

Contents lists available at ScienceDirect

Agricultural Water Management





Estimating cultivar-specific salt tolerance model parameters from multi-annual field tests for identification of salt tolerant potato cultivars

G. van Straten^{a,*}, B. Bruning^{b,1}, A.C. de Vos^{b,1}, A. Parra González^{b,2}, J. Rozema^c, P. M. van Bodegom^d

^a Wageningen University, Farm Technology Group, P.O. Box 16, 6700 AA Wageningen, The Netherlands

^b Salt Farm Texel, Mokweg 41, 1797 SB Den Hoorn, The Netherlands

^c Department of Ecological Sciences, Systems Ecology, Free University, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

^d Department Environmental Biology, Leiden University, Institute of Environmental Sciences, Einsteinweg 2, 2333 CC Leiden, The Netherlands

ARTICLE INFO

Handling Editor: Dr. B.E. Clothier

Keywords: Salinity tolerance Potato Parameter uncertainty Stress factor interaction Multi-annual field tests

ABSTRACT

Having salt-tolerant potatoes is of paramount interest to farmers in salt affected areas, but reliable cultivarspecific parameters on salt tolerance are lacking. To address this issue existing field data on tuber yield on sandy soil at six levels of saline irrigation (0.5, 4, 8, 12, 16, 20 dS m⁻¹) of 13 varieties for which data in two or more consecutive years were available, were analysed year-by-year with the method developed earlier. The method provides estimates of the zero-observed-effect yield (YO), and two typical salt tolerance parameters, - i.e., a characteristic salinity level and a decline parameter -, as well as information about the uncertainties and correlations between these estimates. The results indicate that all varieties have a similar lethal soil salinity (20-24 dS m⁻¹). However, both yield YO as well as salt tolerance parameters differ among cultivars, but for a single variety the estimates vary year by year, and have large uncertainties, underlining the difficulty to obtain robust parameters from single year experiments. The annual variety also hampers the discrimination between varieties. To remedy this, the data from multiple years were united in a single analysis by introducing another unknown, annually varying - factor that is limiting the yield in the trials. Two ways to describe co-current limitations often used in models were tested. In contrast to the minimum rule, the multiplicative rule is found to provide an acceptable description of the observed yields over all years. This results in a single set of salt tolerance parameters with a narrower uncertainty bound than from single year estimation. It shows that with due account of uncertainties, field tests can be used to identify relatively salt tolerant cultivars, while accounting for between-year yield differences. Most potato cultivars have an ECe_{90} of about 4–5 dS m⁻¹, but for some it is roughly double, while maintaining good yield, suggesting that these varieties are good candidates for salt adapted agriculture.

1. Introduction

Salinization of soils is a significant threat to crop production in many parts of the world. It is aggravated by climate change induced effects, such as increased sea water intrusion in coastal areas and the need for more irrigation due to droughts. One possibility to abate the negative effects on agriculture is to search for crops and crop varieties that are salt tolerant. The target crop in the current study is potato, which is a

globally important cash crop.

Despite some scepticism about the potential of breeding programs to counteract salinization (Plaut et al., 2013), there is wide consensus that commercially interesting potato varieties can be found or created that are more salt tolerant than others (Jaarsma et al., 2013; Levy and Veilleux, 2007; Velásquez et al., 2005), and should, in fact, be adopted in daily practice (Pradel et al., 2019). A common avenue to arrive at promising varieties for crops in general is by fast screening tests,

* Corresponding author.

https://doi.org/10.1016/j.agwat.2021.106902

Received 26 May 2020; Received in revised form 28 March 2021; Accepted 29 March 2021 Available online 12 April 2021

0378-3774/© 2021 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

E-mail addresses: gerrit.vanstraten@wur.nl (G. van Straten), bas@thesaltdoctors.com (B. Bruning), arjen@thesaltdoctors.com (A.C. de Vos), aparra@cebas.csic.es (A.P. González), j.rozema@vu.nl (J. Rozema), p.m.van.bodegom@cml.leidenuniv.nl (P.M. van Bodegom).

¹ Present address: The Salt Doctors, www.thesaltdoctors.com

² Present address: Irrigation Department CEBAS-CSIC, Murcia, Spain.

focussing on quantitative traits that can be measured in vitro within a limited period of time (Munns et al., 2002). A screening test on a large number of North American and European potato cultivars is presented in Khrais et al. (1998). Other studies for potato are Khenifi et al. (2011); Morpurgo, (1991); Naik and Widholm, (1993). However, the artificial root zone environment of fast screening tests, the limited number of tested salinity levels and the short duration in *in vitro* screening make it hard to link observed growth rates to final yields in the field. Hence, several of these authors stress the need for additional full field tests. In addition, screening tests do not provide the parameters of salt tolerance functions, which would be of paramount interest in crop yield production models.

