

Performance of the SUBSTOR-potato model across contrasting growing conditions

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Abstract

Crop models are essential tools in climate change impact assessments, but they often lack comprehensive field testing. In this study, we tested the SUBSTOR-potato model with 87 field experiments, including 204 treatments from 19 countries. The field experiments varied in potato species and cultivars, N fertilizer application, water supply, sowing dates, soil types, temperature environments, and atmospheric CO₂ concentrations, and included open top chamber and Free-Air-CO₂-Enrichment (FACE) experiments. Tuber yields were generally well simulated with the SUBSTOR-potato model across a wide range of current growing conditions and for diverse potato species and cultivars, including *Solanum tuberosum*, *Solanum andigenum*, *Solanum juzepczukii* species, as well as modern, traditional, early, medium, and late maturity-type cultivars, with a relative RMSE of 37.2% for tuber dry weight and 21.4% for tuber fresh weight. Cultivars 'Desiree' and 'Atlantic' were grown in experiments across the globe and well simulated using consistent cultivar parameters. However, the model underestimated the impact of elevated atmospheric CO₂ concentrations and poorly simulated high temperature effects on crop growth. Other simulated crop variables, including leaf area, stem weight, crop N, and soil water, differed frequently from measurements; some of these variables had significant large measurement errors. The SUBSTOR-potato model was shown to be suitable to simulate tuber growth and yields over a wide range of current growing conditions and crop management practices across many geographic regions. However, before the model can be used effectively in climate change impact assessments, it requires improved model routines to capture the impacts of elevated atmospheric CO₂ and high temperatures on crop growth.

Keywords: [SUBSTOR-potato](#); [Potato](#); [Crop modeling](#); [Model performance](#); [CO₂](#); [High temperature](#)

1 Introduction

Potato is the most important non-grain crop worldwide with a production of 330 million tonnes globally in 2010 (FAO, 2010). Potato production has increased dramatically during the last decade in the developing world, surpassing the production levels of the developed world (FAO, 2010). Potato constitutes the main source of food security and income in the developing world (Lutaladio and Castaldi, 2009), and will become increasingly important as the population is growing more rapidly in the developing world than developed regions (Lutz and KC, 2010; Lutz and KC, 2010). A growing population, along with climate change and increasing climate variability, will put additional pressure on potato food systems. Assessing the implications of these trends requires integrating crop models when evaluating the impact of new technologies and strategies for adapting to climate change.

Atmospheric concentration of carbon dioxide (CO₂) is expected to increase from 400 ppm in 2010 to ~550 ppm by 2050 (IPCC, 2013). Potato, a C3 crop, will respond with higher photosynthesis rate (Finnan et al., 2008) and water use efficiency under elevated atmospheric CO₂ concentrations (De Temmerman et al., 2002b; Fleisher et al., 2013). But high levels of atmospheric CO₂ are the main driver of climate change and will increase global temperature and higher rainfall variability, leading to heat waves and more droughts in some regions (IPCC, 2013). Studies in controlled experiment chambers suggest that elevated atmospheric CO₂ concentrations can mitigate stresses due to water shortage, but high temperatures can also negate the positive effects of increased atmospheric CO₂ concentrations on crop production (Kaminski et al., 2014).

Crop models are powerful tools that describe crop development and growth as a function of crop management, weather, and soil conditions (Haverkort and Top, 2011). More than 30 crop models have been developed for potato, and many of them have been used to study the impacts of climate change on potato production (Raymundo et al., 2014). Overall, these studies highlight that despite the positive effect of atmospheric CO₂ concentrations, potato production will decline across many regions in the world by 2100 (Raymundo et al., 2014). However, Stockle et al. (2010) indicated that, taking into account the effect of CO₂, adaptation strategies on crop production might guarantee the current production levels under future climate change conditions in the state of Washington in the United States. Others have used potato crop models to assess the impact of climate change on regional (Tubiello et al., 2002; Supit et al., 2012) and global potato production (Hijmans, 2003). Nevertheless, models have been developed for specific cultivars and geographic domains (Griffin et al., 1993; MacKerron, 2004). Global simulations require taking into account the crop variability across the globe and testing the model functionality with a standard cultivar across latitudes. In most of the climate change studies, potato models were used with cultivars and species from the developed world (Tubiello et al., 2002; Hijmans, 2003; Supit et al., 2012), neglecting the cultivar diversity of other cultivated species, as well as traditional and modern cultivars. Cultivars of the species *Solanum tuberosum* are most widely grown, whereas seven cultivated potato species, including *Solanum andigenum* (floury potato), and *Solanum juzepczukii* (bitter potato), coexist in the tropical Andes (Huaman and Spooner, 2002). Also, several hybrids of various species are grown in the developing world (Thiele et al., 2007), where the use of potato models is limited.

Most published potato crop models had limited exposure to field measurements for testing, and none of them have ever been tested with observed data under high temperature and drought conditions (Raymundo et al., 2014). Some potato crop models still ignore the effect of increasing atmospheric CO₂ concentrations on crop growth (Hijmans, 2003; Gobin, 2010; Saue and Kadaja, 2011). Most models include a theoretical C3 crop response to elevated atmospheric CO₂ (Raymundo et al. 2014), but only two potato models, LOPTCO and AQUACROP, were tested with experimental data of yield response to elevated levels of CO₂ concentrations (Wolf and Van Oijen, 2003; Vanuytrecht et al., 2011). The SUBSTOR-potato and the LINTUL potato models are the most widely used models for climate change studies (Franke et al., 2013; Haverkort et al., 2013; Raymundo et al., 2014); however, both models lack model testing with experimental data under elevated atmospheric CO₂ concentration expected in the future. Currently, publications of model applications outnumber publications of model performance testing (Raymundo et al., 2014). Therefore, field testing with current and possible future scenarios is required to build confidence in any crop model application. The most extensive field potato experimental dataset from around the world has been assembled to evaluate the performance of the SUBSTOR-potato model to guide model improvement needs and support future model applications.

2 Material and methods

2.1 The model

The SUBSTOR-potato model belongs to a family of crop models in the DSSAT-CSM (Decision Support Systems for Agro-technology Transfer—Crop Simulation Model) software (Jones et al., 2003; Hoogenboom et al., 2012). The model inputs are daily weather data, soil profile parameters, cultivar parameters, and crop management information. The SUBSTOR-potato model simulates the daily dynamics of phenology, biomass, and yield accumulation. The model accounts for soil water deficit factors that reduce photosynthesis (SWFAC) and growth (TURFAC) (Ritchie, 1998; Ritchie et al., 1995). Similarly, the model uses a nitrogen deficiency factor (NFAC) computed by the actual leaf nitrogen content, the critical leaf nitrogen content and minimum leaf nitrogen content to reduce photosynthesis (NSTRES) and growth (AGEFAC) (Godwin and Singh, 1998). Under water or nitrogen stress, SWFAC and NSTRES hasten tuber initiation and increase the carbon demand of tubers. The model has been extensively described by Griffin et al. (1993), Ritchie et al. (1998) and Singh et al. (1998). Following is a brief summary of the model.

The SUBSTOR-potato model simulates five phenological stages, including (1) pre-planting, (2) planting to sprout elongation, (3) sprout elongation to emergence, (4) emergence to tuber initiation, and (5) tuber initiation to harvest. Five cultivar-specific parameter control crop development and growth. The parameters tuber initiation sensitivity to photoperiod (P2, dimensionless) and upper critical temperature for tuber initiation (TC, °C) affect phenology; and leaf area expansion rate (G2, cm² m⁻² day⁻¹), potential tuber growth rate (G3, gm⁻² day⁻¹), and an index that suppresses tuber growth (PD, dimensionless) affect biomass accumulation (Griffin et al., 1993).

The SUBSTOR-potato model has different trapezoidal temperature impact functions, which simulate the effect of temperature on leaf growth (RTFVINE), root and tuber growth (RTFSOIL), photosynthesis (PRFT), and tuber initiation (RTFTI). Each of these functions has a range from zero to one. For RTFVINE, daily mean temperature is optimal between 18 °C and 24 °C and potential leaf expansion stops at <2 °C and >35 °C. For RTFSOIL, soil temperature (computed in the model from daily mean temperature) is optimal between 15 °C and 23 °C, and root and tuber growth stops at <2 °C and >35 °C. For PRFT, mean daily temperature is optimal between 15 °C and 30 °C, and photosynthesis stops at <3 °C and >42 °C. For RTFTI, a weighted average temperature is used (mean of 0.7 times the minimum temperature plus 0.25 times the maximum temperature) and is optimal between 10 °C and the upper critical temperature set with the cultivar parameter TC. Tuber initiation stops at <4 °C and >TC + 8 °C (Griffin et al., 1993).

2.1.1 Tuber initiation

Parameters TC and P2 play a key role at tuber initiation. If temperature is above TC, the tuber initiation and tuber bulking is reduced or inhibited. Thus, the upper value of TC can be interpreted as representing high temperature tolerance. P2 describes the sensitivity to day length and has a dimensionless value between 0 and 1. The closer P2 is to 0, the less sensitive a cultivar is to long photoperiods. Both parameters, TC and P2, are embedded in functions that determine the tuber initiation and influence tuber bulking.

The relative temperature function for tuber initiation (RTFTI) is described as follows:

$$RTFTI = 0 ; (TEMP \leq 4)$$

$$RTFTI = 1 - (1/36) \cdot (10 - TEMP)^2 ; (TEMP > 4 \ \& \ TEMP \leq 10)$$

$$RTFTI = 1 ; (TEMP > 10 \ \& \ TEMP \leq TC)$$

$$RTFTI = 1 - (1/64) \cdot (TEMP - TC)^2 ; (TEMP > TC \ \& \ TEMP \leq TC + 8)$$

Here, RTFTI is a function of weighted average temperature (TEMP = tmin*0.75 + tmax*0.25) and critical temperature (TC).

The relative daylength function for tuber initiation (RDLFTI) is described as follows:

$$RDLFTI = (1 - P2) + 0.00694 \cdot P2 \cdot (24 - PHPER)^2$$

Here, RDLFTI is a function of daylength in hours (PHPER) and sensitivity to daylength (P2). RDLFTI equals 1 when photoperiod is less than 12 **hours**.

2.1.2 Biomass accumulation after tuber initiation and partitioning

In the SUBSTOR-potato model, CO₂ concentrations affect the daily potential carbon fixation and potential tuber growth. The potential carbon fixation rate is described as follows:

$$PCARB = RUE * PAR / PLANTS * (1 - \exp(-0.55 * LAI)) * PCO_2$$

Here, the PCARB is a function of radiation use efficiency (RUE, g MJ⁻¹), photosynthetically active radiation (PAR, MJ m⁻²), and leaf area index (LAI, dimensionless), where plant density (PLANTS, plants m⁻²) is used to express the potential carbon fixation per unit area. RUE is 3.5 g MJ⁻¹ from emergence to tuber initiation and 4.0 g MJ⁻¹ from tuber initiation to harvest. PCARB is modified with increased atmospheric CO₂ by applying a relative CO₂ response factor (PCO₂) for C3 crops (Curry et al., 1990). This factor is 1 at atmospheric CO₂ concentration of 330 ppm and increases asymptotically up to 1.43 at a CO₂ concentration of 990 ppm. The actual carbon fixation rate is calculated by multiplying the potential carbon fixation rate with the minimum reduction factors for water shortage (SWFAC), nitrogen stress (NSTRES), or temperature factor that affects photosynthesis (PRFT) (Griffin et al., 1993).

