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Drought response in field grown potatoes and the interactions between canopy growth and yield

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ABSTRACT

Potato is an important food crop with high yields. However when exposed to drought it suffers major yield losses. Considering its global importance and the increasing incidence of drought due to climate change, research toward drought tolerance in potato remains imperative. We have studied a set of 103 commercial cultivars representing the genetic diversity in the European potato market. The cultivars were grown in different field locations in three subsequent years (2013–2015). Our aim was to understand how different field drought regimes affect canopy growth in potato, and how these effects translate to tuber yield. The field environmental conditions were monitored, and pictures of canopy ground cover during the growing season were taken. Canopy growth parameters were extracted by an iterative method using the beta sigmoid growth function to model canopy growth. At harvest, tuber yield was scored and tuber size was graded. The GGE (Genotype and Genotype-by-Environment) bi-plot and Finlay Wilkinson's Regression were used to investigate Genotype x Environment interactions. We observed that the timing of the drought occurrence differentially affected canopy growth and tuber yield. Under drought stress, fast attainment of exponential growth and maximum canopy cover had negative effects on tuber formation and tuber bulking. Growth rate, maximum canopy cover, and area under the canopy curve (photosynthetic capacity over the growth season) were more important for tuber bulking than they were for tuber formation under drought stress. Cultivars with high yield were identified as potential material for improvement to drought tolerance. These findings will contribute to the breeding for drought-tolerant potato amidst the threats of climate change.

1. Introduction

Climate change negatively impacts agricultural production, especially in marginal regions with limited inputs like fresh water. The negative effects of water limitation on crop yield are critical for drought-sensitive crops of high importance for food production and security, like potato. Potato is the world's 3rd most important food crop, and its production in the developing world has increased in the last two decades, demonstrating its important contribution to food security (Acton, 2013). The global production of potato is estimated at 377 million tonnes in about 19 million hectares (FAOSTAT, 2016). When compared to grain-producing crops, a hectare of potato can yield about two- to four-fold more calories (CIP, 2013). Potato is known for its efficiency in water usage (Shahnazari et al., 2007; Vreugdenhil et al., 2007). In comparison with other major crops, potato produces the highest amount of calories per unit water input and it is seven times more efficient than some cereals, like wheat, maize, etc. (CIP, 2013; FAO, 2008). However, potato is generally drought-sensitive (Schafleitner et al., 2008), with losses in yield that can reach 79% reduction if water requirements are not met (Binod et al., 2015).

The Palmer Drought Severity Index predicts a widespread drought in many regions of the globe including Europe in the next 30–90 years arising from reduced rainfall and/or increased evaporation (Dai, 2013). The drought sensitivity of potato may be attributed to the stress effects on its foliage characteristics (Deblonde and Ledent, 2001; Schittenhelm et al., 2006; Soltys-Kalina et al., 2016; Romero et al., 2017;) and its shallow root system (van Loon, 1981; Yamaguchi and Tanaka, 1990; Iwama et al., 1993; Opena and Porter, 1999; Stalham et al., 2007; Zarzyńska et al., 2017) that make water uptake inefficient (Luisa et al., 1997). In comparison with many other crops, leaf stomatal closure occurs in potato at relatively low soil moisture deficits perceived by the roots (Sadras and Milroy, 1996). This leads to a significant drop in

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transpiration even before significant reduction in leaf water potential occurs (Liu et al., 2005). Stomatal closure at relatively high leaf water potential (-0.4 MPa and −0.6 MPa) may already limit photosynthesis, with reduced production of assimilates and canopy growth, and a resultant drop in tuber yield and quality (Luisa et al., 1997). Therefore, the drought response in potato and possibly, tolerance, may be closely linked to a bias-free quantification of the progress of canopy growth. (Bojacá et al., 2011).

Many techniques have been developed to facilitate the monitoring of canopy growth. These include the grid system that measures ground area covered; near-infrared reflectance, which measures interception of solar radiation; picture image capture of canopy cover and image analysis; and remote sensing using satellite data (Bojacá et al., 2011; Bouman et al., 1992; Korva, 1996; Prashar and Jones, 2014; Sivarajan, 2011). In addition to monitoring canopy growth as described above, accurate quantification, extraction and interpretation of canopy growth parameters will give deeper insight into the traits of interest for crop improvement (Chen et al., 2014). Potato canopy growth has been described by several authors using growth models of good fit to show the progress of canopy from emergence towards senescence (Khan, 2012; Ospina et al., 2014). Under drought conditions several growth measurements in field grown potato have been reported, which have enhanced our understanding on how to manage different drought regimes in the field (Jefferies and Mackerron, 1993; Mackerron et al., 1988; Ouiam et al., 2003; Shiri et al., 2009; Steyn et al., 2007). The modelling of potato growth under drought, however, still requires more research to understand canopy cover dynamics. Moreover, due to the difficulties in managing field experiments, potato field drought reports are often based on only a few genotypes. This challenges the generalization of conclusions from such field reports.