Tests to evaluate salinity effects on tuber yield under field conditions are scarce. Table 1 summarizes studies from which salinity tolerance parameters can be deduced. Because field tests are scarce, also some open air lysimeter and pot plant tests that can serve this purpose have been included.

Table 1 reveals several common problems in field experimentation. The number of saline irrigation levels is limited, and researchers do not always report on the resulting soil salinities. Without careful design, soil salinities may vary over the season due to changes in evapotranspiration. The maximum soil salinity measured in the reported field tests is not higher than about 6 or 7 dS m⁻¹. Since the 50%-yield salinity (*ECe*₅₀) has about the same value, such experiments provide no information on the entire yield reduction function, which is required in dynamic crop growth models. Decline rates also have a wide range, and interaction with water limitation was not always excluded.

In view of this limited scientific evidence on salt tolerance of potato crops under field conditions and the lack of reliable model parameters, Salt Farm Texel executed extensive field trials with several potato varieties over several years (2012–2018), under well irrigated conditions, thus avoiding both waterlogging and drought stress. With these extensive data at our disposal, and in combination with the evaluation method we developed earlier (van Straten et al., 2019), we set out to answer the following question: which of the tested potato varieties differ significantly in salt tolerance? Our specific objectives are:

- To report on annually observed salinity effects on tuber yield under field conditions for a large number of potato varieties, with particular emphasis on variability and uncertainty in salt tolerance model parameter estimates.
- To present a model-oriented method to unite multiple-year results into a single set of cultivar-specific salt tolerance parameters.

- To apply this new method to identify relatively salt tolerant varieties.

2. Materials and methods

2.1. Source of the data

The data in this study were acquired from Salt Farm Texel (Texel, The Netherlands) and originate from field trials with several potato varieties over the years 2012-2018 on sandy soils (organic fraction 2%, soil particle density 2.5 mg m⁻³, bulk soil density at saturation 1.5 mg m^{-3}). Groups of fields consisting of 4 or 8 replicates – depending on the year - were irrigated after emergence of the first leaves from the tubers with saline water with salinities of 0.5-1.7 (fresh water), 4, 8, 12, 16, and 20 dS m⁻¹. Salinity treatments were built up gradually, with the highest salinity reached within 3 days, to avoid osmotic shocks at the higher salinity levels. The irrigation frequency and quantity were chosen such that there was never shortage of water, which was verified by soil water sensors and regular soil sampling. The seasonal mean soil salinity was determined by taking the average of 8-10 soil- and soil moisture samples during the growing season (De Vos et al., 2016). In general, after a period of 7-10 days after the start of the irrigation, the soil salinity was roughly constant within 25% of the mean. The areal yield was determined from tuber weights of 8 plants per plot. In view of the variation in soil salinities, we chose to consider each data point separately, since in our previous work (van Straten et al., 2019) it was established that the benefits of prior averaging the soil salinities per treatment group were not decisive.

In this study all results pertain to the sub-set of cultivars with a minimum of two years of testing. Three or more years of data were available for Achilles (2012–2016), Miss Mignonne (2012–2017), Focus (2015–2017) and Metro (2015–2018), cultivars with two years of testing were '927' (2015–2016), Actrice, Caruso, Connect, Elgar, Magistral, Nicola, Rivola and Ultra (2017, 2018). The tubers of these varieties were acquired from commercial breeders and suppliers in The Netherlands.

2.2. Yield reduction functions

Two alternative functions were considered to describe the relationship between soil water salinity and observed yield. The first is the common threshold function according to Maas and Hoffman (1977), described by

Table 1

Salinity tolerance parameters from field experiments with potato, including some open air lysimeter and pot plant tests.

Threshold ECe (dS m^{-1})	Slope (% per dS m^{-1})	50% yield ECe (dS m^{-1})	# of irrigation Salinity levels	Max. soil salinity ECe (dS m^{-1})	Source	Comments
		6.2	4	6.5	Bernstein et al. (1951)	Source of values cited by Shannon and Grieve (1999)
1.7	12	5.9			Maas and Hoffman (1977) quoting Bernstein et al. (1951)	Source of values cited by Maas (1993); Tanji and Kielen (2002)
		6 ^a	3	6.2-6.9	Levy (1992)	(1990), Taiji ald Refei (2002)
1.55-1.85	(34–57) ^b	0	1	3.5	Nagaz et al. (2007)	
0	5.6		3	5.9	Katerji et al. (2000)	Lysimeter, Spunta
		~6	4	~14 ^c	Elkhatib et al. (2005)	Lysimeter, Cara > Alpha > Spunta > King Edward
			2	3.5	Zhang and Donnelly (1997)	Lysimeter, for comparison with bioassays
		$\sim 5^d$	3	4.3	Levy et al. (1988)	Pots outdoor
			3	~9 ^{ce}	Nadler and Heuer (1995)	Focus on tuber quality; no clear effect on tuber yield

^a Wide range around 6 depending on start of saline irrigation.

