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A model-based approach to analyse genetic variation in potato using standard cultivars and a segregating population. II. Tuber bulking and resource use efficiency

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ABSTRACT

Quantitative differences in tuber bulking of 100 genotypes in a segregating F1 population, their parents (SH, RH) and five contrasting cultivars of potato (*Solanum tuberosum*) grown in six environments were analysed using a piece-wise expolinear function. Tuber bulking was characterised by three parameters: c_m, *ED* and w_{max}, where c_m and *ED* were growth rate and effective duration, respectively, of the linear phase of tuber bulking, and w_{max} was the final tuber dry weight at the end of the linear phase (t_E). We also analysed radiation (RUE_T) and nitrogen use efficiency (NUE_T), and their relationships with the model parameters. Values of c_m and RUE_T were highest for early-maturing genotypes. Late-maturing genotypes had largest *ED* and NUE_T. As a result, w_{max} was higher in late genotypes than in early genotypes. Most traits exhibited high heritability and high genetic correlations with w_{max}. Path analysis showed that RUE_T, c_m and a previously quantified parameter for total canopy cover A_{sum}, had a major influence on w_{max}. Sixteen QTLs were detected for all traits explaining the phenotypic variance by up to 66%. One particular QTL on paternal linkage group V was detected for all traits with a major additive effect and maximum total phenotypic variance. Additional QTLs mostly associated with RH (c_m, t_E and *ED*) or both SH-RH linkage groups (NUE_T, w_{max}). Our study demonstrates that there are opportunities for improving tuber dry matter yield by selecting an optimal combination of important physiological traits.

1. Introduction

Tuber formation in potato (*Solanum tuberosum* L.) consists of a complex and dynamic sequence of several independently regulated events (Ewing and Struik, 1992; Jackson, 1999), including induction, initiation, set, bulking and maturation (Vreugdenhil and Struik, 1989). These events are only possible when environment-dependent steps occur in an orchestrated way, including the arrest of stolon growth (Vreugdenhil and Struik, 1989), initiation of radial growth (Vreugdenhil and Struik, 1989; Ewing and Struik, 1992) and resource storage (Park, 1990; Müller-Röber et al., 1992). The different steps and events are regulated by specific genes (Struik et al., 1999; Kloosterman et al., 2005). The resulting, economically relevant process of tuber bulking is, therefore, regulated by a large set of genes (Bachem et al., 2000).

The onset of tuber bulking greatly impacts subsequent growth, development and physiology of the entire potato crop (Ewing, 1990; Ewing and Struik, 1992; Van Dam et al., 1996; Walworth and Carling, 2002), mainly because the developing tubers become the dominant sink of both carbon and nitrogen assimilates (Oparka and Davies, 1985). The onset of tuber bulking leads to a more or less abrupt preferential partitioning of assimilates to the tubers, thereby causing a reduction in the growth rate and ultimately a complete halting of growth of foliage and roots (Ewing and Struik, 1992). However, the abruptness depends on the maturity type and other aspects of the genotype-specific physiology; early onset of tuber bulking may result in small plants with limited canopy cover and consequently low final tuber yields, whilst late onset of tuber bulking leads to large plants with high final tuber yields (Struik, 2007).

Information on the different processes involved and factors affecting

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plant development and tuber formation in potato is abundant (Ewing and Struik, 1992; Kolbe and Stephan-Beckmann, 1997; O'Brien et al., 1998; Jackson, 1999; Struik et al., 1999; Claassens and Vreugdenhil, 2000, and references therein). However, most studies have focused on one or very few of these developmental processes, or on one or very few genotypes (cultivars). Moreover, the physiological and genetic basis of variability among such traits have not been thoroughly investigated, although some efforts have been made to study the temporal dynamics of important potato developmental processes under diverse environmental conditions on a set of contrasting genotypes. For instance, Spitters (1988) analysed the genotypic differences in tuber bulking of potato on a large set of commercial varieties. Celis-Gamboa et al. (2003) used a highly segregating diploid population of potato to study the temporal relationships underlying the dynamics of tuber formation and other developmental processes.

Difficulties in manipulating yield are related to its genetic complexity: polygenic nature, interactions between genes (epistasis), and environment-dependent expression of genes (Ribaut and Hoisington, 1998). Many environmental and physical factors, such as temperature, day length, light intensity, water availability and nitrogen (N), influence tuberisation (Ewing and Struik, 1992; Jackson, 1999). For example, temperature exerts a major influence on tuberisation and dry matter partitioning to tubers (Ewing, 1981, 1985), with cool air temperatures favouring induction to tuberise (Gregory, 1965; Epstein, 1966; Ewing, 1981; Manrique et al., 1984), whereas an increase in air temperature may reduce tuber dry matter content and yield (Struik et al., 1989). Nitrogen helps to attain complete canopy cover early in the season, especially under relatively resource-poor conditions (Haverkort and Rutavisire, 1986; Vos, 2009) and to extend the period of full canopy cover thus leading to increased light interception and tuber yield (Martin, 1995). Radiation is important for dry matter accumulation (Monteith, 1977; Goudriaan and Monteith, 1990), and affects the early processes in tuber formation (Ewing and Struik, 1992), the rate of tuber bulking (Burstall and Harris, 1983) and its duration. Therefore, resource (radiation, N) use efficiency may have a strong bearing on tuber bulking and final tuber yields.

In a companion paper (Khan et al., 2019), we quantitatively analysed potato canopy cover dynamics, using a set of varieties covering a wide range of maturity types and a well-adapted diploid F1 segregating population. Here, using the same set of plant materials, we analyse the dynamics of tuber bulking and its variability by breaking them down into biologically meaningful and genetically relevant component traits. We also analyse radiation use efficiency (RUE) and nitrogen use efficiency (NUE) and study their relationships with the tuber bulking traits and genotype maturity type. We quantify the genetic parameters (variance components and heritability), phenotypic and genetic correlations, path coefficients of these traits and explore possibilities for indirect selection for yield based on physiological component traits. Finally, we perform QTL mapping of the traits and discuss their genetic basis. The combined information from the two papers should give insights into the most vital processes that can be used to explore the possibilities of genetically manipulating potato tuber yield.

2. Materials and methods

2.1. F1 segregating population of SH × RH and standard cultivars

The plant material used in this study consisted of 100 F1 diploid ($2n = 2x = 24$) potato genotypes derived from a cross between two diploid heterozygous potato clones, SH83-92-488 × RH89-039-16 (Rouppe van der Voort et al., 1997; Van Os et al., 2006), or simply the 'SH × RH population'. The population segregates for maturity type (Van der Wal et al., 1978; Van Oijen, 1991).

Besides the individual F1 genotypes and their two parents, we also included five standard cultivars: Première, Bintje, Seresta, Astarte, and Karnico. These cultivars were chosen because of their differences in maturity type when grown in the Netherlands, ranging from early (Première) to very late (Karnico) and thus allowed benchmarking of consequences of maturity type on the temporal dynamics of tuber bulking. Further information about plant materials is given in Khan (2012).

2.2. Field experiments and measurements

Six field experiments were carried out in Wageningen (52 °N latitude), the Netherlands, during 2002, 2004, and 2005, with two experiments in each year, using the aforementioned plant materials. Karnico was not present in the two experiments in 2005. These experiments differed in year, soil and N availability regime. For details on the methodology and the environmental conditions see Khan et al. (2019).

Tuber dry matter was measured at three harvests during the growing period. The first and second harvests were scheduled to allow assessing the linear tuber dry matter bulking, while the last harvest was performed at maturity. Tubers of each plot were harvested and dried in an oven at 70 °C to constant weight. For samples of the growing seasons of 2004 and 2005, N concentration in tubers sampled at the end of the growing season was determined by micro-Kjeldahl digestion and distillation (Association of Official Analytical Chemistry (AOAC, 1984). Total amount of N in tubers was calculated from the N concentration and tuber dry weight.

The physiological based maturity criteria developed by Khan et al. (2013) was used to classify the F1 genotypes into four different maturity classes (very early, early/mid-early, mid-late/late, and very late).

2.3. Model approach

2.3.1. A model for tuber bulking dynamics

Potato tuber growth follows a sigmoid pattern over time, including an early accelerating phase, a linear phase and a ripening phase (Fig. 1). We used the expolinear function of Goudriaan and Monteith (1990) to describe the tuber growth during the exponential phase:

$$w = \frac{c_m}{r_m} \ln[1 + e^{r_m(t-t_B)}] \text{ with } t \leq t_B \quad (1)$$

where w is tuber mass, t is time, t_B is the moment at which the linear phase of tuber bulking effectively begins, r_m is the relative growth rate in the 'exponential phase', and c_m is the growth rate in the 'linear phase'.

Eq. (1) can, in principle, be used to describe the tuber growth of the linear phase as well. However, Eq. (1) tends to under-estimate the true growth rate because of its curvilinear nature. To obtain an objective estimation of the growth rate of the linear phase, we used the following linear model to quantify the second phase:

$$w = w_B + c_m(t - t_B) \text{ with } t_B < t < t_E \quad (2)$$

where t_E is the end time of the linear phase, w_B is the tuber weight at time t_B. If we know r_m and c_m, then w_B can be estimated from Eq. (1) as $0.693\ c_m/r_m$.

To represent a deflection in growth towards the third phase, Goudriaan and Monteith (1990) suggested a truncated curve that terminates growth at the time t_E, when the maximum weight (w_{max}) is achieved. This is a brutal method, because growth stops gradually rather than abruptly. However, given the limited number of measurements in the time series (see above), we adopted the truncated curve approach, with:

$$w = w_{max} \text{ with } t \geq t_E \quad (3)$$

where t_E is calculated as $t_B + (w_{max} - w_B)/c_m$.

