

# Svensk potatisförädling: Breeding the new table and crisp potatoes

*Potatisförädling för Sverige: Växtförädling av nya sorter av kok- och chipspotatis*

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As Jonathan Swift (1726) puts it, “*whoever makes two ears of corn, or two blades of grass to grow where only one grew before, deserves better of mankind, and does more essential service to his country than the whole race of politicians put together.*

”Gulliver’s Travels Part 2 A Voyage to Brobdingnag

The potato (*Solanum tuberosum* L.) crop is the third most important world’s food after rice and wheat in human diets (Bruins, 2018). Potatoes are eaten after baking, boiling, steaming, roasting, deep-oil frying, microwave cooking or processing. They were grown near Lake Titicaca (Perú-Bolivia) about 4,000 BCE (Ortiz, 1995). After Columbus’ voyages, some Spaniards took potato tubers to Europe where it spread between the 16th and 18th centuries, thus becoming a staple crop in this continent (Nunn and Qian, 2010). This introduction of the potato accounts for approximately ¼ of the growth in European population and urbanization between 1700 and 1900 (Nunn and Qian, 2011). Potato, indeed, brought caloric and nutritional improvements vis-à-vis other existing staples, and had an important effect on the evolution of local cuisines.

There were 2,929 registered farms in Sweden with commercial table potato production in 2014 (Eriksson et al., 2016), while its total harvest was about 538,200 t in 2019 (SCB, 2019). The average yield for table potato was slightly above 33 t ha<sup>-1</sup> in 2019, which is a relatively low tuber yield when compa-

ring it with main potato producing European countries such as Germany (47 t ha<sup>-1</sup>) and Belgium (48 t ha<sup>-1</sup>). Although, the total potato acreage accounts for ca. 1% (about 25,000 ha) of the total land agricultural area in Sweden, this crop is sprayed with the largest amount of fungicides per hectare (SCB, 2012). Furthermore, the potato market value (crisp, fast food restaurants, industry, table) in Sweden ranges between 5 and 6 billion SEK per year (Eriksson et al. 2016). Such market depends on a stable supply of high-quality potato with diverse quality traits. Late blight – caused by the oomycete *Phytophthora infestans* (Mont.) De Bary – is a serious constraint in potato cultivation because it can infect the entire plant, including stems, leaves and tubers, thus leading to global tuber yield loss of 16% that translates into US\$ 5 billion annually. Investments in potato breeding have great potential to yield a high gross return as well as avoiding risks for human and environmental health due to fungicide use.

## History facts

Sweden shows a long history of plant breeding. It dates back towards the end of the 19th century when Walfrid Weibull began a breeding company in 1870 at Landskrona (later known as W. Weibull AB), while Svalöf AB was established in 1876 with funding from the Swedish Seed Association. The first targeted and scientific potato breeding activities started at Svalöf AB in 1903. Prof. E. Åkerberg – a former director of the Swedish Seed Association – bred many crops

including potato (Schlegel, 2018). The early breeding targets were high tuber yield, early maturation, consumption quality, and host plant resistance to pathogens. The Swedish University of Agricultural Sciences (SLU) began breeding potatoes in 2006 in Skåne (with staff based in its Alnarp campus) with the aim of developing new table potato cultivars for Sweden. The Government of Sweden provides limited public funding since 2006, which does not cover the total costs of the program. Hence, additional funding has been sought and obtained from various sources are noted in acknowledgments. This article provides an overview of potato breeding at SLU (hereafter *Svensk potatisförädling*), main outputs plus past and ongoing related research both for cultivar development and population improvement.

The main goal of *Svensk potatisförädling* is to develop potato cultivars with durable host plant resistance to late blight (and resulting tuber rot), which is a disease with devastating effects on tuber yield as well-known by growers of this crop elsewhere. Besides the economic gains, potato resistant cultivars bring environmental benefits by contributing

to reduced fungicide use and allows organic potato farming. Moreover, the rising non-availability of approved pesticides and increased environmental awareness by the public call for breeding resistant potato cultivars. Furthermore, potato breeding based in Sweden offers to the growers of this country a cultivar for prevailing farming environments and needs rather than relying, as happens today in the market, on foreign cultivars. Cultivars bred elsewhere are not always very suitable the challenging Nordic sites, as some lacking knowledge on this subject recently advocated as an approach for not doing potato breeding in Sweden (Rosengren, 2019). Last but not least, the significant genotype-by-environment interaction for a medium broad-sense heritability ( $H^2 = 0.563$ ) trait such as tuber yield (kg plant<sup>-1</sup>), which was noted in *Svensk potatisförädling* cultivar trials across sites in Sweden (Table 1, Figure 1) calls for specific adaptation; i.e., breeding germplasm with available genetic resources locally for the target population of environments in this Nordic country facing various factors affecting potato productivity, e.g. short crop season, long daylength, or pathogens thriving in these latitudes.