Biomass accumulation at this stage is influenced by the three remaining cultivar-specific parameters, PD, G3, and G2. After tuber initiation, the model computes tuber growth in two steps. First, it estimates the priority for maximum tuber growth (TIND) using the sink strength (DTII) and the carbon demand of tubers after tuber initiation (DEVEFF):

$$TIND = DTII_{avg} * (1 / NFAC) * DEVEFF; NFAC > 1$$

$$TIND = DTII_{avg} * DEVEFF; NFAC < 1$$

$$DTII = RTFTI; \text{if no stress}$$

$$DTII = RTFTI + 0.5 * (1 - \min(SWFAC, NSTRES, 1))$$

$$DEVEFF = \min((XSTAGE - 2) * 10 * PD, 1)$$

$$XSTAGE = 2.0 + (CUMRTFVINE) / 100$$

DTII_{avg} is a three-day moving average of daily values of the sink strength (DTII). DTII is estimated as a relative function of temperature (RTFTI) and stress conditions. DEVEFF represents the carbon demand of tubers after tuber initiation, where XSTAGE indicates the progression through each phenological stage as a function of the cumulative leaf thermal time (CUMRTFVINE); the parameter PD ranges between 0 and 1 and determines how fast tubers get full priority over leaf growth. The constant 10 multiplies the factors to maintain the result between 0 and 1.

Second, the model estimates the potential tuber growth (PTUBGR, g plant⁻¹ day⁻¹) as a function of potential tuber growth rate (G3), relative temperature factor for root growth (RTFSOIL), and plant density (PLANTS, plants m⁻²):

$$PTUBGR = G3 * PCO_{2e} * RTFSOIL / PLANTS$$

Actual tuber growth (GROTUB, g plant⁻¹ day⁻¹) is a function of potential tuber growth affected by TIND, and water and nitrogen shortages:

$$GROTUB = PTUBGR * \min(TURFAC, AGEFAC, 1) * TIND$$

Actual leaf expansion (PLAG) is a function of potential leaf expansion (G2), limited by temperature (RTFVINE), water (TURFAC) and nitrogen (AGEFAC) shortages:

$$PLAG = G2 * RTFVINE / PLANTS * \min(TURFAC, AGEFAC, 1)$$

Leaf (GROLF), stem (GROSTM) and root (GRORT) growth are computed as follows:

$$GROLF = PLAG / LALWR$$

$$GROSTM = GROLF * 0.75$$

$$GRORT = (GROLF + GROSTM) * 0.2$$

where the leaf area to leaf weight ratio (LALWR, 270 cm g⁻¹) is a constant through the crop development.

The model converts tuber dry weight to tuber fresh weight assuming a dry matter content of 20%. Otherwise, the model estimates only dry weight for leaves, stems, and roots.

Finally, in DSSAT-CSM, including the SUBSTOR-potato model, atmospheric CO₂ concentration of 550 ppm increases the stomatal resistance by 37% (Allen, 1990). This effect, which is associated with the boundary layer and canopy resistance, causes an increase in transpiration efficiency.

3 Experimental data

For this study, we used data from experiments conducted in potato production regions across the world (Fig. 1a). The experiments were classified into temperate, subtropics, and tropic regions (CIP, 1992). The average photoperiods for experiments in temperate, subtropics, and tropic regions were 14.90, 11.21, and 12.06 hours, respectively. In the subtropics, the photoperiod was short to moderately long depending on the season, whereas in the tropics the photoperiod was constant throughout the year (Fig. 1b). The experiments represent a wide range of growing environments, including different elevations and soil types. Thus, the experiments covered different temperature regimes (Fig. 1c) and also a wide range of cultivar types, cultivar species, and crop management practices, across a total of 87 experiments conducted from 1970 to 2013 in 19 countries, consisting of 12 soil types, 32 cultivars, and 204 treatments. The experiments have been carried out to study dry matter allocation; yield response to various treatments, including nitrogen (N) fertilizer applications, water supply rates, radiation deficit, impact of high temperature; the adaptability of cultivars across locations and years; and the effect of increased atmospheric CO₂ concentrations on crop development in Open Top Chambers (OTC) and Free-Air-CO₂-Enrichment (FACE) facilities (Table 1a). Experiments selected for this study were fully controlled to prevent, pests, diseases, and weeds.

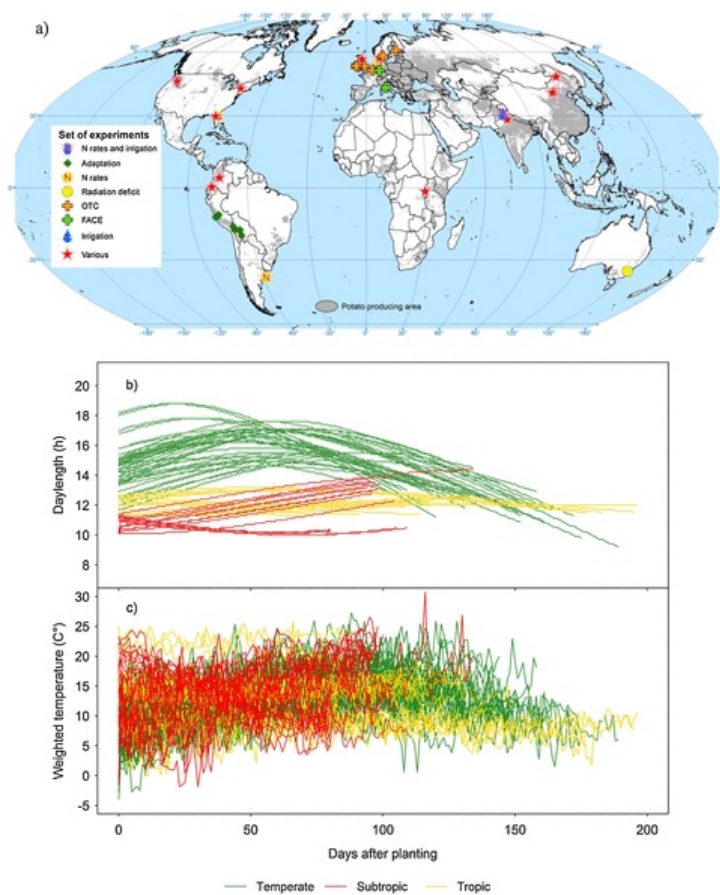


Fig. 1 (a) Global potato producing areas (gray) with model test sites (Monfreda et al., 2008), (b) photo-period, and (c) weighted average temperatures ($=0.75 \times \text{minimum temperature} + 0.25 \times \text{maximum temperature}$) during crop growth periods at model test sites.

alt-text: Fig. 1

Table 1 (a) Experimental sites and measured variables used in the simulation – observation comparisons – sorted alphabetically by country name. (b) Experimental sites and management treatments used in the model testing—sorted alphabetically by country name.

alt-text: Table 1

(A) Location	Year	lat ^a	lon ^b	alt ^c	Objective ^d	tr ^e	cult ^f	rep ^g	In-season sampling	Measured variables ^h	Soil Texture ⁱ	Reference
Argentina, Balcarce	1991	-37.8	-58.3	97	N rates	4	1		5	tu	CL	Travasso et al. (1996)
Australia	1970	-35.0	149.0		Radiation deficit	3	1		10	tuf,LAI	SC	Hoogenboom et al. (2012)
Belgium, Tervuren	1998–1999	50.8	4.5	97	CO ₂ OTC	1	1	3–6	2	tu,le,st,to,LAI	SiL	De Temmerman et al. (2002a)
Bolivia, Belen	1997	-16.0	-68.7	3640	Cultivar adaptation	1	3	3	3	tu,le	CL	Condori et al. (2010)
Bolivia, Chinoli	1997	-19.6	-65.3	3450	Cultivar adaptation	1	1	3	4	tu,le,st,ro,to	SL	Condori et al. (2010)
Bolivia, Koari	1997	-17.4	-65.6	3500	Cultivar adaptation	1	3	3	3	tu,le,st	CL	Condori et al. (2010)
Bolivia, Patacamaya	1997	-17.2	-68.0	3780	Cultivar adaptation	1	2		3–4	tu,le,st,ro	SiCL	Condori et al. (2010)
Bolivia, Patacamaya	1998 (2)	-17.2	-68.0	3780	Cultivar adaptation	1	2	3	3–4	tu,le,st,ro	SCL	Condori et al. (2010)
Bolivia, Toralapa	1993	-17.5	-65.7	3430	Cultivar adaptation	2	3	4	7	tu,le,st,ro,	CL	Condori et al. (2010)
China, Huhhot	1996	40.5	111.4	1065	Partitioning	1	1		6	tu,LAI	SL	Gao et al. (2003)
China, Huhhot	1998	40.5	111.4	1065	Partitioning	1	2		6	tu,le,st,to	SL	Liu et al. (2003b)
China, Jining	1999	41.0	113.0		Partitioning	1	2		6	tu,le,st,to	SL	Gao et al. (2004)
China, Zhalan	1997	48.0	123.0		Various	1	2		7	tu,le,st,to	SL	Liu et al. (2003a)
China, Zhalan	1998	48.0	123.0		Partitioning	1	3		7	tu,le,st,to	SL	Gao et al. (2004)
Colombia, Cundinamarca	1999	4.4	-74.1		Model validation	1	1		9	tu,le,st,to,LAI	SiL	Forero Hernandez and Garzon Montaño (2000)
Denmark, Jyndevad	1982–1983	54.9	9.1	10	Various	3	4		14–15	tu,to	S	Jørgensen (1984)
Denmark, Jyndevad	1990–1993	54.9	9.1	10	N rates	4	1		6–7	tu,ro,to,tuN,roN,toN	S	Edlefsen (1991)
Denmark, Jyndevad	1984–1986	54.9	9.1	10	N rates	2	1		5–7	tu,to,tuN	S	Jørgensen and Edlefsen (1987)
Denmark, Tylstrup	1981–1983	57.2	10.0	10	Various	4	4		13–14	tu,to	S	Bach and Nielsen (1985)
Ecuador, San Gabriel	1985	0.6	-77.8		N rates	3	2		4	tu	SL	Clavijo Ponce (1999)
Finland, Jokioinen	1998–1999	60.8	23.5	84	CO ₂ OTC	1	1	3	2	tu,le,st	SL	De Temmerman et al. (2002a)
Germany, Giessen	1998–1999	50.6	8.7	68	CO ₂ OTC	1	1	1–6	2	tu,le,st,to,LAI	SL	De Temmerman et al. (2002a)
Germany, Giessen	1998–1999	50.6	8.7	68	CO ₂ FACE	1	1	2–6	2	tu,le,st,to,LAI	SL	De Temmerman et al. (2002a)
India, Ludhiana	2008–2011	30.9	75.8	244	N rates and irrigation	4	1		1	tuf	SL	Arora et al. (2013)
India, Modipuram	2002–2009	28.7	77.2	228	Various	1	1		1	tuf	L,SiCL	
Ireland, Carlow	1998–1999	52.9	-6.9	57	CO ₂ OTC	1	1	3	2	tu,le,st,to	SiC	De Temmerman et al. (2002a)
Italy, Rapolano	1998–1999	42.7	11.9	38	CO ₂ FACE	1	1	3–4	2	tu,le,st,to,LAI	SL	De Temmerman et al. (2002a)
Peru, La Molina	2003–2010	-12.1	-77.0	244	Cultivar adaptation	1	1		1	tuf	SL	
Peru, La Molina	2013	-12.1	-77.0	244	Cultivar adaptation	1	3	3	5	tu,le,st	SL	

