	15.5 + 1.3
Czechia ('Magda')	1	9.9	3	22	35	40	15.1
Denmark ('Folva')	1	13.4	4	25	48	23	16.0
Finland ('Timo')	1	10.8	3	17	39	41	13.5
France [W]	16	9.2 + 0.6	7	27	37	29	13.9 + 0.4
Germany [W]	53	10.5 + 0.4	7	29	39	25	14.2 + 0.3
Great Britain [W]	17	10.1 + 0.6	9	27	36	28	16.3 + 0.4
Ireland [W]	3	12.5 + 1.4	3	13	33	50	14.3 + 0.3
Switzerland [W]	2	8.3 + 0.2	7	43	34	16	13.2 + 0.02
The Netherlands [W]	34	11.8 + 0.4	5	23	41	31	16.0 + 0.5
U.S.A. [W]	2	11.4 + 0.1	4	23	42	32	14.5 + 0.5

Note: [Z] Number of cultivars or breeding clones. [Y] Crop wild relatives. [X] 'Blå Mandel' (yield in 10-plant plot: 6.6 kg), 'Perlo' (11.0), 'Sparris' (12.3). [W] See Annex 1 for cultivar list. [V] Market tuber size: gourmet cuisine <40, table medium 40–50, table large 50–60, crisp/fry industry >60.

site included 5 Svensk potatisförädling clones and 3 cultivars (2 from the Netherlands and 1 from Germany) released in Europe (Table 8). The three Svensk potatisförädling clones showing the highest tuber yield (SW 0101011, SLU 1209001and SLU 1201001) were among the top yielding at the high yield potential site under fungicide treatment at Helgegården (Table 3), while the firth performing breeding clone (SLU 1415001) was

Table 3. Best Svensk potatisförädling clones (9) and EU released cultivars (9) for tuber yield (based on BLUPs) evaluated in 10-plant plots using a simple 13 × 13 square lattice design at Helgegården under fungicide treatment against late blight. Five reference cultivars or checks [†] are also tabulated to compare them in this site with most promising breeding clones and high yielding released cultivars.

			Weight within each tuber size (kg)				
Breeding clone or released cultivar	Generation or country release year (pedigree in brackets)	Tuber yield	<40	40–50	50–60	>60	Flesh's starch
SW 0101011	T_8 (93-1015 × 'Vivaldi')	19.21	0.26	1.54	4.59	12.52	14.33
SW 0003022	T_8 (93-1015 × 93-1081)	17.49	0.43	2.39	5.27	9.06	14.44
'Connect' [†]	Netherlands 2012	17.06	0.53	1.87	5.13	9.17	14.34
'Linda'	Germany 1974	16.73	0.89	5.17	7.27	2.83	15.15
SLU 1402009 [Z, Y]	T_5 [(04-3262 × 'Ora' × 'Satina')]	16.49	0.15	1.31	3.76	11.11	16.32
2-IV-4	T_6 [(grr × 'Superb' × MPI50.140.5)]	16.35	1.01	5.85	6.65	2.31	13.69
SW–SLU 0502047	T_9 ('Superb' × 'Fakse')	16.24	0.24	2.02	6.34	7.13	10.26
'Kingsman'	Great Britain	16.03	0.44	1.71	6.33	7.31	15.78
'Fontana'	Netherlands 1999	15.90	0.51	2.81	7.30	4.77	16.40
'Hind'	Netherlands 2018	15.88	0.21	2.85	6.13	6.28	14.75
'Taisiya'	Netherlands 2011	15.74	0.57	2.77	6.23	5.82	12.70
'Galactica'	Ireland 2003	15.63	0.46	2.04	4.64	8.35	13.79
SLU 1201001 [Y]	T_6 (D09 1:2 1701 × 'Fontane')	15.46	0.21	1.04	2.57	11.67	14.47
SLU 1209001	T_7 (93-1015 × 'Fontane')	15.42	0.31	2.10	5.27	7.30	16.62
'Purple Rain'	Netherlands 2019	14.80	0.34	1.87	6.02	6.19	13.04
SLU 1429006	T_4 [('Desiree' × '93-1015) × 'Arielle']	14.71	0.42	2.33	5.54	5.89	14.84
'Maestro'	France 2001	14.56	0.28	1.99	4.57	7.49	13.14
SLU 1314015 [Z]	T_6 (D09 1:2 1701 × 'Carolus')	14.54	0.32	1.94	5.19	6.83	16.93
'Carolus' [†]	Netherlands 2012	11.90	0.49	3.13	4.98	3.00	15.50
'Bintje' [†]	Netherlands 1910	11.43	0.62	3.91	5.53	0.92	15.77
'King Edward' [†]	Great Britain 1902	10.50	0.48	2.73	4.34	2.94	16.84
'Solist' [†]	Germany 1989	10.08	0.25	2.70	4.74	2.19	13.35
Trial grand mean		10.98	0.63	2.79	4.13	3.27	15.00
$LSD_{0.05}$		2.56	0.40	1.13	1.71	2.25	1.10
Coefficient of variation (%)		12.32	32.71	21.77	22.98	36.64	3.60