Combining Eqs. (1–3) yields a model with four parameters: r_m, c_m, t_B and w_{max}, while the two other parameters w_B and t_E are calculated as $0.693\ c_m/r_m$ and $t_B + (w_{max} - w_B)/c_m$, respectively. Obviously an over-

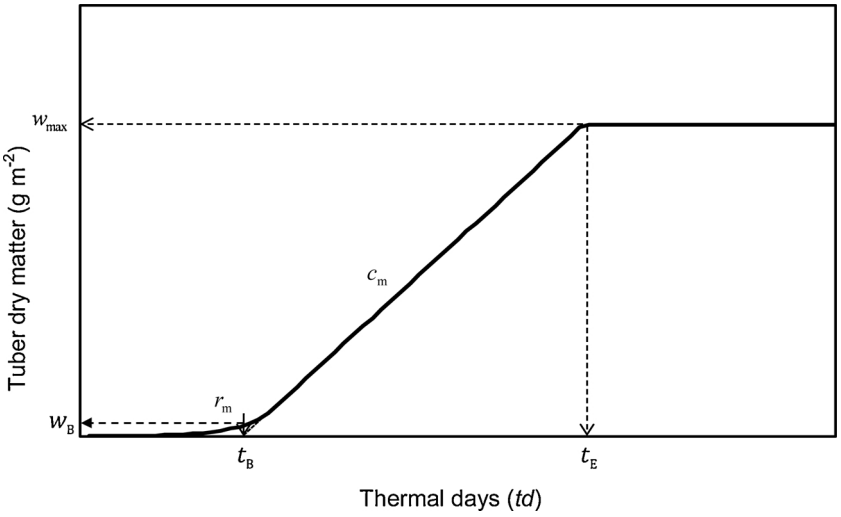

Fig. 1. Tuber bulking dynamics in potato represented by the piece-wise expolinear growth function.

fitting would be obtained if all four parameters were to be directly fitted from our limited data points for each genotype. Ingram and McCloud (1984) and Van Dam et al. (1996) reported that r_m was conserved across potato cultivars at a given temperature. Their r_m value 0.34 d^{-1} at the optimum temperature was used here for all genotypes. We also fixed parameter w_{max} as the average of two blocks of the final measured weight. The two remaining parameters (i.e. c_m, t_B) can be estimated, but with the value of t_B having large standard error, probably due to insufficient data points for the early season. Using these estimated values, we found that the initial weight (w_0) at time zero, calculated using Eq. (1), did not vary much across genotypes. We, therefore, used the value for w_0 = 0.13 (g m^{-2}), the averaged w_0 across all six experiments and all genotypes, to further reduce the number of parameters to be estimated. When w_0 is fixed, parameter t_B can be calculated from Eq. (1) as:

$$t_B = -\frac{1}{r_m}\ln\left(e^{\frac{w_0 r_m}{c_m}} - 1\right) \quad (4)$$

This is in accordance with Goudriaan (1994), who suggested that it may be a more natural sequence to express t_B as a function of initial weight (w_0) at emergence.

Eq. (4) and the formulae for calculating w_B and t_E, were combined with Eqs. (1–3), for curve fitting. The fitting was performed for each genotype of every experiment with the iterative nonlinear least-square regression using the Gauss method, as implemented in the PROC NLIN of the SAS software (SAS Institute Inc., 2004). Obviously, our procedure estimated only c_m, which together with w_{max} as primary model parameters, characterises genotypic and environmental effects on tuber growth. Parameters t_B, t_E and w_B were calculated from the equations described earlier. The effective duration of tuber bulking (*ED*), an additional useful trait, was calculated as $t_E - t_B$.

As in our previous analysis for canopy cover (Khan et al., 2019), all time variables and duration were expressed as thermal days (*td*) to account for the influence of daily and seasonal temperature fluctuations on tuber growth. The method for conversion of the actual days into *td* was given by Yin et al. (2005) and its application to our potato genotypes has been described in Khan et al. (2019). Note that the *td* is equal to or smaller than the number of chronological days.

2.4. Calculation of radiation use efficiency

The radiation use efficiency (RUE; g DM MJ^{-1} PAR$_{int}$) refers to the slope of the relation between total plant dry matter (g m^{-2}) and cumulative intercepted radiation (MJ m^{-2}) (Haverkort and Harris, 1987). However, due to lack of detailed measurements of total plant biomass for our large set of genotypes, RUE was estimated for each individual genotype/cultivar by dividing the total tuber dry matter at maturity (g DM m^{-2}) by the cumulative intercepted PAR (MJ PAR$_{int}$ m^{-2}) for the entire growth period. Data of incident global solar radiation were obtained from a weather station in Wageningen located nearby the experimental sites. Daily incident PAR was calculated as half of the global solar radiation (Spitters, 1988). To calculate cumulative PAR$_{int}$, our extensive data on the percentage green canopy cover (Khan et al., 2019) were converted to PAR-interception percentage, using a linear relationship given by Burstall and Harris (1983) as PAR$_{int}$ (%) = 0.956 × canopy cover (%) – 4.95. Daily values of PAR$_{int}$ were summed and the obtained cumulative PAR$_{int}$ was used to calculate seasonal average RUE on the tuber-dry weight basis (i.e. RUE_T).

2.5. Calculation of nitrogen use efficiency

As we did not measure dry weight and N content in the organs other than tubers, nitrogen use efficiency (NUE; g DM g^{-1} N) was expressed on the tuber-dry weight basis (i.e. NUE_T), as was RUE_T, by dividing the total tuber dry matter (g DM m^{-2}) by total tuber nitrogen uptake (g N m^{-2}). Thus NUE_T is mathematically equivalent to the inverse of tuber N concentration (g N g^{-1} DM).

2.6. Statistical and genetic analyses

All statistical analyses were performed in Genstat (Payne et al., 2009). Combined analysis of variance across experiments (i.e. environments) was performed to test the significance and extent of differences among environments and genotypes (including the F1 population, the parents, and standard cultivars). Means of genotype and environment terms were compared using the Fisher's least significant difference (LSD) test. Further statistical analyses were performed only using the F1 population means (100 genotypes) across six environments as described below.

2.6.1. Estimation of variance components

The variance components for genetic, environmental and experimental error effects were estimated through the REML procedure to assess their contribution to the total phenotypic variance of the traits c_m, t_E, *ED*, RUE_T, NUE_T and w_{max}. Significance levels were determined with a likelihood ratio test (Morrell, 1998), which tests the change in deviation after removing the respective variance component from the model. The change in deviation is approximately chi-square distributed (Littell et al., 1996). Once these variance components were estimated, phenotypic variance (σ^2_{Ph}) was calculated as per following equation (Bradshaw, 1994; Falconer and Mackay, 1996; Lynch and Walsh, 1998):

$$\sigma^2_{Ph} = \sigma^2_G + \sigma^2_E + \sigma^2_\varepsilon \quad (5)$$

where σ^2_G is genetic variance, σ^2_E represents environmental variance, and σ^2_ε is experimental error variance.

2.6.2. Phenotypic and genetic coefficients of variation

Coefficients of variation (%) were calculated according to the following equation:

$$CV_X = \frac{\sqrt{\sigma^2_X}}{\mu} \times 100 \quad (6)$$

where μ is the grand mean of the population, and σ^2_X is a variance component (i.e. σ^2_{Ph} or σ^2_G or σ^2_E).

2.6.3. GGE biplot analysis

GGE biplot analysis was performed to analyse the interrelations among genotypes and environments. GGE biplots were constructed by plotting the first principal component (PC1) scores of the genotypes and the environments against their respective scores for the second principal component (PC2). The environment-standardised method of Yan (2002) was used.

2.6.4. Heritability

Estimates of percent broad-sense heritability (H^2) were calculated by using the estimated variance components (Falconer and Mackay, 1996; Holland et al., 2003) as:

$$H^2 = \frac{\sigma^2_G}{\sigma^2_G + \frac{\sigma^2_\varepsilon}{n_t}} \times 100 \quad (7)$$

where n_t is the product of number of blocks and environments.

2.6.5. Phenotypic and genetic correlation

Phenotypic correlations were calculated using the Pearson Correlation Coefficient. The genetic correlations were calculated using the following equation (Holland, 2006):

$$r_{Gij} = \frac{\sigma^2_{Gij}}{\sqrt{\sigma^2_{Gi}\sigma^2_{Gj}}} \quad (8)$$

where σ^2_{Gij} is the estimated genetic covariance between traits i and j; σ^2_{Gi} and σ^2_{Gj} are the genetic variances of traits i and j, respectively. The variance and covariance components were estimated from multivariate REML analyses (Meyer, 1985; Holland, 2006). The significance of genetic correlations was determined using a t-test after a z-transformation of the correlation coefficients (Sokal and Rohlf, 1995; Gutteling et al., 2007).

2.6.6. Path coefficient analysis

The inter-associations between the important yield determining component model traits were ascertained across all six experiments by working out the path coefficient analysis following the procedure of Dewey and Lu (1959). This was accomplished by partitioning the direct and indirect effects of various physiological traits upon the final tuber dry matter. The final tuber dry matter (i.e. w_{max}) was considered as the response variable while traits c_m, ED, A_{sum}, RUE_T and NUE_T were assumed to be the predictor variables, where A_{sum} is the area under the whole green canopy curve and reflects the capability of the crop to intercept solar radiation during the whole growing season as quantified in the companion paper (Khan et al., 2019) and could be used as an index of crop maturity (Khan et al., 2013). The direct effects of predictor variables were the path coefficients computed through multiple regression. A path coefficient is a standardised regression coefficient (Li, 1975). Indirect effects were computed as the product of the correlation coefficient between two variables and the path coefficient from the second variable to the response variable. Let variables x_1 to x_5 refer to c_m, ED, A_{sum}, RUE_T and NUE_T, respectively. The total effect of a predictor variable x_1 correlated with other predictor variables x_2, x_3, x_4 and x_5 on response variable z, would be given by, for example:

$$r_{zx1} = P_{zx1} + (P_{zx2} \times r_{x1x2}) + (P_{zx3} \times r_{x1x3}) + (P_{zx4} \times r_{x1x4}) + (P_{zx5} \times r_{x1x5}) \quad (9)$$

where r_{zx1} is total correlation between z and x_1, P_{zx1} represents path coefficient from x_1 to z, r_{x1xi} (i = 2, 3, 4 and 5) is correlation coefficient between variables x_1 and x_i, and P_{zxi} denotes path coefficient from x_i to z. The same logic was applied to compute r_{zx2}, r_{zx3}, …, r_{zx5}.

2.6.7. QTL detection

The parental (SH, RH) genetic map described in Khan et al. (2019) was used for QTL mapping of model traits. Eighty-eight genotypes of our 100 F1 lines were covered in the extended ultra-dense genetic map of 250 lines of SH × RH population (cf. Khan, 2012); data of these 88 lines were therefore used for detection of QTLs for model parameters, derived traits and (N, radiation) use efficiencies. QTL analysis was done individually for all six experiments (environments) using Genstat version 14 (Payne et al., 2009) software. For more details about the mapping procedure, see Khan (2012). We do not present results of a QTL analysis across all six environments. QTL mapping across environments implies that trait observations are averaged and usually this will not reveal QTLs that were not already significant within one environment.

