



New Potato-Life Cycle Loci Identified by Using an *StCDF1*-Fixed Population

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Abstract

Photoperiodic insensitivity has been the selected trait that allowed cultivation of potato outside its centre of origin, to the northern latitudes of Europe and North America. More than a decade ago, *Solanum tuberosum* *CYCLING DOF FACTOR 1* (*StCDF1*) was identified as the maturity locus, regulating both above and below-ground maturity traits, also referred to as life cycle length and tuberization onset. Following its identification, several genomic studies contributed to the inventorization of the *StCDF1* alleles carried by potato cultivars and their wild relatives. At the same time, the role of *StCDF1* beyond plant development has started to be elucidated. While the importance of this locus has been widely shown, the presence of this strong QTL hotspot has hampered the identification of additional QTL and genes. Here, we report the use of a *StCDF1*-fixed biparental population to map minor QTL for developmental and generative traits. Remarkably, we identified another region on Chr5 controlling several of the analyzed traits, i.e., tuberization onset, anthesis and senescence traits, and harbouring promising candidate genes for further characterization. Furthermore, the study dissected the contribution of self-compatibility to berry and seed set in a field setting prone to open pollination. The use of an *StCDF1*-fixed population resulted in a straightforward and cost-effective approach to identify additionally agronomically relevant loci that could be used in future potato breeding.

Keywords Generative sexual reproduction · Maturity · Senescence · *Solanum tuberosum* · *StCDF1* · Tuberization

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Introduction

Potato (*Solanum tuberosum* L.) is the third most important food crop for human consumption. It is produced for the fresh ware market and for popular processed products such as chips and French fries. In addition, high-value products can be extracted, such as starch and high-quality protein, the latter with a major role as a plant-based alternative to animal protein (Semeijn and Buwalda 2018; Natarajan et al. 2019; Awogbemi et al. 2022). Lastly, potato is used beyond human nutrition, among others as animal feed, glue and fuel-grade ethanol. The cultivation of potato is widespread in the world, with very variable yields of 40–50 tons/ha in Central Europe and North America and much lower yields, often less than 10 tons/ha, in other geographic regions, mainly in low-income countries (Gildemacher and ter Steeg 2023). In all cases, yield is far from reaching its full potential. Many factors contribute to the potato yield gap, and changes in the climate due to global warming may further increase this gap in the crop yield by altering plant performance, with current cultivars being sensitive to most environmental stresses.

Breeding plays an important role in developing higher-yielding resilient varieties. However, the tetraploid and highly heterozygous nature of cultivated varieties has historically hampered the traditional potato breeding process, compared to other important crops. Recently, diploid hybrid breeding has been proposed as a promising alternative (de Vries et al. 2023). Hybrid breeding is based on the generation of inbred parental lines carrying favourable genetics that then are crossed to produce uniform heterotic F1 hybrid offspring, carrying the favourable alleles of both parents. Furthermore, technological advances in genome sequencing of complex genomes are providing a wealth of sequence data, fostering the development of markers for genotyping and the identification of genes responsible for the traits of interest (Hamilton et al. 2011; Vos et al. 2015; Zhang et al. 2021). As a result, new traits can easily be introduced by a series of marker-assisted backcrossing cycles while maintaining the genetic composition of the parent lines (Su et al. 2020). This detailed genetic information combined with the emerging hybrid breeding technology promises to accelerate the modest genetic gains achieved over the past decades (Lindhout et al. 2011; Jansky et al. 2016; Zhang et al. 2019).

Quantitative trait locus (QTL) mapping is an established approach for identifying genetic loci associated with specific traits (reviewed in McCough and Doerge 1995; Collard et al. 2005; Xu et al. 2017). Simple markers like single nucleotide polymorphisms (SNPs) well distributed over the complete potato genome are used as a comprehensive set of genome-wide markers suitable for QTL mapping (Os et al. 2006). Recently developed genotyping platforms greatly facilitate the identification of molecular markers linked to specific traits that can then be used as diagnostic markers (Hamilton et al. 2011; Vos et al. 2015). So far, diagnostic markers for monogenic traits with clear phenotypes are relatively easy to identify. Markers for disease resistance, pigmentation, tuber shape and many other traits are readily available in potato (e.g., Gebhardt et al. 2007; Moloney et al. 2010; Clot et al. 2020). However, there is an increasing demand for diagnostic markers for diverse developmental traits. Typically, such traits are polygenic, meaning

that these traits are the result of multiple interacting major and minor loci, and that such loci may remain obscure when their effects are confounded by major effect loci. Furthermore, agronomically important traits are influenced by phase transitions, life cycle length and environmental conditions. Although statistical approaches such as MQM mapping may help to identify minor loci, preferably major loci should be fixed in the population used to identify loci with a minor effect.

In potato, a robust major-effect QTL on the short arm of Chromosome 5 corresponds to above-ground maturity (leaf senescence). The same locus also appears to influence other important potato agronomic traits, such as flowering, plant height, tuber yield, tuber number and disease resistance (Visker et al. 2005; Anithakumari et al. 2012; Hurtado-Lopez et al. 2015; Rak et al. 2017; Tai et al. 2018; Clot et al. 2023). This major-effect QTL co-locates with *CYCLING DOF FACTOR 1* (*StCDF1*) (Kloosterman et al. 2013), which encodes a transcription factor that integrates circadian and light signalling, mediating photoperiodic responses in plants. Different alleles of *StCDF1* have been identified, and their roles have been partially elucidated, demonstrating not only an involvement in above-ground maturity but also in tuberization onset (below-ground maturity), a trait that is generally difficult to assess in the field (Kloosterman et al. 2013; Shi et al. 2024). Under long-day conditions, *StCDF1.1*, the wild type allele, is associated with late tuberization and late senescence, whereas the truncated proteins encoded by the *StCDF1.2* and *StCDF1.3* alleles promote early tuberization and shorter life cycle length, irrespective of day length (Kloosterman et al. 2013). Although the *StCDF1* locus has a profound impact on multiple aspects of potato plant development via regulating diverse pathways that are tightly linked to each other, not all phenotypic variation can be attributed to this locus. Clot et al. (2023) mapped tuber yield of potato plants grown in pots to a major QTL coinciding with *StCDF1*. They compensated for the very strong effect of the *StCDF1* locus by subdividing the diploid C × E population into three groups based on their *CDF1* genotypes and performing QTL analysis on each maturity subgroup. In this way, five novel yield QTL were detected in greenhouse-grown plants, highlighting the necessity of eliminating *StCDF1* effects when studying genetic components of agronomic traits in potato (Clot et al. 2023).