Peru, La Molina	1985	-12.1	-77.0	244	Cultivar adaptation	2	3		5	tu,le,st,to,LAI	SL, SCL,SL	Trebejo and Midmore (1990)
Peru, San Ramon	1984	-11.1	-75.3	800	High temperature tolerance	1	3		4	tu,le,st,to	SL	Nelson (1987)
Peru, San Ramon	2013	-11.1	-75.3	800	High temperature tolerance	1	3	3	5	tu,le,st,to	SL	
Scotland, Dundee	1984–1985	56.5	-3.1	40	N rates	2	1		8	tu,le,st,to,LAI,de,tuN,leN,stN,toN	SL	Marshall and Van Den Broek (1995)
Scotland, Dundee	1986–1987	56.5	-3.1	40	Irrigation	4	1		8	tu,le,st,to,LAI,SWC	SL	Marshall and Van Den Broek (1995)
Sweden, Goteborg	1998–1999	57.9	12.4	58	CO ₂ OTC	1	1	4–6	2	tu,le,st,to	SL	De Temmerman et al. (2002a)
Uganda, Kalengyere	2001–2009	-1.2	29.8	2400	Various	1	1		1	tuf	C	
United Kingdom, Sutton	1998–1999	52.8	-1.3	87	CO ₂ OTC	1	1	3	2	tu,le,st,to,LAI	SL	
United States, Benton	2003	45.9	-119.5		N rates	2	1		5–6	tu,le,st,to,LAI,tuN,leN,stN,toN	S	Alva et al. (2010)
United States, Hastings	2011–2012	29.7	-81.5	2	N rates	2	3	3	1	tu,le,st,tuN,leN,stN,toN,soN	S	Zotarelli et al. (2014)
United States, New York	1980	42.4	-76.5		Various	1	1		5	tu,le,st,to	SL	Hoogenboom et al. (2012)
United States, Idaho	1988	45.8	-119.3		Various	1			9–15	tu,le,st,to,LAI	SL	Hoogenboom et al. (2012)
United States, Suwanee	2010–2013	30.1	-83.1	13.7	N mass balance	1	1	12	1	tuf	S	Prasad et al. (2015)
United States, Suwanee	2001	30.1	-83.1	13.7	N mass balance	1	1	4	3–5	tu,le,st,soN,SWC	S	Albert (2002)
United States, Suwanee	2003	30.1	-83.1	13.7	N mass balance	1	1	8	3–5	tu,le,st,soN,SWC	S	Warren (2003)

(B) Location	Year	N tr*	Sowing date DOY	Emergence date DOY	Harvest date DOY	N application (kg ha ⁻¹)**	Irrigation (mm)	Rainfall (mm)	Type of irrigation	CO ₂ (ppm)	Cultivar
Argentina, Balcarce	1991	1	298	n.a.	64	0	113	540	Mixed	Default	Spunta
		2	298	n.a.	64	60 ₍₁₎	113	540	Mixed	Default	Spunta
		3	298	n.a.	64	120 ₍₁₎	113	540	Mixed	Default	Spunta
		4	298	n.a.	64	160 ₍₁₎	113	540	Mixed	Default	Spunta
Australia	1970	1	222	273	356	425 ₍₂₎	n.a.	219	Full	Default	Sebago
		2	222	273	356	425 ₍₂₎	n.a.	219	Full	Default	Sebago
		3	222	273	356	425 ₍₂₎	n.a.	219	Full	Default	Sebago
Belgium, Tervuren	1998+	1 ^N	127	135	257	205 ₍₂₎	373	423	Mixed	380	Bintje
		2 ^N	127	135	257	205 ₍₂₎	373	423	Mixed	386	Bintje
		3 ^N	127	135	257	205 ₍₂₎	373	423	Mixed	676	Bintje
	1999+	1 ^N	131	144	250	220 ₍₂₎	182	204	Full	365	Bintje
		2 ^N	131	144	250	220 ₍₂₎	181	204	Full	370	Bintje
		3 ^N	131	144	250	220 ₍₂₎	183	204	Mixed	664	Bintje
Bolivia, Belen	1997	1	288	316	84	110 ₍₁₎	n.a.	264	Full	Default	Waycha
		2	288	316	84	110 ₍₁₎	n.a.	264	Full	Default	Lucky
Bolivia, Chinoli	1997	1	301	340	62	124 ₍₁₎	n.a.	275	Full	Default	Desiree

Bolivia, Koari	1997	1	281	329	111	100_(1)	–	540	Rainfed	Default	Waycha ^{cal}
		2	281	329	111	100_(1)	–	540	Rainfed	Default	Alpha ^{cal}
		3	281	329	111	100_(1)	–	540	Rainfed	Default	Lucky ^{cal}
Bolivia, Patacamaya	1997	1 ^N	300	351	112	110_(1)	n.a.	341	Full	Default	Waycha
		2 ^N	300	351	112	110_(1)	n.a.	341	Full	Default	Lucky
Bolivia, Patacamaya	1998–1	1	292	347	110	110_(1)	n.a.	334	Full	Default	Waycha
		2	292	347	110	110_(1)	n.a.	334	Full	Default	Lucky
Bolivia, Patacamaya	1998–2	1 ^N	292	342	110	110_(1)	n.a.	334	Full	Default	Waycha
		2 ^N	292	342	110	110_(1)	n.a.	334	Full	Default	Lucky
Bolivia, Toralapa	1993	1 ^N	295	351	103	120_(1)	n.a.	440	Full	Default	Waycha
		2 ^N	295	351	103	120_(1)	n.a.	440	Full	Default	Alpha
		3 ^N	295	351	103	120_(1)	n.a.	440	Full	Default	Lucky
		4 ^N	295	351	103	120_(1)	–	440	Rainfed	Default	Waycha
		5 ^N	295	351	103	120_(1)	–	440	Rainfed	Default	Alpha
		6 ^N	295	351	103	120_(1)	–	440	Rainfed	Default	Lucky
China, Huhhot	1996	1	118	n.a.	250	150_(2)	n.a.	252	Full	Default	Desiree
China, Huhhot	1998	1	115	n.a.	253	150_(2)	n.a.	470.9	Full	Default	Desiree
China, Jining	1999	1	119	n.a.	234	74_(2)	n.a.	156	Full	Default	Desiree
		2	119	n.a.	234	74_(2)	n.a.	156	Full	Default	Kexin 1 ^{cal}
		3	119	n.a.	234	74_(2)	n.a.	156	Full	Default	Jinguan ^{cal}
China, Zhalan	1997	1	119	n.a.	253	180_(2)	n.a.	89	Full	Default	Desiree
China, Zhalan	1998	1	119	n.a.	242	90_(2)	–	754	Rainfed	Default	Kexin 1
		2	119	n.a.	242	90_(2)	–	754	Rainfed	Default	Neishu 7 ^{cal}
Colombia, Cundinamarca	1999	1	119	143	262	100_(1)	–	392	Rainfed	Default	Capiro
Denmark, Jynde vad	1981	1	119	149	225	155_(1)	169	431	Mixed	Default	Bintje
	1982	1	119	148	236	155_(1)	222	521	Mixed	Default	Bintje
	1983	1	122	148	215	155_(1)	156	370	Mixed	Default	Bintje
Denmark, Jynde vad	1990	1	107	n.a.	267	180 (1)	107	499	Mixed	Default	Bintje ^{cal}
		2	107	n.a.	267	180 (4)	104	499	Mixed	Default	Bintje ^{cal}
		3	107	n.a.	267	180 (4)	105	499	Mixed	Default	Bintje ^{cal}
	1991	1	101	149	273	180 (1)	137	390	Mixed	Default	Bintje
		2	101	149	273	180 (3)	137	390	Mixed	Default	Bintje

	1999+	1	149	159	264	80_(2)	–	122	Full	550	Bintje
Germany, Giessen	1998+	1 ^N	124	134	250	150_(2)	67	365	Mixed	373	Bintje
		2 ^N	124	134	250	150_(2)	67	365	Mixed	541	Bintje
		3 ^N	124	134	250	150_(2)	67	365	Mixed	690	Bintje
	1999+	1 ^N	130	147	258	116_(2)	152	267	Full	380	Bintje
		2 ^N	130	147	258	116_(2)	152	267	Full	541	Bintje
		3 ^N	130	147	258	116_(2)	148	267	Full	708	Bintje
Germany, Giessen	1998 + +	1 ^N	125	135	257	150_(2)	186	417	Mixed	401	Bintje
		2 ^N	125	135	257	150_(2)	186	417	Mixed	429	Bintje
	1999 + +	1	130	145	239	156_(2)	128	250	Full	374	Bintje
		2	130	145	239	156_(2)	126	250	Full	491	Bintje
India, Ludhiana	2008	1	290	n.a.	29	0	80	18	Mixed	Default	Kufri Bahar
		2	290	n.a.	29	136_(2)	80	18	Mixed	Default	Kufri Bahar
		3	290	n.a.	29	180_(2)	80	18	Mixed	Default	Kufri Bahar
		4	290	n.a.	29	224_(2)	80	18	Mixed	Default	Kufri Bahar
		5	290	n.a.	29	0	160	18	Mixed	Default	Kufri Bahar
		6	290	n.a.	29	136_(2)	160	18	Mixed	Default	Kufri Bahar
		7	290	n.a.	29	180_(2)	160	18	Mixed	Default	Kufri Bahar
		8	290	n.a.	29	224_(2)	160	18	Mixed	Default	Kufri Bahar
		9	290	n.a.	29	0	200	18	Mixed	Default	Kufri Bahar
		10	290	n.a.	29	136_(2)	200	18	Mixed	Default	Kufri Bahar
		11	290	n.a.	29	180_(2)	200	18	Mixed	Default	Kufri Bahar
		12	290	n.a.	29	224_(2)	200	18	Mixed	Default	Kufri Bahar
	2010	1	285	n.a.	29	0	80	32	Mixed	Default	Kufri Bahar
		2	285	n.a.	29	136_(2)	80	32	Mixed	Default	Kufri Bahar
		3	285	n.a.	29	180_(2)	80	32	Mixed	Default	Kufri Bahar
		4	285	n.a.	29	224_(2)	80	32	Mixed	Default	Kufri Bahar
		5	285	n.a.	29	0	160	32	Mixed	Default	Kufri Bahar
		6	285	n.a.	29	136_(2)	160	32	Mixed	Default	Kufri Bahar
		7	285	n.a.	29	180_(2)	160	32	Mixed	Default	Kufri Bahar
		8	285	n.a.	29	224_(2)	160	32	Mixed	Default	Kufri Bahar
		9	285	n.a.	29	0	200	32	Mixed	Default	Kufri Bahar
		10	285	n.a.	29	136_(2)	200	32	Mixed	Default	Kufri Bahar

