Virtual potato crop modeling
A comparison of genetic coefficients of the DSSAT-SUBSTOR potato model with breeding goals for developing countries[*]

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Abstract

Virtual crop modeling is the representation of future genetic improvements from plant breeding in crop growth simulation models through changes in genetic coefficients or other crop model parameters with the objective of analyzing *ex-ante* the impacts of improved traits on crop yields and assisting breeders in their breeding efforts.

As a first step towards virtual crop modeling for the potato crop, the present report provides a comparison of priority breeding targets for developing country regions with genetic coefficients and other parameters of the SUBSTOR-potato model, thereby showing the potential uses of the model for that purpose.

It is shown that SUBSTOR provides scope for virtual crop modeling. Out of nine priority target traits, five can currently be dealt with in model. Adaptation to long day conditions and heat tolerance can directly be represented by adjusting the genetic coefficients of the model. High yields and drought tolerance would require changes in parameters that are currently included in the model code. Earliness would require the implementation of a new parameter in the code. Additional traits related to crop quality and resistance to biotic stress factors will require more profound changes in either the model structure or the coupling of the crop growth model with disease models.

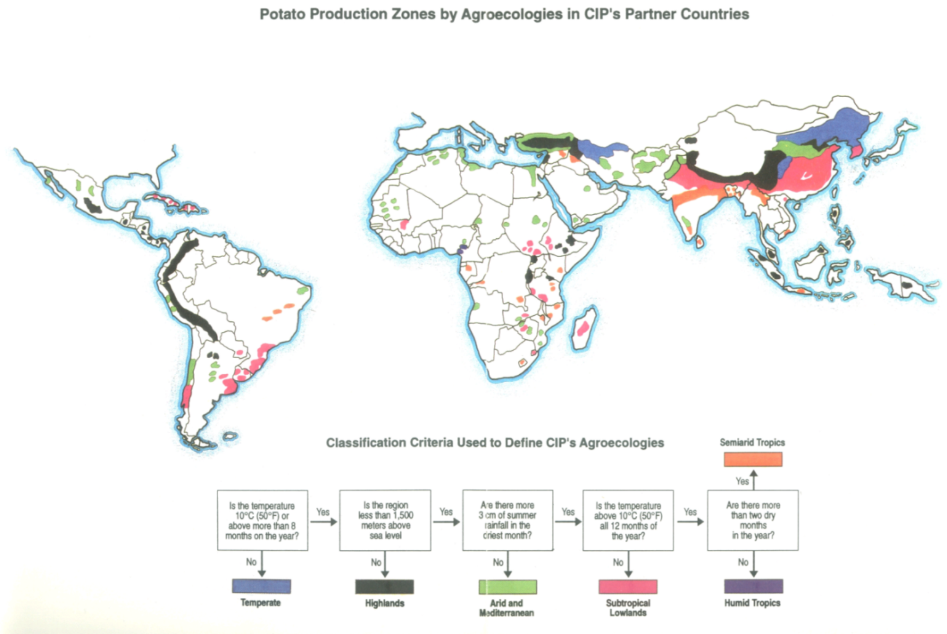
Keywords: DSSAT-SUBSTOR, potatoes, virtual crop modeling, crop improvement, breeding, impact assessment

1 Introduction

Potato is the most important non-grain food crop in the world (FAO, 2011). Up to the early 2000s developed countries were the major producers and consumers, but during the last decade developing countries' production has surpassed that of developed countries (Walker et al., 2011). In developing countries and under marginal growing conditions, potato is a cheap source of nutrients, thus a crop to guarantee food security, besides being an important source of income and employment (Lutaladio and Castaidi, 2009).

The center of origin of the potato is the Andes mountain range, where the International Potato Center (CIP) was established in Peru in 1971. CIP was founded with the objective of broadening the genetic base of the crop through the use of the large collection of potato germplasm and to develop varieties tailored to the needs of potato producers in the tropics and subtropics (CIP, 1985). In the 1990s, a delimitation exercise assisted to target new agro-ecological zones within the tropics and subtropics (Figure 1) (CIP, 1992). During the 2000s CIP's target regions expanded from the tropics and subtropics toward temperate countries of Asia (Theisen and Thiele, 2008). To date, target regions for CIP breeding are located across Latin America, Asia and Africa.

Figure 1: Potato production zones by agro-ecologies in CIP's partner countries. Reproduced after (CIP, 1992).