Previously, we mapped the *S-locus inhibitor* (*Sli*) in population 18SC11 in a greenhouse experiment (Eggers et al. 2021). Aside from a clear segregation for self-compatibility, we noticed additional segregation for several other traits. Notably, we observed segregation for tuber number and weight, plant vigour and flowering abundance and duration (unpublished data). Moreover, the 18SC11 population is fixed for the *StCDF1* locus, offering the opportunity to identify novel minor QTL for developmental traits. To gain more insight into these greenhouse observations and correlate them to performance in the field, the 18SC11 population was assessed in more detail in field trials under conventional potato growing conditions. Here, we report our findings on above- and below-ground development, the latter being assessed directly by performing intermediate plant harvest. Additionally, generative reproduction in the open field was compared to controlled greenhouse experiments. These experiments confirmed some previously identified QTL but also revealed new loci responsible for phenotypic variation that will be important for potato breeding

and for unraveling the biology underlying these traits (Kloosterman et al. 2013; Hurtado-Lopez et al. 2015; Eggers et al. 2021; Clot et al. 2023).

Materials and Methods

Plant Materials

The 18SC11 population is an F1 population derived from the cross between the self-compatible mother 17SC25-8 and the self-incompatible father 17SC11-27. This population segregates for the *Sli* gene and was used to confirm the map position of *Sli* on Chr12 in a previous study (Eggers et al. 2021). The 18SC11 population, consisting of 161 individuals, was grown from true potato seeds (TPS) in a greenhouse in 2018. All individuals that produced more than four tubers in the greenhouse were used in the 2019 field trial ($n=159$). Additionally, remaining tubers from all individuals that produced more than nine tubers in the greenhouse ($n=151$) were used for seed tuber production to enable the field experiment of 2020. From the 2019 seed tuber production, 97 genotypes were selected that produced enough tubers to be used in the 2020 field trial.

Field Trials

The phenotype data for genetic mapping are based on two field trials in Heelsum (51.990 N, 5.770 E) and Wageningen (51.990 N, 5.660E) in 2019 and 2020, respectively. Both locations are characterized by light sandy soil. The weather data from the 2 years were collected from the Veenkampen weather station (51.981 N, 5.620 E) and plotted in Fig. S1. During the growing season, common agronomical practices of irrigation, fertilization and plant protection were applied.

2019 Field Trial

True seeds from population 18SC11 were sown in the greenhouse in the first week of July 2018. After 4 weeks, seedlings were transplanted to 4-L pots, and the plants were grown until harvest in the first week of December 2018. Tuber number and weight at harvest were recorded. The tubers were stored at 4 °C until the end of March 2019. After acclimatization to greenhouse temperature, sprouting was further induced by submerging the tubers in 90 mg/l gibberellic acid for 1 h, followed by immediate planting in trays in the glasshouse on 17 April 2019. After 3 weeks, emerging plants were pruned to one main stem and transplanted in the soil on 16 May 2019 in Heelsum (NL). Planting distance was maintained at 75 cm between ridges and 50 cm between plants on a ridge. The experiment was conducted in a randomized incomplete block design with four replications per genotype. The field was divided into four blocks, and each block contained one plot with one plant per genotype. Each block was again subdivided into four subblocks, one containing the smallest plants to avoid shading by neighbouring plants. Blocks were separated by

border plants. The experiment was terminated, and tubers per plot were harvested on 15 October 2019.

2020 Field Trial

First generation greenhouse grown seed tubers were planted in a seed tuber production field in the north of the Netherlands from the end of April and grown until haulm killing in the beginning of September 2019. The tubers were harvested in the last week of September and stored at 4 °C until April 2020. Seed tubers were planted directly on 29 April 2020 in Wageningen (NL). The experiment was conducted in a randomized incomplete block design with eight replications (blocks) and four clones per plot. In each block, genotypes of the mapping population and control varieties were randomized (132 plots/block). Due to the limited seed tuber availability, 86 genotypes were planted in all 8 blocks, whereas 11 genotypes were present in only 4 blocks. Planting distance was maintained at 75 cm between ridges and 25 cm between plants on a ridge. Additionally, three commercial varieties, Markies, Innovator, and Premiere, were included as controls. Each of the control varieties was present with 8 plots/block. The purple variety Bergerac was used to border each plot and block. The experiment was terminated and tubers were harvested on 30 September and 1 October 2020.

Amplification and Sequencing of the *StCDF1* Alleles

Genomic DNA was extracted from the parental genotypes of the 18SC11 population (17SC11-27 and 17SC25-8). The primer pair 5'-AAGGAAAATCAAGAATTGAGAAG-3' and 5'-CAATGATTGGTACTAGGCAAC-3' designed in the UTRs was used to amplify the genomic region covering the *StCDF1* gene. PCR amplicons were cloned in the plasmid ZERO Blunt (Invitrogen) and sequenced using Sanger sequencing.

DNA Extraction and SNP Genotyping

Leaf disks were sampled from all 159 genotypes planted in the 2019 field trial. Based on the seed tuber production, samples from genotypes that had produced 10 or more seed tubers were selected ($n = 117$) for DNA extraction. Aardevo B.V. performed DNA extraction of the 117 genotypes and of the two parental lines using the 96-well Macherey-Nagel NucleoSpin kits, following the manufacturer's instruction. Extracted DNA was eluted in 10 mM TRIS/HCl and 0.1 mM EDTA. A custom XT Infinium BeadChip containing a selection of 6025 SolCap (Hamilton et al. 2011) and Potvar (Uitdewilligen et al. 2013) SNPs was used for genotyping. SNP markers were renamed according to their position on the DM4.04 reference genome (Hardigan et al. 2016). Markers that are located in unmapped contigs in DM4.04 kept their Potvar and SolCap names.

