Genetic mapping of tuber size distribution and marketable tuber yield under drought stress in potatoes

Ernest B. Aliche · Marian Oortwijn · Tom P. J. M. Theeuwes · Christian W. B. Bachem · Herman J. van Eck · Richard G. F. Visser · C. Gerard van der Linden

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Abstract Drought sensitivity of potato leads to a reduction in total tuber yield and marketable yield. An investigation of drought effects on tuber yield attributes will facilitate our understanding of how to reduce such huge yield losses. We have evaluated tuber yield, tuber size distribution and marketable yield of a set of 103 European commercial potato cultivars under irrigated and non-irrigated conditions in the field. The multi-year results from two locations, Connantre, France (2013–2015) and Nieuw-Namen in Zeeland, The Netherlands (2013–2014), were analysed. We used Normal and Gamma Distribution models to describe the tuber size distribution of tuber fresh weight and tuber number, respectively. The interactions among parameters of tuber size distribution and total/marketable tuber yield traits were

analysed using correlation matrices and biplots. Finally, we used a 14K Infinium SNP marker array to find associations between the parameters or traits and genetic loci on the potato genome. Late foliage maturity facilitated a wider spread of tuber size distribution in favour of larger-sized tubers. Drought effects on total yield were representative of their impact on marketable yield, however, absolute values of total tuber number may not be indicative of marketable number of tubers. We found significant marker-trait associations between a region on chromosome 3 and the spread of tuber number distribution, size class with maximum tuber number and marketable fractions of tuber number and tuber weight. These findings will contribute to improvement and selection for drought tolerance in potato.

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E. B. Aliche · M. Oortwijn · T. P. J. M. Theeuwes · C. W. B. Bachem · H. J. van Eck · R. G. F. Visser · C. G. van der Linden (✉)
Plant Breeding, Wageningen University & Research, Droevendaalsesteeg 1, 6708 PB Wageningen, The Netherlands
e-mail: gerard.vanderlinden@wur.nl

E. B. Aliche
Graduate School Experimental Plant Sciences,
Droevendaalsesteeg 1, 6708 PB Wageningen, The Netherlands

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Abbreviations

<i>TBW</i>	Tuber fresh weight
<i>TBN</i>	Tuber number
<i>TBW MX</i>	Maximum tuber fresh weight observed among size classes
<i>TBW mcs</i>	Average tuber size of the class at which <i>TBW MX</i> occurs
<i>TBW spread</i>	Wideness or spread of tuber size distribution of tuber fresh weight
<i>TBN ms</i>	Tuber number mean size

<i>TBN</i>	Wideness or spread of tuber size
<i>spread</i>	distribution of tuber number
<i>TBW CV</i>	Coefficient of variation for tuber fresh weight
<i>TBN CV</i>	Coefficient of variation for tuber number
<i>TBW mf</i>	Marketable fraction of tuber fresh weight
<i>TBN mf</i>	Marketable fraction of tuber number
<i>TSD</i>	Tuber size distribution

Introduction

Potato is a perennial plant that is cultivated today as an annual crop (Zarka et al. 2009). It is grown for its underground storage organs, the tubers. Potato is consumed by more than a billion people globally, and more than 230 million tonnes is consumed yearly (Devaux et al. 2014). Therefore, it is recognized as a food security crop by the Food and Agriculture Organization (FAOSTAT 2014). Additionally, potato tubers are utilized for industrial production of starch and other uses (Kraak 1992; Stearns et al. 1994). Potato yield under optimal conditions of growth is over 47 tonnes/ha (FAOSTAT 2014), even up to about 50–60 tonnes/ha in The Netherlands. However, under sub-optimal conditions like water limitation, yield is drastically reduced (Trebejo and Midmore 1990).

Climate change makes it increasingly difficult to predict the occurrence and scale of drought periods (Lal 2014). The most devastating effects of drought stress on potato occur when water limitation coincides with the tuberization stage of plant development (Daryanto et al. 2016). Tuberization in potato involves the differentiation of stolon tips into young tubers (tuber initiation) and the bulking of the young tubers (Catchpole and Hillman 1969; Dutt et al. 2017; Minhas et al. 2004; O'Brien et al. 1998; Ozgen et al. 2003). Drought may affect tuberization by reducing the number of tubers that are initiated (Mackerron et al. 1988). Also, drought may reduce the filling of the tubers with assimilates in the tuber bulking phase of plant growth (Lahlou et al. 2003). In both cases, the result is a reduction in tuber yield. Most potato drought research efforts have focussed on understanding the reduction in total tuber yield. However, the implication for marketable tuber yield requires attention as well. In many studies, the attention was limited to few genotypes at a time while only a few studies used

variety panels, thus not allowing the identification of genetic factors influencing the behaviour of the selected varieties.

Marketable tuber yield consists of the fraction of total yield that meets the size, shape, weight and quality requirements of the intended market (Love and Thompson-Johns 1999). It has been demonstrated that marketable tuber yield is dependent on mean tuber size, that is, both total tuber weight and total number of tubers (Harris 2012). Therefore, it was recommended to grow potato cultivars that produce fewer tubers in drought-prone areas (Mackerron et al. 1988). The lower number of tubers are more likely to be bulked when photo-assimilates are limited during drought, thus increasing the average size of the tubers. However, the bulking of the tubers also depends on the time of tuber initiation in the growing season and the maturity type of the potato (van der Zaag 1992). Drought is known to delay tuber initiation (Walworth and Carling 2002). When the drought persists to later stages of the growing season, tubers that are formed towards the end of the growth cycle may hardly be bulked. In this way, drought reduces the marketable fraction of potato tuber yield (Cantore et al. 2014; Luitel et al. 2015; Nouri et al. 2016; Vayda 1994).