3. Results

3.1. Model performance in describing tuber bulking dynamics of genotypes

The model for tuber bulking dynamics (i.e. combined Eqs. (1)–(3)) fitted well for each genotype of the potato segregating population, the parents and the standard cultivars in the entire data set, with R^2 values ranging from 0.90 to 1.00 (n = 6). The estimated tuber bulking curves for the two parents (SH and RH) and four standard cultivars are shown in Fig. S1 and the frequency distributions of the model parameters across the F1 genotypes are shown in Fig. 2. The transformation of calendar days into thermal time resulted in a more stable parameter estimation (data not shown). Overall, combined Eqs. (1)–(3) proved very useful in analysing the tuber bulking dynamics of a diverse set of potato genotypes under various environments.

3.2. Assessing effect of genotype on model traits and resource use efficiencies

Results of combined analysis of variance showed highly significant ($P < 0.01$) effects of genotype (including 100 F1 genotypes, the parents, and standard cultivars) across experiments on all model traits and resource use efficiencies (data not shown). Not surprisingly, in most cases, performance of the commercial potato cultivars was superior to that of the diploid F1 population (Tables 1 and 2; Fig. 3). Differences between genotypes and across environments in the onset of tuber bulking (t_B) were very small, because, as mentioned earlier, t_B was calculated by Eq. (4) where w_o and r_m were fixed due to limited data points for the early growth phase. Similarly, the tuber weight (w_B) achieved at t_B was calculated in relation to r_m and c_m (see Materials and Methods). Therefore, we will not analyse the variation in t_B and w_B further.

There were significant differences ($P < 0.05$) among the standard cultivars for c_m, t_E, ED, w_{max}, RUE_T and NUE_T (Table 1). The tuber bulking rate (c_m) was higher for early-maturing cultivars than for late-maturing ones. Late-maturing genotypes had longest period of tuber bulking (ED). As a result, crops matured (t_E) later and tuber yields (w_{max}) were higher in late genotypes than in early genotypes. The values of RUE_T ranged between 1.9 and 2.7 g DM MJ^{-1} (Table 1). They

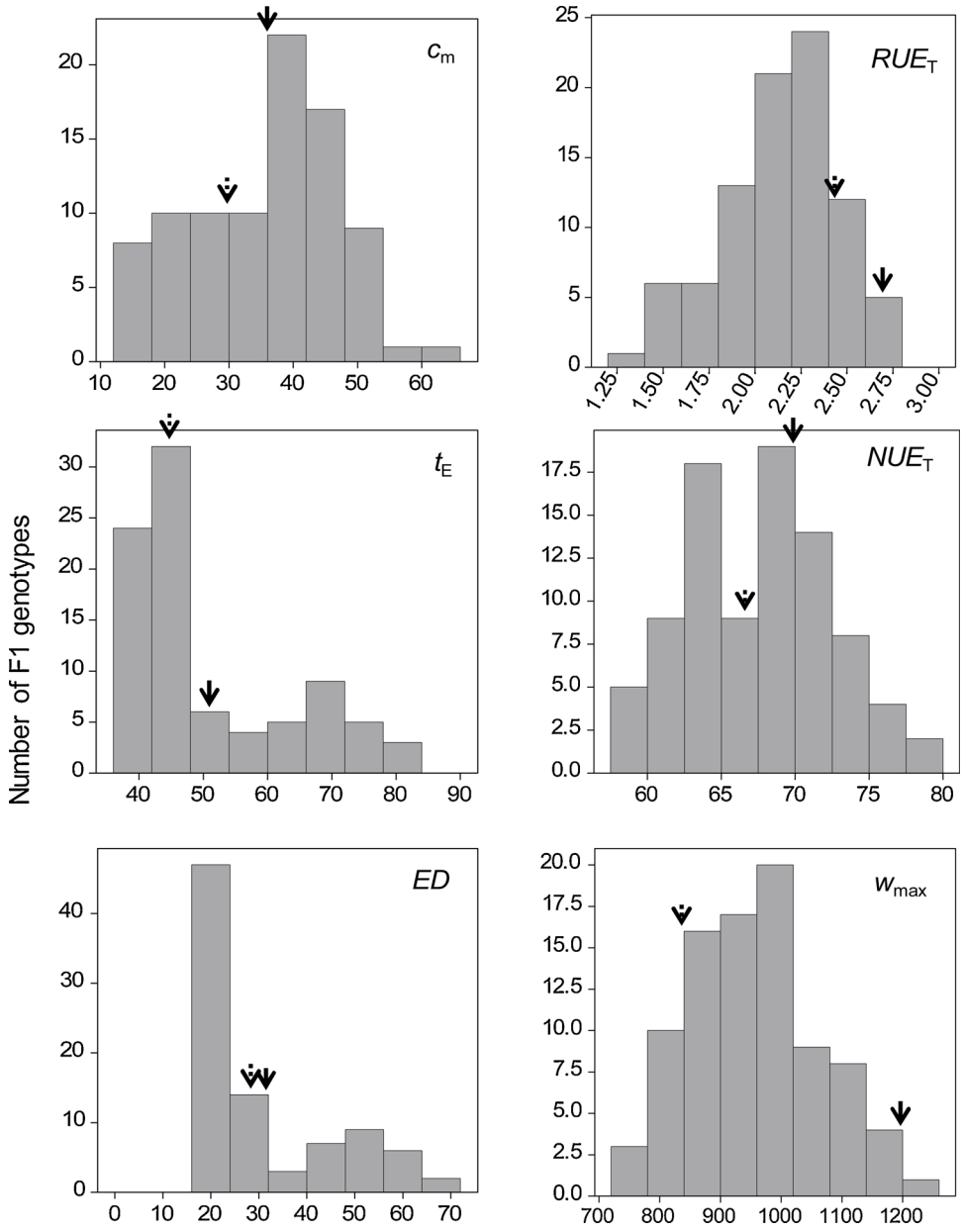

Fig. 2. Distribution of five model parameters among F1 genotypes across six experiments (environments). The values of two parents 'SH' and 'RH' are indicated by full arrow and dashed arrow, respectively. Values on the X-axis represent *td* (thermal days) for t_E and *ED*, g for w_{max}, g DM m^{-2} td^{-1} for c_m, g DM MJ^{-1} for RUE_T, and g DM g^{-1} N for NUE_T. Values on Y-axis indicate number of F1 genotypes.

Table 1
Estimated mean values of different traits for five standard cultivars (listed in order of increasingly longer crop cycle), as obtained from combined ANOVA across six environments. *td* stands for thermal day.

Cultivar	c_m (g DM m^{-2} td^{-1})	t_E (*td*)	*ED* (*td*)	RUE_T (g DM MJ^{-1})	NUE_T (g DM g^{-1} N)	w_{max} (g DM m^{-2})
Première	55.7 a	37.3 c	16.1 c	2.7 a	70.4 c	1122 b
Bintje	48.2 ab	47.9 b	27.4 b	2.4 a	72.1 c	1375 ab
Seresta	36.7 bc	62.4 a	42.8 a	2.4 a	88.5 b	1579 a
Astarte	35.4 bc	63.0 a	43.5 a	2.2 ab	90.9 b	1533 a
Karnico	31.2 c	63.7 a	44.4 a	1.9 b	101.8 a	1487 a
LSD	13.2	10.1	10.7	0.5	7.7	263

Means within a column followed by different letters are significantly different according to Fisher's least significant difference test ($P < 0.05$).

Table 2
Estimated mean values of different traits (across six environments) for two parents (SH and RH) and mean, minimum (Min.), maximum (Max.), and range within the F1 population. *td* stands for thermal day.

Parameter	SH	RH	Mean (±S.E.)[1]	Min.	Max.	Range
c_m (g DM m^{-2} td^{-1})	39.8	29.0	35.5 (±4.2)	19.9	47.4	27.5
t_E (*td*)	50.8	46.9	51.0 (±2.9)	42.5	62.9	20.4
ED (*td*)	30.9	27.8	31.8 (±3.3)	22.4	45.1	22.7
RUE_T (g DM MJ^{-1})	2.7	2.4	2.1 (±0.2)	1.5	2.6	1.1
NUE_T (g DM g^{-1} N)	69.6	67.2	68.2 (±5.6)	54.4	81.6	27.2
w_{max} (g m^{-2})	1219	847	955.6 (±50.0)	830.4	1115.7	285.3

[1]Mean of F1 segregating population (100 genotypes) across six environments.