Note: [Z] Rated among the three most highly resistant breeding clones to late blight in 2020 'sister' trial at Mosslunda where the oomycete *Phytophthora infestans* seems to be ubiquitous. [Y] Unselected due to very large tuber size percentage (>2/3).

Table 4. Mean (± standard error) of best linear unbiased predictors (BLUPs) of potato tuber yield (kg in 10-plant plot) using a simple 16 × 16 square lattice design and starch content (%, estimated based on specific gravity recording using weight in air and under water) in Svensk potatisförädling clones and available cultivars for farm planting in Sweden at late blight-prone site (Mosslunda, Skåne, Sweden).

Country/Programme	N [Z]	Tuber yield	Weight within each tuber size (%) [P]				Flesh's starch	AUDPC [O]
			<40	40–50	50–60	>60		
Svensk potatisförädling table	36	12.24 + 0.54	5	20	30	45	12.64 + 0.26	157.18 + 6.33
Svensk potatisförädling crisp	8	7.35 + 0.60	8	35	38	19	14.59 + 0.74	277.21 + 4.48
Svensk potatisförädling derived from CWR [Y]	3	14.66 + 2.08	13	37	28	22	13.60 + 0.90	140.69 + 5.10
Austria [X]	4	5.93 + 1.19	23	48	23	7	10.92 + 0.38	275.22 + 6.04
Czechia ('Magda')	1	9.78	4	11	46	38	13.13	279.38
Denmark [X]	2 [W]	5.23 + 2.41	14	35	38	12	12.94	268.79 + 7.68
Finland [X]	2	5.66 + 1.70	13	37	27	23	11.34 + 0.37	285.56 + 2.81
France [X]	21 [V]	5.62 + 0.55	14	34	29	23	10.98 + 0.20	261.73 + 7.08
Germany [X]	73 [U]	6.88 + 0.31	14	39	32	16	11.59 + 0.22	251.57 + 3.70
Great Britain [X]	25	6.77 + 0.44	14	36	30	21	12.42 + 0.38	248.79 + 8.26
Hungary ('Sarpo Mira')	1	10.60	7	30	36	27	16.12	161.49
Iceland ('Raudar')	1	3.14	34	41	14	11	11.56	289.54
Ireland [X]	5	11.01 + 0.88	5	22	21	43	13.10 + 0.31	194.42 + 20.90
Poland/Norway ('Marius')	1	6.85	22	44	24	10	17.10	177.56
Sweden [X]	8 [T]	3.98 + 0.51	17	26	43	14	11.13 + 0.53	277.21 + 4.49
Switzerland [X]	2	3.57 + 0.51	28	43	16	14	10.01 + 0.01	270.89 + 4.10
The Netherlands [X]	61 [S]	8.91 + 0.36	7	27	37	29	12.45 + 0.35	238.60 + 6.37
U.S.A. [X]	3	6.48 + 0.70	9	40	37	14	11.81 + 0.26	289.67 + 10.72