		11	285	n.a.	29	180 ₍₂₎	200	32	Mixed	Default	Kufri Bahar
		12	285	n.a.	29	224 ₍₂₎	200	32	Mixed	Default	Kufri Bahar
India, Modipuram	2002	1	288	n.a.	3	181 ₍₂₎	n.a.	0	Full	Default	Kufri Bahar
	2003	1	299	n.a.	18	181 ₍₂₎	n.a.	30	Full	Default	Kufri Bahar
	2004	1	293	n.a.	11	181 ₍₂₎	n.a.	0	Full	Default	Kufri Bahar
	2005	1	289	n.a.	8	181 ₍₂₎	n.a.	1	Full	Default	Kufri Bahar
	2006	1	294	n.a.	13	181 ₍₂₎	n.a.	0	Full	Default	Kufri Bahar
	2007	1	298	n.a.	17	181 ₍₂₎	n.a.	0	Full	Default	Kufri Bahar
	2008	1	290	n.a.	8	181 ₍₂₎	n.a.	12	Full	Default	Kufri Bahar
	2009	1	302	n.a.	21	181 ₍₂₎	n.a.	0	Full	Default	Kufri Bahar
Ireland, Carlow	1998 ^N	1	128	138	280	250 ₍₂₎	61	343	Full	372	Bintje
		2	128	138	280	250 ₍₂₎	31	343	Full	693	Bintje
	1999 ^N	1	140	152	249	250 ₍₂₎	89	392	Full	372	Bintje
		2	140	152	249	250 ₍₂₎	91	392	Full	670	Bintje
Italy, Rapolano	1998 ⁺⁺	1	141	149	237	240 ₍₂₎	309	554	Full	366	Bintje
		2	141	149	237	240 ₍₂₎	294	554	Full	552	Bintje
		3	141	149	237	240 ₍₂₎	285	554	Full	367	Bintje
	1999 ⁺⁺	1	126	147	237	250 ₍₂₎	462	146	Mixed	367	Bintje
		2	126	147	237	250 ₍₂₎	462	146	Mixed	552	Bintje
		3	126	147	237	250 ₍₂₎	462	146	Mixed	367	Bintje
Peru, La Molina	2003	1	181	n.a.	314	310 ₍₂₎	450	0	Irrigated	Default	Amarilis
	2004	1	177	n.a.	307	310 ₍₂₎	350	0	Irrigated	Default	Amarilis
	2005	1	164	n.a.	281	298 ₍₂₎	450	0	Irrigated	Default	Amarilis
	2006	1	186	n.a.	319	310 ₍₂₎	350	0	Irrigated	Default	Amarilis
	2007	1	152	n.a.	275	350 ₍₂₎	400	0	Irrigated	Default	Amarilis
	2008	1	182	n.a.	294	235 ₍₂₎	350	0	Irrigated	Default	Amarilis
	2009	1	183	n.a.	292	235 ₍₂₎	400	0	Irrigated	Default	Amarilis
	2010	1	196	n.a.	307	227 ₍₂₎	350	0	Irrigated	Default	Amarilis
Peru, La Molina	2013	1	179	200	288	210 ₍₂₎	215	14	Full	Default	Achirana
		2	179	198	288	210 ₍₂₎	215	14	Full	Default	Atlantic
		3	179	198	288	210 ₍₂₎	215	14	Full	Default	Sarnav ^{cal}
Peru, La Molina	1985	1	30	60	122	160 ₍₂₎	449	3	Irrigated	Default	DTO-33
		2	30	60	130	160 ₍₂₎	480	3	Irrigated	Default	LT1

		3	30	60	144	160 ₍₂₎	485	3	Irrigated	Default	Revolucion
		4	176	206	285	160 ₍₂₎	315	1	Irrigated	Default	DTO-33
		5	176	206	291	160 ₍₂₎	257	1	Irrigated	Default	LT1
		6	176	206	274	160 ₍₂₎	272	1	Irrigated	Default	Revolucion
Peru, San Ramon	1984	1	109	122	199	200 ₍₂₎	n.a.	336	Full	Default	DTO-33
		2	109	126	199	200 ₍₂₎	n.a.	336	Full	Default	Desiree
		3	109	128	199	200 ₍₂₎	n.a.	336	Full	Default	Revolucion
Peru, San Ramon	2013	1	213	228	301	300 ₍₂₎	449	303	Mixed	Default	Achirana ^{sal}
		2	213	228	301	300 ₍₂₎	449	303	Mixed	Default	Atlantic
		3	213	228	301	300 ₍₂₎	449	303	Mixed	Default	Sarnav
Scotland, Dundee	1984	1 ^N	104	150	268	0	187	202	Mixed	Default	Maris piper
		2 ^N	104	150	268	240 ₍₁₎	187	202	Mixed	Default	Maris piper
	1985	1 ^N	114	154	262	0	15	373	Mixed	Default	Maris piper
		2 ^N	114	154	262	240 ₍₁₎	15	373	Mixed	Default	Maris piper
	1986	1 ^N	135	166	266	175 ₍₁₎	91	200	Mixed	Default	Maris piper
	1987	1 ^N	119	155	258	175 ₍₁₎	39	346	Mixed	Default	Maris piper
Sweden, Goteborg	1998+	1 ^N	145	154	252	88 ₍₂₎	480	357	Mixed	708	Bintje
		2 ^N	145	155	252	88 ₍₂₎	480	357	Mixed	404	Bintje
Uganda, Kalengyere	2004	1	61	n.a.	169	100 ₍₁₎	–	294	Rainfed	Default	Asante
	2005	1	80	n.a.	189	100 ₍₁₎	–	318	Rainfed	Default	Asante
	2006	1	82	n.a.	186	100 ₍₁₎	–	399	Rainfed	Default	Asante
	2009	1	273	n.a.	355	120 ₍₁₎	–	501	Rainfed	Default	Asante
United Kingdom, Sutton	1998+	1 ^N	126	136	239	110 ₍₂₎	98	251	Full	379	Bintje
		2 ^N	126	136	239	110 ₍₂₎	97	251	Full	563	Bintje
		3 ^N	126	136	239	110 ₍₂₎	99	251	Full	673	Bintje
	1999+	1 ^N	132	144	249	250 ₍₂₎	131	247	Full	399	Bintje
		2 ^N	132	144	249	250 ₍₂₎	134	247	Full	543	Bintje
		3 ^N	132	144	249	250 ₍₂₎	132	247	Full	694	Bintje
United States, Benton	2003	1	87	110	231	324 ₍₉₎	666	164	Mixed	Default	Russet Burbank
		2	87	110	231	669 ₍₅₎	666	164	Mixed	Default	Russet Burbank
United States, Hastings	2011	1	12	43	108	168 ₍₃₎	n.a.	255	Full	Default	Atlantic
		2	12	43	108	224 ₍₃₎	n.a.	258	Full	Default	Atlantic
		3	19	45	117	168 ₍₃₎	n.a.	258	Full	Default	Atlantic

		4	19	45	117	224 ₍₃₎	n.a.	258	Full	Default	Atlantic
		5	20	45	116	168 ₍₃₎	n.a.	258	Full	Default	Atlantic
		6	20	45	116	224 ₍₃₎	n.a.	258	Full	Default	Atlantic
United States, New York	1980	1	143	157	257	275 ₍₂₎	209	297	Full	Default	Kathadin
United States, Idaho	1988	1	105	129	264	367 ₍₁₀₎	669	136	Full	Default	Russet Burbank
		2	89	115	174	354 ₍₁₅₎	580	123	Full	Default	Russet Burbank
		3	98	118	174	433 ₍₁₆₎	687	136	Full	Default	Russet Burbank
		4	117	134	264	349 ₍₁₅₎	644	136	Full	Default	Russet Burbank
		5	75	105	221	771 ₍₁₇₎	598	123	Full	Default	Russet Burbank
		6	81	114	250	375 ₍₁₁₎	669	123	Full	Default	Russet Burbank
		7	107	131	174	375 ₍₁₁₎	605	123	Full	Default	Russet Burbank
		8	91	120	174	175 ₍₇₎	686	135	Full	Default	Russet Burbank
		9	116	136	264	375 ₍₁₁₎	686	136	Full	Default	Russet Burbank
		10	98	125	174	375 ₍₁₁₎	740	136	Full	Default	Russet Burbank
United States, Suwanee	2010	1	41	74	140	265 ₍₄₎	281	758	Mixed	Default	Red Lasoda
	2011	1	28	57	118	278 ₍₅₎	297	537	Mixed	Default	Red Lasoda
		2	43	62	140	285 ₍₅₎	291	558	Mixed	Default	Red Lasoda
	2012	1	31	51	123	285 ₍₅₎	349	320	Mixed	Default	Red Lasoda
		2	50	69	141	248 ₍₄₎	343	356	Mixed	Default	Red Lasoda
	2013	1	45	65	140	248 ₍₄₎	287	448	Mixed	Default	Red Lasoda
United States, Suwanee	2001	1	46	62	141	313 ₍₅₎	507	290	Mixed	Default	Red Lasoda
		2	46	62	141	280 ₍₅₎	507	290	Mixed	Default	Red Lasoda
	2002	1	43	60	137	292 ₍₅₎	343	481	Mixed	Default	Red Lasoda
		2	46	64	138	261 ₍₅₎	272	489	Mixed	Default	Red Lasoda
	2003	1	41	64	138	278 ₍₄₎	242	576	Mixed	Default	Red Lasoda

cal: Treatments used for calibration.

N: Treatments with estimated initial soil N.

*: Number of treatments.

**: Number of nitrogen applications are in parenthesis.

+: OTC.

++: FACE.

n.a.: Not available.

-: Not applicable.

Full: Automatic irrigation.

Default: Atmospheric CO₂ concentration calculated by DSSAT-CSM.

^a Latitude.

^b Longitude.

^c Altitude.