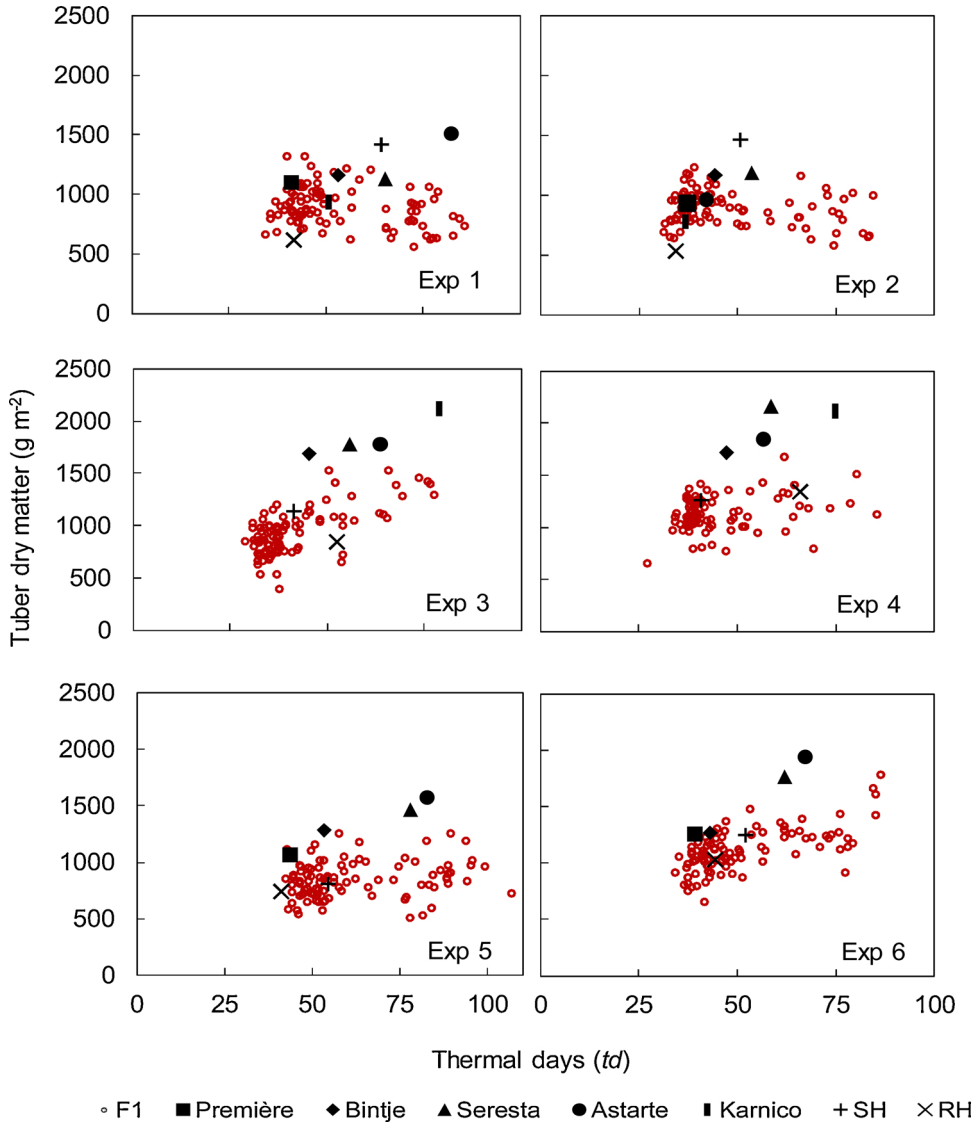

Fig. 3. Final tuber yields of 100 F1 genotypes, 5 standard cultivars, and 2 parental genotypes (SH and RH), measured in each individual experiment.

were higher for the early-maturing cultivar (Première) followed by the mid-late (Bintje, Seresta) and late (Karnico) cultivars. Mean estimates for NUE_T ranged between 69.6–101.8 g DM g^{-1} N (Table 1). They were higher for late-maturing cultivars like Karnico and Astarte than for mid-early and early cultivars such as Bintje and Première.

Table 2 compares the mean, and ranges of model traits and resource use efficiencies between the two parents (SH and RH) and the F1 segregating population. Wide ranges were observed for all traits. Most traits were nearly normally distributed but t_E and *ED* were not (Fig. 2). The mean RUE_T of the F1 population was lower than the value of either parent, associated with a wide variation in the population for RUE_T with values ranging from 1.5 g DM MJ^{-1} to 2.6 g DM MJ^{-1} (Table 2). NUE_T in the F1 population was, on average, 68.2 g DM g^{-1} N which was close to the values of the two parents (SH: 69.6 g DM g^{-1} N; RH: 67.2 g DM g^{-1} N). However, there was a very wide variation in NUE_T within the F1 population; it ranged from 54.4 g DM g^{-1} N to 81.6 g DM g^{-1} N (Table 2).

3.3. Assessing effect of environment on model traits and resource use efficiencies

Environment had a highly significant ($P < 0.01$) effect on all model traits and resource use efficiencies. There were significant differences ($P < 0.05$) between the experiments for c_m, t_E, *ED*, w_{max}, RUE_T and NUE_T within the five standard cultivars (Table 3). This was at least partly due to the purposeful variation in availability of N across trials. Fig. 4 illustrates the variation of these model parameters and derived traits for the F1 population per individual experiment. The ranges of parameters c_m and w_{max} were consistently wider in Exp. 3 than in the other experiments (Fig. 4). In case of t_E and *ED*, wider ranges were observed in Exps 4 and 5, respectively (Fig. 4). This could be attributed

Table 3
Estimated mean values of different traits for each individual environment as obtained from combined ANOVA across five standard cultivars. *td* stands for thermal day. '–' means no data.

Parameter	Exp. 1	Exp. 2	Exp. 3	Exp. 4	Exp. 5	Exp. 6	LSD
c_m (g DM m^{-2} td^{-1})	30.6 d	41.6 c	46.1 b	50.0 a	30.9 d	48.3 a	2.2
t_E (*td*)	55.4 d	42.9 f	61.1 b	59.4 c	64.6 a	53.0 e	1.7
ED (*td*)	36.3 d	22.8 f	40.8 b	38.8 c	45.5 a	32.5 e	1.8
RUE_T (g DM MJ^{-1})	2.1 d	2.0 e	2.8 a	2.6 b	2.0 e	2.4 c	0.09
NUE_T (g DM g^{-1} N)	–	–	102.5 a	80.8 c	69.4 d	84.8 b	1.5
w_{max} (g m^{-2})	1086 e	1003 f	1834 b	1954 a	1341 d	1555 c	44

Means within a row followed by different letters are significantly different according to Fisher's least significant difference test ($P < 0.05$).

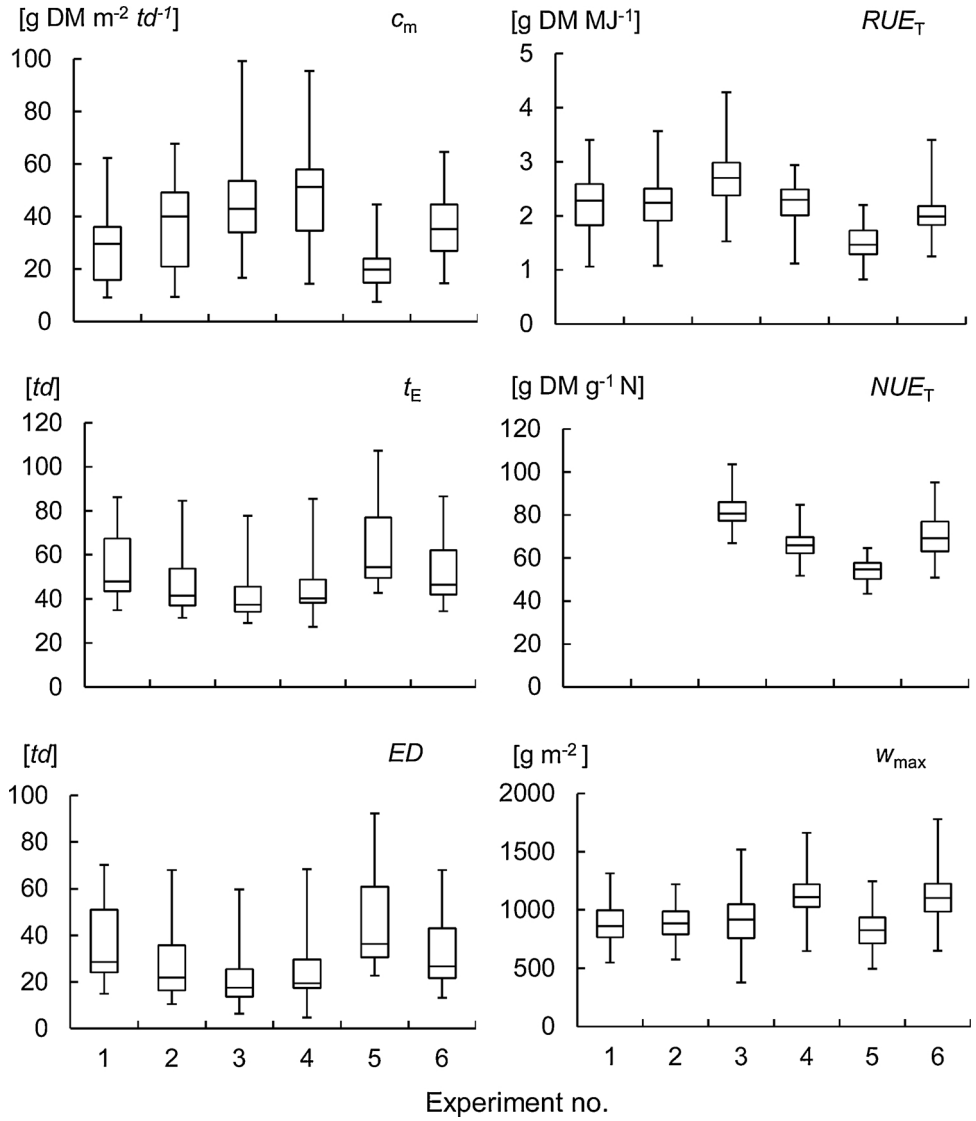

Fig. 4. Box plots of genetic means of an F1 population of different traits in all six experiments. The boxes span the interquartile range of the trait values, so that the middle 50% of the data lay within the box, with a horizontal line indicating the median. Whiskers extend beyond the ends of the box as far as the minimum and maximum values.

to varied availability of N per experiment (Khan et al., 2019) in interaction with genotype-specific behaviour, causing different trade-offs between rate and duration of tuber bulking and tuber final dry matter production. In case of RUE_T, wider and lower ranges of variation for RUE_T were observed in Exp. 3 and Exp. 5, respectively, than in the other experiments (Fig. 4). For the standard cultivars, a similar trend was observed (Table 3). The highest NUE_T was recorded in Exp. 3 and the lowest in Exp. 5, in line with lower tuber N uptake (11.3 g m^{-2}) observed in Exp. 3 and higher tuber N uptake (15.3 g m^{-2}) observed in Exp. 5. The NUE_T also varied within the experiments, with wide ranges of variation observed in Exp. 6 (Fig. 4).

3.4. Assessing effect of maturity classes in F1 segregating population

The results were further evaluated based on the variation among maturity classes within the F1 population. For the sake of simplicity, here we only discuss the relationship between maturity and resource use efficiencies.

There were wide ranges of variation for both RUE_T and NUE_T for each maturity class within the F1 population, except for RUE_T for the very early genotypes and for NUE_T for the very late genotypes (Fig. 5). RUE_T values were highest for very early to early/mid-early genotypes. In contrast, results indicated high NUE_T estimates for very late genotypes (Fig. 5).

3.5. Variances, coefficients of variation and heritability

Table 4 presents estimated values of phenotypic, genetic and environmental variances for all the parameters and the derived traits in the F1 population. The results revealed considerable phenotypic and genetic variances for all traits studied. All genetic and environmental components of variation were significant ($P < 0.01$) (Table 4). The genetic variance component contributed a major portion to the phenotypic variance in traits c_m, t_E and *ED* (Table 4). The contribution of the environmental variance to the phenotypic variance was relatively large in w_{max}, RUE_T and NUE_T (Table 4), probably because these traits were sensitive to N as we purposefully applied varied doses of N for creating contrasting environments (see Materials and Methods).