Crop modeling is a tool of using bio-physical knowledge through mathematical equations to simulate the dynamics of the plant-soil-atmosphere system. Crop modeling has supplied insights into the growth and development of crops as affected by environmental conditions like temperature, solar radiation, CO_2, water and nitrogen (van Ittersum et al., 2003). Crop modeling has assisted in irrigation management (Shae et al., 1999; Snapp and Fortuna, 2003), the reduction of nitrogen leaching (Peralta and Stockle, 2002) and can complement conventional procedures for breeding, especially in the improvement of resistances and tolerance to abiotic factors (Hammer et al., 2006).

As a more recent development, efforts are underway in the agricultural research for development community to use crop models for the ex-ante assessment of improved crop varieties. In these modeling efforts, called "virtual crop modeling", future genetic improvements through breeding shall be represented in crop models through changes in genetic coefficients or other crop parameters. Such an approach would offer the possibility to analyze *ex-ante* the impacts of improved traits on crop yields in a wide range of target environments. Results provided by these analyses could help to assist breeders in their breeding efforts and provide information for strategic research planning, priority setting and the design of future research programs.

Focusing on potatoes and the potato crop growth model SUBSTOR, the present report takes a first step into that direction by comparing relevant breeding goals for developing countries with the set of traits that can currently be represented in the model. The report starts with the identification of target traits for potato breeding for developing countries based on the particular case of CIP's potato breeding program. Next, an overview is supplied of the SUBSTOR-potato model. The general structure of the model is described and aspects relevant for virtual crop modeling are highlighted. A subsequent section compares the target traits identified with the genetic coefficients and other parameters of SUBSTOR, thus describing the potential uses of the model for virtual crop modeling.

2 Target traits in potato breeding for developing countries

Modern potato breeding started in the beginning of 18th century and till the 19th century was carried out in Europe and North America mainly (Birch et al., 2012). In China and India, as the most important potato producers in the developing world and currently the main potato producing countries, modern potato breeding started in the 1930s (Birch et al., 2012). Over the past

40 years, CIP has played an important role in developing and distributing improved potato cultivars for developing countries (CIP, 2010). Through CIP's breeding program, 107 varieties have been released in 26 countries since 1972 (CIP, 2013; Thiele et al., 2007).

Most breeding programs worldwide are oriented to improve cultivars for high yields, table quality, processing quality, high starch content, specific maturity types and dormancy (Birch et al., 2012; Bradshaw, 2009; CIP, 2006; Simakov et al., 2008). These characteristics are combined with regional-specific disease-resistance traits, leading to some variation among breeding programs and regions. For example, at the Scottish Crop Research Institute (SCRI), the biotic priorities are potato cyst nematode, late blight, powdery scab, blemish diseases, storage diseases, and viruses; while abiotic factor are heat, drought, cold and salinity tolerance (Bradshaw, 2009). For the Russian breeding program biotic priorities are viruses, late blight, *Alternaria solani*, potato cyst nematodes and heat and drought stress tolerance (Simakov et al., 2008).

For developing countries, we consider that the breeding targets of CIP provide a good representation of relevant traits for the respective regions. As Table 1 illustrates, CIP's breeding priorities have evolved over time. At the time of its establishment, CIP's breeding program had the objective of improving tuber and adaptation characteristics like yield, earliness and tuber nutrient quality. Also, tolerance to frost and drought as well as resistance to a range of biotic stresses like viruses, late blight, phoma blight, nematodes, bacterial wilt and *Erwinia* were targeted by breeders.

By the 2000s, adaptation to long photoperiod and processing quality had been added to the tuber and adaptation characteristics (Table 1). Among the abiotic stress tolerance traits, breeding for frost tolerance has been abandoned in favor of drought tolerance while heat tolerance has been maintained as a target trait. Crop improvement for the latter two gained particular attention during the last decade because regions with less favorable environments such as drought prone areas and warm conditions have been incorporated into potato producing areas in the Mediterranean region, in Asia, and Brazil (Benites and Pinto, 2011; CIP, 1985; Frusciante et al., 1999). In addition, projections of climate change indicate an increase of temperature and variability of rainfall (intensity and frequency) which may exacerbate the effect of droughts and heat waves (IPCC, 2007). Breeding for biotic has been the main priority focusing on virus resistance and resistance to late blight.

Accordingly, current target traits for potato breeding for developing countries as carried out by CIP comprise breeding for high yields, earliness, adaptation to long photoperiods, processing and tuber nutrient quality, heat

Table 1: Timeline of CIP's breeding priorities.