Note: [Z] Number of cultivars or breeding clones. [Y] Crop wild relatives. [X] See Annex 1 for cultivar list. [W] 1 for flesh's starch. [V] 18 for fresh's starch. [U] 70 for flesh's starch. [T] 4 for flesh's starch. [S] 56 for flesh's starch. [P] Market tuber size: gourmet cuisine <40, table medium 40–50, table large 50–60, crisp/fry industry >60. [O] Area under disease progress curve.

the top yielding at late-blight prone site in Mosslunda (Table 5). The best performing reference cultivar was the early maturing 'Solist' (as also noticed in previous years' trials at this testing site).

Discussion

The breeding of new cultivars is a powerful approach to increase both the quantity and quality of potato harvest per land unit. Potato breeding programmes aim to

Table 5. Best Svensk potatisförädling breeding clones (9) and EU released cultivars (1) for tuber yield (based on BLUPs) evaluated in 10-plant plots using a simple 16 × 16 square lattice design at Mosslunda under late blight. Five reference cultivars or checks [†] are also tabulated for comparison in this site with most promising breeding clones and high yielding released cultivars.

Breeding clone or released cultivar	Generation (pedigree), crossing or country release year	Tuber yield	Weight within each tuber size (kg)				Flesh's starch	AUDPC [Y]
			<40	40–50	50–60	>60		
SLU 1415001	T_5 (C08I69 × 'Solist')	22.10	1.10	3.71	6.78	10.11	10.78	161.78
SLU 2-IV-6	T_6 [(grr×'Superb') × MPI50.140.5)]	18.56	1.37	5.24	5.97	5.45	12.59	145.07
SLU 1402009 [Z]	T_5 [(04-3262×'Ora') × 'Satina')]	17.61	0.33	1.68	3.86	11.86	13.83	95.63
'Connect'	The Netherlands 2012	17.39	0.59	2.12	6.20	9.24	12.60	120.99
SLU 1429006 [Z]	T_4 [('Desiree'×'93-1015) × 'Arielle']	17.18	0.37	1.65	2.47	12.60	12.04	148.00
SLU 1314015 [Z]	T_6 (D09 1:2 1701 × 'Carolus')	16.99	0.40	1.81	3.64	11.20	12.69	99.19
'Papageno'	Germany 2019	16.80	0.60	3.46	6.70	5.72	16.15	150.18
SLU 1402003	T_5 [(04.3262 × 'Sarpo Mira') × 'Satina']	15.83	0.45	2.30	3.83	9.35	13.35	133.80
SLU 2-IV-4 [Z]	T_6 [(grr×'Superb' × MPI50.140.5)]	15.55	1.53	4.92	4.82	3.72	12.42	148.64
SLU-SW 0502047 [Z]	T_9 ('Superb' × 'Fakse')	15.34	0.49	3.25	5.93	5.40	9.96	137.02
SLU 1433005	T_5 ('Lady Balfour' × 'Sarpo Mira')	15.19	0.74	2.33	3.08	9.00	13.84	122.03
'Carolus'	The Netherlands 2012	12.58	0.70	3.22	3.59	4.71	13.28	157.73
'Solist'	Germany 1999	8.94	0.26	2.72	4.89	0.91	10.82	289.33
'King Edward'	Great Britain 1900	6.52	0.73	2.62	2.54	0.53	12.74	272.81
'Bintje'	The Netherlands 1910	5.83	0.97	2.17	1.25	0.89	N/A	290.37
Trial grand mean + standard error		8.04 + 0.04	0.77 + 0.01	2.43 + 0.01	2.56 + 0.01	2.17 + 0.06	12.16 + 0.27	234.24 + 0.01
$LSD_{0.05}$		4.04	0.63	1.31	1.66	2.74	1.14	40.33
Coefficient of variation (%)		26.38	45.27	29.78	34.26	66.85	6.74	8.65

Note: [Z] Among top yielding breeding clones and cultivars in 2020 trial at high yield potential site under fungicide treatment. [Y] Area under disease progress curve.