Estimates of phenotypic (CV_{Ph}), genetic (CV_G) and environmental (CV_E) coefficients of variation for traits across the six experiments are presented in Table 5. Estimates of CV_{Ph} ranged from 19.5 to 54.7%. These estimates were smallest for NUE_T and highest for *ED*. The CV_G

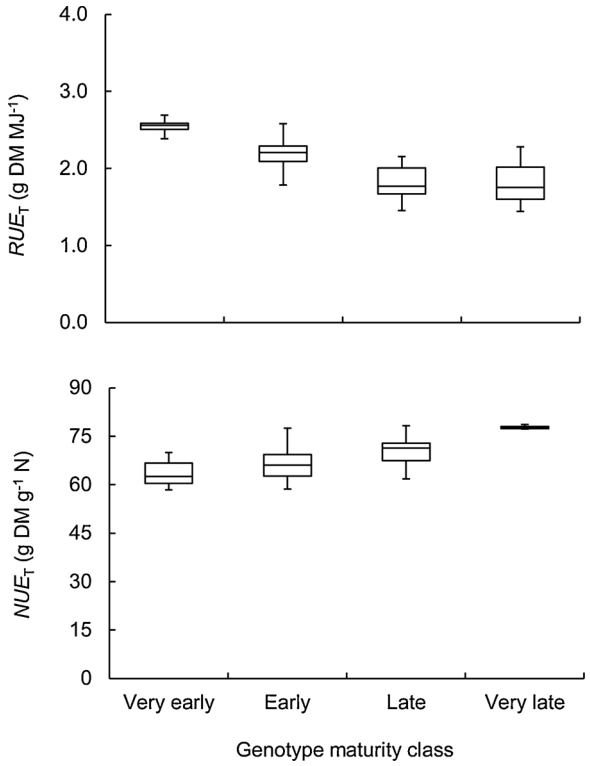

Fig. 5. Box plots illustrating the ranges of variation within an F1 population for resource (radiation, N) use efficiencies in four maturity classes as assessed by a physiological based maturity criterion developed by Khan (2012). The boxes span the interquartile range of the trait values, so that the middle 50% of the data lay within the box, with a horizontal line indicating the median. Whiskers extend beyond the ends of the box as far as the minimum and maximum values.

Table 4
Variance components for different traits within the F1 population across all six experiments. *td* stands for thermal day.

Parameter	σ^2_{Ph}	σ^2_E	σ^2_G	σ^2_ε
c_m (g DM m^{-2} *td*$^{-1}$)	297.5	107.6**	120.6**	69.2
t_E (*td*)	253.9	51.1**	169.1**	33.7
ED (*td*)	301.0	65.1**	197.3**	38.6
RUE_T (g DM MJ^{-1})	0.34	0.15**	0.09**	0.10
NUE_T (g DM g^{-1} N)	177.2	125.9**	20.7**	30.6
w_{max} (g m^{-2})	47025	14706**	9902**	22417

σ^2_{Ph}= phenotypic variance, σ^2_E = environmental variance, σ^2_G = genetic variance, σ^2_ε= residual variance.
** Significant at 1%.

Table 5
The phenotypic coefficient of variation (CV_{Ph}), genetic coefficient of variation (CV_G), environmental coefficient of variation (CV_E), and broad-sense heritability (H^2) of different traits within the F1 population across all six experiments. *td* stands for thermal day.

Parameter	Mean[1]	CV_{Ph} (%)	CV_G (%)	CV_E (%)	H^2 (%)
c_m (g DM m^{-2} *td*$^{-1}$)	35.5	48.6	30.9	29.2	91.3
t_E (*td*)	51.0	31.3	25.5	14.0	96.8
ED (*td*)	31.7	54.7	44.3	25.5	96.8
RUE_T (g DM MJ^{-1})	2.1	27.1	17.9	13.9	84.2
NUE_T (g DM g^{-1} N)	68.1	19.5	16.5	6.7	80.2
w_{max} (g m^{-2})	957	22.7	12.7	10.4	72.6

[1]Grand mean of the F1 segregating population across all six experiments.

estimates were higher than CV_E estimates for all traits investigated. However, the ratio of CV_G over CV_E was much greater in traits NUE_T, t_E and *ED* followed by RUE_T and w_{max}, whereas the lowest ratios were observed in c_m.

Broad-sense heritability (H^2) estimates across environments were high for most traits (Table 5). H^2 values >80% were recorded for c_m, t_E, *ED*, RUE_T, and NUE_T; H^2 for w_{max} was only 72.6%.

Table S1 provides detailed information on the most relevant traits of the 10 best performing genotypes of the F1 population.

3.6. GGE biplot analysis for NUE_T

The GGE biplots revealed that the 1st and the 2nd principal components accounted for 84.04% of the G × E variation (Fig. S2). The results further showed that two environments (Exps 4 and 5) were grouped together, suggesting they were highly correlated and relatively similar in the manner they discriminated among genotypes. These environments (Exps 4 and 5) fell relatively close to the origin, and apparently had little variability across genotypes. Markers of Exps 3 and 6 were standing furthest apart from the origin suggesting that these environments caused maximum variability across the genotypes. These environments might therefore be the main contributors to the overall G × E because of their lower and higher N availability, respectively, than the other environments.

3.7. Phenotypic and genetic correlations of model parameters and the secondary traits

Table 6 illustrates the phenotypic correlation coefficients among all the model parameters and secondary traits within the F1 population across all six experiments. All phenotypic correlations were highly significant ($P < 0.01$) (Table 6). There were strong negative phenotypic correlations between c_m and t_E ($r = -0.83$) and between c_m and *ED* ($r = -0.84$), suggesting trade-offs between tuber bulking rate and duration of tuber bulking. As mentioned earlier t_B was stable, which means that *ED* was almost exclusively determined by t_E; so, unsurprisingly, there was a strong positive correlation between t_E and *ED*. The results further revealed a negative correlation ($r = -0.37$) between RUE_T and NUE_T. This suggests trade-offs between RUE_T and NUE_T, mainly caused by their negative and positive relationships with *ED*, respectively (Table 6).

There were weak but negative ($r = -0.10$) phenotypic correlations between c_m and w_{max} (Table 6). However, the results indicated strong and positive phenotypic correlations between t_E, *ED* and w_{max} ($r = 0.55$ and 0.53, respectively). Apparently, both rate and duration of tuber bulking are important in determining final tuber yield. The positive role of NUE_T was evident from these results due to its positive phenotypic correlation with w_{max} ($r = 0.43$): genotypes with high NUE_T tended to yield high. The underlying relationships of w_{max} with important traits are described in detail in the next section.

Table 6 also illustrates the genetic correlation coefficients between the model parameters and secondary traits within the F1 population. The results of genetic correlations were in line with those of phenotypic correlations. As a whole the coefficient values for genetic correlations were comparatively higher than phenotypic correlations.

Table 6
Phenotypic (lower triangle) and genetic (upper triangle) correlation coefficients among all pair wise comparisons of different traits across six experiments of an F1 population of potato. *td* stands for thermal day.

Parameter	c_m	t_E	*ED*	RUE_T	NUE_T	w_{max}
c_m (g DM m^{-2} *td*$^{-1}$)	–	−0.91**	−0.93**	0.95**	−0.41**	−0.20**
t_E (*td*)	−0.83**	–	1.00**	−0.91**	0.65**	0.66**
ED (*td*)	−0.84**	1.00**	–	−0.93**	0.64**	0.64**
RUE_T (g DM MJ^{-1})	0.69**	−0.65**	−0.65**	–	−0.75**	−0.25**
NUE_T (g DM g^{-1} N)	−0.28**	0.53**	0.52**	−0.37**	–	0.43**
w_{max} (g m^{-2})	−0.10**	0.55**	0.53**	−0.02**	0.43**	–

** Significant at 1%.

Table 7
Path coefficient analysis of direct and indirect effects of different traits on the tuber dry yield (w_{max}) of an F1 population. *td* stands for thermal day.

Variable	[a]Effect
A_{sum} (*td* %)	
Direct effect	1.34
Indirect effect via	
c_m	−0.20
ED	0.05
RUE_T	−0.47
NUE_T	−0.02
Total correlation	**0.69**
c_m (g DM m^{-2} td^{-1})	
Direct effect	0.32
Indirect effect via	
A_{sum}	−0.85
ED	−0.05
RUE_T	0.47
NUE_T	0.01
Total correlation	**−0.10**
ED (*td*)	
Direct effect	0.06
Indirect effect via	
A_{sum}	1.21
c_m	−0.27
RUE_T	−0.46
NUE_T	−0.02
Total correlation	**0.53**
RUE_T (g DM MJ^{-1})	
Direct effect	0.69
Indirect effect via	
A_{sum}	−0.91
c_m	0.22
ED	−0.04
NUE_T	0.01
Total correlation	**−0.02**
NUE_T (g DM g^{-1} N)	
Direct effect	−0.04
Indirect effect via	
A_{sum}	0.78
c_m	−0.09
ED	0.03
RUE_T	−0.25
Total correlation	**0.43**

[a] Across six environments.

3.8. Assessing direct and indirect effects of model traits on tuber yield

Table 7 presents the results of the path coefficient analysis describing the direct and indirect effects of different traits on tuber dry matter yield (w_{max}), while Fig. 6 presents the path coefficient structural model describing important relationships among selected traits. The traits A_{sum}, RUE_T and c_m had the highest direct effects on tuber dry matter yield (w_{max}) (Table 7). Very low direct effects on w_{max} were observed for traits *ED* and NUE_T (0.06 and −0.04, respectively). The results further illustrated that the strong, direct effect of A_{sum} on w_{max} was the result of significant, strong, positive correlation of A_{sum} with *ED* ($r = 0.90$) and NUE_T ($r = 0.59$).