^b High values probably due to combined water stress.

 $^{\rm c}\,$ Not measured but calculated as 1.5*EC_{\rm irr}

^d Estimated from their Fig. 3.

^e increasing soil salinity during experiment.

$$\frac{Y}{Y0} = \begin{cases} 1 & \text{if } 0 \le ECe < ECe_{thr} \\ 1 + s(ECe - ECe_{thr}) & \text{if } ECe_{thr} \le ECe < ECe_{lethal} \\ 0 & \text{if } ECe \ge ECe_{lethal} \end{cases}$$
(1)

where *ECe* is the seasonal average soil water EC, expressed as saturated paste extract equivalence (dS m⁻¹), *Y* is the yield at salinity *ECe* (tons ha⁻¹), *Y*0 the zero-observed-effect yield (tons ha⁻¹), *ECe*_{thr} the threshold soil water salinity (dS m⁻¹), below which the yield is *Y*0, and *s* is the decline slope (a negative number) for salinities beyond the threshold, expressed as the fraction of the yield lost per unit dS m⁻¹. Note that S = s Y0 is the absolute slope (in tons ha⁻¹ per dS m⁻¹). *ECe*_{lethal} is the salinity beyond which no yield occurs; it is derived from the other quantities by

$$ECe_{lethal} = ECe_{thr} - \frac{Y0}{S}$$
(2)

The salt tolerance parameters of the Maas-Hoffman (MH) model are ECe_{thr} and *s*. In addition, the zero-observed-effect yield must be considered as a parameter to be estimated from the data. Hence, the parameter vector of this model is $\beta_{MH} = [ECe_{thr}, s, Y0]$.

The second is the S-shaped function according to Van Genuchten and Hoffman (1984), given by

$$\frac{Y}{Y0} = \frac{1}{1 + \left(\frac{ECe}{ECe_{50}}\right)^p}$$
(3)

The salt tolerance parameters in this model are ECe_{50} (dS m⁻¹), i.e., the equivalent soil water salinity at which the yield has dropped to 50% of Y0, and a dimensionless slope parameter *p*. The parameter vector of the vanGenuchten-Hoffman (vGH) model therefore is $\beta_{vGH} = [ECe_{50}, p, Y0]$.

2.3. Parameter estimation and uncertainty assessment for individual years

The three parameters for each variety and each model were estimated by ordinary least squares (OLS), for each year separately, according to the method described by van Straten et al. (2019). It was shown there that OLS gives satisfactory results for the typical conditions of the field trials, despite the fact that there are (unavoidable) errors in the independent variable. The method does not only provide the least squares parameter estimates, but also their ellipsoid uncertainty regions and mutual correlations. Correlation implies that changing one parameter value requires a shift in one or both of the other parameters too, in order to maintain a credible fit within the yield data uncertainty bounds. The uncertainty ellipsoids are, in fact, approximations resulting from linearization of the response surface about the estimates. The true uncertainty region is given by the surface in 3-D parameter space with equal sum of squares defined by Draper and Smith (1966):

$$V(\mathbf{\beta}) = \left(1 + \frac{n_p}{N - n_p} F\{n_p, N - n_p, 1 - \alpha\} V(\widehat{\mathbf{\beta}})\right)$$
(4)

where $V(\beta)$ is the sum of squares at parameter vector β , defined before (Section 2.1), and $V(\hat{\beta})$ is the minimum sum of squares obtained at the best fit parameter vector $\hat{\beta}$. The factor F is the F-distribution available in tables as function of *N*, the number of data points, n_p the number of parameters, $N - n_p$ the number of degrees of freedom, and α the probability level that the actual parameter is outside the region. Our choice for α is 5%. If the model is linear-in-the-parameters the 2-D projections of the surface are ellipsoidal, and the confidence level is 95%, but in our case the model is non-linear in the salt tolerance parameters, and hence the contours are no longer ellipsoidal, and the label 95% is only approximate.

In contrast to the ellipsoids, which can be obtained easily from the estimation procedure (see appendix A2 in van Straten et al. (2019)), the determination of the equal-sum-of-squares surface in the 3-D parameter

space is computationally intensive. For this reason, equal-sum-of-squares contours, called uncertainty contours hereafter, have been evaluated for the salt tolerance parameters only, and only in the 2-D cross-section at the estimated yield.