Potato cultivars with different genetic backgrounds respond differently to drought in terms of tuberization. Some cultivars have a fixed tuber initiation period, while others may initiate tubers several times during the growing season (Celis-Gamboa et al. 2003; Walworth and Carling 2002). These genotypic variations and the corresponding unique drought responses complicate the understanding of potato tuber yield marketability under dry conditions. Consequently, modelling techniques are used to study potato tuber size distribution in order to gain more insight. For instance, potato tuber size distribution has been modelled using the truncated Gaussian or normal distribution model to describe tuber weight and tuber number distribution across various size classes (Mackerron et al. 1988; Ospina et al. 2014; Sands and Regel 1983). Also, the gamma distribution model has been shown to have a better fit than the normal and log-normal models for describing tuber number distribution into size classes (MAFF 2000). Some of the insights gained from the modelling approaches include the spread and skewness of tuber size distribution, which can provide information on the

marketable proportion of tuber yield. However, not much research has been conducted towards understanding the genetic basis of the model parameters that describe total and marketable tuber size distribution, although there is an indication that tuber size distribution in potato is under quantitative inheritance (Celis-Gamboa 2002). Also, the factors that influence tuber size distribution and marketable yield, including stolon branching, the duration of the stolon tip swelling period and tuber resorption, are genotype-dependent (Celis-Gamboa et al. 2003; Pasare et al. 2013). These observations indicate the need to further investigate the role of genetic factors in determining tuber size distribution and marketable yield, and how these are influenced by stress conditions.

In this study, we have used the best fitting models after comparing different models to extract tuber size distribution parameters in order to evaluate their effects on marketable yield in a set of 103 potato cultivars grown in two locations—Connantre (France) and Zeeland (The Netherlands) in three and two years, respectively. Furthermore, we have used a 14K SNP array from the potato genome to identify genetic loci that may be associated with total yield, marketable yield, and any of the tuber size distribution parameters.

Materials and methods

Planting and data collection

A set of 103 commercial potato cultivars representing a significant proportion of the European potato gene pool was used in this study. This set consists of different genetic backgrounds, maturity classes, and market niches (Supplementary Table 2). The maturity classes comprise 10 late, 46 intermediate and 47 early maturing cultivars. Foliage maturity was scored on a scale of 4 (very late maturing) to 8.5 (very early) according to the scoring scheme of CBSG (Centre for Biosystems Genomics), The Netherlands (Björn et al. 2010). The plants were grown in the field at Connantre, France in 3 years (2013–2015) and at Nieuw-Namen, Zeeland (abbreviated as Zeeland throughout the paper), The Netherlands in 2 years (2013–2014). Plants in the control block were irrigated weekly with an average of 13 mm per irrigation session during the dry period of the growing season, which lasted for

about 2 months in Connantre and 2 weeks in Zeeland, amid limited and light showers respectively. Irrigation was withheld from the stress block during the early plant growth phase in Connantre (2014 trial) and at later developmental stages in the Connantre 2015 trial as determined by the rainfall patterns in both years (Aliche et al. 2018). There was no defined rainfall pattern in Zeeland trials and as such irrigation was minimal. The 103 cultivars were randomized as plots in each block. Each plot had eight plants and there were two plots for each cultivar within a block. The environmental conditions were monitored on site in the Connantre trial in 2014 and 2015 but not at the site in The Netherlands. Foliage development was measured weekly using a SONY DSC-W610 digital camera mounted on a rectangular frame and placed above the plants to capture canopy ground cover. Using DIPimage toolbox in MATLAB, the canopy pictures were analysed to extract quantitative data of foliage development. At the end of the growing season, tuber fresh weight (TBW) and tuber number (TBN) were measured. Also, a Smart Grader was used to grade the tubers into the various tuber size classes: 0–40 mm, 40–50 mm, 50–60 mm, 60–70 mm and > 70 mm. TBW and TBN per size class were scored as well.

Processing tuber size data

The data of tuber fresh weight per size class and tuber number per size class formed unique tuber size distributions. The tuber size distribution for tuber fresh weight per size class was modelled using a Gaussian normal distribution equation in DataFit (version 9.1.32) (Ospina et al. 2014):

$$TBW = MX * \exp(-(mcl - B)^2 / A) \quad (1)$$

where TBW is the tuber fresh weight, MX is the maximum fresh weight observed among the size classes, mcl is the mid-point of each size class boundaries, B is the average size of the class at which MX occurs, and A is the dispersion parameter showing the spread of the distribution across the size classes. An illustration of the model parameters is shown in the graphical representation in Fig. 1. For clarity, in the results section MX is used as *TBW MX*, B as *TBW mcs*, and A as *TBW spread*.

Fig. 1 Graphical representation of a normal distribution graph showing the spread (σ) and mean (μ) of the distribution. In our dataset, σ represents the dispersion parameter (A or *TBW spread*) and μ represents the maximum tuber weight (MX or *TBW MX*)

The Gaussian normal distribution model did not appropriately describe the distribution of number of tubers across the tuber size classes. The gamma distribution model was demonstrated to give a better fit (MAFF 2000). The gamma model was fitted in NCSS (version 11), which predicts the model parameter estimates of the distribution using a maximum likelihood estimate (MLE) approach. The gamma distribution model is given as:

$$TBN = \frac{(w^{\alpha-1} \exp^{-\beta w})}{(\beta^{\alpha} \{ \int_1^5 w^{\alpha-1} \exp^{-w} \Delta w \})} \quad (2)$$

where TBN is the tuber number; w is the tuber size class ranging from 1 to 5, representing the five size classes (0–40 mm, 40–50 mm, 50–60 mm, 60–70 mm and > 70 mm, respectively); α is the shape of the curve; and β the is the rate. The mean (μ) of the distribution and the standard deviation (σ) are determined by the equation:

$$\mu = \alpha/\beta; \text{ and } \sigma = (\sqrt{\alpha})/\beta$$

where μ is the size class with the maximum tuber number (tuber number mean size), and σ describes the spread of the distribution. In the results section, μ is represented as *TBN ms*, and σ as *TBN spread*.

Calculated data and statistical analyses

The marketable fractions of tuber fresh weight and tuber number were calculated by dividing the tuber fresh weight and tuber number of size classes ≥ 50 mm by the total tuber fresh weight and tuber number,

respectively. The ≥ 50 mm size threshold refers to the longitudinal length of a tuber. The coefficients of variation for both tuber fresh weight and tuber number were computed as $((\sigma/\mu)*100)$, that is, $((TBN \text{ spread}/TBN \text{ ms})*100)$ in the case of tuber number, for instance. We analysed the Spearman's correlation of the calculated traits and parameters from tuber size distributions with overall tuber fresh weight and tuber number. This was implemented in R-Studio 3.2.3. Principal Component Analysis (PCA) bi-plots were used to investigate the contribution of the various traits and parameters to the variation in the dataset. Heritability (H^2) was calculated as: $V_g/(V_g + V_e)$ where V_g is genotypic variance and V_e is environmental variance. Statistical analyses were effected at 0.05 level of significance.