^d FACE: Free-Air-CO₂-Enrichment, OTC: Open Top Chambers.

^e n Number of treatments.

^f n Number of cultivars.

^g s Sampling repetitions.

^h tu: Tuber dry weight (Mg ha⁻¹), tubf: Tuber fresh weight (Mg ha⁻¹), le: Leaf dry weight (Mg ha⁻¹), st: Stem dry weight (Mg ha⁻¹), to: aboveground dry weight (Mg ha⁻¹), LAI: leaf area index, de: dead tissue dry weight (Mg ha⁻¹); tuN: tuber N uptake (kg ha⁻¹); leN: Leaf N uptake (kg ha⁻¹); stN: Stem N uptake (kg ha⁻¹), toN: aboveground nitrogen uptake (kg ha⁻¹), SoN: Soil N content (ppm), SWC: Soil water content (m³ m⁻³).

ⁱ C: clay; S:sand; Si: silt; L:loam.

Measurements in many of these potato experiments differed. For example, 65 of the experiments had information about tuber dry weight, while 22 experiments had information about tuber fresh weight. Most experiments had in-season tuber growth measurements (often with more than two measurements), and 21 experiments only had information about the final tuber yield. Table 1a and b lists the experiments we used with the measured experimental variables and the manager information.

3.1 Weather data

The experiments included daily measurements of solar radiation, maximum and minimum temperatures, and precipitation. Missing data were filled in with data from NASA Prediction of Worldwide Energy Resource (<http://power.larc.nasa.gov/cgiwrap/solar/agro.cgi>).

3.2 Soil parameters

Several of the field experiments had measurements of soil parameters. If this information was not available, it was computed using the Sbuild soil parameter estimation tool available in the DSSAT-CSM suite of applications when quantitative information of soil texture and organic carbon were available. Generic soil profiles, available in DSSAT-CSM, were assigned only when qualitative soil type information was available.

3.3 Calibration of cultivar parameters

Cultivar parameters P2, TC, G2, G3, and PD were obtained from literature and otherwise from the DSSAT-CSM database (Table 2). To estimate new parameters for new cultivars we used the Generalized Likelihood Uncertainty Estimation (GLUE) tool of DSSAT-CSM (Jones et al., 2011), which requires a default set of parameters and observed data. The default set of parameters was assigned from a randomly selected cultivar or was assigned from a specific cultivar only if a new cultivar shared the pedigree (Berlo et al., 2007; Berlo et al., 2007) with a known cultivar in Table 2. Table 1b shows the treatments used for calibration. We evaluated the model performance with the default set of parameters and with the new set of parameters estimated with GLUE. Parameters TC and P2 were manually adjusted if tuber yield simulations failed in one of contrasting locations (La Molina and San Ramon). These results were discussed with potato experts (breeders) who provided the experimental datasets. After cultivar parameters were determined, they were kept unchanged across experiments and locations. Table 2 lists the cultivar parameters used in simulations performed with the SUBSTOR-potato model.

Table 2 Cultivar parameters used in the SUBSTOR-potato model.

alt-text: Table 2

Cultivar	Species	Maturity type	Country	G2 (cm ² m ⁻² day ⁻¹)	G3 (g m ⁻² day ⁻¹)	PD (-)	P2 (-)	TC (°C)	Source
Achirana	<i>S. tuberosum</i>	Early	Peru	2000	21	0.8	0.5	17	
Alpha	<i>S. tuberosum</i>	Late	Bolivia	1000	25	0.9	0.4	20	
Amarilis	<i>S. tuberosum</i>	Medium	Peru	2000	30	0.9	0.9	20	(U. Kleinwechter, pers. comm., 2014)

Asante	<i>S. tuberosum</i>	Medium	Uganda	2000	26	0.7	0.9	21	(U. Kleinwechter, pers. comm., 2014)
Atlantic	<i>S. tuberosum</i>	Early	Peru, United States	1000	25	0.9	0.6	17	Hoogenboom et al. (2012)
Bintje	<i>S. tuberosum</i>	Late	Europe	1000	30	0.8	0.1	19	
Capiro	<i>S. tuberosum</i>	Late	Colombia	1000	22	0.6	0.7	17	Bowen et al. (1999)
Desiree	<i>S. tuberosum</i>	Early	China, Peru, and Bolivia	2000	25	0.9	0.6	16	Hoogenboom et al. (2012)
Dianella	<i>S. tuberosum</i>	Late	Denmark	1500	24	0.6	0.3	18	
DTO-33	<i>S. tuberosum</i>	Early	Peru	2000	25	0.7	0.6	17	Bowen et al. (1999)
INIAP-Gabriela	<i>S. tuberosum</i>	Late	Ecuador	2000	19	0.9	0.3	19	Bowen et al. (1999)
INIAP-Maria	<i>S. tuberosum</i>	Late	Ecuador	2000	22	0.4	0.5	19	Bowen et al., (1999)
Jinguan	<i>S. tuberosum</i>	–	China	2000	24	0.9	0.8	17	
Kaptah	<i>S. tuberosum</i>	Late	Denmark	1800	24	0.6	0.4	18	
Kathadin	<i>S. tuberosum</i>	Late	United States	2000	25	0.5	0.7	20	Hoogenboom et al. (2012)
Kexin 1	<i>S. tuberosum</i>	–	China	2000	25	0.9	0.8	17	
Kufri Bahar	<i>S. tuberosum</i>	Early	India	2000	22	0.9	0.8	23	(U. Kleinwechter, pers. comm., 2014)
LT-1	<i>S. tuberosum</i>	Early	Peru	2000	25	0.9	0.8	17	Hoogenboom et al. (2012)
Luky	<i>S. juzepczukii</i>	Late	Bolivia	2000	21	0.4	0.8	15	
Maris Piper	<i>S. tuberosum</i>	Late	Scotland	2000	25	0.8	0.4	17	Hoogenboom et al. (2012)
Neishu 7	<i>S. tuberosum</i>	–	China	1600	23	0.7	0.8	18	
Posmo	<i>S. tuberosum</i>	Late	Denmark	1500	24	0.6	0.3	18	
Ranger Russet	<i>S. tuberosum</i>	Late	United States	1100	26	0.9	0.6	17	Hoogenboom et al. (2012)
Red Lasoda	<i>S. tuberosum</i>	Medium	United States	2000	22	0.7	0.4	19	Hoogenboom et al. (2012)
Revolucion	<i>S. tuberosum</i>	Late	Peru	2000	30	1	0.6	17	Bowen et al. (1999)
Russet Burbank	<i>S. tuberosum</i>	Late	United States	1100	26	0.9	0.6	17	Hoogenboom et al. (2012)
Sarnav	<i>S. tuberosum</i>	Late	Peru	1000	30	0.2	0.6	18	
Sava	<i>S. tuberosum</i>	Late	Denmark	1300	24	0.6	0.4	21	
Spunta	<i>S. tuberosum</i>	Medium	Argentina	1800	24	0.5	0.1	19	Travasso et al. (1996)
Tilva	<i>S. tuberosum</i>	Late	Denmark	1500	24	0.9	0.3	18	
Waycha	<i>S. andigenum</i>	Late	Bolivia	1200	23	0.6	0.3	15	
Zibaihua	<i>S. tuberosum</i>	–	China	2000	25	0.9	0.8	17	

G2: Leaf expansion rate, G3: **T**uber growth rate, PD: **I**ndex that suppress tuber growth after tuber induction, P2: **S**sensitivity to photoperiod, TC: **U**pper critical temperature for tuber initiation (°C).

–: **n**Not available.

3.4 Simulations

Simulated experiments were set to non-water-limiting conditions (automatic irrigation), when irrigation was known to be applied but actual rates were missing and when the involved researchers confirmed non-water-limiting conditions. Additionally, some

experiments were confirmed to be non-nitrogen limited by the researchers. Initial soil conditions were missing in about 20% of the experiments; in these cases, simulations with various amounts of initial mineral soil N were carried out for one treatment and the amount of initial mineral N that fitted the final yield best was applied to all other treatments. This process was repeated for every experiment with no information of initial soil N. In experiments with N rate treatments, the plant N uptake of the lowest N treatment (usually a treatment without N fertilizer) was set as the initial mineral soil N (Ritchie et al., 1995). In experiments with information on soil organic carbon, we initialized the soil carbon pools with the CENTURY model (Basso et al., 2011; Porter et al., 2014), providing the stable organic carbon for each soil layer. We assumed 82% and 90% of the total organic carbon as stable organic carbon between 0 and 60 cm and below 60 cm, respectively.

We performed simulations with the SUBSTOR-potato model embodied in DSSAT-CSM for all experiments. Evapotranspiration was calculated with the Priestley-Taylor/Ritchie formula; soil water infiltration was computed with the capacity approach method; soil evaporation was estimated with the Suleiman-Ritchie method; and the dynamic of carbon and nitrogen was simulated with the CENTURY model (Hoogenboom et al., 2012).

Finally, we simulated the experiments from emergence to harvest date with information about weather, soil and cultivar characteristics, and crop management practices, as given in Table 1a and b. Simulations started at planting date if the emergence day was not available.

3.5 Evaluation of model performance

Crop model performance was evaluated by comparing simulated and observed in-season and end-of-season values. Experimental crop measurements included tuber dry weight (Mg ha^{-1}), tuber fresh weight (Mg ha^{-1}), aboveground dry weight (Mg ha^{-1}), root dry weight (Mg ha^{-1}), leaf dry weight (Mg ha^{-1}), stem dry weight (Mg ha^{-1}), dead material dry weight (Mg ha^{-1}), leaf area index (LAI, -), aboveground N (kg N ha^{-1}), tuber initiation (days), tuber N content (kg N ha^{-1}), root N content (%), leaf N content (kg N ha^{-1}), and stem N content (kg N ha^{-1}). Experimental soil measurements included soil water content ($\text{m}^3 \text{ m}^{-3}$), soil NO_3

N (ppm), and soil NH_4

N (ppm). We evaluated the model simulations by comparing with measured data from experiments, using statistical indices of coefficient of determination (R^2), slope of a linear regression (m), root mean square error (RMSE) (Wallach and Goffinet, 1987), and relative RMSE (RRMSE). The regression to calculate the R^2 was for the 1:1 line and forced through the origin. This R^2 value measures the true deviation of the estimates from the observations (Yang et al., 2014). The slope m quantifies a possible overestimation or underestimation by the model. The RMSE was computed to provide a measure of the absolute magnitude of the error. All calculations and graphs were made using the R statistical software (R Core Team, 2015).

4 Results

Fig. 2 shows a comparison of simulated and observed yields of three potato species, *S. andigenum* (cv. 'Waycha'), *S. tuberosum* (cv. 'Alpha'), and *S. juzepczukii* (cv. 'Lucky') at Toralapa, Bolivia (1993) at 3430 m.a.s.l. The in-season tuber dry weight was well-simulated for these three species. The simulated in-season leaf dry weight accumulation (Fig. 2b, d, and f) followed the trend of the observations, although it was less accurate than the tuber dry weight simulations (Fig. 2a, c, and e).