Trait Phenotyping

Flowering, Berry and Seed Set Evaluation

In the 2020 field trial, the presence of flower buds and open flowers was scored every week during the growing season. For each individual plant, flowering was scored as growing degree days after planting using temperature data from the weather station next to the field with the following formula:

$$GDD = \left[\frac{T_{max} + T_{min}}{2} \right] - T_b$$

where T_{max} is the maximum temperature measured per day, T_{min} is the minimum temperature per day and T_b is the base temperature under which the growth of the crop stops. In this experiment, T_b was set to two degrees. Overall, the flowering and berry set were scored ten times over the field season at 902, 1088, 1211, 1331, 1430, 1519, 1609, 1737, 1862 and 1984 GDD.

Berries from two blocks were harvested from all plants in each plot on 11 August 2020 at 1984.1 GDD, and the total number and fresh weight were measured. Seeds from the 10 largest berries of each plot were extracted and then weighed and counted.

Tuberization Onset Evaluation

In the 2019 field trial, two blocks were harvested at intermediate time points during the growing season. Plants of the first block were harvested 32 days after transplanting to the field, and stolons were assessed for the presence/absence of swelling stolon tips. A genotype was considered non-tuberizing when all stolons still showed the typical apical hook (Kloosterman et al. 2005). A genotype was considered to be tuberizing when at least one stolon showed swelling of the subapical region. Plants of the second block were harvested 63 days after transplanting to the field. Since 93% of the genotypes had undergone the transition to tuberization, early total tuber number and early total tuber weight were measured as indicators of tuberization onset time.

In the 2020 field trial, two blocks were harvested at the same time 54 days after planting of the tubers into the field, and stolons were assessed for presence/absence of swelling stolon tips. Again, since ca. 87% of the genotypes had undergone the transition to tuberization, early total tuber number and early total tuber weight were measured as indicators of tuberization onset time.

Senescence Evaluation

In 2019, the observation period of senescence started from 126 days and ended 173 days after transplanting. During the observation period, the evaluation was

performed every 6–10 days. Senescence progress evaluation was done by using the scale described by Hurtado et al. (2012). Some changes were made to adapt the scale to the field:

- Score 6: Plants show signs of senescence (from the lower part, within a small range), and some of them still have a few flowers.
- Score 7: Plants with visible signs of senescence, around 30–50% of the tissues are brown. The stems remain firm and upright. The bottom leaves are brown or yellow, while the upper leaves are green.
- Score 8: > 50% brown tissues. Some stems become soft and lay on the ground. Some upper leaves stay green.
- Score 9: Plants are dying, most stems are dry and lying on the ground. Leaves have fallen and turned brown already.
- Score 10: Plants are dead. All stems are dry, grey, and lying on the ground.

Based on the data from 2019 and plants' performance in the field, in 2020, we evaluated senescence at two time points: 106 and 133 days after planting the tubers in the field. The same scale was used in the evaluation as described above.

In the 2020 field trial, two additional traits related to senescence were evaluated on 11 September 2020: presence of anthocyanin and regrowth. All plants in the field were phenotyped based on the visible production of anthocyanin and using a binary score (0 = absence of anthocyanin, 1 = presence of anthocyanin). Above ground regrowth, or secondary growth, was assessed based on the following scale: 0, no secondary growth on foliage; 1, plants show visible new leaves or newly grown shoot from ground; 2, presence of early-stage regrowth, the leaves budding on developing stems, fewer than 20% of the total leaf canopy; 3, approximately 30% of the plant canopy resulted from new leaf growth; 4, 30–50% of the foliage consisted of newly developed leaves; 5, about half of the leaves were from regrowth; 6, 50–70% new foliage, and some plants began forming buds or flowers; finally, the highest score of 7 was assigned when more than 70% of the leaves were newly formed, with regrowth stems remaining vigorous and green, and in some cases, open flowers were observed.

Tuber Traits Evaluation

In 2019 and 2020, tubers were harvested 182 and 149 days after (trans)planting, respectively. Two weeks before harvest, haulm-killing reagent was applied to the plants. In each plot, all the tubers were collected in a net bag and dried under ambient conditions. The tuber number and yield were counted and weighed.

Statistical Analysis

The spatial variation within and between blocks was tested using SpATS packages in R (Rodríguez-Álvarez et al. 2018). Genotype was set as a fixed effect, and Best Linear Unbiased Estimates (BLUES) for each trait were generated. This was done

for all measured traits in both 2019 and 2020 except for tuberization onset in 2019 for which we had only one block per early harvest moment. Broad sense heritability within years was calculated by the *getHeritability* function in the SpATS package. Pearson's correlation coefficients were calculated using BLUEs.

A generalized linear mixed model, allowing a gamma distribution, was used to study berry set and seed set in self-incompatible (SI) and self-compatible (SC) clones. The following model was applied:

$$\text{logit}(y_{ij}) = \eta_{ij} = \mu + \alpha_i + \beta_j + \epsilon$$

where y_{ij} is the observed trait value of the i^{th} self-compatibility type in j^{th} block, η_{ij} is the logit linear predictor of y_{ij} , μ is the population mean, α_i is the fixed effect of compatibility type, β_j is the random effect of j^{th} block and ϵ is the residual. The model was fitted in lme4/r package (Bates et al. 2015).

Genotyping, Genetic Map Creation and QTL Analysis

The population and their parents were genotyped using XT Infinium BeadChip containing 6025 potato SNPs. SNPs were renamed according to their position on DM4.04, and the genotype data were recoded according to Joinmap 4.1 segregation types and loaded into a cross-pollinated (cp) population type (Van Ooijen 2006). SNPs were assigned to linkage groups using the independence LOD parameter, and groupings with an independence LOD score of at least 4 were selected for further analysis. SNPs for which the assigned linkage group disagreed with its chromosome position on the DM4.04 genome were excluded from the analysis. BLUEs extracted from SpATS were used as the trait values. QTL analysis was performed using interval mapping with default settings in MapQTL 6 (Van Ooijen 2009). A 1000× permutation test was performed for each trait to determine the LOD threshold ($P < 0.05$).