Association mapping

The set of commercial cultivars was used as a panel for mapping marker-trait associations. A dataset of 14,402 Infinium SNP markers was used in mapping the association of the traits and parameters to physical positions on the potato genome. This marker dataset has been fully described (Vos et al. 2015). SNP markers were available for approximately 94% of the cultivars. The assignment of allele dosage classes to the markers was done using the freely available R package fitTetra algorithms (Voorrips et al. 2011). Numeric score of dosage classes was applied on the markers from 0 to 4 representing nulliplex (aaaa), simplex (Aaaa), duplex (AAaa), triplex (AAAa) and quadruplex (AAAA) marker dosages, respectively. The Q + K linear mixed model for GWAS approach was used to map the marker-trait associations (Yu et al. 2006). The GWAS model was implemented as follows:

$$t = X\beta + ZS_{\zeta} + ZQv + Zv + \varepsilon \quad (3)$$

where t is phenotypic trait or parameter; $X\beta$ accounts for covariates like environmental effects; ZS_{ζ} describes the SNP effects using the genetic model to map genotype to phenotype; ZQv accounts for sub-populations of the given population size in the association panel; Zv considers polygenic effects and its covariance matrix is proportional to the kinship (K) matrix; and the residual (ε) is based on the model assumptions of independence, normality, and equality

of variance (*iid*—*independent and identically distributed*). The variance of the random effects is given as follows, $\text{Var}[\varepsilon] = \text{I}\sigma_{\varepsilon}^2$ and $\text{Var}[v] = \sigma_g^2\text{K}$.

Kinship (relatedness of the association panel) was calculated using the realized relationship matrix (Rosyara et al. 2016). The population structure groups of the association panel were accounted for by using the structure grouping information (Björn et al. 2010). Different gene models were imposed on the marker associations including: general, additive, simplex dominant, and duplex dominant. The quantile–quantile plot was used to check the association of the markers on a log scale to avoid spurious associations. The significance threshold of marker–trait association was determined using the Bonferroni method. Manhattan plots were used to visualize trait-associated loci on the physical map of potato. The entire association mapping procedure was implemented in R Studio version 3.2.3, using the GWASpoly package for autotetraploids (Rosyara et al. 2016).

Results

The foliage development and tuber yield at Zeeland, which is a coastal region of The Netherlands, were much less affected by drought than the Connantre trials, indicating that the trial in Zeeland only suffered minor water limitation stress. The foliage of the plants in the irrigated block of the Connantre (2013) trial at some time points in the growing season turned yellowish green (data not shown), which may be indicative of a lack of nitrogen. We speculate that the irrigation may have resulted in the leaching of nutrients to lower soil depths beyond the reach of the plant roots. Environmental information was collected in the Connantre trials of 2014 and 2015. The environmental data showed that at the Connantre 2014 trial, total rainfall was 258.2 mm and the drought occurred during the early stages of plant growth. The total rainfall in Connantre 2015 was only 42 mm and the drought occurred at a later stage of plant development (See Aliche et al. 2018—Supplementary files). Therefore, the Connantre 2014 and Connantre 2015 trials are described as early and late drought stress trials, respectively.

Size distribution of tuber fresh weight and tuber number

The tuber size with maximum fresh weight (*TBW mcs*) and the spread of the tuber size distribution (*TBW spread*) were significantly negatively affected by drought in Connantre (2014 and 2015) and in Zeeland 2014 (Fig. 2). The size class with the maximum tuber number (*TBN ms*) was significantly smaller under drought in Connantre (2013–2015) but not in Zeeland. The spread of the distribution of tuber number in the various sizes (*TBN spread*) was only significantly reduced in Connantre 2014 and 2015 (Fig. 2).

Marketable tuber size fraction

A tuber size threshold of ≥ 50 mm along the longitudinal plane of the tuber was used to determine marketable fraction of tuber yield under irrigated and non-irrigated conditions. This size threshold was applied to both tuber fresh weight (TBW) and tuber number (TBN). Drought stress significantly reduced the fresh weight of the marketable tuber size fraction in Connantre (2014 and 2015). Also, the number of marketable tubers was reduced in the three trial years at Connantre (Fig. 3). The reduction in marketable yield was most severe in Connantre 2015. However, there was no significant reduction of marketable yield in the Zeeland trials.

Correlation of tuber size distribution parameters

Generally, foliage maturity correlated negatively with most tuber size distribution (TSD) parameters in all trials under irrigated as well as non-irrigated conditions (data not shown), which means that late maturing cultivars had higher values for the TSD parameters (data not shown). However, in the late drought trial (Connantre 2015), foliage maturity was more negatively correlated with tuber size distribution parameters under stress than under irrigated conditions (Fig. 4). Also, marketable fractions of tuber yield (*TBN mf* and *TBW mf*) were higher in late maturing cultivars than in early maturity types, especially under drought. We computed the coefficient of variation for both tuber number (*TBN CV*) and tuber fresh weight (*TBW CV*) as a way of investigating the variability in yield distribution in our dataset. The negative and positive correlations of foliage maturity with *TBN CV*

Fig. 2 **a** Tuber size with the maximum tuber fresh weight (*TBW mcs*), **b** spread of the tuber size distribution in weight (*TBW spread*), **c** tuber size with the maximum tuber number (*TBN ms*), and **d** spread of tuber size distribution in tuber number (*TBN spread*); under irrigated (WR) and non-irrigated (DR)

conditions, at CON (Connantre), ZEE (Zeeland) in the years, 2013–2015. Error bars are standard errors of the mean values of 103 cultivars. Significant differences between WR and DR are given by asterisks at 0.05 level of significance. TSD is tuber size distribution

Fig. 3 **a** Marketable fractions of tuber fresh weight (*TBW mf*) and **b** tuber number (*TBN mf*); under irrigated (WR) and non-irrigated (DR) conditions, at CON (Connantre) and ZEE (Zeeland) in the years, 2013–2015. Error bars are standard

errors of the mean values of 103 cultivars. Significant differences between WR and DR are given by asterisks at 0.05 level of significance