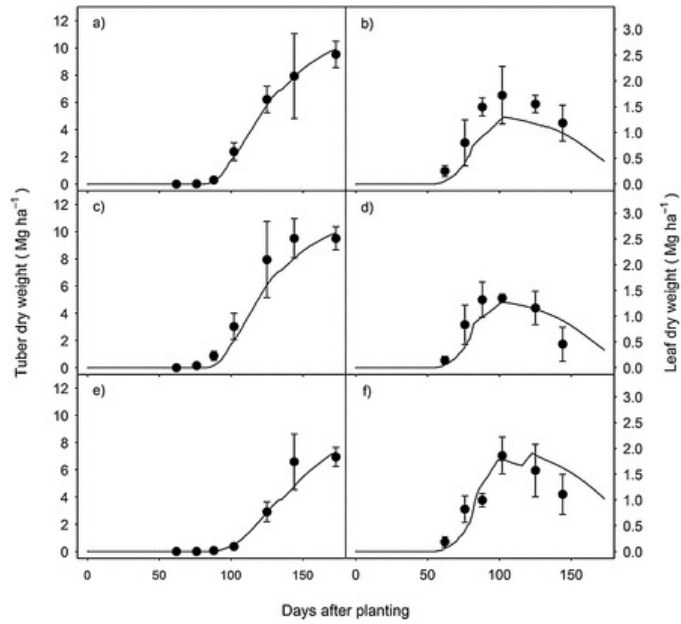


Fig. 2 Simulated (—) versus observed (●) tuber dry weight (Mg ha^{-1}) and leaf dry weight (Mg ha^{-1}) for three potato species: (a,b) *Solanum andigenum* – cv. 'Waycha', (c,d) *Solanum tuberosum* – cv. 'Alpha' and (e, f) *Solanum juzepczukii* – cv. 'Lucky' in Toralapa, Bolivia, 1993. Error bars indicate standard error of measurements when available.

alt-text: Fig. 2

Fig. 3 shows the performance of the model for cv. 'Desiree' in different locations with contrasting temperature and photoperiod environments. The photoperiod in these four locations ranged from 11.4 hours in Peru (San Ramon) to 14.8 hours in northern China (Huhhot and Wumeng). In Huhhot (Fig. 3a) and Wumeng (Fig. 3b), the simulation captured the dynamics of the observations well, but tended to overestimate final yields in Huhhot (Fig. 3a). In San Ramon and Chinoli, the simulated tuber growth corresponded well with the observed tuber growth during the initial part of the growth period (Fig. 3c and d). However, at these locations observed tuber growth stopped earlier than assumed in the simulation, resulting in a difference in the final tuber yield.

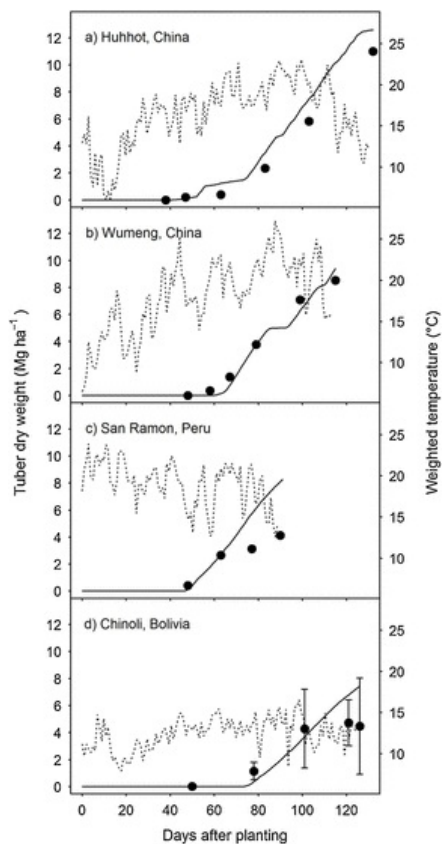


Fig. 3 Simulated (—) versus observed (●) tuber dry weight (Mg ha^{-1}) for cv. 'Desiree' at (a) Huhhot, China, 1996, (b) Wumeng, China, 1999, (c) San Ramon, Peru, 1984, and (d) Chinoli, Bolivia, 1997. Dotted lines show the weighted average temperature for each location. Error bars indicate standard error of measurements when available.

alt-text: Fig. 3

Fig. 4 shows a comparison of simulated and observed values of tuber dry weight, leaf area index, and tuber N uptake for two N treatments (N0 and N240, with application rates of 0 and 240 kg N ha^{-1} , respectively) on a sandy loam soil at Dundee, Scotland in 1985. The model simulated accurately the time course of the observed tuber dry weights for the two N treatments (Fig. 4a). The simulated results for both LAI and tuber N uptake sometimes differed from the measured values (Fig. 4b and c). For example, the model overestimated the tuber N uptake for the N0 treatment but showed a good agreement for the N240 treatment. These results show that in general the model can predict tuber production well for different N fertilizer treatments, although sometimes the simulated time courses of LAI and tuber N uptake may differ from the observed values (Fig. 4).

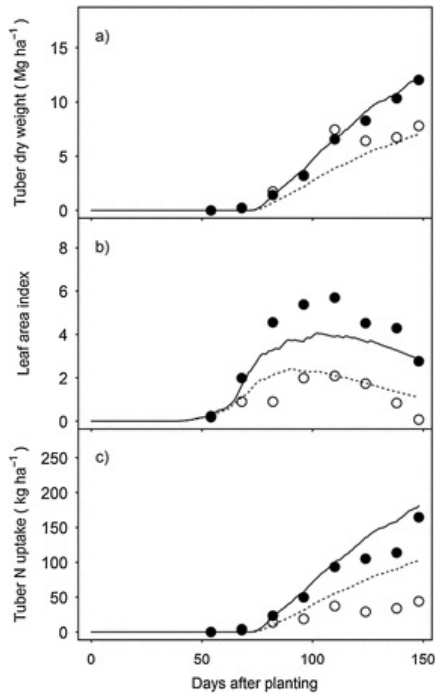


Fig. 4 Simulated (lines) versus observed (symbols) tuber dry weight (Mg ha^{-1}), leaf area index (LAI), and tuber N uptake (kg N ha^{-1}), for two nitrogen treatments: N0, and N240 at Dundee, Scotland, 1985. Treatment N0 (dotted lines, open symbols) and treatment N240 (solid lines and solid symbols).

alt-text: Fig. 4

Fig. 5 presents the model results for 87 experiments under various treatments and conditions, including non-stress, water limited, high temperature, and N limited conditions, and both current and elevated atmospheric CO_2 concentrations. Overall, the model results corresponded well with the observed tuber dry and fresh weights (Fig. 5a, b). Note that for some OTC treatments the model underestimated the tuber dry weight despite the non-limiting conditions of water and N manager (Fig. 5a). For leaf dry weight, stem dry weight and LAI (Fig. 5c–f) the correspondence between simulated and observed values appeared to be limited. The tuber initiation period was generally simulated well for all regions, although some underestimate values were simulated for the high Andes (Patacamaya ~~3700 m.~~ 3700 m.a.s.l) and high temperature conditions.

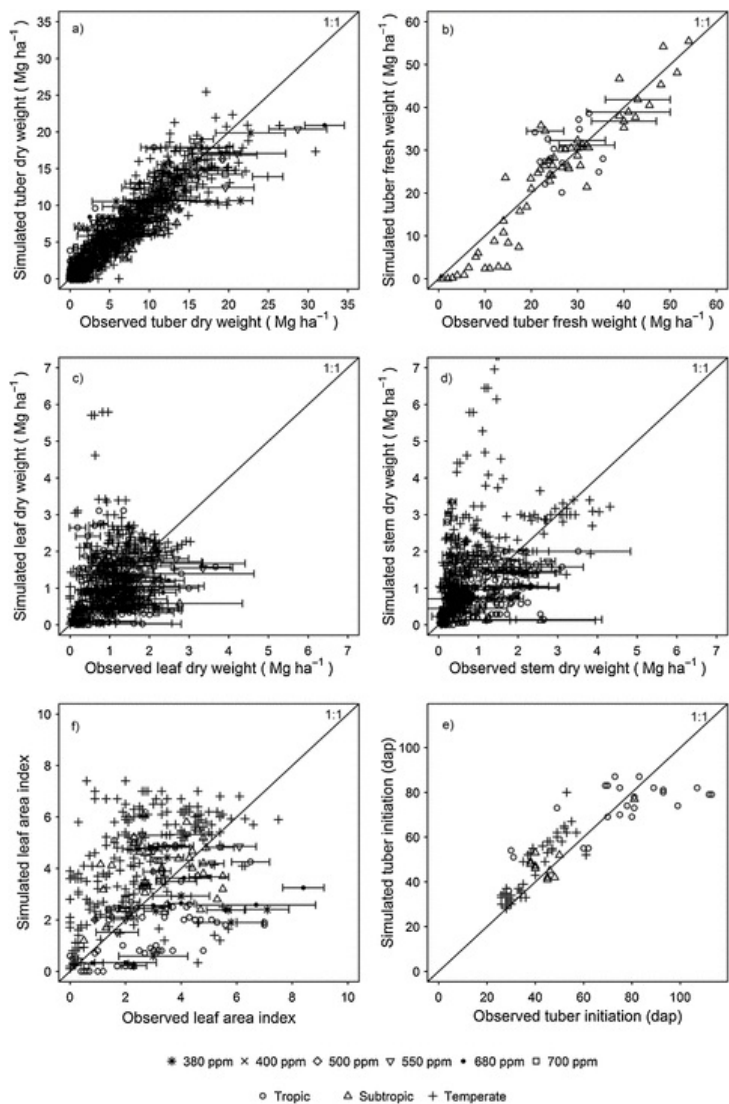


Fig. 5 Model performance for (a) tuber dry weight (Mg ha^{-1}), (b) tuber fresh weight (Mg ha^{-1}), (c) stem dry weight (Mg ha^{-1}), (d) leaf dry weight (Mg ha^{-1}), (e) leaf area index, and (f) tuber initiation (dap) days after planting in tropical (\circ), subtropical (Δ), and temperate ($+$) regions and for atmospheric CO_2 concentrations: 380 ppm ($*$), 400 ppm (\times), 500 ppm (\diamond), 550 ppm (∇), 680 ppm (\bullet), 700 ppm (\square), for FACE and OTC experiments. Error bars indicate standard error of measurements when available.

alt-text: Fig. 5

The simulated tuber N contents and leaf N contents corresponded well with the observed values (Fig. 6a and c), but the simulated aboveground and stem N contents showed large discrepancies (Fig. 6b and d). Fig. 6e and f present

N and $\text{NH}_4\text{-N}$ and NH_4

N (not shown in figure) were poorly simulated; additionally, the observed data had large measurement errors. The soil water contents were moderately well simulated for Suwannee but underestimated for Dundee.