Table 6. Host plant resistance to late blight as measured by area under disease progress curve (AUDPC) using a simple 16 × 16 square lattice design in Mosslunda (Skåne, Sweden) during the 2020 cropping season. The frequency distribution groups defined considering as very susceptible those showing non-significantly different AUPDC than 'Bintje', i.e. mean – standard error = 288.2. The other 3 group clusters defined by range intervals as noted in table and showing high partial resistance if the AUDPC is below 100.

						Frequency distribution (%)			
Group	N [Z]	Mean	St. error	Min.	Max.	<100	101–199	200–288	>288
Svensk potatisförädling for table	39	149.6	7.1	83.25 [Y]	199.8	3 (7.7)	33 (84.6)	3 (7.7)	0 (0)
Svensk potatisförädling for crisps	8	206.0	10.1	172.5 [X]	273.8	0 (0)	2 (25)	6 (75)	0 (0)
Old Nordic cultivars kept at NordGen	6	255.4	21.3	174.5 [W]	311.8	0 (0)	1 (17)	3 (50)	2 (33)
EU released cultivars	203	246.4	3.2	82.0 [V]	310.5	1 (0.5)	27 (13.3)	138 (68.0)	37 (18.2)
'Bintje' spreader row plots	52	291.7	1.7	267.0	316.2	0 (0)	0 (0)	25 (48)	27(52)

Note: [Z] Number of breeding clones or cultivars. [Y] High tuber yielding SLU 1314015, [X] SLU 131, [W] 'Marius', [V] 'Nofy'.

Table 7. Mean (± standard error) of best linear unbiased predictors (BLUPs) of potato tuber yield kg in 10-plant plot using a simple 16 × 16 square lattice design and starch content (%, estimated based on specific gravity recording using weight in air and under water) in Svensk potatisförädling clones and available cultivars for farm planting in Sweden at a long daylength, short season and relatively low temperature testing site (Umeå, Sweden).

			Weight within each tuber size (%) [W]					
Country/Programme	N [Z]	Tuber yield	<40	40–50	50–60	> 60	Flesh's starch	Reducing sugars [V]
Svensk potatisförädling table	36	8.93 + 0.30	13	36	31	19	10.04 + 0.27	0.34 + 0.02
Svensk potatisförädling crisp	8	6.34 + 0.67	20	44	27	9	13.41 + 0.76	0.25 + 0.03
Svensk potatisförädling derived from CWR [Y]	3	7.85 + 1.72	23	44	25	7	9.24 + 0.82	0.29 + 0.03
Austria [X]	4	5.95 + 0,92	45	42	10	3	9.63 + 0.63	0.44 + 0.05
Czechia ('Magda')	1	8.46	14	35	35	17	11.65	0.18
Denmark [X]	2	6.67 + 2.23	21	41	26	12	10.89 + 0.23	0.28 + 0.07
Finland [X]	2	8.43 + 0.44	29	30	21	20	10.18 + 0.38	0.38 + 0.00
France [X]	21	6.79 + 0.44	29	42	20	8	9.76 + 0.32	0.49 + 0.09
Germany [X]	73	6.73 + 0.26	22	42	26	10	9.75 + 0.24	0.39 + 0.04
Great Britain [X]	25	6.32 + 0.40	28	41	22	9	10.76 + 0.34	0.29 + 0.02
Hungary ('Sarpo Mira')	1	6.15	16	43	25	16	11.14	0.50
Iceland ('Raudar')	1	6.24	32	52	14	2	12.58	0.25
Ireland [X]	5	7.52 + 1.04	16	36	34	15	9.87 + 0.55	0.26 + 0.05
Poland/Norway [X] ('Marius')	1	4.66	47	39	11	3	13.17	0.25
Sweden [X]	8	5.41 + 0.53	38	40	17	5	12.53 + 0.79	0.24 + 0.04
Switzerland [X]	2	3.69 + 0.42	37	45	13	4	8.77 + 0.14	0.31 + 0.04
The Netherlands [X]	60	7.87 + 0.23	18	41	29	12	10.56 + 0.32	0.33 + 0.02
U.S.A. [X]	3	7.72 + 0.01	19	44	30	7	11.17 + 0.47	0.29 + 0.03