Table 1. Analysis of variance based on means per site for tuber yield (kg plant<sup>-1</sup>) of five cultivars grown across testing locations (Helgegården, Mosslanda and Umeå) used by *Svensk potatisförädling* in 2019

Source of variation	Degrees of freedom	Sum of squares	Mean square error	FC	P FC > FT
Locations (L)	2	1.050	0.525	29.882	< 0.0001
Blocks/L	7	0.123	0.018		
Cultivars (C)	4	0.858	0.214	9.459	< 0.0001
L × C interaction	8	0.547	0.068	3.013	< 0.0001
Average pooled error	28	0.635	0.023		

Coefficient of variation (%): 18.72

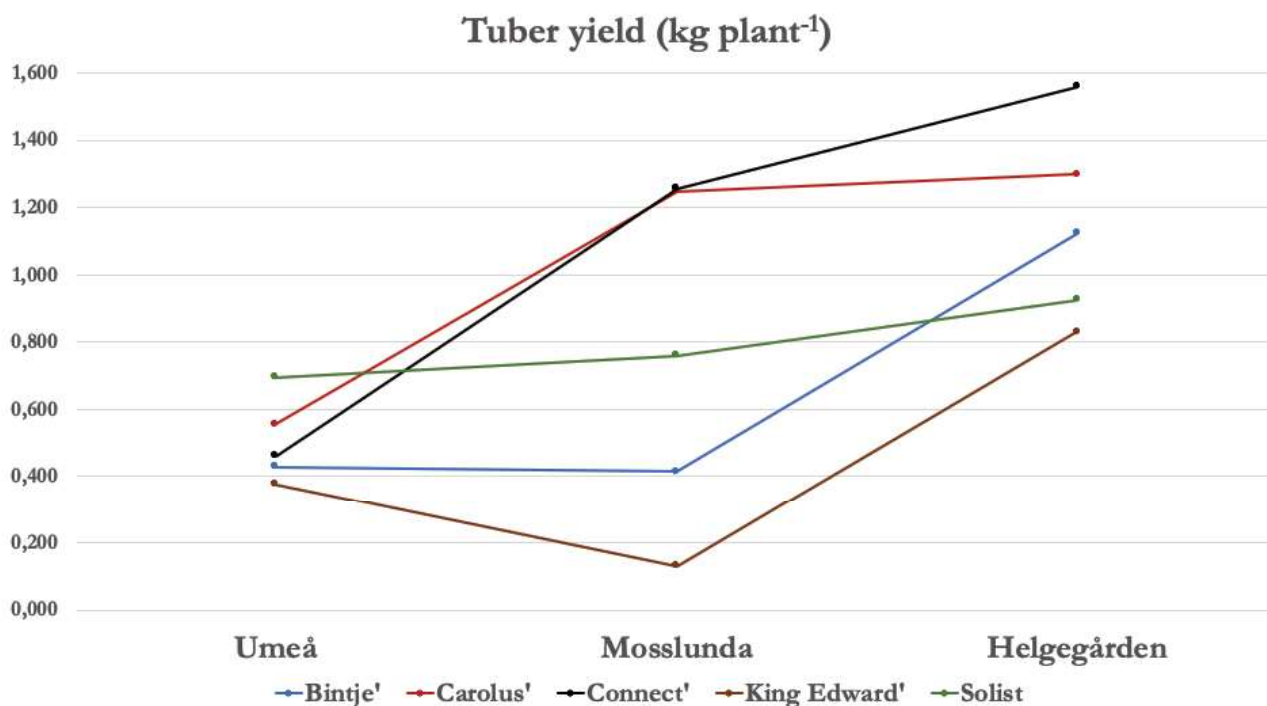


Figure 1. Average tuber yield (kg plant<sup>-1</sup>) of five cultivars grown across testing locations (Helgegården, Mosslunda and Umeå) used by Svensk potatisförädling in 2019. Average tuber yield  $\pm$  standard error of cultivar differences per site:  $0.503 \pm 0.027$  (Umeå),  $0.762 \pm 0.147$  (Mosslunda) and  $1.147 \pm 0.136$  (Helgegården), respectively