Results

The 18SC11 Population Carries Two *StCDF1.1* Alleles

The 18SC11 population was previously developed to map the *Sli* gene conferring self-compatibility in potato (Eggers et al. 2021). From previous genomic studies, there was compelling evidence that only alleles belonging to the *StCDF1.1* class are present in the parents of this population. To confirm the exclusive presence of *StCDF1.1* alleles and assess eventual minor variation, we PCR-amplified, cloned and sequenced a region of approximately 3000 bp covering the whole genomic region between the 5' and 3' UTR of the *StCDF1* gene. Focusing on the coding region, the sequencing results showed that parental line 17SC11-27 carries two forms of the *StCDF1.1* allele that differ in only one nucleotide; this mutation is synonymous and hence does not result in a different amino acid (Fig. S2). Parental line 17SC25-8 carries two alleles encoding two forms of the StCDF1.1 protein. One is identical to one allele of 17SC11-27, while the other differs in three amino acids. Two of these

amino acids are outside functional domains of *StCDF1*. The third is located within the GIGANTEA binding domain; however, being a conservative substitution, it is not likely to affect any biochemical properties. We conclude that the 18SC11 population is functionally fixed at the *StCDF1* locus, making it a potentially very valuable population for the identification of new loci responsible for developmental traits.

Genetic Map Construction

From the 6025 SNP markers present on the XT Infinium BeadChip, 2359 segregate in population 18SC11, of which 896 are heterozygous in the maternal parent (Imx11), 511 are heterozygous in both parents (hkxhk) and 952 are heterozygous in the paternal parent (nnxnp). After the first round of mapping using the maximum likelihood mapping algorithm with default settings, we manually inspected the physical and genetic positions of each SNP marker. Next, we excluded SNP markers for which the genetic position was not syntenic with DM4.04 and proceeded with a second round of mapping. The second mapping round resulted in a genetic map of 1366 markers divided over 12 linkage groups (Supplementary Information).

QTL Mapping for Flowering, Berry Set, and Seed Set

We assessed the transition to open flowers in 2020, as described in the “Materials and Methods” section. QTL analysis for transition to open flowers (GGD4_2020 and DIFF_4-1_2020) revealed a significant QTL on Chr05 and a moderate effect size QTL on Chr11 (Fig. 1, S3, Table S1). To gain more insight into the generative

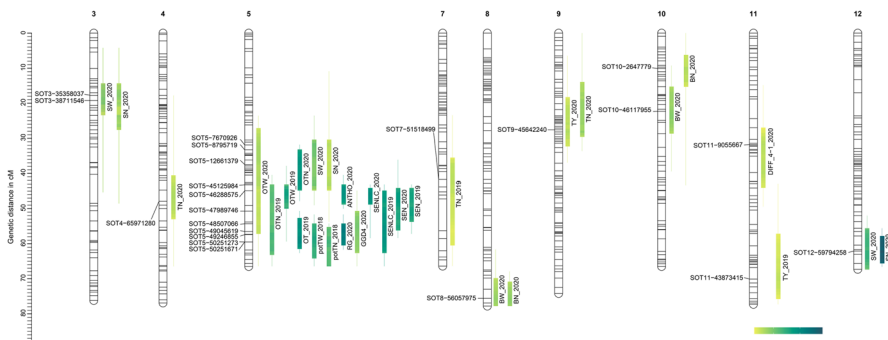


Fig. 1 Overview of QTL identified in this study. SEN_2019, Senescence 2019; SEN_2020, Senescence 2020; SENLC_2019, Senescence life cycle length 2019; SENLC_2020, Senescence life cycle length 2020; RG_2020, Senescence regrowth 2020; ANTHO_2020, Senescence anthocyanin 2020; GGD4_2020, Transition to anthesis 2020; DIFF_4-1, transition to anthesis from GGD1 to GGD4 2020; BN_2020, Total number of berries 2020; BW_2020, Total weight of berries 2020; SN_2020, Number of seeds 2020; SW_2020, Total seed weight 2020; potTN_2018, number of tubers in pots 2018; potTW_2018, total tuber weight in pots 2018; OT_2019, Tuberization onset 2019; OTW_2019, Early tuber weight 2019; OTN_2019, Early tuber number 2019; OTW_2020, Early tuber weight 2020; OTN_2020, Early tuber number 2020; TN_2019, Tuber number 2019; TN_2020, Tuber number 2020; TY_2019, Tuber yield 2019; TY_2020, Tuber yield 2020

reproduction in the population, we harvested all berries per plot at 105 days after planting (DAP). Based on knowledge of self-compatibility of the genotypes (Eggers et al. 2021), we compared the number of berries on self-compatible (SC) and self-incompatible (SI) genotypes and observed that SC genotypes set significantly more berries than SI genotypes (Fig. 2a, $p < 0.001$). However, QTL analysis on the total number of berries (BN_2020) revealed no QTL on the *Sli* locus; instead, we found a QTL on Chr08 (LOD=4.46) and on Chr10 (LOD=3.44) explaining 19.4% and 15.4% of phenotypic variation, respectively. The QTL analysis on the total fresh weight of the berries (BW_2020) showed a similar pattern albeit with slightly different LOD scores and percentages of explained phenotypic variance (Fig. 1 and Table S1). Next, we compared the number of seeds per berry in SC and SI genotypes and found that SC genotypes have significantly more seeds per berry than SI genotypes (Fig. 2b, $p < 0.001$). Interestingly, QTL analysis on the number of seeds (SN_2020) from the ten largest berries of each plot resulted in the identification of a large effect QTL on Chr12 at the position of the *Sli* locus (LOD=14.05), which explained 50.1% of the phenotypic variance, and a moderate effect QTL on Chr03 (LOD=4.67, $R^2=20.7\%$). As expected, the QTL on Chr12 was also observed in the QTL analysis on the total seed weight (SW_2020),