2.4. ECe₉₀ as alternative

As an alternative to the standard parameterization with ECe_{thr} or ECe_{50} , we proposed ECe_{90} as an agronomically more meaningful alternative (van Straten et al., 2019). In the Maas-Hoffman model the determination of ECe_{90} is more robust than that of ECe_{thr} . The conversion from the standard parameterization to the alternative parameterization is straight-forward by some simple manipulation of Eq. (1) or, for vanGenuchten-Hoffman, Eq. (3). Repeating the estimation in alternative parameter space provides the uncertainty ellipsoids in alternative space. However, the uncertainty is better represented by the true uncertainty contour according to Eq. (4). The true uncertainty contour in alternative parameter space, by conversion of the points of the uncertainty contour found in standard parameter space.

2.5. Evaluating salinity tolerance from individual year estimations

If salinity would be the only limiting factor affecting potato tuber growth, a single set of salt tolerance parameters would exist of which the uncertainty contours of the individual years would overlap to form a cluster. Presenting the clusters of all varieties in one plot would make the tolerant varieties stand out as detached from the others. However, if the zero-observed effect yield would be influenced by other limiting factors, the overlap may get lost since the estimates are correlated with each other.

Another way to obtain an overview over the multiple year data is to simply ignore the correlations between estimates, and only take into account the uncertainties. To this end the centre of the cluster of ellipsoids for each multiple-year cultivar is computed as the weighted mean of the parameters, by taking the reciprocal of the estimation variance as the weight:

$$\overline{\beta} = \frac{\sum_{i=1}^{N_{y}} \overline{\sigma_{i}^{2}} \widehat{\beta}_{i}}{\sum_{i=1}^{N_{y}} \overline{\sigma_{i}^{2}}}$$
(5)

2.6. Hypotheses on simultaneous yield limiting factors

It appears that there are large yield variations between the years. Hence, we hypothesize that there is another factor during the experiments, unknown and annually different, that limits the yield. Let $g_k\{\cdot\}$, between 0 and 1, represent the unknown reduction factor in year k, where the notation $\{\cdot\}$ serves as a reminder that this is a function of stress factors other than salt. Suppose, furthermore, that there exists a potential maximum yield for each cultivar Y_{pot} , i.e. a yield that would be observed when no limitations would be active. While potential yield is unknown, it can be approximated by the ever-observed maximum yield. When $g_k = 1$, and in the absence of salt limitation, the observed yield will be equal to the potential yield. Because the yield in the absence of salt limitation in any year is estimated as \widehat{YO}_k , it follows that an estimate of the unknown annual reduction factor other than soil salinity is given by

$$\widehat{g}_k = \frac{\widehat{Y0_k}}{Y_{pot}} \tag{6}$$

Let the function that describes the reduction of the yield at a specific salinity with respect to the zero-observed-effect yield in the absence of other limitations formally be denoted as $f{E, \beta_{ST}}$, where *E* stands for the

seasonal mean soil water salinity of the field (ECe) and β_{ST} is shorthand for the salt tolerance parameters. It has a value between 0 and 1 and a shape given by the right-hand side of the functions in Section 2.2. A central element in the current hypothesis is that the salt reduction function and its parameters do not depend on the year of testing, for if it does it would mean that the whole idea that a cultivar is characterized by a cultivar-specific salt tolerance would be void.

We examine two popular hypotheses for the occurrence of multiple limiting factors, namely the multiplicative rule and the minimum rule of Liebig-Sprengel (see Van Der Ploeg et al., 1999, for an argument to use this denomination). So, we have.

Hypothesis 1. multiplicative rule.

$$H_{multi}: \quad Y_k\{E\} = f\{E, \beta_{ST}\}g_k\{.\}Y_{pot}$$
(7)

Hypothesis 2. minimum rule.

$$H_{minim}: Y_k\{E\} = \min(f\{E, \beta_{ST}\}, g_k\{.\}) Y_{pot}$$
(8)

Fig. 1 illustrates the difference between the two hypotheses for the vanGenuchten-Hoffman model. Under the multiplicative rule, the shape is maintained. Note that the minimum rule gives rise to data patterns that in the presence of observation noise could just as well be described by the Maas-Hoffman model, with a threshold that varies with the actual zero-observed-effect yield.

2.7. Joint multiple-year parameter estimation

With data pairs of yield and salinities $E_{i,k}$, $Y_{obs,k}(E_{i,k})$ for each available year $k = 1, ..., N_y$, each with $i_k = 1, ..., N_k$ data points, the OLS multiple year parameter estimation is formulated as

$$[\widehat{\boldsymbol{\beta}}_{ST}, \ \widehat{\boldsymbol{g}}_{1}, ..., \widehat{\boldsymbol{g}}_{Ny}] = \operatorname{argmin}\left(\sum_{k=1}^{N_{y}} \sum_{i_{k}=1}^{N_{k}} \left(Y_{obs,k}(E_{i,k}) - Y_{k}(E_{i,k}, \boldsymbol{\beta})\right)^{2}\right)$$
(9)

Here $Y_k(E_{i,k}, \beta)$ is the yield predicted by either Eqs. (7) or (8), as function of the entire parameter vector $\beta = [\beta_{ST}, g_1, ..., g_{Ny}]$. The number of to-beestimated parameters is $2 + N_y$.