Percentage ground cover by canopy is known as a good measure of intercepted solar radiation in potato, which is also reflected in dry matter production (Haverkort et al., 1991; Lemaga and Caesar, 1990; Vreugdenhil et al., 2011). Interception of solar radiation is reduced under drought conditions depending on the severity of the stress, due to reduced leaf expansion and reduction in total number of leaves (Harris, 2012). Potato canopy growth has been described in three phases including the build-up phase, maximum canopy cover phase, and decline or senescence phase (Khan, 2012). The build-up phase includes the period from emergence till full canopy cover, and this often coincides with tuber initiation stage of the plant (Haverkort and Mackerron, 1995). The maximum canopy cover and decline phases are periods during which the tubers have to be filled with assimilates (bulking). The duration of these phases depend on the tuber growth rate and foliage maturity class of the potato genotype (Haverkort and Mackerron, 1995). Potato genotypes that invest a major part of their life cycle in canopy growth (late maturity genotypes) can intercept about 700 MJ/m^2 (Zaag, 1992), while early maturity potato genotypes start investing photosynthetic assimilates in their tubers much earlier, and thus complete their life cycle early (Kooman and Rabbinge, 1996). These differences in genotype and maturity type imply different effects of canopy cover on yield. Our study is the first to investigate these canopy cover effects on potato yield using an extensive set of genotypes representing different foliage maturity types under field drought conditions in different environments. Potato yield is the resultant of the number of tubers formed, and the volume (weight and size) of the tubers. Deblonde and Ledent (2001) reported that tuber number was reduced under drought, which was compensated by a higher tuber dry weight. Some reports indicate that drought causes more reduction in tuber weight than tuber number (Binod et al., 2015), but this may be highly dependent on genotypic differences and timing of the drought. Partitioning of assimilates to tubers for tuber formation as well as bulking and the interaction between these processes may be important for drought tolerance improvement of potato.

In this study we have evaluated the growth and yield of 103 potato cultivars in three different locations in three years. The aim was to investigate the genotypic variation of the drought response in cultivated potato with respect to canopy growth and yield under field conditions. Our objectives were to understand (i) how the timing of drought in the growing season affects potato growth and yield in the field (ii) which canopy growth characteristics are critical for potato tuber yield under drought in the field (iii) the stability of drought tolerance of potato cultivars across locations and in different years (iv) which aspects of yield are adversely affected in the field during drought.

2. Materials and methods

2.1. Field location and planting

A selection of 103 commercial potato cultivars with different genetic backgrounds and foliage maturity classes (early, intermediate, and late) were used in this study (Supplementary Table 1). The cultivars are part of the European potato gene pool used by D'Hoop et al. (2010) for genome-wide association studies. Field trials were conducted in partnership with four potato breeding companies (HZPC Holland BV, C. Meijer, KWS POTATO, and Averis seeds). Tubers used for the trials of each year were multiplied in the previous year at a single breeding station ensuring uniformity of seed tuber conditions. A split-plot design was used for each of the trials in three consecutive years (2013, 2014 and 2015), with irrigation levels assigned in the main plots as blocks and genotypes assigned in subplots. The fields were located in Connantre, France (48.7258°N, 3.9219° E) from 2013 to 2015; and in the Netherlands, Zeeland (51.5667°N, 3.7500° E) in 2013 and 2014; Emmeloord (52.7097°N, 5.7508° E) in 2013; and Grolloo (52.9305°N, 6.6943° E) in 2014. The field structure in each location and year included two blocks, irrigated (IR) and non-irrigated (NI) treatments. In each block, the cultivars were randomized as sub-plots within the blocks. Each subplot (experimental unit) had eight plants of a single cultivar in two rows (four plants per row). The spacing between plants in a row was 30 cm, and 70 cm between rows. Border plants were planted in between subplots of each row. The rows were set on ridges. The tubers were planted in April 2013 at Connantre, Zeeland, and Emmeloord; April 2014 at Connantre and Zeeland, and May 2014 at Grolloo; and April 2015 at Connantre. The plants remained in the field until harvest at the beginning of Fall in the respective locations and years. Environmental conditions of rainfall, temperature (aerial and soil), radiation, relative humidity, wind speed, and wind direction were monitored at the Connantre field in 2014 and 2015 using facilities provided by Dacom B.V. Environmental data from nearby weather stations were used for the other trials. The control blocks were irrigated weekly during periods of the drought (less rainfall) (e.g. Fig. 6D).

2.2. Phenotyping and data collection

Potato tubers germinated within three weeks of planting. The emergence date was recorded as days after planting when more than half of the plants per plot had germinated. Canopy ground cover was monitored by taking pictures of each plot weekly with a SONY DSC-W610 digital camera, to infer canopy growth. The camera was mounted on a rectangular frame at a specific height from the frame throughout the trial, and the frame was positioned just above the canopy. The dimension of the rectangular frame was set to capture the inner two plants of each plot. *Plant height* was scored within a month from emergence using the highest apex of each plot. At harvest various yield traits were measured including *tuber fresh weight* (TBW), *tuber number* (TBN), *underwater weight* (UWW), *dry matter percentage* (DMP, only in Connantre), and tuber quality by visual impression. A sample of 5.05 kg of harvested tubers per plot was used to measure UWW. The 5.05 kg was lowered in water and the weight under water measured according to EU-direction (https://webgate.ec.europa.eu/agriportal/angebleu/pdf.download?docNum=32009r0571&lg=EN). UWW is used to infer

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