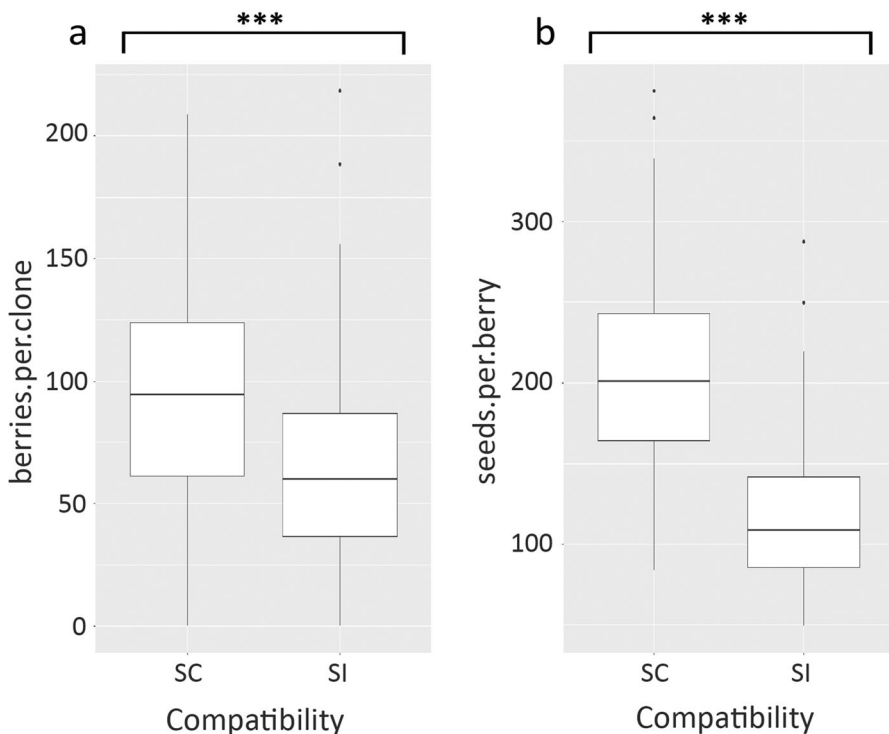


Fig. 2 Berries and seeds of self-compatible (SC) and self-incompatible (SI) genotypes. **a** Number of berries per clone; **b** Number of seeds per berry from the 10 largest berries of each plot

although with a lower LOD score of 7.29 ($R^2=30.6\%$), while the Chr03 QTL now had a higher LOD score (LOD=5.13, $R^2=22.6\%$) and an additional QTL on Chr05 appeared with a similar LOD score (LOD=5.62, $R^2=24.5\%$) (Fig. 1, Table S1). Taken together, we concluded that while berry set and seed set in the field are controlled by multiple moderate effect size QTL, the presence of *Sl*i has a significant effect on the number of seeds per berry.

QTL Mapping for Tuberization Onset

Despite the non-segregating *StCDF1.1* allele configuration in 18SC11, we observed early induction of tuber formation to occur within weeks from shoot emergence. To phenotype tuberization onset, all the genotypes from one or more blocks were subjected to early harvests within 2 months from planting in the soil. Depending on the stage of tuberization, traits such as presence/absence of induced swelling stolons, total early tuber weight and total early tuber number were measured as indicators of the differences in tuberization time among the genotypes. In the first early harvest in the 2019 field trial, approximately 40% of the genotypes had undergone tuberization onset, while 60% were still in a vegetative state when harvested 32 days after transplanting (DAT) in the field (60 DAP in the glasshouse) (Fig. S3, OT_2019). Using these phenotyping data, a significant QTL was identified on Chr05 with a LOD score of 10.03, explaining 34.3% of the variation (Fig. 1 and Table S1). In a second intermediate harvest 63 DAT in the field, 93% of the genotypes had undergone tuberization. Total early tuber weight (OTW_2019) and number (OTN_2019) were measured and mapped as well to the long arm of Chr05 (Fig. 1, S3 and Table S1).

In 2020 field trial, two blocks were harvested at the intermediate time of 54 DAP. At this time, 85% of genotypes from both blocks had already undergone tuberization. The total early tuber number (OTN_2020) and total early tuber weight (OTW_2020) were measured and showed a heritability of 0.86 and 0.82, respectively, suggesting a large genetic contribution to this trait (Table 1 and Fig. S3). Moreover, the two 2020 measurements showed a Pearson correlation of 0.68 between each other but up to 0.47 with tuberization onset traits measured in 2019 (Fig. 3). Both early total tuber number and weight gave a significant QTL on Chr05 (Fig. 1). For total early tuber number, we identified a QTL on Chr05 with a LOD score of 9.42, explaining 39.6% of the variation (Fig. 1 and Table S1). Likewise, for total early tuber weight, we identified a QTL on Chr05 with a LOD score of 3.83, explaining 18.7% of the variation (Fig. 1 and Table S1). Additionally, we analyzed available data from tuber pot yield (potTW_2018) and tuber number (potTN_2018) obtained from first generation F1 plants grown from true potato seeds in the glasshouse in 2018 (Fig. S3). In both cases, we identified a QTL on Chr05 with LOD score of 7.88 for pot yield and 6.88 for tuber number (Fig. 1 and Table S1).

Taken together, analysis of tuberization onset in all years revealed QTL on Chr05 that map to different locations than *StCDF1*, which is located on the short arm of Chr05 at ~17 cM on Chr05 in this genetic map. Although the QTL associated with tuberization onset were consistently detected on Chr05 between approximately 33

Table 1 Heritability of measured traits

Trait	Year	Heritability
Transition to anthesis (GDD4_2020)	2020	0.95
Number of seeds (SN_2020)	2020	0.88
Tuber number (TN_2020)	2020	0.95
Tuber Yield (TY_2020)	2020	0.96
Early tuber weight (OTW_2020)	2020	0.82
Early tuber number (OTN_2020)	2020	0.86
Tuber number (TN_2019)	2019	0.71
Tuber yield (TY_2019)	2019	0.73
Senescence (SEN_2019)	2019	0.70
Senescence (SEN_2020)	2020	0.90
Senescence onset	2019	0.36
Senescence onset	2020	0.84
Senescence life cycle (SENLC_2020)	2020	0.94
Senescence life cycle (SENLC_2019)	2019	0.85
Senescence regrowth (RG_2020)	2020	0.85

and 59 cM, the map positions of the peak markers and the corresponding confidence intervals did not always coincide. To assess whether this pattern reflected the presence of two linked QTL in this region, we conducted a cofactor analysis in which the peak marker of one QTL was used to condition the detection of the other (data not shown). This analysis abolished QTL detection, suggesting that the apparent positional shifts are more likely attributable to phenotypic stochasticity across harvest times, years and experimental setups rather than to multiple linked loci.

QTL Mapping for Senescence Progression and Total Life Cycle Length

The 18SC11 population offered also a great opportunity to detect loci controlling senescence, other than the previously identified *StCDF1* (Kloosterman et al. 2013). In potato breeding programmes, maturity (senescence) is generally scored once, at a time point where the breeder observes the greatest variation among the genotypes. In this study, we phenotyped senescence at multiple time points to obtain trait values for senescence onset, senescence (breeder's score, SEN_2019 and SEN_2020), and total life cycle length (SENLC_2019 and SENLC_2020) in both 2019 and 2020. A scale was used for visual evaluation (see "Material and Methods" section).