Fig. 4 Spearman's correlation of tuber size distribution parameters and yield traits under **a** irrigated and **b** non-irrigated conditions, at Connantre 2015 trial. MAT (maturity on a scale of late (–, that is, 4) to early (++ , that is, 8.5)), *TBN ms* (tuber number mean size), *TBN spread* (tuber number size distribution spread), *TBN CV* (Coefficient of variation in tuber number), *TBN mf* (tuber number marketable fraction), *TBN* (tuber number), *TBW MX* (maximum tuber fresh weight among size

classes), *TBW mcs* (size class with the maximum tuber fresh weight), *TBW spread* (tuber fresh weight size distribution spread), *TBW CV* (Coefficient of variation in tuber fresh weight), *TBW mf* (tuber fresh weight marketable fraction), *TBW* (tuber fresh weight). Correlation coefficients threshold for *p* values 0.1, 0.05 and 0.01 are 0.18, 0.21 and 0.26, respectively. The *p* value matrices for all correlation coefficients are given in Supplementary Fig. SF2

and *TBW CV* respectively under drought conditions suggest that, contrary to normal conditions, the

variability in tuber number distribution among size classes was more pronounced in late maturing

cultivars than for early maturing cultivars, whereas the early maturing cultivars showed more variability in tuber weight distribution among size classes.

Interestingly, the positive correlation of *TBN CV* and *TBW CV* under irrigation as opposed to their negative correlation under drought stress suggests that irrigation similarly affected the variability in distribution of tuber number and tuber weight among size classes, while the drought may have caused a differential response in variability of tuber number and tuber weight distribution. In both treatments, cultivars producing many tubers (high *TBN*) also showed high variability in their tuber weight distribution among size classes (high *TBW CV*), but only under drought was high variability in tuber number distribution among size classes (high *TBN CV*) associated with a high total tuber fresh weight (high *TBW*) (Fig. 4). Conversely, low variability in tuber number distribution among size classes (low *TBN CV*) was observed in cultivars with high total tuber number (high *TBN*) under drought. But under irrigation, *TBN CV* and *TBN* were positively correlated.

Generally higher marketable fraction of tuber yield and wider spread of tuber size distribution were observed when the variability in tuber weight distribution among size classes (*TBW CV*) was low under irrigation and drought. Under stress, however, high variability in tuber number distribution among size classes (*TBN CV*) coincided with a high marketable fraction and wide spread of tuber size distribution, but not under irrigation. The marketable fractions of tuber yield (*TBN mf* and *TBW mf*) correlated positively with spread of tuber size distribution (*TBN spread* and *TBW spread*). That is, a wider tuber size distribution meant that marketable fraction was high.

Remarkably, high total number of tubers (*TBN*) tended to skew size distribution towards smaller size classes, narrower distribution curves, and loss of tuber marketability, as shown from its negative correlation with maximum tuber yield (*TBN ms* and *TBW mcs*), spread of tuber size distribution (*TBN spread* and *TBW spread*), and marketable fractions (*TBN mf* and *TBW mf*). These negative correlations of total tuber number were observed under irrigated as well as non-irrigated conditions.

Bi-plots of principal components analyses were used to further investigate the effects of foliage maturity and cultivar-specific differences. Only the

late drought (Connantre 2015) showed an observable contrast between irrigated and non-irrigated conditions in terms of maturity type influences (Fig. 5a and b). Under irrigated conditions, cultivars of the different maturity classes were evenly distributed and strongly overlapped with no distinction of maturity groups (Fig. 5a). However, in non-irrigated condition there was an apparent maturity grouping along the PC1 (Dim1) axis, with a less even distribution especially in the late maturity types (Fig. 5b). Most of the tuber size distribution parameters made similar contribution to the variation in the dataset under the respective conditions except *TBW MX* (maximum tuber fresh weight among size classes). The parameter with the lowest contribution to the variation among the cultivars is the spread of tuber size distribution for fresh weight (*TBW spread*) as indicated by the relatively shorter length of its vector along PC1 (Dim1) axis (Fig. 5).

Under non-irrigated conditions, the later maturity types tended to have higher total tuber weight (*TBW*) and higher values of tuber size distribution parameters than early maturity types. However, a few cultivars escaped the trend of their maturity class. Some of these 'outlying cultivars' were selected from the bi-plots for a closer study of their tuber size distributions. The selection was based on the position of the outliers on the bi-plots and also on the uniqueness of the cultivar's tuber size distribution. These include: Jazzy, Kuroda, Hansa, Terragold, Valiant, and Avano (numbers 39, 46, 34, 91, 93 and 10, respectively in the bi-plots of Fig. 5).

The better-performing cultivars in each maturity class among the six are Kuroda (46-early type), Terragold (91-intermediate type), and Avano (10-late type). These three cultivars had their maximum tuber fresh weight or tuber number in the 50–60 mm size class under stress (Fig. 6). On the other hand, Jazzy (39-early type), Hansa (34-intermediate type) and Valiant (93-late type) had their maximum tuber weight or tuber number in lower classes under stress. Hansa and Jazzy produced the highest number of tubers in the dataset in all trials under irrigated and non-irrigated conditions, but most of their tubers were within 0–40 mm (non-marketable) size class. Under drought conditions, Jazzy had no marketable tuber while only 3% of the total number of Hansa was marketable as shown in the Online Resource 1 (Supplementary Table 1). In the Connantre 2014 trial (early drought),

Fig. 5 PCA bi-plots of tuber size distribution parameters and yield traits at the Connantre 2015 trial under **a** irrigated condition, and **b** non-irrigated condition. The numbers represent individual cultivars according to their maturity classes: Early (red), Intermediate (green), and late (blue). The vectors represent tuber size distribution parameters and yield traits: *TBN ms* (tuber number mean size), *TBN spread* (tuber number size distribution spread), *TBN mf* (tuber number

marketable fraction), *TBN* (tuber number), *TBW MX*. (maximum tuber fresh weight among size classes), *TBW mcs* (size class with the maximum tuber fresh weight), *TBW spread* (tuber fresh weight size distribution spread), *TBW mf* (tuber fresh weight marketable fraction), *TBW* (tuber fresh weight). Cultivars with contrasting results from the respective maturity classes studied in further details: Jazzy (39), Kuroda (46), Hansa (34), Terragold (91), Valiant (93) and Avano (10)

the performance of these six cultivars in terms of their tuber size distribution parameters, marketable yield and total yield, followed a trend that was similar to the Connantre 2015 trial. However, in general drought had a more severe effect on the cultivars in the Connantre 2015 trial (Supplementary Table 1).