## Crossbreeding for cultivar development

The commonly cultivated *Solanum tuberosum* is a self-compatible polysomic tetraploid ( $2n = 4x = 48$ ), which shows tetrasomic inheritance and inbreeding depression after continuous self-fertilizing (Ortiz and Mihovilovich, 2020). Potato is a vegetatively propagating crop in which each tuber is identical with its mother plant, thus allowing that favorable traits are fixed in the F1 hybrid generation. The clones are highly heterozygous and tuber yield benefits from heterosis that is the most important goal in potato breeding, which has a long and successful history in Sweden.

Potato breeding includes the crossing of parents showing complementary features with the goal of producing enough genetic variation to apply thereafter phenotypic selection across various vegetative generations for clones with many desired traits and further release as new cultivars. Figure 2 illustrates the steps involved in *Svensk potatisförädling*. The parents are grown on bricks at a SLU's

greenhouse in Alnarp (available space allows planting 64 plants for the crossing block every year) to remove easily any forming tubers and facilitate producing berries with F1 hybrid seed. For a small breeding program with limited funding the size of the first tuber generation (T1) in the field remains key. Since 2013, the aim has been to produce 12,000 to 15,000 F1 hybrid seeds (resulting from crossing heterozygous parents) that the following year there will result in 10,000 unique T1 in the field, which should be regarded as the lowest threshold for having a reasonable chance of identifying and selecting enough good breeding clones, but not so large that it may be overly labor- and cost-demanding. After crossing and berry harvest, F1 seeds are planted in individual pots at a greenhouse, and one tuber (the best for size) for each plant taken at harvest. This harvest yields the T1 generation for planting in the field at Mosslunda (Skåne), where *Phytophthora infestans* seems to be widespread thus facilitating the field-screening of host-plant resistance



for this pathogen in a site with neighboring farmers producing potatoes for the markets. The potato breeding fields are regularly inspected and plants that look healthy, particularly regarding late blight are noted. At the end of the season, plants are dug up to assess their number and size of tubers plus their appearance and health, which are the selection criteria for obtaining the T2.

In 2017, there were 8,257 hybrid tuberlings resulting from 11,915 seed derived from 30 crosses involving 22 parents (cultivars and breeding clones). They were included for planting as T1 in 2017. The crossing block in 2017 (producing seed for 2018 T1) involved 12 parents (eight released cultivars available for growing in Sweden and four advanced breeding clones). Seed set was, on average,  $201 \pm 71$ ; being the cultivar ‘Lilly’ (527 seeds) the best seed-producing female while the best male was cultivar ‘Bionica’ (303). There were 6,091 hybrid T1 tuberlings resulting from 12,396 seeds derived from 42 crosses involving cultivars and breeding clones as parents in 2018, while there were 12,082 seeds germinated to obtain the 2019 T1 from 48 crosses involving cultivars and breeding clones. The most used were the breeding clone 1201002

and cultivar ‘Sarpo Mira’.

Combining ability (CA) refers to the breeding value of a genotype based on its offspring performance. In this regard since 2015, CA has been estimated in *Svensk potatistföreläring* according to the percentage of selected T1 for each cross and averaging it across to define the parents’ performance. For the last four years, the cultivars ‘Amour’, ‘Aracy’, ‘Carolus’, ‘Cicero’, ‘Lady Balfour’, ‘Maestro’, ‘Mandel’, ‘Sarpo Mira’, ‘Satina’ and ‘Toluca’, as well as breeding clones 0902188, C08II69 and SW93-1015 had the highest percentages of selected T1 offspring.