Given that the zero-observed-effect yield in any year is the yield observed without salinity limitation, we have

$$Y0_k = g_k\{.\}Y_{pot} \tag{10}$$

Hence, from the estimates of the additional limitation factorg_k. in a specific year, the zero-observed-effect yield for that year can be easily determined from Eq. (10) given the pre-defined Y_{pot} . In the case of the multiplicative limitation it is easy to see that the estimated annual YO_k does not depend upon the particular choice of Y_{pot} , because in the calculation of the predicted yield in Eq. (7), it is actually the product of g_k and Y_{pot} that is estimated, and another choice of Y_{pot} will simply lead to proportionally adjusted g_k estimates, such that YO_k (Eq. (10)) remains the same. With the minimum model the result may depend upon the actual Y_{pot} . This will be investigated by evaluating the sensitivity of the solution. The performance of each hypothesis is evaluated by comparing the root mean square error, by visually judging the predicted fits to see whether the fits are within the data uncertainties for each year separately, and by examining the residual histogram for absence of systematic bias and skewness.

3. Results

3.1. Parameter estimates for individual years

Fig. 2 shows a typical example of the parameter estimation for an individual year, here Miss Mignonne in 2014.

The uncertainty in the curve as a whole is represented by the area within the simultaneous prediction error bounds, whereas no more than 5% of the observations are expected to be outside the non-simultaneous prediction error bounds. The parameter values in this year for the Maas-Hoffman model are $ECe_{thr} = 4.4 \text{ dS m}^{-1}$, $s = -6.8\%/(\text{dS m}^{-1})$, Y0 = 42.6 tons ha⁻¹, and for the description according to vanGenuchten-Hoffman we have $ECe_{50} = 11.4 \text{ dS m}^{-1}$, p = 3.3, Y0 = 43.2 tons ha⁻¹. From the figures, the unavoidable noise in the yield data is immediately clear. Variation in yields at the lower ECe have the largest effect on the predicted zero-observed-effect yield. Both descriptions result in a similar zero-observed-effect yield of roughly 43 tons ha⁻¹. In some cases the data did not have enough structure to get useful estimates by the current models, especially when in the low range of ECe there is not enough data, or too much noise. In such cases the Maas-Hoffman estimation problem becomes ill-conditioned, and the uncertainty in the parameters becomes extremely large. In the vanGenuchten-Hoffman model it may result in unrealistic high Y0 and extremely low p (<1). In the analysis, a warning is issued when this happens.

Some statistics of the valid single year estimates over all cultivars and all years are provided in Table 2. On average, over all potato cultivars, the threshold ECe is about 3 dS m⁻¹ and the ECe_{50} about 11 dS m⁻¹.

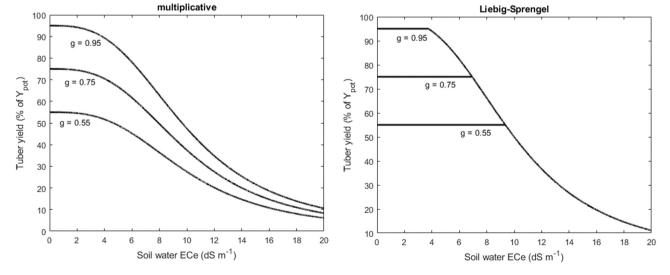


Fig. 1. Yield-salinity curves according to the vanGenuchten-Hoffman model in the presence of another limitation. Left: multiplicative rule; Right: minimum rule.

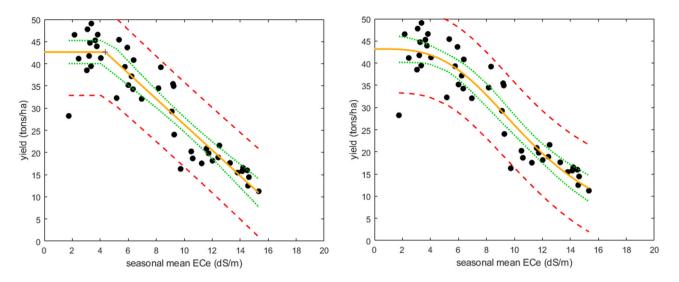


Fig. 2. Ordinary least squares fit; Miss Mignonne 2014. Left: Maas-Hoffman; Right: vanGenuchten-Hoffman. Solid (orange) centre line: fitted curve; dotted (green) line on both sides: simultaneous prediction error; outer (red) dashed: non-simultaneous prediction error. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

 Table 2

 Statistics of the parameter estimates across all years and all potato cultivars.