Heritability of yield traits in all locations

The tuber size distribution parameters were derived from the means of the size-graded tuber yield traits (total tuber number and total tuber weight) for each cultivar. In order to evaluate the breeding value of the parameters, we calculated the broad-sense heritability (H^2) of the yield traits from which the parameters were derived (Table 1). Tuber number had high heritability ($H^2 \geq 0.5$) in all locations under irrigated (WR) and non-irrigated (DR) conditions. Tuber fresh weight also had high heritability ($H^2 \geq 0.5$) except in Zeeland 2013 (irrigated treatment) and Zeeland 2014 (non-irrigated treatment). Among the locations, Connantre 2015 had the lowest environmental noise as shown by

the environmental variance for TBW under DR, which was lowest in this trial. Therefore, we further studied the performance of the cultivars in Connantre 2015 in order to discover the genetic factors that may be associated with the tuber yield variations in the dataset.

Association mapping

An Infinium array of 14,402 SNP markers was used for discovering associations of the tuber size distribution parameters for the Connantre 2015 trial to physical positions on the potato genome. Quantile–quantile plots confirmed the absence of spurious associations of the markers on a log scale (data not shown). We observed significant associations of tuber fresh weight under irrigated conditions with three SNP markers in close proximity to the *StCDF/Maturity* locus on Chromosome 5 as shown in the Online Resource 2 (Supplementary Fig. SF1a), which was found to be strongly associated with tuber yield in other studies (Kloosterman et al. 2013; Schönhals et al. 2016;

Fig. 6 **a–c** Number of tubers in the size classes (0–40 mm, 40–50 mm, 50–60 mm, 60–70 mm and > 70 mm) for selected cultivars of late, intermediate, and early maturity types, respectively. **d–f** Fresh weight of tubers in the size classes (0–40 mm, 40–50 mm, 50–60 mm, 60–70 mm and > 70 mm) for selected cultivars of late, intermediate, and early maturity types respectively. In each maturity class, the tuber size distribution of two cultivars with contrasting drought response are compared under irrigated (WR) and non-irrigated (DR) condition

Anithakumari et al. 2012). Under drought conditions in the Connantre 2015 trial we found significant association of a SNP marker with *TBN spread*, *TBN ms*, *TBN mf* and *TBW mf* at 0.05 significance threshold (Fig. 7), and with *TBN mcs* at 0.1 significance level (Supplementary Fig. SF1b). This marker, Pot-Var0030768, is found at position 55,657,256 bp on the scaffold PGSC0003DMB000000062 of Chromosome 3 of the potato genome. We also observed SNP markers on Chromosome 6 that tended to associate with the yield traits, but these markers did not reach the significance threshold and so were not further analysed.

The SNP marker PotVar0030768 has an A/G polymorphism with an additive allele dosage effect. An evaluation of the effect of its additivity on the

parameters, *TBN spread*, *TBN ms*, *TBN mf* and *TBW mf*, is illustrated in Fig. 8a and b. For every allele dosage increase from nulliplex through quadruplex, there is an increase in parameter value. Among the cultivars with contrasting drought responses illustrated in Fig. 6 above, the following dosages of this SNP marker were observed for the favourable allele: quadruplex (Kuroda), triplex (Avano and Terragold), simplex (Valiant), nulliplex (Hansa). These allele dosages fitted our expectation based on the variation among these widely contrasting cultivars for the traits (*TBN spread*, *TBN ms*, *TBN mf* and *TBW mf*). No marker information for Jazzy was available. Among the entire set of cultivars, the allelic distribution (number of cultivars in the respective allele dosage classes) is as follows: quadruplex (5), triplex (20),

Table 1 Heritability (H^2) of yield traits in Connantre and Zeeland under irrigated and non-irrigated conditions

Year	Location	Trait	TRT ^a	Mean	Min. ^b	MAX ^c	* <i>F.pr</i>	V_g	V_e	H^2
2013	CONNANTRE	TBW	WR	10.49	4.003	17.05	< .001	4.408	1.98	0.69
		TBW	DR	8.666	3.118	13.78	< .001	2.9785	1.573	0.65
		TBN	WR	79.82	29	223	< .001	566.9	139.4	0.80
		TBN	DR	79.68	32	188	< .001	476.2	296.6	0.62
2014	CONNANTRE	TBW	WR	15.53	7.2	26.96	< .001	9.0095	3.902	0.70
		TBW	DR	10.27	5.44	18.34	< .001	3.3985	1.366	0.71
		TBN	WR	101.8	38	181	< .001	405.6	298.8	0.58
		TBN	DR	87.26	34	182	< .001	603.1	107.3	0.85
2015	CONNANTRE	TBW	WR	12.88	7.4	19.7	< .001	3.701	1.869	0.66
		TBW	DR	5.961	2.3	10.5	< .001	1.247	0.6315	0.66
		TBN	WR	105.8	52	229	< .001	469.2	529.7	0.47
		TBN	DR	93.3	27	168	< .001	472.3	148	0.76
2013	ZEELAND	TBW	WR	12.29	5.52	20.53	< .001	2.2325	4.715	0.32
		TBW	DR	10.76	4.77	15.55	< .001	2.0485	2.251	0.48
		TBN	WR	126.4	56	265	< .001	1135.1	348.6	0.77
		TBN	DR	117.8	40	317	< .001	957.9	386.7	0.71
2014	ZEELAND	TBW	WR	15.38	7.11	26.62	< .001	7.36	4.109	0.64
		TBW	DR	12.26	3.83	24.02	0.004	2.65	10.2	0.21
		TBN	WR	127.5	66	328	< .001	897.75	489.2	0.65
		TBN	DR	118.6	40	317	< .001	1507.4	516	0.74

^aTreatment (WR—Irrigated, DR—Non-irrigated)^bMinimum trait value^cMaximum trait value, TBW—tuber fresh weight in kg, TBN—tuber number V_g —genotypic variance, V_e —environmental variance, **F.pr*—*p* values

duplex (38), simplex (20) and nulliplex (13), forming a normal distribution (Fig. 8c).