After selection in T1 and derived T2 breeding clones, the aim is having about 100 of the remaining T3 breeding clones, 5 to 10 T5 breeding clones after the 5th year of field-testing, and 1 or 2 T7 breeding clones after the 7th year of field-testing. There are trials of advanced clonal generations (T3 onwards) at two sites in Skåne (only in Hellegården and Mosslanda since 2017) and one site in Umeå every year. In each trial cultivars (newly released and those still grown by farmers, e.g. ‘Bintje’ or ‘King Edward’) are included as reference or checks. This testing approach allows identifying breeding clones whose tuber yields

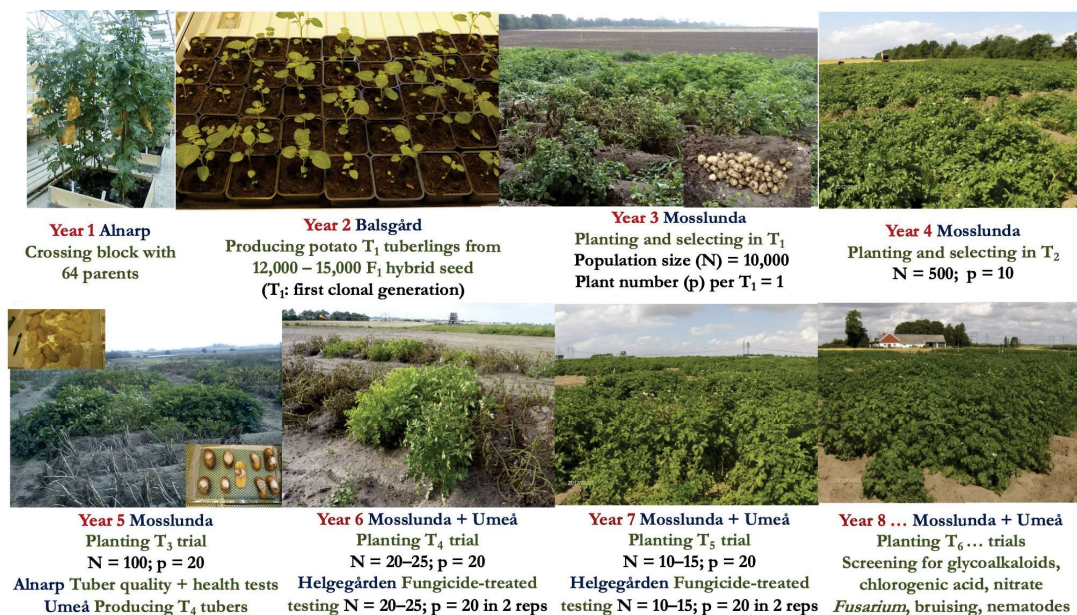


Figure 2. Breeding pipeline in Svensk potatistföreläring. Producing T<sub>i</sub> tubers for multi-site trials begins in T<sub>4</sub> at Umeå onwards thereafter. T<sub>i</sub> refers to the breeding generations after each clonal selection cycle