	Maas-H	offman			vanGenuchten-Hoffman					
	ECe _{thr}	s%	ECe ₉₀	RMSE	ECe ₅₀	р	ECe ₉₀	RMSE		
mean	3.2	6.1	5.0	4.73	11.3	3.1	5.5	4.66		
median	3.0	6.1	4.5	4.73	11.6	3.0	5.4	4.68		
lowest	0.2	4.2	2.2	3.05	7.7	1.8	2.9	2.91		
highest	6.7	8,3	7.9	8.36	13.6	5.0	8.1	8.37		
st. dev.	2.1	1,1	1.7	1.22	1.4	0.9	1.5	1.22		

Both the threshold and the ECe_{50} are higher than the 1.7 and 5.9, respectively, mentioned in tables of the FAO based on Tanji and Kielen (2002). On the other hand, the slope we find is with 6% considerably lower than reported there (12%). The ECe_{90} is between 4.5 and 5.5 dS m⁻¹. The slope parameter in the vanGenuchten-Hoffman model is about 3, which is in accordance with the findings in van Genuchten and Gupta (1993).

The differences in fit quality (root mean square error, RMSE) between vanGenuchten-Hoffman and Maas-Hoffman are marginal. For brevity, in the remainder of the paper we will favour the vanGenuchten-Hoffman model, as it is probably closer to the real salt tolerance behaviour than the discontinuity in slope inherent to the Maas-Hoffman model. The estimation results for all years, cultivars and both models are provided in the Supplementary Material.

In general, a larger *ECe*₉₀ is accompanied by a larger slope parameter (Fig. 3). The same effect is observed with the Maas-Hoffman model (not shown), for which $s(\%) = 4 + 0.6ECe_{thr}$. This implies that the lethal EC is about 20–24 dS m⁻¹ and is about the same for all cultivars and all years.

The estimated individual-year zero-observed-effect yield (Y0) differs between years and over cultivars (not shown) but appears uncorrelated with the salt tolerance parameters. This is an indication that the estimation of Y0 is unbiased by the salinity conditions, which is what one expects since the true Y0 pertains to a non-saline soil.

3.2. Confidence ellipses

The uncertainty region is an ellipsoid in the 3-D parameters space. It can be characterized by three 2-D projections, one for each combination of two out of three parameters, taking the other one at its estimated value (Fig. 4).

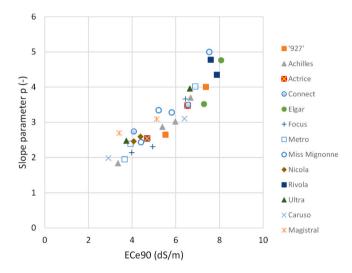


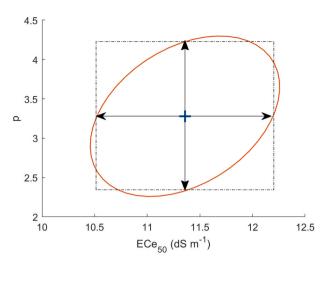
Fig. 3. Individual year estimates of ECe_{90} and p of potato cultivars (vanGenuchten-Hoffman model).

Diagrams such as Fig. 4 have been produced for each cultivar and each year (Supplementary Material). The presentation of the conditional confidence bounds of the individual parameters (arrows) must be considered with care, as the rectangular box does not coincide with the actual uncertainty region defined by the ellipses. The correlations between the estimates define the orientation of the ellipses; unlikely combinations of parameters are more easily reached in the direction of the short axis than along the long axis. Of particular interest are the uncertainty regions of the two salt tolerance parameters (upper left panel in Fig. 4), because these are the parameters by which the salt tolerance of cultivars is evaluated.

3.3. Combining single year estimates

The uncertainty ellipses of the salt tolerance parameters for one cultivar over several years can be combined into one single plot. An example is given in Fig. 5 for Miss Mignonne. For completeness, years where excessive data scatter precluded reliable estimation, as discussed in Sections 2.3 and 3.1, have been included as dashed lines.

A salt-tolerant cultivar would have a high ECe₅₀ and a low decline



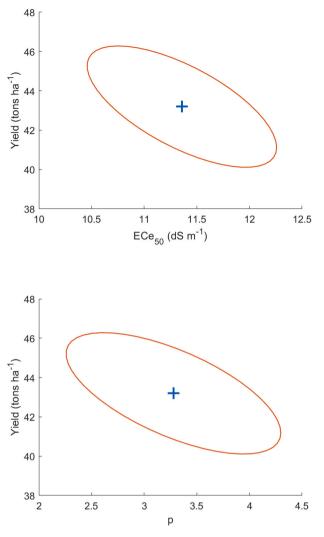


Fig. 4. Approximate 95% confidence ellipses. Miss Mignonne, 2014, model vanGenuchten-Hoffman. Arrows indicate the conditional confidence bounds (for clarity shown for salt tolerance parameters only).

rate, i.e., a low *p*, but it is equally important that there is a good yield. Therefore, the estimated yields are indicated in the figure as well. Years with larger data noise appear as wider ellipses.