Trait	**1970**	**1980**	**1990**	**2000**
Agronomic, adaptation, and quality traits				
Yield	X	X	X	X
Earliness	X	X	X	X
Adaptation to long photoperiod				X
Processing quality		X	X	X
Tuber nutrient quality	X			X
Abiotic stress				
Frost	X	X		
Heat	X	X	X	X
Drought				X
Biotic stress				
Virus (PVX, PVY, and PLRV)	X	X	X	X
Late blight	X	X	X	X
Phoma blight	X			
Nematodes	X	X		
Bacterial wilt	X	X	X	
Erwinia	X			
Tuber moth		X		

Sources: CIP (1974, 1985); Thiele et al. (2007).

and drought tolerance as well as resistance to viruses and late blight.

3 The SUBSTOR potato model

SUBSTOR-potato belongs to a family of crop models embodied in the DSSAT (Decision Support Systems for Agro-technology Transfer) crop modeling software. SUBSTOR was developed from CERES-type crop models, thus uses capacity-type models of soil water and soil N dynamics that are used in other CERES-type models (Griffin et al., 1993). The SUBSTOR-potato model includes subroutines of temperature functions, phenology, biomass accumulation and carbon partitioning. Cardinal values were used to determine temperature functions for vine growth (RTFvine) and tuber and root growth (RTFsoil). Temperature functions differ for above and underground organs, however, due to the lack of data it has been assumed that all organs develop at the same temperature. The model calculates the daily crop growth rates and biomass accumulation. Biomass accumulation and carbon partitioning are controlled by coefficients or crop parameters. In SUBSTOR, these parameters are leaf area expansion rate (G2), potential tuber growth rate (G3), an index that suppresses the tuber growth (PD), tuber initiation sensitivity to photoperiod (P2), and upper critical temperature for tuber initiation (TC).

SUBSTOR-potato describes five phenological stages: pre-planting, planting to sprout elongation, sprout elongation to emergence, emergence to tuber initiation, and tuber initiation to maturity. The stage of sprout elongation to emergence is calculated when an emergence date is not provided. Using the RTFsoil function, the growth and elongations of unsprouted and sprouted tuber are calculated. Emergence in the model occurs when cumulative sprout length is higher than the depth of planting.

Tuber induction is a complex process affected by temperature and photoperiod. Despite of its complexity, a simplistic linear function is used in SUBSTOR to model tuber initiation. This function consists of a linear interpolation between tuber growth rate and the time when the tuber weight is zero. At the stage of tuber initiation, two of the genetic coefficients of SUBSTOR become effective. The model uses genetic parameters for the temperature for tuber initiation (TC) and the sensitivity to photoperiod (P2). If temperature is above TC, the tuber induction is reduced or inhibited. Thus, a higher value of TC can be interpreted as representing higher heat tolerance. P2 has a dimensionless value between 0 and 1. The closer P2 is to zero the less sensitive a cultivar is to long photoperiods. Tuber induction can take place earlier, even under long day conditions.

Biomass accumulation is influenced by the three remaining cultivar-specific genetic parameters, namely the potential leaf area expansion rate

(G2), the potential tuber growth rate (G3), and the index that suppresses tuber growth (PD). The vegetative growth is divided in two parts, before and after tuber induction. During sprout formation to emergence, stem elongation and leaf growth depend on the energy provided by the tuber seed. When leaf area reaches 400 cm^2 plant^{-1} the tuber seed is exhausted. Afterwards, the amount of assimilate available for crop growth is calculated from light interception of leaves and radiation use efficiency (RUE). Thereby, a larger leaf area results in a higher leaf area index, which (up to a saturation point) leads to higher light interception and therefore larger amounts of assimilate. The potential leaf area expansion rate (G2) influences leaf growth and, as a consequence, the availability of assimilate.

Tuber bulking is initiated after tuber induction. At this stage, the allocation of carbon resources to tubers gets priority over foliage. The coefficient PD, the index that suppresses tuber growth after tuber induction, ranges between 0 and 1 and determines how fast the tuber gets full priority over leaf growth. With a high value, assimilate gets allocated to the tuber more quickly. With low values, the period of transition towards giving the tuber full priority on assimilates takes longer (up to 10 days). Tuber growth, in turn, has two components: potential tuber growth and actual tuber growth. Potential tuber growth is calculated from light interception and radiation use efficiency and is influenced by the genetic parameter G3, the potential tuber growth rate. A higher value of P3 implies stronger potential tuber growth. The simulated actual tuber growth is then reduced by water and N deficit and suboptimal temperatures.