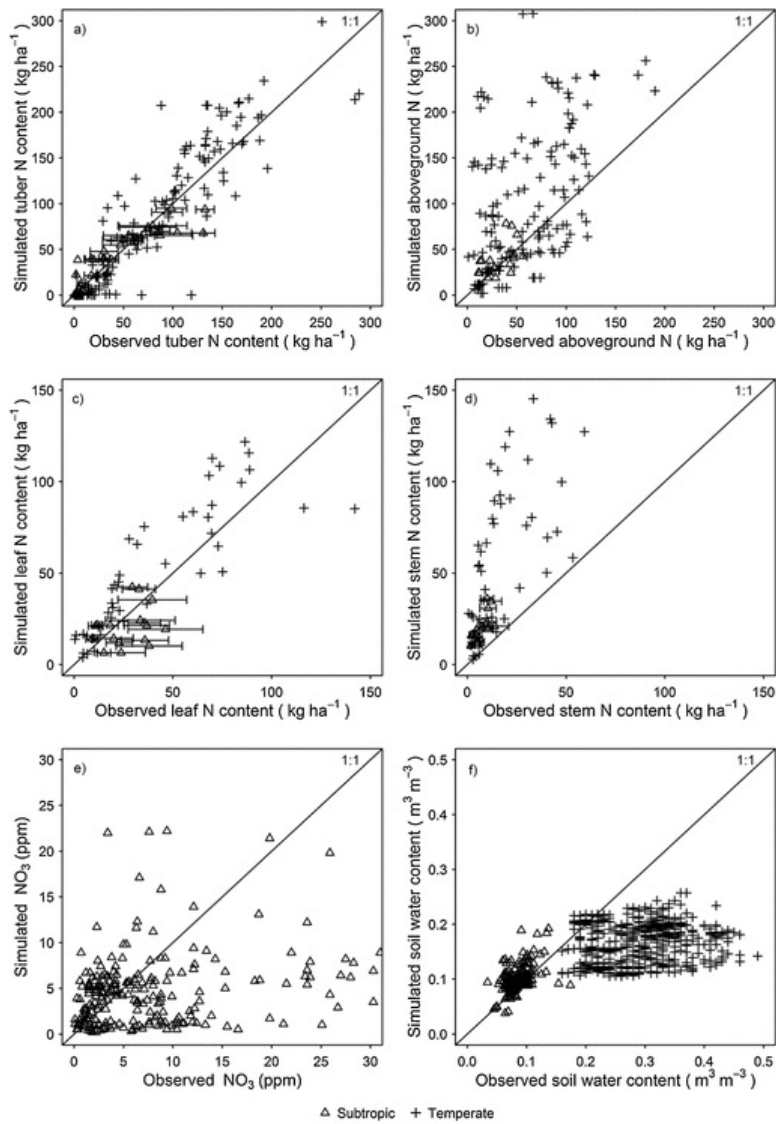


Fig. 6 Model performance of (a) tuber N uptake (kg N ha⁻¹), (b) aboveground N uptake (kg N ha⁻¹), (c) leaf N uptake (kg N ha⁻¹), (d) stem N uptake (kg N ha⁻¹), (e) soil mineral N as a NO₃

N (ppm), and (f) soil water content (m³ m⁻³) for subtropical (Δ), and temperate (+) regions. Error bars indicate the standard deviation of measurements when available. For panel (e) and (f) error bars were available but not shown.

alt-text: Fig. 6

Fig. 7 provides the tuber yield response of cv. 'Achirana' under non-high (La Molina, Peru) and high temperature (San Ramon) environments. This cultivar has a TC of 18 °C; therefore, weighted average temperatures above this threshold inhibited tuber initiation and reduced tuber bulking. In La Molina and San Ramon, weighted average temperatures for tuber initiation were suitable (<17 °C) and unsuitable (>20 °C), respectively. Under non-high temperature conditions, the model provided satisfactory simulations. However, under high temperature conditions, the model reproduced the final yield well, but overestimated the tuber initiation and underestimated the tuber dry weights during the growth period. This shows that under high temperature conditions throughout the growing season, SUBSTOR-potato failed to simulate the observed growth dynamics well.

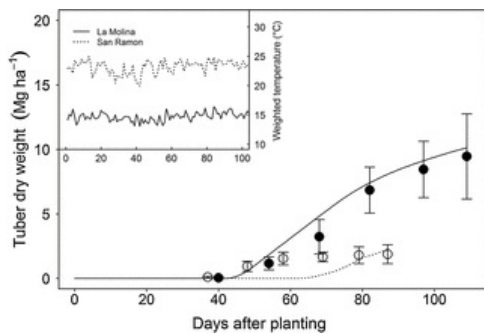


Fig. 7 Simulated (lines) versus observed (symbols) tuber dry weight (Mg ha^{-1}) under high temperature at San Ramon, Peru, 2013 and a low temperature environment at La Molina, Peru, 2013 for cv. 'Achirana'. High temperatures conditions with dotted lines and open symbols, and low temperatures conditions with solid lines and solid symbols. Error bars indicate standard error of measurements when available. Weighted average temperature for both locations is embedded in the graphic.

alt-text: Fig. 7

Fig. 8 shows the tuber yield response to elevated atmospheric CO_2 concentrations in a FACE experiment in 1999 at Rapolano, Italy. SUBSTOR-potato simulated the tuber growth under ambient CO_2 concentrations reasonably well, but failed to simulate the large positive observed yield response to elevated atmospheric CO_2 .

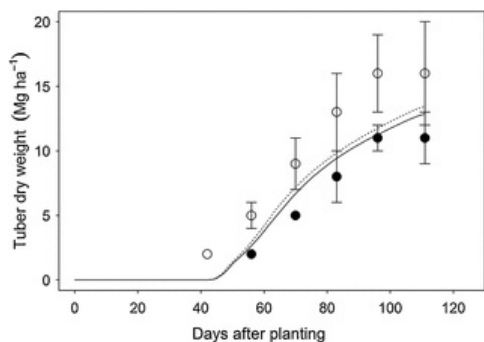


Fig. 8 Simulated (lines) versus observed (symbols) cumulative potato tuber dry weight (Mg ha^{-1}) for cv. 'Bintje', FACE experiment with ambient (370 ppm) and elevated atmospheric CO_2 concentration (560 ppm) at Rapolano, Italy in 1999. Treatment with elevated atmospheric CO_2 with dotted line and open symbols, and treatment with ambient CO_2 with solid lines and solid symbols. Error bars indicate standard error of measurements when available.

alt-text: Fig. 8

Table 3 summarizes the performance of the SUBSTOR-potato model versus experimental observations for 17 variables. Simulations with the model were compared to 5345 actual measurements. Values of RRMSE were 37.2% for tuber dry weight, 21.0% for tuber fresh weight, 22.6% for tuber initiation, 40.4% for tuber N uptake, and 52.3% for leaf N uptake. RRMSE for stem N content, aboveground N content, and soil NO_3 and NH_4 were >80%.

Table 3 Summary of model performance of SUBSTOR-potato modelling for all experiments (see [Table 1](#)).

alt-text: Table 3

Variable	Number of paired data	Observed range	R^2	Slope	RMSE ^a	RRMSE ^b
Tuber dry weight (Mg ha^{-1})	946	0.00–32.08	0.93	1.01	2.12	37.20
Tuber fresh weight (Mg ha^{-1})	79	0.50–54	0.97	0.96	5.23	21.04
Aboveground dry weight (Mg ha^{-1})	758	0.03–9.75	0.69	0.64	1.93	85.33
Roots dry weight (Mg ha^{-1})	213	0.02–1.08	0.63	0.45	0.34	253.07

Leaf dry weight (Mg ha ⁻¹)	504	0.01–3.67	0.61	0.64	0.97	90.34
Stem dry weight (Mg ha ⁻¹)	471	0.02–4.32	0.51	0.48	1.32	141.42
Dead dry weight (Mg ha ⁻¹)	57	0.00–2.56	0.26	0.79	0.62	151.42
LAI	378	0.01–8.39	0.70	0.67	2.24	81.95
Tuber initiation (dap)	116	26.00–113	0.96	0.93	10.54	22.65
Tuber N (kg ha ⁻¹)	184	0.10–318.20	0.92	0.90	44.78	40.40
Aboveground N (kg ha ⁻¹)	160	76.48–132.72	0.78	0.65	76.48	86.23
Roots N (kg ha ⁻¹)	96	0.63–8.19	0.60	0.37	6.95	153.83
Leaf N (kg ha ⁻¹)	64	21.48–52.32	0.86	0.89	21.48	52.31
Stem N (kg ha ⁻¹)	64	0.62–59.25	0.74	0.28	47.18	309.57
Soil water content (m ³ m ⁻³)	891	0.03–0.49	0.89	0.89	1.55	62.08
NO ₃ ⁻ -N (ppm)	240	0.10–58.10	0.42	1.35	9.82	95.45
NH ₄ ⁺ -N (ppm)	240	0.60–185.60	0.05	1.66	19.42	140.09

^a Root mean square error (Mg ha⁻¹).

^b Relative root mean square error (%).

^c 0.00002.

^d 0.00002.

5 Discussion

5.1 Cultivars of the developed world

This study presents a comprehensive model testing for a potato crop model, using multiple cultivars, locations, and treatments. Previous studies also tested various potato cultivars but were often limited in the number of cultivars. Other studies had analyzed model performance for a single cultivar with the models SIMPOTATO and DANUBIA (Hodges et al., 1992; Gayler et al., 2002; Lenz-Wiedemann et al., 2010); six cultivars with the model SUBSTOR-potato (Griffin et al., 1993); seven cultivars with the model DAISY (Heidmann et al., 2008); and 10 cultivars with the model INFOCROP (Aggarwal et al., 2006). Only one model, SOLANUM, was used to compare simulated and observed yields for a large number of potato species (Condori et al., 2010). In our study, we analyzed the performance of the SUBSTOR-potato model for three potato species and 32 potato cultivars. The results indicated that the SUBSTOR-potato model can in general reproduce the tuber and leaf development for different potato species and cultivars.

5.2 Cultivar use across climatic regions

An important test for any crop model is to perform simulations for one cultivar grown across a wide range of climatic regions. Cultivar parameters in such evaluation study must be kept constant across the different environments to be considered truly cultivar specific. Wolf and Van Oijen (2003) used cv. 'Bintje' to test the model LPOTCO across eight locations in Europe, whereas Heidmann et al. (2008) used cv. 'Agria' to test the model DAISY at three locations of Europe. However, the locations used in their studies were all part of the same temperate region. In our study, a crop model was tested for the first time with a cultivar across several climatic regions using constant cultivar parameters. Observed tuber yields were well simulated for cv. 'Desiree' in temperate (China) and tropical (Peru/Bolivia) regions. Similarly, simulations were acceptable for cv. 'Atlantic' in the tropics (Peru) and subtropics (southern United States) regions. Note that conditions between the temperate and tropical regions were more contrasting, whereas conditions of the subtropics and tropics were more alike. Tuber yields of cultivars 'Sarnav' and 'Achirana' were well simulated in the tropics. Despite the lack of experimental measurements of these cultivars in temperate and subtropics regions, we presume that the same set of parameters can be used in temperate regions of Uzbekistan, Argentina, and The Netherlands, where these cultivars were used in various studies (Butzonitch et al., 1994; Inceoglu et al., 2010; Carli et al., 2014). These results indicate that the cultivar parameters in the SUBSTOR-potato model do represent cultivar-specific characteristics and support the general functionality and transferability of this model.