Fig. 5 illustrates that, in contrast to the ideal situation, the ellipses do not fully overlap, indicating differences between years that cannot be described with the current models. More importantly, both variability as well as uncertainty hamper the classification of salt tolerance. It is worth to mention that in the Maas-Hoffman model (not shown) there was even less overlap. The four years with reliable estimates agree well about the parameter ECe_{50} , but there is no agreement on the slope *p*. This means that the more relevant ECe_{90} will differ quite a lot between years (cf. Section 3.4), again making it hard to judge the suitability of the cultivar for salt affected agriculture.

Nevertheless, in an attempt to obtain a quick screening of cultivar tolerances, the annual results were amalgamated to cultivar-specific parameters with the weighted mean method (Eq. 5) of Section 2.5 (Table 3).

A similar table for the Maas-Hoffman model is provided in the Supplementary Material. The lower and upper bounds define the outer rectangular box around the cluster of ellipses, which is quite conservative. The large uncertainties make it hard to find significant differences between the varieties. Yet, by searching for the highest *ECe₉₀* we see that the cultivars Elgar and Rivola might be good candidates for relatively saline soils; of these two, Rivola has the highest yields. Both cultivars, however, also have the highest slope parameter, indicating that they are more sensitive to increases in salinity beyond ECe_{90} than others.

3.4. True uncertainty regions

As a test of the method, Fig. 6 shows the extent to which the ellipsoids (dashed lines) directly generated by the estimation method are close to the true uncertainty regions according to Eq. (4) (solid lines). In general, the true confidence region, i.e., the line of equal sum of squares, is wider than given by the ellipsoid approximation. This is to be expected as the ellipsoids are linear approximations. Overall, based on the true regions, there is somewhat more overlap between the parameter regions of multiple years than suggested by the ellipsoid approximations.

The correlation between ECe_{90} and the slope parameter between years is due to a different mechanism than the estimation correlation for an individual year. The between-year correlation should be absent in the ideal case that there exists a universal ECe_{90} and p per cultivar. A comparison between Figs. 5 and 6 also illustrates that the variation in ECe_{90} between years is larger than the variation in ECe_{50} . This implies that screening on the basis of a single salinity in the neighbourhood of the half-yield value (cf. Table 1) might be inadequate.

3.5. Which potato cultivars are significantly more salt tolerant?

If the combined annual uncertainty regions of one cultivar do not overlap with those of another cultivar, this would be a sign of significant

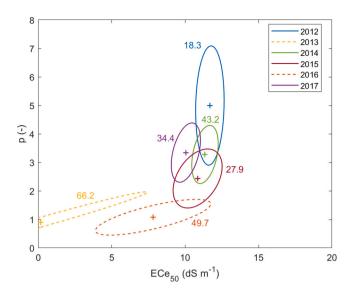


Fig. 5. Uncertainty ellipses of the salt tolerance parameters ECe_{50} and p, estimated for each year separately (Miss Mignonne, vanGenuchten-Hoffman model). Numbers next to the ellipses indicate estimated tuber yields (in tons ha⁻¹). Dashed lines indicate years with excessive data scatter, precluding reliable estimation (see text).

differences in salt tolerance. A complete diagram of all cultivars and all years would be cluttered, but an indication can be obtained by pairwise comparison of cultivars. Fig. 7, comparing Nicola with Rivola, shows that the estimates for Rivola in both years are outside the combined uncertainty region for Nicola, and vice versa, meaning that the two cultivars – on the basis of these two-year measurements – are significantly different in salt tolerance. Graphs like this allow for more accurate statements than by the method of Table 3.

Nevertheless, deceiving results might be obtained if a cultivar were tested for one year only; consider, for instance, Miss Mignonne in 2012 (Fig. 6), that seems significantly different from Nicola when just that year is considered, but this conclusion does not hold when looking at the centre of the uncertainty cluster over multiple years.

3.6. Simultaneous estimation of salt tolerance over multiple years

Although single year estimation already provides some insight, the annual variability and the large uncertainty constitutes a problem, and from a modelling point of view the annual variability would be devastating. Estimating the salt tolerance parameters for each year separately discards the knowledge gained from previous year estimations. In fact, the estimate of one year can serve as a prior to the estimate of a next year, thus possibly allowing to narrow down the region of uncertainty. To investigate this, the expanded method explained in Section 2.6 was used to obtain a simultaneous estimate of a unique set of salt tolerance parameters for each cultivar together with year-by-year varying yield estimates, under the two alternative model hypotheses.