Onset of senescence, measured in both years, did not show any correlation and did not reveal any significant QTL (data not shown). The trait senescence (SEN_2019 and SEN_2020) and total life cycle length (SENLC_2019 and SENLC_2020) show a wide range of phenotypic variation with strong correlations ($R=0.6\text{--}0.75$) between both years (Fig. 3 and S3). Heritability of senescence and life cycle in both years ranges from 0.7 to 0.9 (Table 1), suggesting that the traits related to senescence were mainly controlled by genetic factors.

Interval mapping for senescence resulted in the detection of a significant QTL on Chr05 in 2019 (SEN_2019) with a LOD score of 8.44. This QTL was also identified

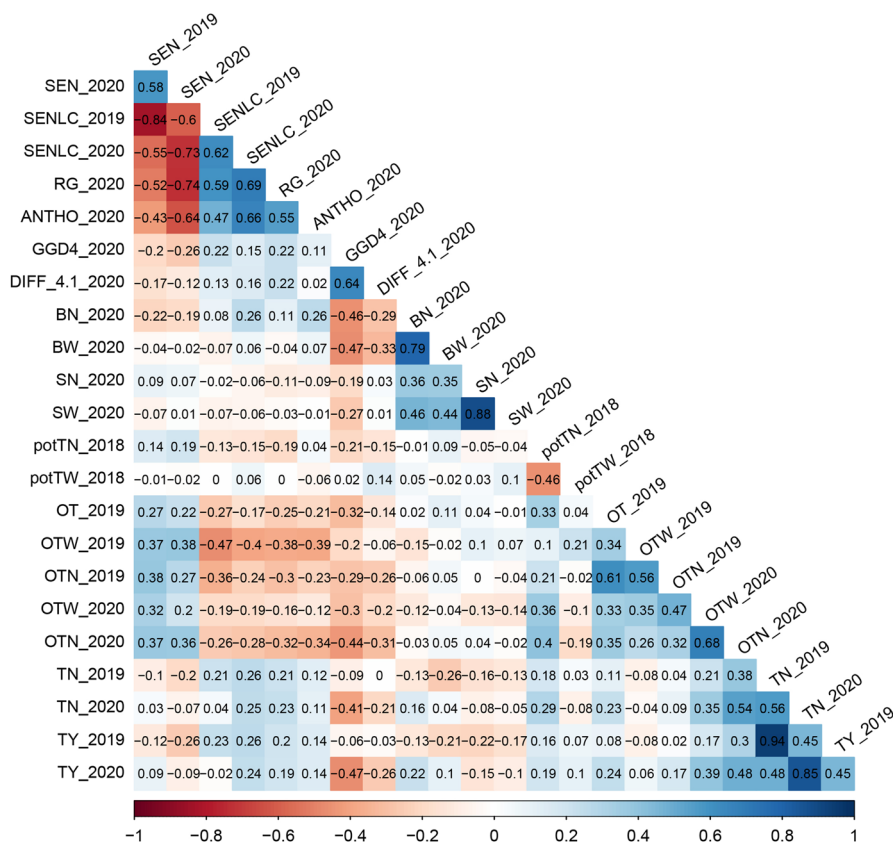


Fig. 3 Correlations between traits and years (locations), based on BLUES. SEN_2019, Senescence 2019; SEN_2020, Senescence 2020; SENLC_2019, Senescence life cycle length 2019; SENLC_2020, Senescence life cycle length 2020; RG_2020, Senescence regrowth 2020; ANTHO_2020, Senescence anthocyanin 2020; GGD4_2020, Transition to anthesis 2020; DIFF_4_1, transition to anthesis from GGD1 to GGD4 2020; BN_2020, Total number of berries 2020; BW_2020, Total weight of berries 2020; SN_2020, Number of seeds 2020; SW_2020, Total seed weight 2020; potTN_2018, number of tubers in pots 2018; potTW_2018, total tuber weight in pots 2018; OT_2019, Tuberization onset 2019; OTW_2019, Early tuber weight 2019; OTN_2019, Early tuber number 2019; OTW_2020, Early tuber weight 2020; OTN_2020, Early tuber number 2020; TN_2019, Tuber number 2019; TN_2020, Tuber number 2020; TY_2019, Tuber yield 2019; TY_2020, Tuber yield 2020. Cells with no significant correlations (p -value < 0.01) are left blank. Pearson's correlation coefficients are indicated in the cells

in 2020 (SEN_2020) with a higher LOD score of 8.8 (Fig. 1 and Table S1). The QTL accounted for between 28.5% and 34.7% of the variation in the trait (Table S1). Interestingly, we discovered that the total life cycle length mapped to a region largely overlapping the QTL for senescence in both 2019 and 2020 (Fig. 1 and Table S1). The LOD score for total life cycle length in this region was 9.52 in 2019 (SENLC_2019) and 9.36 in 2020 (SENLC_2020). The correlation between senescence and total life cycle was -0.85 in 2019 and -0.73 in 2020 (Fig. 3). Overall, we found a negative correlation between the senescence (breeder's score) and total life

cycle in the 18SC11 population, and we identified a new region on the long arm of Chr05 that affects both traits in both years.

Above-ground regrowth occurs during the later stages of plant development. In some genotypes, new shoots develop into a new green canopy distinct from the original senescent canopy during the late senescence stage (Fig. S3). We found a significant QTL for regrowth (RG_2020) near the QTL for senescence and total life cycle length on Chr05, with a LOD value of 11.31 (Fig. 1 and Table S1).

QTL Mapping for Tuber Traits

Tuber number and yield were measured in two consecutive years, 2019 and 2020 (TN_2019, TN_2020, TY_2019 and TY_2020). The distributions of both traits were continuous, reflecting their quantitative nature (Fig. S3). In 2019, the tuber number ranged from one to 60 per plant, while in 2020, it varied from one to 54. In this population, tuber size distribution within and between genotypes is uniform, resulting in a strong correlation between tuber number and yield (Pearson correlation = 0.94 in 2019 and 0.89 in 2020) (Fig. 3). The heritability of tuber number and yield is high, from 0.71 to 0.96 (Table 1), suggesting an important role of genetic factors in regulating these traits.