On the other hand, significant, strong, positive correlations ($r = 0.80$) between RUE_T and c_m were reflected in their strong, direct effects on w_{max}. Results further indicated that total correlation (i.e. sum of direct and indirect effects) between RUE_T and w_{max} was only −0.02. This was mainly due to the strong, negative indirect effect (−0.91) of A_{sum} on RUE_T. The total correlation between c_m and w_{max} was also low (−0.10). In this case the strong, indirect negative effect (−0.85) of A_{sum} on c_m also played its role. The above results were further supported by the strong, negative correlations between A_{sum} and RUE_T ($r = -0.79$) and c_m and A_{sum} ($r = -0.72$) (Fig. 6) and suggest that genotypes with higher A_{sum} exhibited slow tuber bulking rate (c_m) in the linear phase and were less efficient in converting the radiation intercepted into dry matter yield of tubers (i.e. with smaller RUE_T). This could be related with the assimilation of dry matter and its distribution within the plant. Higher investment in terms of biomass allocation to vegetative organs may give high A_{sum} and thereby higher total biomass, but on the other hand a relatively low proportion may be used for the production of tubers, especially if the maintenance requirements are high. Excessive vegetative growth can be compensated to only a limited extent by redistribution of dry matter from vegetative parts to tubers. Therefore, A_{sum}, RUE_T and c_m could be the traits having the strongest influence on the temporal dynamics of yield formation in potato.

3.9. QTL detection

In total, 16 QTLs were identified for our model traits determining tuber bulking dynamics on both SH and RH parental genomes across all

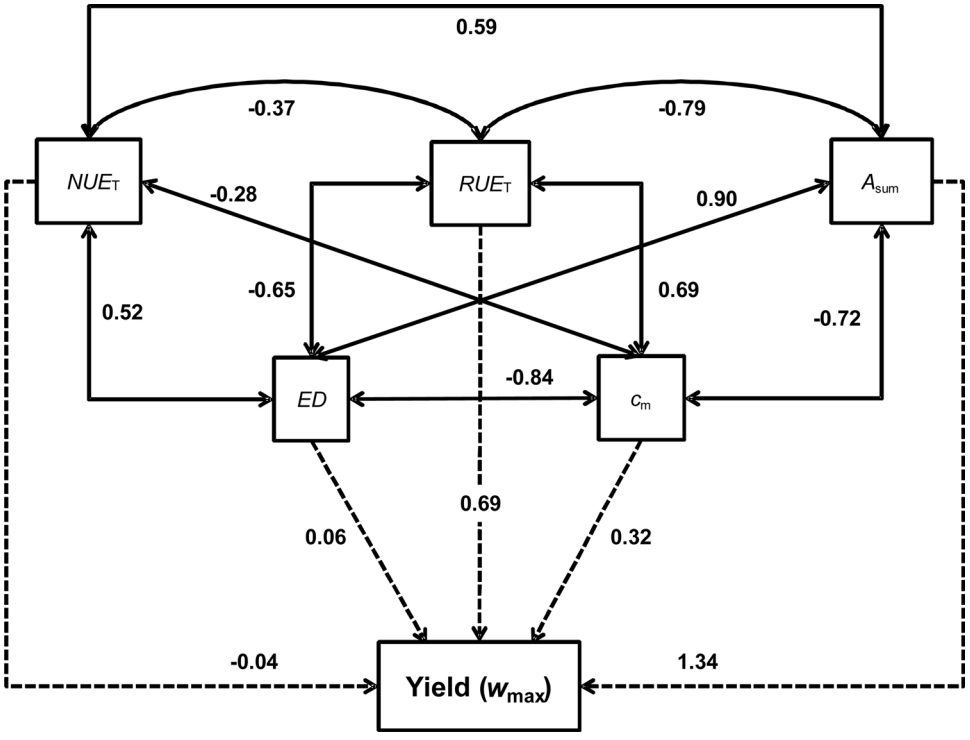

Fig. 6. Path coefficient structural model describing direct and indirect effects of different traits on the maximum tuber dry matter at crop maturity (w_{max}) across six experiments for an F1 segregating population of potato. The solid line represents the correlation coefficient between two predictor variables; dashed line represents the path coefficient from the predictor variable to response variable (w_{max}).

Table 8
Main characteristics of quantitative trait loci (QTL) identified for different traits within the 'SH × RH' population per individual experiment (i.e. environment.). Data given in the table are from the CIM mapping method. QTLs marked as bold are detected only by the CIM method, otherwise by both the CIM and SIM methods. Exp., experiment; position, position of maximum $-\log_{10}(P)$; a, additive effect of the presence of parental allele at a marker; R^2, the individual contribution of one QTL to the variation in a trait; global R^2, the fraction of the total variation explained by QTLs of the same trait within single environment ; *td*, thermal day. Symbols '−' and '*' mean no QTL or data, respectively.

Parameter	Exp.	QTL	Linkage group	Marker name	Position (cM)	$-\log_{10}(P)$	a	R^2	Global R^2
c_m	1	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	24.97	38.833	0.57	0.63
(g DM m^{-2} td^{-1})		**189_8_83**	**RH VIII**	**PAT/MAGG_149.8_8_83**	**74.5**	3.62	12.058	0.07	
	2	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	22.93	53.663	0.56	
	3	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	6.84	35.736	0.24	0.35
		188_8_83	**RH VIII**	**PAG/MAGC_298.8_8_83**	**76.1**	4.01	23.719	0.13	
	4	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	24.54	51.958	0.57	
	5	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	17.74	21.488	0.48	
	6	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	18.80	34.060	0.50	
t_E (*td*)	1	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	67.62	−55.624	0.79	
	2	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	36.78	−54.458	0.68	
	3	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	19.38	−38.459	0.63	
	4	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	34.70	−38.968	0.65	0.70
		48_1_71	**RH IB**	**EACAMCGT_296.2_1_71**	**33.9**	3.67	9.561	<0.1	
	5	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	51.11	−24.133	0.63	
	6	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	52.33	−49.912	0.74	
ED (*td*)	1	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	67.99	−60.873	0.79	
	2	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	37.54	−60.247	0.68	
	3	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	18.76	−41.077	0.62	
	4	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	36.23	−43.013	0.66	0.71
		48_1_71	**RH IB**	**EACAMCGT_296.2_1_71**	**33.9**	3.70	10.369	<0.1	
	5	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	52.34	−66.019	0.74	
	6	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	52.35	−52.988	0.74	
RUE_T	1	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	22.72	1.732	0.55	
(g DM MJ^{-1})	2	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	14.87	1.259	0.43	0.47
		121_5_46	RH V	EAACMCAG_231.8_5_46	52.6	6.74	0.402	0.15	
	3	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	9.862	1.329	0.39	
	4	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	16.32	1.135	0.45	
	5	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	6.67	0.641	0.24	
	6	−	−	−	−	−	−	−	
NUE_T	1	*	*	*	*	*	*	*	
(g DM g^{-1} N)	2	*	*	*	*	*	*	*	
	3	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	3.60	−8.790	0.12	0.39
		84_3_3	RH III	PAT/MAAC_298.3_3_3	0	4.29	8.881	0.11	
		204_10_34	RH X	EAACMCCA_216.8_10_34	31.4	4.99	−10.835	0.17	
	4	75_2_51	RH II	EAGTMCAC_249_2_51	50.9	3.83	−8.352	0.15	
	5	**6_1_2**	**SH I**	**PAC/MACT_232.4_1_2**	**6.6**	3.29	−6.291	0.10	0.27
		68_2_32	RH II	PAT/MAAC_570.4_2_32	32.2	4.69	−8.005	0.16	
	6	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	18.91	−30.187	0.48	0.56
		179_5_77	**SH V**	**PAC/MATA_201.4_5_77**	**77.2**	3.70	10.299	0.03	
w_{max} ($g\ m^{-2}$)	1	117_5_37	RH V	EACAMCGT_250.1_5_37	35.7	3.82	274.016	0.15	
	2	131_5_55	RH V	PAC/MATA_99.4_5_55	62.6	4.36	246.053	0.18	
	3	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	15.84	−630.531	0.44	0.53
		81_2_75	**RH II**	**PAC/MAGG_527.2_2_75**	**79.1**	4.10	−252.070	0.06	
	4	18_1_32	SH I	EAACMCAG_187.9_1_32	36.3	3.52	244.584	0.13	
	5	−	−	−	−	−	−	−	
	6	116_5_17	RH V	EAGAMCTC_470_5_17	18.2	8.94	−458.440	0.29	0.41
		99_4_35	**RH IV**	**EACAMCTG_69.5_4_35**	**11.2**	4.46	256.493	0.08	

Table 9
List of parental linkage groups with major and additional minor QTLs. *td* stands for thermal day.

Parameter	SH linkage group	RH linkage group	
	Minor QTLs	Major QTL	Minor QTLs
c_m (g DM m^{-2} td^{-1})	−	V	VIII
t_E (*td*)	−	V	IB
ED (*td*)	−	V	IB
RUE_T (g DM MJ^{-1})	−	V	−
NUE_T (g DM g^{-1} N)	I, V	V	II, III, X
w_{max} ($g\ m^{-2}$)	I	V	II, IV

six environments. In the SH genome, three QTLs were associated with two linkage groups (I and V). Thirteen QTLs linked to seven linkage groups (IB, II, III, IV, V, VIII, and X) on the RH genome.

Table 8 summarises the list of QTLs detected, their parental chromosomes and map positions and their characteristics (i.e. additive effects and variance explained (R^2)) for each of the traits investigated for individual environments. All QTLs detected were significant at ($P < 0.05$) with $-\log_{10}(P)$ values ranging from 3.52 to 67.99. The total fraction of phenotypic variance explained by effects of individual QTLs ranged from <0.1% to 79%. The percentage of phenotypic variance was even higher when considering their global effects (ranging from 27% to 71%) (Table 8).

QTLs with major effects were associated with paternal (RH) linkage group RH V, where maximum number of four QTLs was detected (Table 9). One particular QTL (i.e. 116_5_17) on paternal (RH) linkage group V at position 18.2 cM was detected for all traits across environments with a major additive effect and explained more than 50% of the total phenotypic variance (Table 9). It was interesting to note that for traits such as NUE_T and w_{max}, results indicated a significant decrease in additive effects of this QTL in the low N environment (i.e. Exp. 3), which might suggest that alleles on paternal chromosome V at position 18.2 cM may reduce NUE_T less drastically under such low N conditions. This also suggests that this particular QTL is sensitive to the

Table 10
List of co-localised QTLs (i.e. QTLs were same for more than one trait), marked as bold and independent QTLs (i.e. QTLs detected only once for a particular trait in any experiment (environment)).