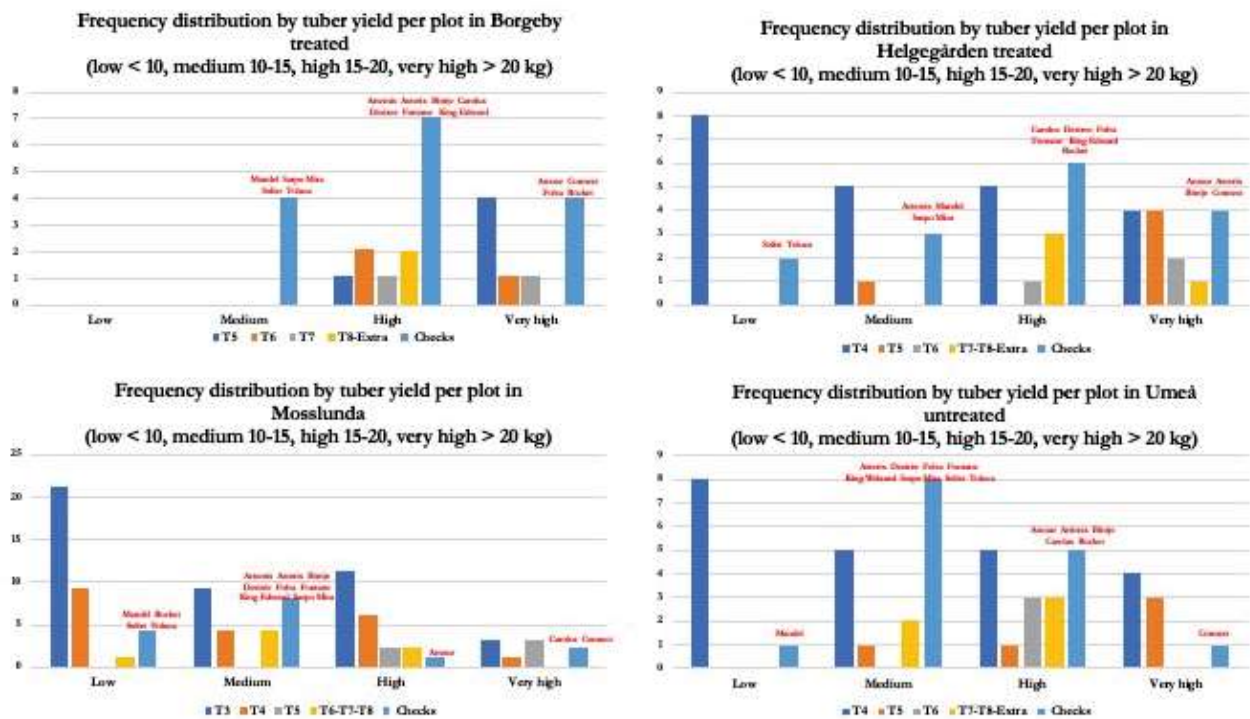


Figure 3. Frequency distribution of tuber yield per plant (kg plant<sup>-1</sup>) in Ti breeding clones after second selection cycle (i.e., T3 onwards) along with testing cultivars across sites in Skåne and Umeå during 2016 by Svensk potatisförädling. Treated (in Borgeby and Helgegården) refers to plots with fungicide sprays. Names of cultivar checks written in red font at the top of each bar showing their tuber yield per plant

are above these cultivar checks (Figure 3).

Some breeding clones had tuber yields above the cultivars checks in 2018 – when drought stress and heat waves led to a historic low production of table potato in Sweden: 449,000 t, which was not only 17% lower than the last 5-year average but also than the years of crop failure in 1867 (causing famine in the country) and 1999 (that led to a large potato import) (SCB, 2018). Details of the most promising breeding clones in 2018 grown in Helgegården and Mosslanda (Skåne) plus Umeå in 2018 are given in Table 2. The results are very encouraging and suggest that *Svensk potatisförädling* may be able to target developing climate-resilient, stable high-yielding table cultivars with desired traits for end-users in the country, particularly when drought and heat may be striking more often.

Durable host-plant resistance to *Phytophthora infestans* remains as a main challenge to achieve. *Svensk potatisförädling* strategy seeks, therefore, gene pyramiding using as sources for crossing, among others, the breeding

clone SW93-1015 and the cultivar ‘Sampo Mira’, both of which are known for their high resistance to late blight and tuber rot in potato. Their host-plant resistance belongs to distinct genetic backgrounds (Lenman et al., 2016). The crossing partner brings traits such as early maturity, good tuber finish, suitable taste and high tuber yield in their hybrid offspring.

Although the focus of *Svensk potatisförädling* has been host plant resistance to *Phytophthora infestans*, other traits are also sought when selecting breeding clones in the Ti generations. For example, economic returns for farmers and consumer benefits are important factors. The desired table potato must therefore show an appropriate specific gravity for food and have good cooking quality; i.e., it does not fall apart or become dark after cooking. Likewise, it should be free from scab and other pathogens, and show an appealing and uniform size and shape that makes it easy to peel. After each year’s field trials, these traits are assessed to select the breeding clones that will be in next year’s multisite trials.



Table 2. Tuber yield [kg plant<sup>-1</sup>, mean  $\pm$  standard error, (S.E.)] at breeding trials of Svensk potatisförädling during the drought stress and heat waves of 2018 in Skåne (Hellegården and Mosslunda) plus Umeå. (Number of tested breeding clones or cultivars in brackets)

Breeding generation	Hellegården		Mosslunda		Umeå	
	Breeding clones	Cultivars	Breeding clones	Cultivars	Breeding clones	Cultivars
T3	N/A		1.031 $\pm$ 0.075 (24)		N/A	
T4	0.915 $\pm$ 0.037 (20)	1.031 $\pm$ 0.137 (5)	1.125 $\pm$ 0.054 (26)		0.635 $\pm$ 0.021 (31)	0.811 $\pm$ 0.046 (4)
T5	1.185 $\pm$ 0.061 (10)	0.990 $\pm$ 0.106 (5)	1.381 $\pm$ 0.106 (10)	1.136 $\pm$ 0.096 (5)	0.777 $\pm$ 0.029 (10)	0.808 $\pm$ 0.083 (4)
T6	1.248 $\pm$ 0.138 (4)	1.025 $\pm$ 0.127 (5)	1.162 $\pm$ 0.196 (4)		0.704 $\pm$ 0.083 (4)	0.642 $\pm$ 0.050 (4)
T7 >	1.269 $\pm$ 0.046 (3)		1.578 $\pm$ 0.045 (3)		0.700 $\pm$ 0.119 (3)	
# promising breeding clones > best cultivars	T4: 1; T5: 2; T6: 2, T7: 2		T3: 3; T4: 3; T5: 4; T6: 2, T7: 2		T4: 4; T5: 2; T6: 2, T7: 1	