The Ensembl Plant database was blasted for the super-scaffold of this significant SNP marker, PGSC0003DMB000000062. The blast result showed many genes including a gene (PGSC0003DMG400019503) encoding a Pentatripeptide repeat-containing protein (PPR) located at 2.9 kb downstream of the PotVar0030768 marker.

Discussion and conclusions

Differences in drought scenarios

The potato crop is known to be generally sensitive to drought stress, leading to severe reduction in tuber yield (Loon 1981). The severity of drought stress, however, may vary between different environments and thus differently impact yield (Aliche et al. 2018).

Information on the environmental conditions in a given region and the type of drought frequently encountered will facilitate targeted and effective drought tolerance breeding for such a region. In this study, we evaluated the performance of 103 commercial potato cultivars in several locations under non-irrigated (drought) and irrigated conditions. Generally, Zeeland, a coastal Westland area of The Netherlands, experiences less drought than Connantre (Northern France). However, different years in these locations presented unique patterns of drought that affected the cultivars differentially. Interestingly, available environmental data enabled us to understand the drought patterns in the Connantre 2014 and 2015 trials in detail (Aliche et al. 2018). The two main aspects of the drought patterns were the timing/duration of the drought and the total amount of water available to the crops in the field during the crop cycle. The Connantre 2014 trial was exposed to early drought (delayed rainfall), and there was also a higher total

Fig. 7 Manhattan plots showing significant association of SNP marker, PotVar0030768, on Chromosome 3 of the potato genome under drought stress with **a** *TBN spread* (size distribution spread of tuber number), **b** *TBN ms* (size class

where maximum tuber number occurred), **c** *TBN mf* (marketable fractions of tuber number), and **d** *TBW mf* (marketable fractions of tuber fresh weight)

amount of rainfall throughout the growth season than in Connantre 2015 (late drought) (Aliche et al. 2018—Supplementary files). Therefore, the stronger effects of drought on traits in the Connantre 2015 trial were a combination of both the timing of the drought and the smaller amount of rainfall. For this kind of locations with highly fluctuating drought patterns between years, the monitoring of environmental information during trials would generate meta-data that facilitates the precise modelling of the crop drought response (Bassam et al. 1990; Kooman and Haverkort 1995; Rey et al. 2016).

Tuber size distribution (TSD) parameters unveil drought impact on potato yield

Grading of potato tubers after harvest is a way of assessing the value of the total yield produced by the crop. With the aid of the Normal distribution and

Gamma distribution models we have used graded tuber size data to interpret the distribution of tuber fresh weight and tuber number, respectively. From these size distributions, we extracted parameters that gave information about the respective distributions. Tuber size distribution (TSD) parameters are especially important for the description of the yield of the crop and to determine which aspects are differently affected by drought between cultivars. For instance, the distribution parameters (*TBW mcs* and *TBN ms*) describe the balance between tuber initiation and the bulking of the formed tubers. Cultivars that make more tubers than they can bulk during the growing season would have a distribution that is skewed towards the smaller sized tubers. In our dataset, Jazzy and Hansa produced lots of tubers, but were not able to bulk them by the end of the growing season (Fig. 6). Also during the drought stress conditions, the distributions were even more skewed towards smaller

Fig. 8 Illustration of the additive effect of allele dosages of the SNP marker, PotVar0030768, on the mean values of the parameters from 95 cultivars: **a** *TBN mf* (marketable fractions of tuber number) and *TBW mf* (marketable fractions of tuber fresh weight), **b** *TBN spread* (size distribution spread of tuber

number) and *TBN ms* (size class where maximum tuber number occurred). **c** Normal distribution of allele dosages for the PotVar0030768 marker on Chromosome 3 of the potato genome showing the number of cultivars that contain each allele dosage (0: nulliplex, 1: simplex, 2: duplex, 3: triplex, and 4: quadruplex)

tubers and higher number of tubers than under non-water limiting conditions, depending on the severity of the drought. Interestingly, we observed that the skewed distribution towards smaller and more tubers in early maturing cultivars compared to the late types was more pronounced under drought than under irrigated conditions at the Connantre 2015 trial (data not shown). The late drought in Connantre 2015 coincided with the tuber bulking stage of the plant growth. During this drought period the early maturity types had a relatively shorter time to bulk their tubers than the later maturity types. The longer crop growth cycle is advantageous for a longer duration of light interception and photosynthesis, which seems to translate to tuber bulking even more under drought. Ishimaru et al. (2008) reported a field trial comparison of a potato cultivar (cv. May Queen) and its transgenic lines (*Ag1203*) overexpressing sucrose-phosphate synthase. The *Ag1203* lines had the same photosynthetic rate as the wild type May Queen. However, the

Ag1203 lines had delayed senescence, which increased their period of photosynthetic activity. They also had an improved translocation of photosynthates to the tubers, resulting in a higher yield (Ishimaru et al. 2008). In our study, this may imply that the later maturity types may have gained the advantage of a delayed senescence to produce more photosynthates that could partly be used for tuber bulking. However, generally, the rate of photosynthesis and the partitioning of photosynthetic products to yield are severely reduced by drought (Ashraf and Harris 2013; Li et al. 2017). We did observe that within the same maturity class, some cultivars bulked a large fraction of their tubers much more than others, indicative of genetic variation in the effective use of photosynthates for tuber bulking under drought stress. Therefore, the photosynthetic duration is maturity-dependent, but the effective use of photosynthates for tubers bulking may be highly genotype-dependent within the maturity class.

The spread of the distribution (*TBN spread* and *TBW spread*) is another important tuber size distribution parameter that describes the degree of variation in the sizes of potato tubers at harvest (Wurr et al. 1993). Often, a wide spread of tuber size would imply that the larger-sized tubers are also present. Marshall and Thompson (1986) reported a linear relationship between spread of distribution and class size with the maximum tuber yield. A wide distribution suggests that the plant translocated assimilates to most of its tuber size classes, and tubers are still being formed, whereas narrow spread would imply that a narrow range of tuber sizes were prioritized during bulking, or tubers were still formed, but hardly bulked. In our drought trials, spread of TSD was reduced for both tuber number (*TBN*) and tuber fresh weight (*TBW*) in Connantre 2014 and 2015 (Fig. 2). Among these trials, however, foliage maturity only affected *TBN spread* and *TBN CV* (coefficient of variation in tuber number) under drought in the Connantre 2015 trial to the advantage of late maturity types (Fig. 4b). This suggests that a longer growth cycle (delayed senescence) facilitated the partitioning of assimilates to a larger range of tuber size classes.