5.3 N response

The SUBSTOR-potato model reproduced the tuber yield response to various N treatments. The results varied with application of N and the levels of soil organic carbon (OC). In soils with high OC, the mineralization of soil organic N contributes to the crop N supply during the growing season (Basso et al., 2011). Therefore, the model simulated high tuber yields for N0 treatments (7.7 Mg ha⁻¹ of dry weight) in Dundee (OC = 2.2%). Also, other models have been shown to reproduce potato yields under optimum N rates (higher than 150 kg ha⁻¹ of N) (Hodges, 1998; Gayler et al., 2002). The SUBSTOR-potato model showed reasonable results for N0 treatments in a soil with low organic carbon content (OC = 0.3%) (Arora et al., 2013); however, using the same experimental soil parameterization did not allow us to reproduce observed plant growth dynamics for the N0 simulations obtained by Arora et al. (2013). The simulated N mass balance suggested that other sources of N must have been available, but the information provided by Arora et al. (2013) did not allow these sources to be identified. Estimates by Bobbink et al. (2010) indicated that atmospheric N deposition in India, calculated with a transport and deposition N model, could range between 15–30 kg year⁻¹ and could potentially be a significant source of additional N for cropping systems, as also shown for other regions of the world (Asseng et al., 2000). Similarly, we could not satisfactorily reproduce the observations for some of the N rate treatments for Argentina where N availability limited crop growth (Travasso et al., 1996).

5.4 Simulation of tuber yield and other variables

The SUBSTOR-potato model simulated tuber dry and tuber fresh weights in current growing conditions reasonably well (Fig. 5a and b). However, the model indicated limitations for simulations under high temperature environments (Fig. 7) and elevated atmospheric CO₂ concentrations (Fig. 8). Crop models for cereals have been shown to simulate elevated atmospheric CO₂ concentrations well (O'leary et al., 2014), but these models still require improvements to simulate the impact of heat temperature stress (Asseng et al., 2015) and interactions of CO₂ with high temperatures (Asseng et al., 2013).

Other crop variables were less well simulated than tuber yields, including aboveground biomass, LAI, and root dry weight. This shows that it is difficult to simulate leaf and stem dry weights and leaf area index precisely, but also measurement errors are often large for these variables (van Oijen and Ewert, 1999). The potential biomass is a function of photosynthetically active radiation (PAR), radiation use efficiency (RUE), and light interception. Light interception saturates at LAI higher than three; therefore, any LAI higher than this value will have the same impact on potential biomass.

Leaf area is modeled by converting the increment of leaf weight into leaf area using the specific leaf area-weight ratio (LALWR, 270 cm g⁻¹). Ng and Loomis (1984) report LALWR from different potato experiments ranging from 202 to 303 cm g⁻¹, however the variability of LALWR in potato crop during the crop development and phenology is not well documented. The use of various methods to measure the LAI of a maize crop have shown substantial differences in a single plot experiment (Yang et al., 2012; Yang et al., 2014). Consequently, some of the discrepancies between simulations and observations are due to field experiments with relative large measurement error comprised from experiments from different sources. In addition, in the potato model, biomass and yield accumulation are a function of LAI, light interception and RUE. However, other factors, such as non-optimal temperatures, water and nitrogen stress can limit actual carbon fixation in the model. In addition, under stress conditions tuber growth has priority for carbon allocation with less carbon allocation to leaves and stems. Hence, while LAI is important for light interception, it is often not the limiting factor for yield.

This partly explains the discrepancies of observed and simulated LAI not affecting growth and yield in the same way. This phenomenon was also reported for other crops (Asseng et al., 1998; Asseng et al., 2000). Other potato models, such as the SPUDSII model, also had difficulties in simulating root dry weight (Dathe et al., 2014). Growth habits (Huaman and Schmiediche, 1999) and rooting traits (Wishart et al., 2013) vary across cultivars, species, and regions. For example, *S. tuberosum* is more robust and taller in temperate regions, and smaller in the tropics (Vander Zaag et al., 1990); this would implicate discrepancies in stem weight of a same cultivar in contrasting regions. Traditional and modern cultivars give higher harvest indexes than non-improved species such as *S. andigenum* and *S. juzepczukii* (Condori et al., 2010). As some of the existing cultivar variability is not taken into account via the current cultivar-specific model parameters, this could partly explain the rather poorly simulated results for aboveground biomass and root weights. In addition, the quality of root measurements in potatoes could be a factor in some model observation discrepancies (Ahmadi et al., 2014).

Some of the model discrepancies with the observed soil water content (SWC) and soil mineral N can be attributed to the one-dimensional water movement (tipping bucket) of the DSSAT model (Ritchie et al., 1995) and the two-dimensional structure of ridges and valleys in potato fields.

5.5 Overestimation at the end of the growing season

In general, the SUBSTOR-potato model results were more accurate in experiments, in which N supply from the soil was exhausted toward the end of the growing season. However, the model often overestimated the final yield in situations in which the soil N supply was large. Such overestimated yields are attributed to the lack of simulating maturity in the SUBSTOR-potato. The simulated crop growth requires constant water and N supplies and stops under terminal water and N limitations. The concept of crop maturity and senescence is widely discussed for potato (Mackerron and Davies, 1986; Khan et al., 2013), and the impact of water or N stress on crop senescence and the maturity type of cultivars (early, medium, or late) is not clear. The model also lacks the ability to accelerate leaf senescence due to high temperatures. Increasing temperatures in the subtropics at the end of the season (Rahman et al., 2014) often accelerate crop senescence (Kooman and Haverkort, 1995). This partly explains why potato cultivars in the subtropics usually have shorter growing periods (Santhosh et al., 2014).

5.6 Simulations under high temperatures

In the SUBSTOR-potato model, high temperature has no effect on aboveground development, but has a direct impact on tuber initiation and tuber development. Therefore, under constantly high temperatures in lowland tropics, the model simulates a delayed tuber

initiation and underestimated the in-season tuber growth. In contrast, experimental observations in San Ramon, Peru, suggested that tuber initiation occurred despite high temperatures. Some studies have explored the effect of high temperatures on tuber initiation (O'Brien et al., 1998; Levy and Veilleux, 2007). Their results indicated that high temperatures affected the allocation of glucose, stimulating aboveground biomass growth and simultaneously reducing tuber accumulation but not necessarily inhibiting tuber initiation (Ewing, 1987; Gawronska et al., 1992; Basu and Minhas, 1999). Our results showed the limited capability of the SUBSTOR-potato model to simulate high temperature responses when high temperatures are frequent throughout the growing season (e.g., lowland tropics). On the other hand, the model matched the observed data when high temperatures occurred after tuber initiation or at the end of the growing season. These conditions were frequent in the subtropics (United States) and in the temperate (northern China) regions.

5.7 CO₂ effect

Finnan et al. (2008) showed that the fertilization effects of increased CO₂ (550 ppm to 680 ppm) on tuber yields of potato in OTC and FACE facilities were highly variable, ranging from -7.3% to +54%. The FACE experiments (550 ppm) from Italy and Germany showed an increase on tuber yield of 46% and 5.75% respectively (Finnan et al., 2008). Jaggard et al. (2010) used the relative change of FACE experiments from Italy to indicate a yield increase of 36% by 2050. Miglietta et al. (1998) indicated an increase of tuber yield of 10% for every 100 ppm of CO₂. The FACE experiments in Italy presented in this study were also used to test the performance of the models LPOTCO and AQUACROP (Wolf and Van Oijen, 2003; Vanuytrecht et al., 2011). The observed yield response of potato to increased CO₂ in these experiments was high but underestimated in the SUBSTOR-potato simulations. An underestimation did also occur but to a lesser extent in the simulation results from the model LPOTCO (Wolf and Van Oijen, 2003). In the SUBSTOR-potato model the potential carbon fixation and potential tuber growth increases by 17%, when atmospheric CO₂ increases from 330 ppm to 550 ppm. For the FACE experiments in Rapolano, Italy in 1999, the model simulations indicated that N stress should have limited the carbon fixation. This resulted in a lower simulated yield response to increased CO₂ of only 3%, whereas the observed yield response was as high as 45%. However, simulations of these experiments under sufficient N supply resulted in overestimation of the observed data. The interactions between increased CO₂ and different N fertilizer rates have not been studied in potato field experiments, although studies in other crops indicated that increasing N shortage reduces the yield response of most crops to increased atmospheric CO₂ (Wolf, 1998; Kim et al., 2003; Franzaring et al., 2011). Note that in the experiments done in the "CHanging climate and potential Impact on Potato yield and quality" (CHIP) project (De Temmerman et al., 2002b), the yield response of potato to increased CO₂ was much lower (i.e., about +20% to +30% if the CO₂ concentration increased from 380 to 550 ppm) than that observed in the FACE experiments in Rapolano (De Temmerman et al., 2002b; Wolf and Van Oijen, 2003).

6 Conclusion

Tuber yields were generally well simulated with the SUBSTOR-potato model for different potato species and cultivars, across a wide range of management and environments under current growing conditions. The simulation results for other crop growth variables (e.g., leaf area index, leaf and stem biomass) were less accurate in comparison to experimental data, which was partly due to the limited parameters for cultivar characterization in the SUBSTOR-potato model. However, some of these variables also had significant large measurement errors. Consistent underestimations occurred under high temperature and elevated atmospheric CO₂ concentrations and require improvements before the model can be used for climate change impact assessments.

Implementing a senescence routine affected by high maximum temperatures and maturity type should improve the model simulations under high temperature environments. The senescence routine should trigger tuber induction, affect the rate and duration of tuber bulking, and decrease the water and nitrogen uptake at the end of the growing season. In the SUBSTOR-potato model, the relative response function to atmospheric CO₂ is too low and does require adjustments based on experimental data. ~~Uncited references~~ Albert (2002), Berloo R. v. Hutten et al. (2007), ZZZZ (2016), Litaladio and Gastaldi (2009), Lutz (2010).

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Highlights

- The SUBSTOR-potato model was tested with 87 experiments and 204 treatments, including 32 cultivars and three potato species.
- The model-observation comparison showed that the SUBSTOR-potato model can in general simulate tuber yields across contrasting environments.
- However, the SUBSTOR-potato model cannot accurately simulate tuber yield under elevated CO₂ concentrations and high temperatures which needs to be improved.

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