QTL	Linkage group	Marker name	Position (cM)	Exp. 1	Exp. 2	Exp. 3	Exp. 4	Exp. 5	Exp. 6
6_1_2	SH I	PAC/MACT_232.4_1_2	6.6					NUE_T	
18_1_32	SH I	EAACMCAG_187.9_1_32	36.3				w_{max}		
179_5_77	SH V	PAC/MATA_201.4_5_77	77.2						NUE_T
48_1_71	**RH IB**	**EACAMCGT_296.2_1_71**	**33.9**				t_E, *ED*		
68_2_32	RH II	PAT/MAAC_570.4_2_32	32.2					NUE_T	
75_2_51	RH II	EAGTMCAC_249_2_51	50.9				NUE_T		
84_3_3	RH III	PAT/MAAC_298.3_3_3	0			NUE_T			
99_4_35	RH IV	EACAMCTG_69.5_4_35	11.2						w_{max}
116_5_17	**RH V**	**EAGAMCTC_470_5_17**	**18.2**	c_m, t_E, *ED*, RUE_T	c_m, t_E, *ED*, RUE_T	c_m, t_E, RUE_T, NUE_T, w_{max}	c_m, t_E, *ED*, RUE_T	c_m, t_E, *ED*, RUE_T	c_m, t_E, *ED*, NUE_T, w_{max}
117_5_37	RH V	EACAMCGT_250.1_5_37	35.7	w_{max}					
121_5_46	RH V	EAACMCAG_231.8_5_46	52.6		RUE_T				
131_5_55	RH V	PAC/MATA_99.4_5_55	62.6		w_{max}				
189_8_83	RH VIII	PAT/MAGG_149.8_8_83	74.5	c_m					
188_8_83	RH VIII	PAG/MAGC_298.8_8_83	76.1			c_m			
204_10_34	RH X	EAACMCCA_216.8_10_34	31.4			NUE_T			

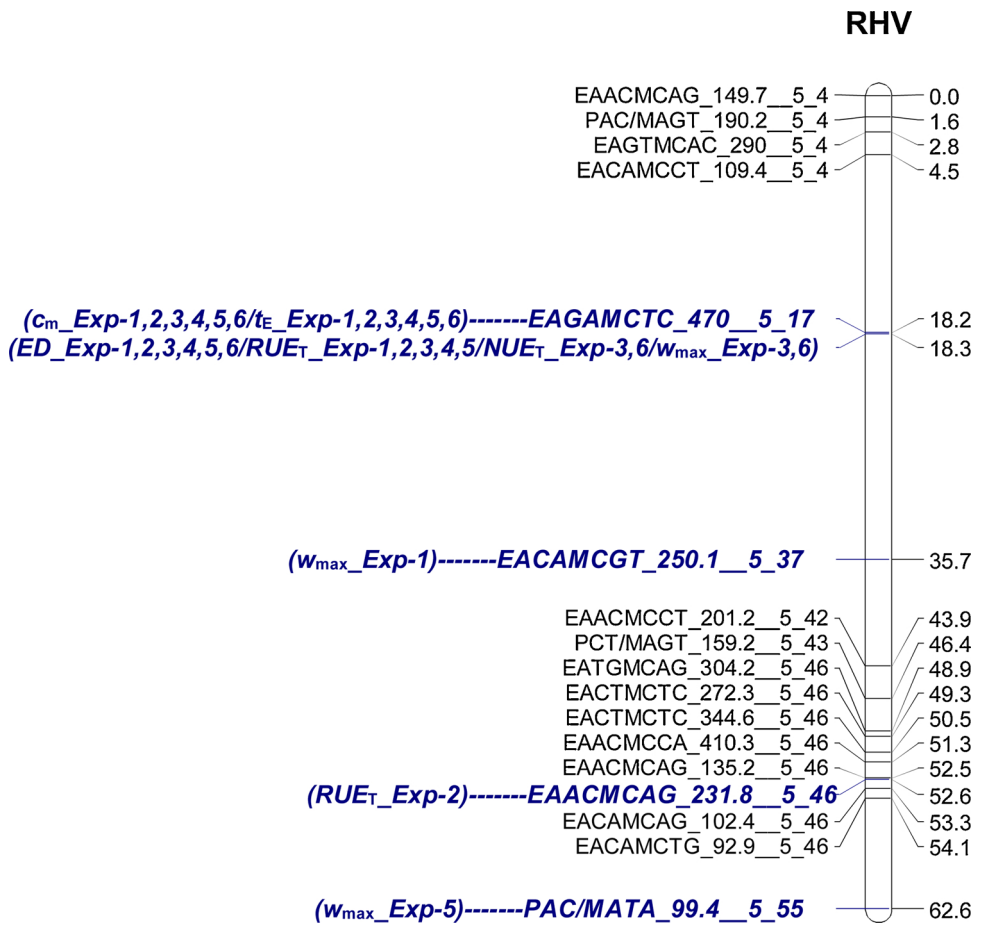

Fig. 7. Locations of AFLP markers on paternal (RH) linkage group V. The number on *right side* is the genetic distance in centiMorgans (cM), codes on *left side* are marker designations. The marker in bold shows the position of QTL associated with traits, across environments.

environment, particularly N, as negative effects caused by alleles associated with this QTL changed in magnitude with respect to N availability. We even found that mean w_{max} for Exp. 3 was even higher than for Exp. 6 with high N availability (Table 3). As previously mentioned, variability among the genotypes was higher in Exp. 3 for most traits. It would be expected that some genotype were most effective in this environment especially for NUE_T as suggested by the biplot analysis (Fig. S2). Therefore a focus on why particular genotypes perform exceptionally well in low or high input situations could enable selection strategies to be developed for improved varieties.

Additional QTLs with minor effects were mostly associated with only paternal (RH) linkage groups for traits (c_m, t_E and ED), whereas both maternal (SH) and paternal (RH) linkage groups were associated with traits NUE_T and w_{max} for minor QTLs (Tables 8 and 9).

Paternal QTL (116_5_17) was associated with its negative additive effects for most of the traits including tuber yield (w_{max}) *per se* except

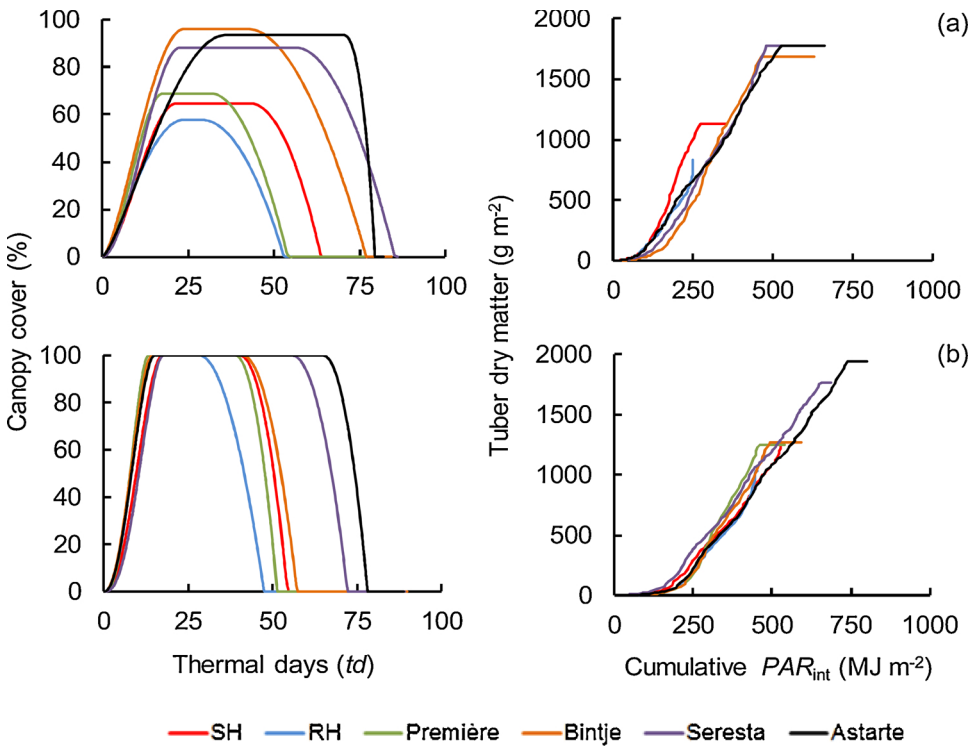

Fig. 8. Schematic representation of the course of green canopy cover (data from Khan, 2012) and tuber dry matter production of 4 standard cultivars, and 2 parental genotypes (SH and RH) for (a) low N situation (Exp. 3) and (b) optimum N situation (Exp. 6) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

for c_m and RUE_T where this QTL showed the positive effects. This indicates that RH alleles for this QTL caused synergistic effects during the early phase of plant growth when the tuber bulking rates (c_m) and RUE_T were at their maximum. It was evident from our results that variation in tuber yield was associated with variation in rate (c_m) and duration (*ED*) of tuber bulking and associated extent of radiation interception (A_{sum}) (Fig. 6). However, these components are not physiologically independent as genotypes with a high tuber bulking rate may effectively limit the crop growth and duration (via enhanced internal plant competition) leading to their identified 'earliness'.

We also observed co-localisation of QTLs with many traits. For instance clustering of many QTLs were found on position 18.2 cM on the paternal (RH) linkage group (Table 10). Here most of the traits (e.g. c_m, t_E and *ED*) were tightly linked with QTL 116_5_17 in most environments (Fig. 7). This could mean that this QTL is playing a pleiotropic role in determining these traits. The strong genetic correlations between these traits confirm these relations (Table 6). This may indicate the difficulties of manipulating correlated traits simultaneously. However, QTLs with similar behaviours could also be interesting targets for breeding programmes as they are more likely to be stable under various environments. Our results also indicated a number of independent QTLs mainly for NUE_T as they did not coincide with other traits (Table 10).

Only one QTL 116_5_17 on RH V showed up in all the experiments (Table 8). This QTL was therefore stable across the environments and did not show much QTL × E.

4. Discussion

4.1. Model performance and limitations

The combined Eqs. (1)–(3) (see also Fig. 1) were useful in assessing the phenotypic, genetic and environmental variation in the most important model traits (Tables 1–2; Figs S1, 2–4). However, due to the limited number of observations per genotype per experiment during the early stages of tuber bulking, it was not possible to properly analyse the genetic variation in t_B and w_B. Parameter t_B was calculated from Eq. (4), in which w_0 and r_m were fixed, whereas w_B was calculated from r_m (fixed) and c_m. *ED*, calculated as $t_E - t_B$, showed a very strong correlation with t_E as t_B was calculated using fixed parameters w_0 and r_m. Our genetic analysis of tuber bulking dynamics is therefore mainly based on the primary model parameters c_m, w_{max}, and t_E. *ED* is closely correlated to t_E. Resource use efficiencies (RUE_T and NUE_T), however, are also relevant as secondary traits.