In earlier studies, coefficient of variation (CV) has also been used to describe the relative variation in TSD. TSD CV is defined as ((spread of distribution/class size containing the highest tuber yield) * 100) (Wurr et al. 1993). The findings from these earlier studies are that a drought treatment did not affect TSD CV (Marshall and Thompson 1986; Wurr et al. 1993). However, in our study we observed a differential effect of drought on TSD CV depending on the drought pattern and possibly the drought severity. In the Connantre 2014 trial (early drought), the drought significantly reduced *TBN CV* but not *TBW CV* (data not shown). On the other hand, in Connantre 2015 the late drought significantly reduced *TBW CV* but not *TBN CV* (data not shown). The timing of the drought coincided with different tuberization stages of plant growth. The early drought of Connantre 2014 coincided with the tuber initiation stage of plant growth, and this may have negatively affected the number of tubers formed. This drought effect on tuber initiation may be the reason for the observed drought effect on *TBN CV* in this trial. The late drought of Connantre 2015 coincided with the tuber bulking stage, with more severe effects on tuber fresh weight, resulting in a stronger effect on *TBW CV*. Moreover, there were

similar levels of variation for *TBN CV* and *TBW CV* under irrigation, but these (*TBN CV* and *TBW CV*) differed widely under stress (Fig. 4). The reason for the disparity in findings between our study and earlier studies may be due to the limited number of genotypes on which the conclusions from these earlier studies were based. For instance, MacKerron et al. (1988) used six genotypes, and they concluded that drought only affects CV of tuber number when it equally affects tuber number (Mackerron et al. 1988). In our study, however, the drought stress in both the Connantre 2014 and 2015 trials significantly reduced tuber number (Aliche et al. 2018), but only in the Connantre 2014 trial was *TBN CV* significantly reduced (data not shown). Also, in the Connantre 2015 trial *TBN CV* associated negatively with *TBN* under drought (Fig. 4). That is, the formation of more tubers did not cause an increased variability of tuber number among size classes. Therefore, tuber size variability under drought may not only be related to tuber number.

Moreover, Wurr et al. (1993) reported not being able to demonstrate that total tuber number affected CV, and they suggested a complex influence. Our findings indicate that the drought pattern, severity, and the tuberization stage of the plant affected by the drought may be more directly responsible for the impact on CV than the supposed relationship between drought effects on tuber number and CV. Furthermore, it has been shown that stolon characteristics, date of tuber initiation and position along the stolon, sugar metabolising enzymes, hormones, mineral compositions and turgor potential contribute to tuber size variability in potato (Struik et al. 1991).

Tuber size distribution (TSD) parameters influence total and marketable yield

Potato tuber yield can be described as total yield, which considers all tubers formed, or marketable yield, which only accounts for the proportion of total yield that can be marketed. Under normal (irrigation) conditions, not all the tubers at the end of the growing season are marketable. The marketable proportion must meet the specific requirements of the intended market, including tuber size. Under drought conditions the marketable proportion of yield is reduced (Abbas and Ranjan 2015). Therefore, we investigated the

relationship of TSD parameters with total yield and marketable yield.

The two total yield components in our study, *TBN* and *TBW*, had differential correlations with their TSD parameters. The TSD parameters of *TBN*, *TBN ms* and *TBN spread*, correlated negatively with *TBN*, while those of *TBW*, *TBW mcs* and *TBW spread*, correlated positively with *TBW* (Fig. 4). Nonetheless, *TBN* and *TBW* were not negatively correlated (Fig. 4). The negative correlations of *TBN* with its TSD parameters indicate that the formation of many tubers reduces spread of the distribution to a range of small-sized tubers, implying a reduction in individual tuber bulking. In an earlier study using the potato cultivar Ostara grown on a nutrient medium, it was shown that the removal of individual tubers with known growth rates from the potato plant increased the growth rate of the remaining tubers within 4 days (Engels and Marschner 1987). Probably a competition for assimilates among the tuber sinks may be responsible for this observation. In our study, the high number of small tubers may be associated with such competition for limited assimilates under stress. Therefore, potato cultivars that produce relatively less tubers but are able to bulk them under drought may be preferred. Furthermore, it was demonstrated that some potato genotypes maintain a single tuber initiation period while some others have multiple tuber initiation periods (Walworth and Carling 2002). In our cultivar set, probably the effect of multiple tuber initiation periods coupled with delays in tuber initiation under drought may have played a role in the proliferation of small-sized tubers in some cultivars. The young tubers formed at the end of the growing season would not have enough time to be bulked. On the other hand, the positive correlation of *TBW* with *TBW mcs* and *TBW spread* indicates a higher tendency to bulk larger-sized tubers, even under drought. It has already been shown that sink tissues with higher sink strength would attract more assimilates (Marcelis 1996). In our study, when tubers of the large size classes are bulked, *TBW spread* widened since there were always some small tubers present.

Interestingly, unlike the differential correlations between the total yield traits (*TBN* and *TBW*) and their TSD parameters, the marketable fractions of tuber yield (*TBN mf* and *TBW mf*) were positively correlated with all TSD parameters under stress and control conditions (Fig. 4a and b). Although the late drought

stress (Connantre 2015) did not generally interfere with the correlations of marketable fractions of tuber yield and the TSD parameters, the correlations with spread of TSD was quite remarkable. There were more positive correlations of *TBN mf* and *TBW mf* with *TBN spread* and *TBW spread*, respectively under the late drought than under irrigation (Fig. 4a and b). This drought effect on correlations between marketable fraction and spread of TSD was not observed in the Connantre 2014 trial or the other trials (data not shown). Moreover, from the Connantre 2015 trial we noticed that a high *TBN CV* was remarkably associated with high values of the TSD parameters and marketable fraction, but only under drought (Fig. 4b). Therefore, depending on the pattern and severity of drought, spread of tuber size distribution may be an indicator of how the drought affects marketable fraction. A wider spread would indicate a higher marketability.