After several years of testing and selection of suitable clones for crisp production by Svensk potatisförädling (Figure 4), two promising breeding clones (97 and 188) were chosen for potential cultivar registration due to the interest shown for growing them in Norrland (Carlson-Nilsson and Reslow, 2017). Their taste and tuber appearance were also evaluated in Umeå. Axel Ljungstrand (Folestad, Ljungbyhed) and his son Henrik did the crossing and the early breeding of these clones, and in 2010 donated them to SLU through a gift letter. They are also suitable as summer table potato (“sommartyp” or second early).

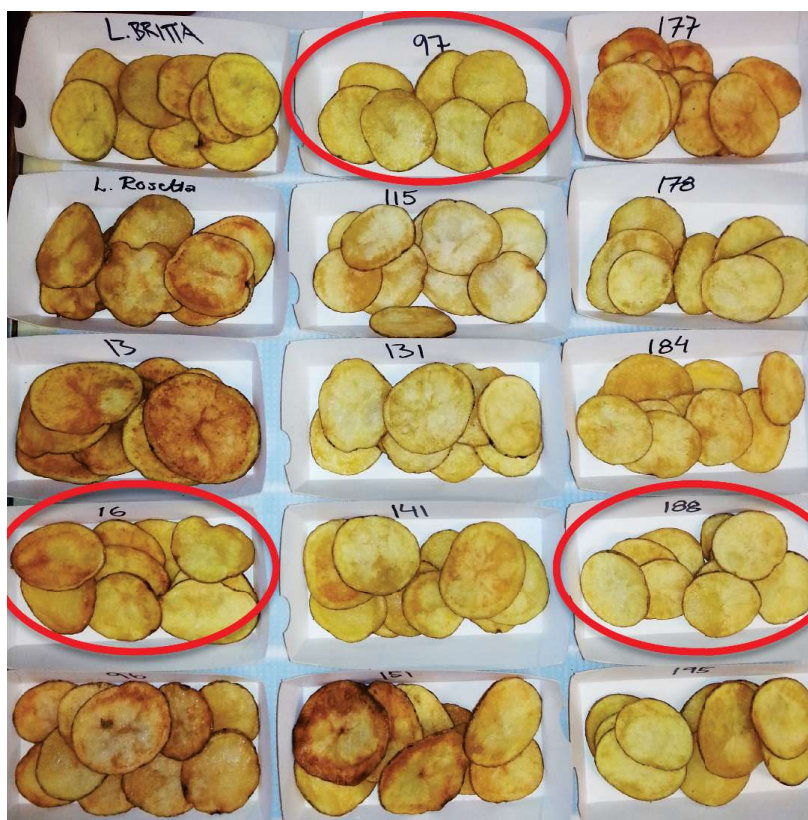


Figure 4. Promising cultivar candidates (97 and 188), among others, selected for their suitability in crisp manufacturing. They may be also used as summer potatoes. Tubers came from harvest at Borgeby, Kävlinge