The required input data for the SUBSTOR model include daily total solar radiation, daily minimum and maximum temperature and daily precipitation. The crop model computes, in daily time-steps, plant phenological development from planting to harvest; photosynthesis and plant growth; carbon allocation to plant organs, and soil water and nitrogen dynamics and uptake. Additional inputs include cultivar parameters (see above), soil characteristics (soil water lower limit, drained upper limit, saturation, rooting depth, bulk density, soil organic carbon), and crop management information (planting date, plant density, sowing depth, irrigation, and fertilization amount, type and schedules).

4 Comparison of breeding goals and potato model parameters

In conventional breeding methods, many genotypes are screened across many environments to select the best adapted genotypes for an environment. Through modeling, breeders have the opportunity to expand their selection process across more environments and also to include varies management options. New potato growing regions could be explored with a model for potential suitability and many years of climate records could be included to analyze the risk of climatic variability on crop yield (Boote and Jones, 2011; Haverkort and Kooman, 1997). By means of virtual crop modeling, the impact of potential new improved traits on crop yields can be assessed. While the SUBSTOR model was not yet used in breeding applications, other potato crop models with similar structures to SUBSTOR, have been used for that purpose (Haverkort and Kooman, 1997; Haverkort and Grashoff, 2004; Khan et al., 2013; Spitters and Schapendonk, 1990).

For virtual crop modeling with SUBSTOR, the genetic coefficients of the model can be assumed to represent plant traits targeted by breeders. The genotype parameters, but also other crop parameters currently not considered as genetic coefficients in the model, can be adjusted to represent new improved traits in order to explore the potential yield impacts of future breeding efforts. As a first step towards such efforts, it is necessary to compare the genetic coefficients and other parameters of the model with the target traits of breeders. Such comparison allows gaining an overview on which traits can actually be represented in the model and therefore can be dealt with by virtual crop modeling. Table 2 contrasts the targets for potato breeding identified above with the genetic coefficients and other crop parameters of the SUBSTOR model.

Radiation use efficiency is the increase in dry matter per unit radiation intercepted (g MJ^{-1}). Higher RUE would allow for the generation of higher amounts of assimilates at a given level of solar radiation. In the case of cereals some cultivars showed higher RUE that would lead to higher yields (Reynolds et al., 2009). The variation of RUE in potato experiments is attributed to the genotypic and environment variation (Kooman et al., 1996). However, in the current version of SUBSTOR, RUE is not a genetic coefficient but rather a hard coded parameter.

With respect to earliness, CIP already has a collection of short (70 days), early (90 days), mid-early (100 days), and medium (110 days) maturity groups. These groups represent a large range of maturing types to be potentially introduced in different cropping systems to avoid biotic and abiotic stresses to improve food security and income in poverty regions of Asia and the tropical highlands (CIP, 1985, 2013). At CIP, a maturity type is evaluated based on the earliness of tuber onset and the senescence of the crop. Earliness of tuber onset is determined by sampling the tuber formation in the tip of stolons. The senescence is determined when a change of color of the vine from green to yellow is observed. The SUBSTOR model includes tuber initiation (TI), while senescence or maturity is defined by the harvest

Table 2: Breeding goals and genetic crop coefficients in SUBSTOR-potato.

	G2	**G3**	**PD**	**P2**	**TC**	**TI**	**RUE**	**HD**	**RD**	**ETBD**
Tuber quality and adaptation										
Yield							X			
Earliness						X		X		X
Photoperiod				X						
Processing quality										
Tuber nutrient quality										
Abiotic stress										
Heat tolerance					X					
Drought tolerance							X		X	
Biotic stress										
Virus resistance										
Late blight resisatance										

Genetic coefficients: G2 - Leaf expansion rate (cm^2 m^{-2}d^{-1}); G3 - Tuber growth rate (g m^{-2}d^{-1}); PD - Index that suppresses tuber growth after tuber induction; P2 - Sensitivity to long photoperiods; TC - Upper critical temperature for tuber induction (°C).

Other crop parameters which could be explored as traits: TI - Tuber induction (code); RUE - Radiation use efficiency (code); HD - Harvest date (X-File); RD - Rooting depth (code); ETBD - Effective tuber bulking duration (to implement).

day and therefore a maturity type is not considered. This is a shortcoming of SUBSTOR and needs to be addressed in future model improvements. Parameters which need to be included for such an improvement could be the effective tuber bulking duration (ETBD), and the duration of maximum canopy cover (Khan et al., 2013).