We identified a total of five QTL associated with tuber number and yield in 2019 and 2020 (Fig. 1 and Table S1). The proportion of explained variance ranged from 15.8% to 19.5%. Map positions, confidence intervals and effect sizes of these QTL are summarized in Table S1. Notably, a major QTL was found for tuber number and yield in 2020 and is located on Chr09 with a LOD score of 4.44 for tuber number and 3.48 for yield. Unfortunately, no QTL was found consistently in both years, suggesting that the Genotype-by-Year interaction has a strong effect on these traits.

Discussion

Advantage of Plant Development Studies in Populations That Are Fixed for the *StCDF1.1* Allele

In previous mapping studies in potato, many developmental traits have been mapped to the *StCDF1* locus on the short arm of Chr05. The effect of the different *StCDF1* alleles on developmental phenotypes is so large in these studies that small effect loci remain obscure. Recently, Clot et al. (2023) neutralized the large effect of *StCDF1* alleles in the diploid C × E population by compartmentalizing the population into three cohorts based on their *StCDF1* genotypes, with one cohort containing the *StCDF1.1* homozygotes, a second cohort with *StCDF1.1/StCDF1.2* heterozygotes and the third cohort containing all individuals with an *StCDF1.3* allele. This strategy allowed the identification of new QTL for (pot) tuber yield that remained undetected when the complete population was analyzed (Clot et al. 2023). While this

approach allowed the identification of interactions between the individual *StCDF1* alleles and other minor QTL, it required a large initial population size.

In this study, we utilized a diploid F1 population, 18SC11, composed of about 100 individuals in which only *StCDF1.1* alleles are present. As expected, none of the traits measured in this study mapped to the *StCDF1* locus, proving that the amino acid variation detected between the two variants of *StCDF1.1* does not play a functional role in any of the traits analyzed in this study. The approach allowed us to identify multiple new QTL for developmental and generative traits.

Flowering, Berry Set, and Seed Set

Since the advent of inbred line-based hybrid breeding in potato, many efforts have been undertaken to better understand flowering and seed set (Peterson et al. 2016; Plantenga et al. 2016, 2019; Clot et al. 2020; Alsahlany et al. 2021; Kaiser et al. 2021). The population 18SC11 was previously used to confirm the position of the *Sli* gene on Chr12, as it segregates for the *Sli* locus (Eggers et al. 2021). In this study, we showed that under field conditions, the presence of *Sli* significantly increases both the number of berries per plant as well as the number of seeds per berry. Interestingly, while the presence of *Sli* clearly improves berry set, no significant QTL for the number of berries was found at the *Sli* locus. In contrast, QTL analysis on the number of seeds per berry resulted in a highly significant QTL on the *Sli* locus with individuals that have the dominant *Sli* allele having more seeds per berry. Apparently, there was enough cross-pollination to allow the plants to set berries even if they are self-incompatible. Nonetheless, having anthers that release compatible pollen near the stigma increases both berry and seed yield, suggesting that wind- or insect-driven cross-pollination is limiting even when there are many compatible plants nearby.

Aside from the Chr12 QTL, several other QTL related to flowering, berry and seed set were identified in this study. For the transition to anthesis, two QTL were identified on Chr05 and Chr11. The Chr11 QTL may be similar to the fruit set QTL identified by Peterson et al. for fruit set in the DRH population (Peterson et al. 2016), whereas the Chr05 QTL may well have the same causal gene(s) as the other developmental QTL identified in this study. To our knowledge, the total berry number QTL on Chr08 and Chr10 have not been reported before, and it is currently unclear how these QTL are involved in increased berry set. It is possible that these QTL improve vigour in general, thus allowing increased berry set, or that these QTL affect flowering, pollinator attraction or male fertility. Previously, Kaiser et al. found a QTL for seed set on Chr03; however, this QTL is likely not the same as the QTL we identified on the same chromosome for number of seed and seed weight, as these are far apart, at 35.3 Mb distance (Kaiser et al. 2021).

The efficient development of inbred lines relies on the potato plant's ability to flower and set self-berries and seed, and as a result, breeders automatically select for fertility in their lines. As a consequence, F1 hybrids resulting from

these inbred lines are self-fertile as well and will produce undesirable berries in the field, which may limit the value of such hybrid cultivars. To ensure the commercial success of F1 hybrid potato varieties, breeders will have to find ways to reduce berry set in the field. For this, cytoplasmic male sterility may be used, which will allow breeders to create male sterile maternal lines that produce male sterile F1 hybrids.

Tuberization Onset

Potato has its centre of diversity in the equatorial Andes where tuberization in wild species is adapted to the prevailing short-day photoperiods at these latitudes. In contrast, in Europe, cultivated potatoes require initiation of tuberization during the long summer days to ensure the production of high yields well before the autumn frosts. *StCDF1* has been identified as the gene selected in Europe during breeding that has allowed cultivation of potato in temperate regions (Kloosterman et al. 2013).

Interestingly, the identification of *StCDF1* as a major player in early tuberization occurred by phenotyping above-ground plant maturity, and this can be explained, at the molecular level, by the multiple mechanisms that CDF proteins and their potato homologues play in plant development. In potato, the link between early tuberization and early plant maturity is often assumed; however, while early tuberization might have been selected in European varieties during seed tuber production, large variation in life cycle length is observed, suggesting the two traits can also be separated.

Tuberization occurs underground, and this hampers routine phenotyping of onset and tuber development in a non-destructive way. In fact, the majority of the studies investigating the genetics and molecular regulation of tuberization onset have been performed under controlled conditions. In our study, we performed early harvests to specifically address variation in tuberization onset in the field. We found that the 18SC11 population tuberizes within the window of early June to mid-July, a period when plants in the field in the Netherlands experience the longest days, with more than 16 h light/day. This is in striking contrast to the expectations for a short-day tuberizing population based on the presence of two copies of *StCDF1.1*. This suggests that other loci, or a previously uncharacterized variation at the *StCDF1* locus, might be responsible for the earliness in the population. Finally, we cannot completely rule out that differences between environmental conditions in controlled vs. field conditions (e.g., differences in light spectra and intensity) affect tuberization onset in addition to photoperiod.

While the 18SC11 population tuberizes under long day photoperiod, variation in tuberization onset was observed and mapped in consecutive years to Chr05. Although consistently mapping to the long arm of Chr05, the location of the QTL confidence intervals varied depending on the year and on the assessed traits, suggesting interaction with the environment and stochastic variation. We found that the QTL for tuber yield and tuber number of plants grown in pots in 2018 also colocalized with tuber onset on Chr05 rather than with any of the QTL detected for tuber number and yield in the field. This finding suggests that the number and weight of

tubers produced in pots, with a generally shorter plant life cycle, are strongly influenced by tuberization onset.