[Z]Number of cultivars or breeding clones. [Y] Crop wild relatives. [X] See Annex 1 for cultivar list. [W] Market tuber size: gourmet cuisine <40, table medium 40–50, table large 50–60, crisp/fry industry >60, **[V]** Based on glucose strip test.

Table 8. Best Svensk potatisförädling clones (5) and EU released cultivars (3) for tuber yield (based on best linear unbiased predictors – BLUPs) evaluated in 10-plant plots using a simple 16 × 16 square lattice design at Umeå under long daylength, short season and relatively low temperature. Five reference cultivars or checks [†] are also tabulated for comparison.

Breeding clone or released cultivar	Generation (pedigree) or country release year	Tuber yield	Weight within each tuber size (kg)				Flesh's starch	Reducing sugars [Z]
			<40	40–50	50–60	>60		
SW 0101011	T_8 (93-1015 × 'Vivaldi')	12.41	1.20	5.16	3.83	1.67	10.01	0.25
'Galactica'	Ireland 2003	12.09	2.03	3.73	3.93	2.23	8.93	0.38
SLU 1209001	T_7 (93-1015×'Fontane')	11.99	1.00	4.65	4.00	1.94	11.31	0.38
'Twister'	The Netherlands 2017	11.66	2.58	4.11	2.86	1.88	8.54	0.25
'7 FOUR 7'	The Netherlands 2016	11.63	1.80	4.09	3,77	1.38	8.18	0.38
SLU 1201001	T_6 (D09 1:2 1701 × 'Fontane')	11.38	1.03	4.19	4.20	1.61	11.03	0.50
SLU 1419010	T_5 ('Carolus' × 'Valor')	11.15	1.31	3.37	3.80	2.30	9.99	0.38
SLU 1415001	T_5 (C08II69 × 'Solist')	11.07	0.61	2.78	3.61	3.82	8.66	0.25
'Solist'	Germany 1999	10.08	1.10	5.23	3.22	0.76	8.95	0.38
'Carolus'	The Netherlands 2012	8.44	1.24	3.66	3.39	0.13	10.98	0.38
'Bintje'	The Netherlands 1910	8.22	3.34	4.37	0.41	0.00	10.67	0.18
'Connect'	The Netherlands 2012	7.79	0.74	2.53	2.59	1.81	9.11	0.38
'King Edward'	Great Britain 1900	7.43	1.43	3.83	1.77	0.25	12.94	0.18
Trial grand mean + standard error		7.22 + 0.04	1.52 + 0.03	2.94 + 0.04	1.91 + 0.02	0.86 + 0.09	10.33 + 0.24	0.36 + 0.01
$LSD_{0.05}$		1.39	0.52	1.08	0.89	0.79	1.21	0.23
Coefficient of variation (%)		13.78	24.45	26.34	33.46	65.93	8.44	46.75

Note: [Z] Based on glucose strip test.

identify superior F_1 offspring after various years of trials and selection. Potato breeding progress for edible yield, however, lags that of other crops because of its out-breeding, heterozygosity, polyploidy, tetrasomic inheritance and multi-genes controlling such a complex quantitative trait sought by farmers and the industry. In this regard, it should be noted that potato breeding was used to pursue all-purpose performing cultivars across a large range of environments that retain their productivity for a long period. Today the focus is, however, to select cultivars in a target population of production environments that may be also defined by its end-uses.