4.2. Genetic variation in model traits and influence of environment on trait expression

Tetraploid potatoes are typically more vigorous and higher-yielding than diploids (DeMaine, 1984; Hutten, 1994). The somewhat decreased vigour and yield in diploids may be due to their ploidy reduction and inbreeding depression (Kotch, 1987). Our results indicated that significant genetic variability existed among standard cultivars and within the F1 population for c_m, t_E, *ED*, w_{max}, RUE_T and NUE_T (Tables 1 and 2, 4 and 5; Table S1; Figs. 2–4). It is therefore possible to utilise such wide genetic variability available for breeding programmes aimed at improving tuber bulking dynamics, resource use efficiency and ultimately tuber dry matter production.

The ranking of genotypes changed across the environments for most model and secondary traits (Table S1), i.e. there were cross-over G × E interactions (*sensu* Baker, 1988). Cross-over types of interactions are important to breeders and agronomists for identifying adapted traits and may enable selection strategies for developing improved varieties. Yet, some genotypes that were best yielding in N sufficient environments also yielded relatively very well under the low N conditions of Exp. 3 (e.g. SHRH42-H12, SHRH-406, SHRH53-J8, SHRH89-M3 and SHRH83-L9; Table S1), demonstrating their wide adaptation.

Overall, results showed that N availability might be one of the key drivers for causing trade-offs between the physiological traits in different environments (Table 3; see Table 6 for phenotypic and genotypic correlation coefficients and Table 7 and Fig. 6 for path coefficient analysis). The GGE biplot analysis (Fig. S2) allowed visual examination of the relationships among the test environments, genotypes, and the G × E interaction (Yan et al., 2000).

N availability and its interaction with the genotype's maturity type

significantly contributed to the G × E interaction of the growth and development related processes in potato in the F1 population of genotypes.

However, the high heritability estimates, especially of c_m, t_E and *ED* (Table 4) prove that some of our model traits are strongly expressed across a range of environmental conditions and therefore may respond to selection (Falconer and Mackay, 1996).

4.3. QTL analysis

We found 16 QTLs for c_m, t_E, *ED*, w_{max}, RUE_T and NUE_T (Table 8), mainly from the RH genome (Table 9; Fig. 7). Many QTLs for different model and secondary traits co-localised (Table 10). This is partly associated with our modelling methods, but also partly with the physiological and genetic linkages between our model and secondary traits.

Several authors have indicated that some yield QTLs coincide with those for component traits, whereas other yield QTLs map independently from component traits (Xiao et al., 1995; Bezant et al., 1997). In our analysis, this was mostly evident for traits RUE_T, NUE_T and w_{max}.

Few QTLs were expressed in one environment but not in the other (Table 8). The low repeatability of some QTLs across the environments suggests QTL × E interaction. For these traits the environmental variance component contributed majorly to the total phenotypic variance for these traits (Table 4). QTLs controlling such traits often show low stability (Veldboom and Lee, 1996; Reymond et al., 2004). Many researchers have identified loci that interacted with the environment in other plant species e.g. yield in barley (Yin et al., 1999; Teulat et al., 2001; Voltas et al., 2001).

4.4. Integrating canopy cover dynamics with tuber bulking dynamics as affected by nitrogen and maturity type

Our results, described in this paper and its companion paper (Khan et al., 2019), indicated that an ideal potato genotype is characterised by green canopy cover that intercepts solar radiation for as long as possible (i.e. with high A_{sum}) during the available growing season to accumulate as much dry matter as possible maintaining a maximum capacity to divert dry matter to the tubers (i.e. with greater period of tuber bulking (*ED*)) without compromising the optimal levels of growth rates (c_m) and RUE_T ensuring highest possible economical tuber yields. Figure 8 schematically highlights various situations of potato ideotypes under both high N and low N conditions. Figure 8 underlines the relation between maximum canopy cover and canopy cover duration on the one hand and rate and duration of tuber bulking on the other hand. It also clearly demonstrates the interaction between nitrogen supply and maturity type in determining canopy cover dynamics and tuber bulking dynamics. Based on an analysis as illustrated in Fig. 8, agronomists and breeders could strive to obtain an optimum combination of yield components that would best suit the requirement for high yielding ability in potato genotypes for any particular environment.

We surmise that such within and between experimental variations (Tables 1–4) are the combined result of differences in A_{sum} associated with variation in maturity class and with varied availability of N (Khan et al., 2013, 2019). Plant N status and crop growth cycle interact to affect RUE_T and NUE_T, in addition to the effects of other factors (Green, 1987; Muchow and Davis, 1988; Sinclair and Horie, 1989; Trapani et al., 1992; Vos, 2009).

Maturity type (as illustrated in Figs. S1, 3, 5 and 8) was a dominant factor in the expression of performance of the cultivars and the F1 genotypes. This is in line with Kooman and Rabbinge (1996) and Spitters (1988), who reported that, compared with late cultivars, early potato cultivars allocate a larger part of the available assimilates to the tubers early in the growing season, resulting in shorter growing periods and also lower yields. On the other hand, late-maturing cultivars combine a long canopy cover with a long tuber-bulking period (*ED*) and therefore achieve more tuber dry matter yield (w_{max}) per unit of N uptake than mid-early and early-maturing cultivars (Zebarth et al., 2008). Physiological model traits could help in elucidating the effects of maturity type of a specific cultivar or genotype on yield-determining processes of potato (Khan et al., 2013).

A number of studies have also shown a varying response to rates of N on the dry matter yield production in potato crops (e.g. Porter and Sisson, 1991a; Maier et al., 1994; Belanger et al., 2000; Vos, 2009). Responses to N can vary greatly from site to site and from year to year. They depend on the capacity of the soil to supply N when the crop needs it (Meyer and Marcum, 1998) and on the capacity of the crop to make efficient use of that N. This might be due to the indirect effects of different maturity groups within the F1 population (Khan et al., 2013).

4.5. Resource use efficiencies

The calculated values of RUE_T (Tables 1–6; Table S1; Figs. 4–5) were within the range reported in the literature for *Solanum tuberosum* genotypes under temperate conditions (Scott and Wilcockson, 1978; Allen and Scott, 1980; Khurana and McLaren, 1982; MacKerron and Waister, 1985; Spitters, 1988; Stol et al., 1991; Kooman and Haverkort, 1995), and significantly differed among environments. They were lower and showed more variation for late-maturity types than for early-maturity types. These results were expected because cumulative light absorption tended to be greater for the later-maturing cultivars (Khan et al., 2019), but they exhibited a lower harvest index (data not shown). Early-maturing cultivars allocate already in an early phase the major part of their current assimilates to tuber growth, at the expense of canopy growth (Spitters, 1988; Kooman and Rabbinge, 1996). Without significant formation of new leaves, the canopy senesces early. Early cultivars had, therefore, a smaller cumulative light absorption but a higher harvest index and RUE_T. On the other hand, late-maturing cultivars maintain green, active foliage for an extended period of time (Spitters and Schapendonk, 1990), but this investment in canopy growth is at the expense of tuber growth.

The calculated values of NUE_T (Tables 1–6; Table S1; Figs. 4–5) were higher and less variable for very late cultivars than for very early cultivars, showed a very large variation among F1 genotypes and significantly differed among environments. A model analysis by Khan et al. (2014) indicated that genotypes with higher N uptake and lower tuber N concentration yielded more. These effects could be mainly associated with differences in maturity type (Van Kempen et al., 1996; Zebarth et al., 2004; Ospina et al., 2014). Late-maturing cultivars combine a long canopy cover with a long tuber bulking period (*ED*) and therefore achieve more tuber dry matter yield (w_{max}) per unit of N uptake than mid-early and early-maturing cultivars (Zebarth et al., 2008). Previous research has also demonstrated that there is significant variation in crop uptake and use efficiency of N among commercial potato cultivars and advanced clones (Kleinkopf et al., 1981; Lauer, 1986; Sattelmacher et al., 1990; Porter and Sisson, 1991a, b; Johnson et al., 1995; Errebhi et al., 1998a, b,1999; Sharifi et al., 2007; Zebarth et al., 2004, 2008; Ospina et al., 2014).

The resource use efficiencies showed relatively high heritability estimates (Table 5). Variation in resource use efficiency within maturity groups could be further genetically manipulated for improving resource (radiation, N) use efficiency characteristics in potato.

5. Conclusions

We presented a robust physiological framework for quantitatively dissecting the phenotypic variation in potato tuber bulking dynamics to aid understanding of underlying causes while simultaneously providing means to predict emergent phenotypic consequences by integrating effects of variation in component factors and processes leading to yield formation in potato.

The parameters of the growth functions determining the temporal

dynamics of tuber bulking have a clear meaning with regards to the processes of resource capture by the crop, thus allowing an easier interpretation of the value and magnitude of the growth components associated with variation in tuber yield among cultivars and/or genotypes. However, these components are not physiologically independent as genotypes with a high tuber bulking rate may have short bulking duration via enhanced internal plant competition.

N availability was the driving factor for causing trade-offs between the physiological traits in different environments. Moreover, results suggested that N availability and its interaction with genotype's maturity type contributed significantly to the G × E interaction of the growth and development related processes in potato.

The QTL results showed that nearly all physiological traits co-localised at one particular chromosomal position at 18.2 cM on paternal (RH) linkage group V with major effects. This QTL was associated with major additive effects on most traits and explained most (> 50%) of the total phenotypic variance. This suggested the pleiotropic nature of the QTL for most traits determining crop maturity and tuber yields. A number of QTLs for traits were not detected when tuber yield *per se* was subjected to QTL analysis. The phenotypic variance explained by the QTLs for tuber yield *per se* was also lower than for other traits.

Our results also confirmed previous studies that most traits linked to linkage group V were related with maturity. This linkage group is mainly controlling earliness in genotypes because of the negative additive effects associated with a major QTL found here for most traits including tuber yield *per se*.

This study along with its companion study (Khan et al., 2019) yielded estimates for agronomically relevant crop physiological and genetic characteristics and/or traits that are promising for defining future breeding strategies in potato. High genetic variability along with high heritability for most of these traits indicated that a more general breeding goal, increased tuber dry matter yield by indirect selection for optimal combination of important physiological traits can be achieved.

Declaration of Competing Interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.fcr.2019.107582.

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