Senescence

The above-ground senescence of potato plants has long been recognized as a quantitative trait that significantly influences the final yield. Senescence, being a complex trait, poses challenges in performing QTL analysis due to the involvement of diverse genetic loci. Additionally, the growth environment plays a crucial role in the occurrence and development of senescence. The most well-known genetic locus relating to above-ground senescence is *StCDF1*, which has been repeatedly mapped in several potato populations and in different years (Visker et al. 2005; Kloosterman et al. 2013; Song and Endelman 2023).

In this study, we identified a region on the long arm of Chr05 that influences senescence progression and total lifecycle length. In previous studies with populations segregating for *StCDF1*, the timing of senescence onset was strongly linked with senescence progression and total life cycle length (Celis-Gamboa 2002; Kloosterman et al. 2013). In contrast, in the 18SC11 population, we found that senescence onset is not so strongly linked with senescence progression and total life cycle length, suggesting that these aspects of senescence can be independently regulated when segregation of *StCDF1* alleles is absent.

Tuber Number and Yield

Tuber number and tuber yield are complex traits of great importance for breeders and farmers. Earlier studies identified a QTL on the short arm Chr05, associated with both traits (Hurtado-Lopez et al. 2015; Rak et al. 2017; Marand et al. 2019; Clot et al. 2023), which co-localized with *StCDF1*. It is not surprising that tuber number and yield were confounded with maturity in these studies because wild type genotypes, exhibiting *StCDF1.1/1.1*, tend to tuberize late under long day conditions while individuals with *StCDF1.2/1.3* alleles produce fewer tubers and lower yield compared to other genotypes because of their shorter growing period.

In this study, tuber number and yield mapped to Chr07 and Chr11, respectively, in the 2019 trial, while one major QTL on Chr09 was identified for both traits in 2020. In 2019, seed tubers underwent GA treatment prior to planting, and only one main stem was retained. Earlier studies have shown that GA treatment influences tuber number and size by inducing the development of stems and stolons (Holmes et al. 1970). However, it is not established whether the influence persists when only one stem remains. Moreover, stem number is correlated with tuber number (Iritani et al. 1983). In 2020, when stem number was not controlled, tuber number and yield were mapped to Chr09. This QTL was not identified in 2019. Therefore, we speculate that the locus regulating the development of stems might be underlying this QTL, which is supported by Tessema et al. (2019).

Chromosome 5 QTL

In this study, the long arm of Chr5 was identified as associating with several developmental transitions, namely days to anthesis, tuberization onset, and senescence. Since the significant regions of the different QTL shift, depending on experimental years and analyzed traits, and overall they span a large area of the chromosome, we cannot conclude that one same locus confers variation for all traits without further fine mapping studies to address this question. However, at the molecular level, the two potato's reproductive strategies, tuberization and flowering onset, are regulated by similar pathways leading to the expression of tuberigen SELF PRUNING 6A (*StSP6A*) and florigen *StSP3D* (Navarro et al. 2011). *StSP6A* is located on the long arm of Chr5, at 51.32 Mb (DM4.04), which is rather external to the detected QTL, including tuberization onset QTL, and therefore unlikely to represent the underlying causative locus. Transcript levels of *StSP6A* are known to be regulated by another member of the same protein family, *StSP5G* (Navarro et al. 2011; Abelenda et al. 2016). In potato DM, a tandem duplication of *StSP5G* is located on Chr5 at position 49.30 Mb, in a region shared by several of the identified QTL in the 18SC11 population. Interestingly, different potato genotypes appear to carry a various number of tandemly repeated copies of *StSP5G* (data not shown). Molecular investigation of *StSP5Ga* function has elucidated a repressive role in both flowering and tuberization in potato (Abelenda et al. 2016). Furthermore, in tomato, *cis* regulatory variation at the *SP5G* ortholog has been selected to confer photoperiodic insensitivity of flowering in commercial tomato cultivars (Soyk et al. 2017). *StSP5Gs* represent, therefore, very strong candidates that could explain variation in tuberization onset and time to anthesis in the 18SC11 population, whereas a role for these genes in senescence has not been reported to date.

Practical Consequences

In this study, we extensively phenotyped a small-size population to identify loci controlling potato life cycle traits. Multiple QTL for generative and developmental traits were identified. Although the QTL resolution might be impacted by the size of the population, the results represent promising leads for further identification of genes involved in potato developmental pathways that may well prove agronomically relevant.

Further elucidation of the developmental QTL would assist breeders in designing hybrids with specific maturity types and field performance. For instance, depending on the specific market conditions, a breeder may want to design a hybrid with early tuberization but a long life cycle length. With the results of this study, it could be possible to develop markers that allow breeders to select for these QTL in diverse genomic backgrounds. However, the QTL presented here are still not accurately mapped and do not allow the targeted introgression of small segments. Future identification of the causal genes would allow breeders to utilize these QTL more efficiently, as that would make it easier to develop highly specific markers that work in

diverse genomic backgrounds, with very little recombination between these markers and the causal genes.

In conclusion, by using a *StCDF1*-fixed segregating mapping population, we were able to identify new loci responsible for the control of many important potato developmental and agronomic traits. In addition to development, *StCDF1* controls also abiotic and biotic stress responses. The 18SC11 population or a similar *StCDF1*-fixed population could represent valuable material to identify loci regulating those non-developmental complex traits as well.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11540-025-09972-9>.

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Author Contribution The 18SC11 population was generated and provided by Solynta through E-JE and PL. CWBB, SB and PL conceived and supervised the research and edited the manuscript. E-JE, LS, XW and SB designed the trials, supervised and performed data collection and genetic analysis, wrote the manuscript. MO collected phenotypic data and cloned the *StCDF1* alleles. SUM provided the genotyping of the 18SC11 population. RGFV and MEDV supervised E-JE and edited the manuscript. CWBB obtained funding for the research. All authors read and approved the final manuscript.

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Data Availability The availability of data is on the basis of personal request.

Declarations

Conflict of interest R.G.F.V. is a member of the editorial board of Potato Research. The authors do not foresee any potential conflict of interest.

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