## Breeding related research and population improvement

Early breeding research at *Svensk potatisförädling* included assessing host plant resistance to pathogens such as late blight and Potato virus Y (PVY) in wild relatives of potato and their derived offspring (Zoteyeva et al. 2014) or in Nordic potato-bred germplasm (Zoteyeva et al. 2017). Some wild tuber-bearing *Solanum* species bear alleles that provide host plant resistance to both *Phytophthora infestans* and PVY. A couple of cultivars ('Hårek' and 'Sarpo Mira') and two breeding clones (SW04-2662 and SW04-2085) show resistance to late blight but did not get virus infection. Likewise, previous collaborative research with SLU's Department of Plant Protection Biology included understanding host plant resistance to late blight and early blight. For example, the hyper-sensitive response to *Phytophthora infestans* in breeding clone SW93-1015 was characterized as a constitutive expressor of pathogenesis-related genes. This clone was among the first plants showing a protein-based defense being expressed constitutively, but without any known metabolic costs or spontaneous cell death lesions (Ali et al. 2012). Furthermore, it seems that SW93-1015 may bear a functional homolog of the R2 resistance gene as shown by Lenman et al. (2016), who also developed a new DNA marker for this resistance gene found in this breeding clone. Phenotyping research on host plant resistance to early blight –caused by *Alternaria solani* (Ellis & G. Martin) L.R. Jones & Grout– revealed that detached-leaf assays for screening potato germplasm to this pathogen does not seem to be accurate (Odilbekov et al., 2014). This finding led to developing new screening protocols that pave the way for mapping quantitative trait loci related to host plant resistance to early blight in potato (F. Odilbekov et al., SLU, unpublished). Ongoing joint PhD research (across both Departments) includes a transcriptomics study to ensure that these QTL are specific for host

plant resistance to early blight.

Modern potato breeding methods following a genomic-led approach provide means for shortening breeding cycles and increasing breeding efficiency across selection cycles. For example,

genomic estimated breeding values (GEBVs) for selection are used in a predictive model that has been trained with a number of individuals (i.e., the training population) that reflects the diversity of the breeding program being evaluated at the phenotypic and genotypic level (Abera Desta and Ortiz, 2014). As the number of dense DNA markers increases in the model, the prediction accuracies of GEBVs are likely to increase, whereas the single DNA marker effect is expected to decrease in absolute magnitude. Once the predictive model has proven successful, the plant breeder is able to estimate the GEBVs for the next breeding cycle through the incorporation of only genomic data. These GEBVs give an ideal criterion for selecting the best performing clones to be the parents of such a breeding cycle in a vegetatively propagated crop such as potato (Ventorim Ferrao et al. 2017). The first cycle of selection (T1) is the most time consuming, thus introducing selection based on GEBVs at this step would have the largest impact for *Svensk potatisförädling*. A PhD student does her research recording genotyping and phenotyping data for two potato populations which are both part of *Svensk potatisförädling* (Selga et al., 2017a,b). One consists of elite breeding material (T3 onwards; N = 208) grown in 3 locations (2 in Skåne and 1 in Umeå) and having data from previous years. The genotypes in the second population have not undergone selection and can be viewed as a T1. This population was grown in two replicates in one environment (Mosslunda, Skåne; N = 465) in 2018 and in same environment without replicates in 2016. The genotype data consist of a 22K single nucleotide polymorphism (SNP) array (GGP Potato), and the phenotypic data

consists of 10 phenotypic traits including tuber yield and quality. Combining these data sets along with co-ancestry and population structure allows estimating GEBVs and assess their accuracy for selection in potato breeding. A cross-validation approach, in which data are divided into reference and validation sets with the former used for training the model, indicates that high accuracy may be achieved for traits with a high heritability such as specific gravity or in an environment that facilitates trait scoring in the field such as host plant resistance to scab that is caused by a few *Streptomyces* species (Table 3).

The PhD research also includes developing a pipeline to reduce the number of SNPs to lower the cost of genotyping large populations (Selga et al., 2018). A limited number of SNPs was validated by their use on identifying useful markers for indirect assisted selection, and for applying genomic selection (GS) in potato. First, the number of individuals to be genotyped was reduced with a modern, high-throughput method according to the multi-trait variation as defined by principal component analysis of phenotypic characteristics previously recorded in field trials. Next, the lowering of number of SNPs was also pursued by pruning for linkage disequilibrium. By adjusting the square of the correlation coefficient between two adjacent loci ( $r^2$ ) reduced subsets of SNPs were obtained. Subsequently the reliability of the SNP subsets was assessed in a genome-wide association study (GWAS) for marker identification and GEBV. The results indicate that both GWAS and GEBV can be done in potato breeding without losing information after reducing the numbers of SNPs. The pipeline allows for

creating custom SNP subsets to cover all variation found in any particular breeding population. Low-throughput genotyping will reduce the genotyping cost associated with large populations, thereby making genomic breeding methods applicable to large potato breeding populations by reducing genotyping costs.