The accuracy and efficiency of the assessment of breeding clones remain key for succeeding in the genetic enhancement of potato. In this regard, the use of multi-site testing from the T_4 generation (when enough planting material becomes available), along with the use of mixed models for data analysis provide means for improving selection in the potato cultivar pipeline (Tables 3, 5 and 8). In recent years, the linear mixed model and its resulting BLUPs (with information from relatives or across testing sites and replicated plots) are being used in potato breeding to be more accurate and closer to the true values of testing genotypes. For example, BLUPs seem to be efficient when doing family selection for tuber yield, as well as for clonal selection for both tuber yield and specific gravity/starch in tetraploid potato (Ticona-Benavente and da Silva Filho 2015). Likewise, BLUPs were used for efficiently selecting superior diploid breeding clones with yellow tuber flesh and high yield potential (Pacheco et al. 2020). Furthermore, BLUPs along with the additive main effects and multiplicative interaction (AMMI) model provided means for predicting tuber yield in an unbalanced set of testing potato genotypes across sites and over years (Mijić et al. 2019). Our research (Tables 2, 4 and 7) also shows that mixed models and BLUPs are useful for assessing potato breeding progress for tuber yield, grading by tuber size, tuber starch, reducing sugars in tuber flesh and host plant resistance to late blight when testing selected T_is along with available cultivars to growers in Scandinavia. Integrating as random effect the genotype-by-environment interaction, which was significant for all traits evaluated in our multi-site trials, may further improve the prediction *per se* of breeding clones.

Pedigree analysis for the top performing breeding clones in our multi-site trials (Tables 3, 5 and 8) shows the diversity of their parents that are often a breeding clone and a cultivar. In this regard, Sood et al. (2020) indicated that BLUPs based on pedigree relationship may improve selection efficiency, as well as save both time and resources for multiplication and testing when breeding for high tuber yield and host plant resistance to late blight. Their BLUPs used data from historical replicated preliminary yield evaluation trials at a main potato breeding station in India. The use of BLUPs for selecting promising breeding clones for further cultivar release(s) may lead to increased genetic gains.

Trials of newly bred potato clones always include released cultivars to determine their potential for the market(s). Although there were only 41 breeding clones for table potato from Svensk potatisförädling, they were always at the top across the three testing sites (Tables 3, 5 and 8), which also included up to 207 released cultivars in Europe. These results are outstanding since these breeding clones were selected from starting T_1s with a total size below 50,000. Some of the most promising breeding clones combine high tuber yield (even under stress) and late blight resistance, but their tuber starch is often below of the most preferred 'mealy' cultivar 'King Edward' (Tables 3, 5 and 8). The breeding clones also had big size tubers, as noted by the high percentage of their tuber size exceeding 60 mm. Hence, Svensk potatisförädling must emphasize improving both tuber size for table potato as well as having tuber dry matter content to meet consumers' preferences. It should be indicated that 30–40 mm tubers may provide a uniform harvest of large number of small tubers. There is also an emerging 'niche' demand for high value 'little' potatoes with 20–40 mm size for new culinary markets. Crop husbandry (such as plant density, irrigation and early harvest), weather and cultivar determine the tuber size at harvest.

In summary, potato breeding based in Scandinavia offers to the growers of the Nordic Region of Europe cultivars for prevailing farming environments and end-user needs (Tables 2, 4 and 7) rather than relying, as happens today in the market, on foreign cultivars. These cultivars bred elsewhere are not always very suitable for the challenging Nordic agroecosystems, as shown by the results of the multi-site testing herein. Such an approach on relying on foreign cultivars may be advocated for not funding potato breeding in, and for Fennoscandia by those ignoring the results shown by this research.

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Author contributions

Rodomiro Ortiz (RO), Fredrik Reslow (FR), Ulrika Carlson-Nilsson (UC-N) and José Crossa (JCr) conceptualisation and field-testing layouts; FR field data recording, JCr and Jaime Cuevas (JCu), methodology for data analysis, RO, JCr and JCu writing first manuscript draft, RO, FR, JCr, JCu and UC-N review and editing draft, RO project grants acquisition and management. All authors have read and agreed to the final version of the manuscript.