Adaptation to long photoperiods is a relevant trait because CIP aims to introduce advanced material into the subtropics and temperate regions where *tuberosum* type cultivars are predominant. This advanced material of tropical origin is usually adapted to short day conditions only. Three traits are considered at CIP for photoperiod adaptation: the capability of cuttings to form tubers after plants are exposed to long day conditions, the pedigree of genotypes which may include traits from higher latitude, and the compensatory effect of heat unit accumulation. In SUBSTOR, sensitivity to long photoperiods is an index that ranges from 0 to 1. The closer the value is to zero the less sensitive the cultivar is to long photoperiod. A high sensitivity to photoperiod means that a cultivar will not form tubers in a long day environment. Reducing the value of the coefficient allows to model less photoperiod sensitive virtual cultivars. The sensitivity to the photoperiod (P2) has been quantified for *tuberosum* cultivars, but not yet for *andigena* cultivars.

Drought is the major abiotic stress affecting growth and tuber yields.

With future climate change and an increased frequency of drought, selecting cultivars for effective use of water is important (Blum, 2009; Levy et al., 2013; Monneveux et al., 2013). Results of Cabello et al. (2012) show a high sensitivity of the potato crop to water stress with 38-58% less yield under several reduced irrigation regimes. Results of Schafleitner et al. (2007) suggest that stomata conductance and chlorophyll content are not effective traits to distinguish susceptible and tolerant genotypes. A characteristic observed in tolerant drought stress potatoes is an increased rooting system (rooting ability and higher root density) to increase access to more soil water (Cheng et al., 2013).

Several drought tolerance traits have been suggested for other crops like maize and beans, but less is known about possible effective drought tolerance traits in potato (Monneveux et al., 2013). Critical for drought tolerance is also the type of drought (early and late) and the type of cultivar (early and late) (Spitters and Schapendonk, 1990).

In standard cultivars drought stress reduces RUE; meanwhile cultivars with higher rooting depth probably maintain optimal RUE under drought stress conditions. RUE and rooting depth are parameters included in SUBSTOR, the interaction of both parameters under drought stress can be modified to explore their impact on drought tolerance. Root water uptake is influenced by rooting depth, root length density in each soil layer, water available in each soil layer, and resistance to water flow in roots. Distribution and root growth rate is also affected by the soil moisture and texture characteristics.

Since 1976, CIP started selecting for heat stress tolerance in potato (CIP, 1985). A crop characteristic identified for heat tolerance is earliness (CIP, 1985; Levy et al., 1991). Temperature has an impact on photosynthesis. The optimum temperature of gross photosynthesis is between 24-30°C and the optimum temperature for net photosynthesis is 25°C. A response of susceptible plants to high temperature include a shift of carbon partitioning affecting the harvest index, a reduction of stomata conductance, and an acceleration of the senescence process (Gawronska et al., 1992; Reynolds et al., 1990). In SUBSTOR, the tolerance to heat stress is currently expressed by the upper critical temperature threshold for tuber initiation (TC). By increasing its value, this coefficient can be explored to model heat tolerant potato cultivars.

Target traits that cannot be modeled with the current version of the SUBSTOR model are quality characteristics like processing or nutrient quality and biotic stresses like virus or late blight resistance. For the former group of traits, it would be required to further develop the model to be able to capture quality aspects of crop growth. In case of biotic stresses, an option worth exploring could be to couple the crop model with disease models.

5 Conclusions

By identifying target traits of potato breeding for production regions in developing countries and comparing these traits with the genetic coefficients and other parameters of the SUBSTOR potato model, the present report explores the options for using this specific crop model for virtual crop modeling aimed at assisting breeding programs and carrying out ex-ante impact assessment of potential new improved crop varieties.

The analysis shows that the SUBSTOR model provides scope for virtual crop modeling. Out of the nine traits currently targeted by potato breeders at CIP, five can currently be dealt with by the SUBSTOR model. Two traits – adaptation to long day conditions and heat tolerance – can directly be represented by adjusting the genetic coefficients of the model. The two further traits âĂŞ- high yields and drought tolerance – would require changes in parameters that are currently included in the model code. The fifth trait – earlines – would require the implementation of a new parameter in the code. Additional traits that are among the target traits identified will require more profound changes in either the model structure (quality traits) or the coupling of the crop growth model with disease models.

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