Although genomic prediction of breeding values appears to be feasible in potato, these predictions across breeding populations still remain unreliable (Ortiz, 2020 and references therein), perhaps due to the high allelic diversity in this crop that calls for enlarging the training sets. Thus, the overall goal of a new 3-year project (involving a 2-year post-doc from 2021) is to develop a novel and high accuracy genomic prediction model to estimate breeding values for tuber yield and its components in potato by including high-throughput phenotyping data across two sites (one each in Skåne and Umeå) in model building (by collaborating with other staff at SLU's Department of Plant Breeding), as well as researching on the effects of training sets (based on available cultivars and *Svensk potatisförädling* advanced breeding clones) plus their sizes, and inbreeding. This and the PhD project will also allow answering questions such as, *inter alia*, What to be done to make accurate and cheap modern potato crossbreeding? Which training set to use (a panel of cultivars and breeding clones, or a segregating first generation of potato derived seedlings or T1 generation) for estimating best linear unbiased predictors in potato breeding? How big show the training population size and how many DNA markers will suffice for predicting breeding values?

Table 3. Accuracy of genomic-estimated breeding values after cross-validation for various traits in *Svensk potatisförädling* selected population (T2 and above) grown in replicated plots at Mosshunda (Skåne, Sweden; 2018)

Trait	Accuracy	Trait	Accuracy
Total tuber yield (kg plant <sup>-1</sup> )	0.15	Specific gravity ( $\approx$ dry matter content)	0.62
Tuber number	0.20	Host plant resistance to scab (based on field screening)	0.45
Tuber size uniformity	0.21		



## Outlook

*“Ignorance is not, not knowing something. It is knowing, what isn’t so.”*

Mark Twain

As noticed recently in a special feature of the weekly journal *Science*, the “breeding revolution in the making” elsewhere will allow unleashing the potential of potato (Stokstad, 2019). It has been also indicated that genomic prediction of breeding values for selection is a “far-reaching innovation” in potato research (Andrivon, 2017). Indeed, newly bred high-yielding potato cultivars with increased input-use efficiency and host plant resistance to pathogens and pests will allow an integrated approach of reduced fertilizer and fungicide usage.

In the long-term, the main output of *Svensk potatisförädling*; i.e., newly bred cultivars, will allow potato farming with resilience to the changing climate while following sustainable agriculture intensification practices in Sweden. The limited program funding, in spite of short-term project grants, remains, however, as a main shortcoming for realizing this potential. Although the Government instructed recently SLU to implement, measures within the framework of the food strategy to achieve the overall objective for increased production that is sustainable and competitive, and increased the funding (50 million SEK for 2020 budget) to SLU Grogrund – Centrum för växtförädling av livsmedelsgrödor – (Regeringskansliet, 2019), its manager indicated that “the problem is that *potato breeding is almost non-existent in Sweden. Potato breeding mainly takes place in The Netherlands by a company in which Lantmännen is a partner. We are interested in running operations on potato breeding for northern Sweden but today there is no Swedish company to cooperate with*” (Rosengren, 2019). Such a discouraging view appears to ignore the recent achievements of *Svensk potatisförädling*, as noted in this article,

and that “*Governments must provide incentives for businesses to fix the global food system*” – as stated by World Food Prize Laureate Lawrence Haddad (2018) in the weekly journal *Nature*.

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## Sammanfattning

*Svensk potatisförädling* började 1903 vid ett halvstatligt institut, och bedrivs sedan 2006 i form av ett förädlingsprogram vid Sveriges lantbruksuniversitet (SLU). Arbetet utförs av en heltids (1 FTE) praktiskt arbetande förädlare och en professor (0,1 FTE). En doktorand gör sin forskning om genomledd förädling sedan 2016, och en ny postdoc kommer under en 2-årsperiod att arbeta med genomisk prediktion i kombination med högkapacitetsfenotypning från 2021. Inom

förädlingsprogrammet produceras runt 35 korsningsfamiljer (unika korsningskombinationer) årligen för att erhålla runt 10 000 fröplantor i den första urvalscykeln. Denna är baserad på knölegenskaper (skalfinish och färg plus knölstorlek och enhetlighet i form). Knölkvalitetsegenskaper och motståndskraft mot *Phytophthora infestans* (orsakar bladmögel och brunröta) är viktigare i senare urvalscykler. Knölkvalitetsegenskaper inkluderar matlagnings- och frityrkvalitet, köttfärg och specifik vikt. För att säkerställa virusfritt utsäde odlas alla genotyper efter den andra urvalscykeln i Umeå, där växtsäsongen är kort och förekomsten av virusspredande insekter är låg.



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