Notes on contributors

Fredrik Reslow works at the Swedish University of Agricultural Sciences (SLU) in Alnarp running the daily work of Svensk potatisförädling: from crossings through screening in the greenhouse or cooking for quality in the kitchen and field testing prior to selection of promising bred potato germplasm for further cultivar release.

Ulrika Carlson-Nilsson was the former breeder at Svensk potatisförädling at SLU, where she did her PhD education and got this academic degree, before taking her current job at the Nordic Genetic Resource Center (NordGen) in Alnarp as Senior Scientist. At NordGen, Dr. Carlson-Nilsson deals with conservation, characterisation, evaluation, and documentation of Nordic legume germplasm.

Jaime Dionisio Cuevas Domínguez is Doctor in Statistics from the College of Postgraduates of Mexico and Research Professor at the University of Quintana Roo Mexico since 1992. Prof. Cueva is member of the National System of Researchers in Mexico since 2016. His research includes genomic selection, statistical prediction, and Bayesian models. He has been first or corresponding author in 11 articles in indexed journals and has other 11 articles as co-author in prestigious journals along the above areas of interest.

José Crossa is a Fellow of the Agronomy Society of America and of the Crop Science Society of America, Member of the Mexican Academy of Science, Member of the National Research System of the National Council of Research and Technology (CONACYT) of Mexico, invited professor at Universities in Mexico and Uruguay, and Adjunct Professor at the University of Nebraska – Department of Statistics and Department of Agronomy and Horticulture, U.S.A. In 2018 Prof. Crossa was awarded as the best CGIAR scientist for his work on genetic resources conservation and utilisation. Recently, he and colleges impacted plant breeding by being one of the first researchers in showing genomic-enabled predictions models with high accuracy using pedigree and markers information applied in massive maize and wheat field data. Prof. Crossa has over 400 scientific articles published in referee journals and 40 book chapters. A new book written with another colleague in modern phenotypic and genomic selection indices methods for plant breeding was published in 2018. In 2019, the *Web of Science Group* rated Prof. Crossa among the elite group recognised for the exceptional research influence, demonstrated by the production of multiple highly-cited papers that rank in the top 1% by citations for field and year in *Web of Science*.

Rodomiro Ortiz is Faculty Professor and Chair of Genetics and Plant Breeding at the Swedish University of Agricultural Sciences. Prof. Ortiz holds a PhD in Plant Breeding & Genetics from the Univ. Wisconsin–Madison, and worked as young researcher at UNALM (Perú) and Rutgers Univ., was scientist and director of various CGIAR Consortium Centers, and held a Nordic professorship on plant genetic resources at the then Royal Veterinary and Agricultural Univ. He has written > 900 reports, of which about 50% are journal articles or edited book chapters with h-index of 70 and cited by 18749 [as per Google Scholar on 2021.10.22]. The CGIAR awarded to IITA the prestigious 1994 King Baudouin Award for the multidisciplinary research of the team working in plantain and banana improvement, in which he was programme leader. In 2012, *Plant Breeding Reviews* dedicated him its vol. 36. He was PI of SLU/ICARDA–led research development partnership project *Adapting durum wheat varieties to the Senegal Basin for food security* that won the 2017 Olam Prize for Innovation in Food Security. Ortiz was member of CGIAR Independent Science and Partnership Council (2015–2019) and of the Commission on Sustainable Agriculture Intensification (2020–2021). He is also international fellow of the Royal Swedish Academy of Agriculture and Forestry since 2019 and member of the Royal Physiographic Society (Lund) from 2021 onwards.

Data availability statement

The datasets presented in this study can be found in online repository Dataverse at https://hdl.handle.net/11529/10548617

ORCID

José Crossa http://orcid.org/0000-0001-9429-5855
Rodomiro Ortiz http://orcid.org/0000-0002-1739-7206

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