Marketable yield has received far less considerations from scientific reports than total yield. This may be because of the rigorous process of scoring marketable yield from total yield. In our study, under irrigated conditions in Connantre 2015 about 73% of *TBW* and 54% of *TBN* were marketable (Fig. 3). In Connantre 2014 under irrigated conditions, 82% of *TBW* and 62% of *TBN* were marketable. However, in the late drought (Connantre 2015), 36% of *TBW* and 21% of *TBN* were marketable, while under the early drought conditions (Connantre 2014), 73% of *TBW* and 54% of *TBN* were marketable (Fig. 3). The marketable yield percentages for Connantre 2013 trial were within these limits, and there was no drought effect on marketable yield in Zeeland. The late drought led to a more severe reduction in marketable yield than the early drought. Moreover, in the late drought the plants also had less water available in the growing season (Aliche et al. 2018—Supplementary Fig. S2). The overall most severe drought effect on *TBW* was a 54% reduction (Connantre, 2015) and on *TBN* a 14% reduction (Connantre 2014) (data not shown). Interestingly, the most severe effect of drought on *TBW mf* is 51% reduction (Connantre, 2015) and on *TBN mf* is 13% reduction (Connantre 2014). This suggests that drought impact on total yield may be representative of its impact on marketable yield. But *TBN mf* was always negatively correlated with *TBN* under irrigated and non-irrigated conditions. Therefore, reduction in *TBN* and *TBW* due

to drought may be used to infer reduction in *TBN mf* and *TBW mf*, respectively; and high absolute *TBN* values would be indicative of low marketable number of tubers. However, some genotypes may not show this relationship between marketable fraction and total yield. For instance, a comparison between two late maturity types, Avano and Valiant, showed that Valiant was more drought tolerant than Avano in terms of *TBW* in the Connantre 2015 trial as shown in the Online Resource 1 (Supplementary Table 1), but the *TBW* of Valiant under drought (7.35 kg) only had 50% marketable fraction, while of the 7.65 kg total yield of Avano under drought 67% was marketable. Therefore, in addition to evaluating drought tolerance in breeding trials, marketable fractions of tuber yield under drought conditions need to be carefully considered.

Maturity effects on TSD parameters, marketable fraction and total yield under drought versus control

The cultivars in this study were classified into three groups based on their foliage maturity types: early, intermediate and late maturity types. This classification enabled us to investigate the role of maturity differences and the genotype variation within the maturity groups. Using a biplot analysis we observed that the effect of drought on the TSD parameters was quite dependent on maturity grouping in the Connantre 2015 trial (Fig. 5), probably due to the pattern and/or severity of the drought in this trial. The late maturing cultivars and some intermediate maturing cultivars had higher values of the TSD parameters than most of the early maturity types. Interestingly, the level of variation within a maturity class was highest within the early maturity class and lowest within the late maturity class, as shown by the convex hulls of the maturity groups (Fig. 5b). The late maturity types had less variation under drought than under irrigation (Fig. 5a and b). Therefore, late foliage maturity facilitated the attainment of high values for the TSD parameters (and yield). This advantage of late maturity towards high TSD parameter values is also indicated from the correlation coefficients under drought (Fig. 4). The late maturing cultivars had more large-sized tubers and a wider spread of tuber size distribution than the early maturing cultivars, especially under drought (Fig. 4a and b). Therefore, late

maturing cultivars may provide a more robust background material in the breeding for drought tolerance improvement of potato.

Marker-parameter associations

One of the aims of studying tuber yield and yield distribution parameters is to understand the extent of genetic control on the variation in these phenotypic characteristics under environmental stress conditions like drought. We have investigated a set of 95 cultivars that showed significant genotypic variation in tuber yield parameters in our dataset for which genetic markers are available. The population size of this selected set of cultivars is relatively less than what is commonly used in GWAS studies, but the limited experimental size made it possible to properly manage the difficulties in multi-year-multi-environment drought trials in order to obtain reliable results. Nevertheless, due to the level of genotypic variation, the rich pedigree represented by the cultivar set and the marker density, it was possible to detect important associations that are reliable leads for further studies of which the most promising has been reported in this paper. In another related GWAS study in tetraploid potatoes (Khlestkin et al. 2019), the authors also used a limited set of 90 genotypes and a 15K SNP marker dataset, and were able to find genomic loci associated with phosphorylated starch content although they could not establish a functional protein-level effect of the associations.

Based on the existence of relatively high heritability for the tuber yield traits in our dataset, we have used a 14K SNP marker array to search for associations between regions of the potato genome and the TSD parameters in 95 of the cultivars. Under drought in the Connantre 2015 trial we found significant marker-trait associations of the TSD parameters, *TBN spread* and *TBN ms*, and marketable yield (*TBN mf* and *TBW mf*), with a region on chromosome 3 of the potato genome. Increases in the allelic dosage in this region improved parameter value and marketable fraction, indicating additive effects. Amongst other genes, a pentatricopeptide repeat-containing protein (PPR) is present in this region. PPR proteins were recently discovered (Schmitz-Linneweber and Small 2008), and are known to recognize RNA editing sites and bind to the upstream sequences of such editing sites through their repeat elements (Ichinose and Sugita 2017;

Schmitz-Linneweber and Small 2008). In literature, this gene family is shown to be involved in Arabidopsis in the tolerance to abiotic stresses including drought (Jiang et al. 2015; Liu et al. 2010; Lv et al. 2014; Sharma and Pandey 2015; Yuan and Liu 2012; Zhu et al. 2012; Zsigmond et al. 2008). A role of PPRs has not yet been reported in potato. In other plant systems, PPRs have been reported to be involved in the restoration of fertility to cytoplasmic male sterile lines in *Petunia* (Bentolila et al. 2002) and *Brassica napus* (Brown et al. 2003). However, their role in stress tolerance has not been demonstrated in any other plant systems apart from Arabidopsis. Further work is therefore necessary to understand the possible role of this gene in crop systems during stress. Also, this significantly associated SNP locus on Chromosome 3 will need more dedicated investigation to understand its functional involvement in yield, and how it can be integrated into the breeding for stress tolerance in crops.

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Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

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