3.6.1. Discriminating between yield limiting hypotheses

Fig. 8 shows the model predictions for all years of Miss Mignonne obtained with a single set of jointly estimated salt tolerance parameters under the two hypotheses, based on the vanGenuchten-Hoffman model. Fig. 9 presents the associated histograms of the residuals (i.e., the differences between the model predictions according to Eqs. (7) or (8) and the observed yield).

Visual inspection of the model fits (Fig. 8) shows that unlike the minimum rule, the multiplicative model is able to provide fits that are within the data uncertainty range for all years, even for years where the individual estimations failed (such as Miss Mignonne in 2013 and 2016). Also, the RMSE is lower. This result is confirmed by the histograms of the residual error, which under the multiplicative hypothesis is close to a Gaussian distribution (Fig. 9 Left), whereas under the minimum rule the histograms are clearly skewed (Fig. 9 Right). In principle, under the minimum rule, the result may depend on the choice of the potential yield Y_{pot} (here formally set to 70 tons ha⁻¹; the choice is immaterial under the multiplicative rule, see Section 2.7), but a test in the plausible range

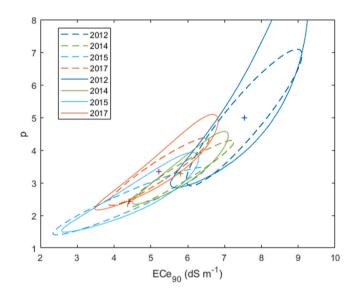


Fig. 6. Comparison of ellipsoid uncertainty regions (dashed lines) with the true uncertainty regions (solid lines). Four years of Miss Mignonne.

Table 3

Potato cultivar-specific parameters of the van Genuchten-Hoffman model, obtained by combining single year estimates across all years (#yr: number of years with data, L-min: lowest minimum, w-Mn: weighted mean, H-max: highest maximum).

	#yr	ECe50			р			YO			ECe ₉₀		
		L-min	w-Mn	H-max	L-min	w-Mn	H-max	L-min	w-Mn	H-max	L-min	w-Mn	H-max
927	2	11.5	12.7	14.0	1.9	2.8	5.9	41.1	48.3	53.7	4.1	6.1	9.4
Achilles	4	9.1	11.8	14.1	0.7	2.2	5.0	23.9	30.7	55.2	2.0	4.9	8.8
Actrice	2	9.5	12.1	13.2	1.7	2.9	4.4	35.6	43.5	47.7	2.9	5.9	7.9
Caruso	2	7.3	11.5	14.1	1.4	2.2	4.1	38.3	41.8	47.6	1.7	4.2	8.0
Connect	2	7.7	11.6	13.0	1.9	3.1	4.3	53.4	59.3	67.0	2.6	5.6	7.7
Elgar	2	11.8	13.0	15.2	2.1	4.0	6.6	36.8	43.2	48.8	5.0	7.8	9.8
Focus	3	9.2	11.5	16.4	0.0	1.6	4.7	18.7	44.3	54.7	0.1	5.2	9.7
Magistral	2	6.6	9.2	11.4	1.9	2.9	4.0	48.9	58.1	65.2	2.3	4.1	6.5
Metro	4	8.9	11.2	12.6	1.4	2.4	5.3	40.4	51.9	67.0	2.3	4.7	8.1
Miss Mignonne	4	9.1	11.0	12.7	1.4	3.2	7.1	16.8	25.7	46.3	2.3	5.8	9.1
Nicola	2	8.5	10.0	12.0	1.4	2.5	3.8	46.3	52.0	68.5	2.2	4.1	6.5
Rivola	2	10.8	12.8	13.8	2.9	4.5	6.7	45.0	57.2	63.5	5.7	7.8	9.5
Ultra	2	7.5	11.1	12.4	1.6	3.0	5.0	37.8	50.7	57.5	2.2	5.5	7.9

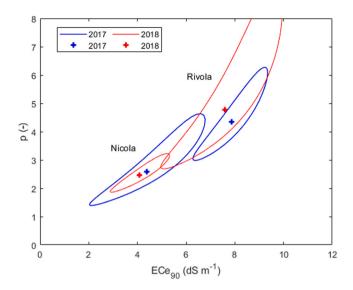


Fig. 7. Parameter estimates (crosses) and uncertainty regions for salt tolerance parameters (vanGenuchten-Hoffman in alternate form) for individual years 2017 and 2018, for cultivars Nicola and Rivola.

from 50 to 90 tons/ha revealed that the RMSE remains around 5.8, so that the comparison is allowed. Similar plots with other cultivars, all show the same tendencies (Supplementary Material, including the Maas-Hoffman model as well).

Hence, the multiplicative hypothesis gives a better representation of the data than the minimum rule. As it produces plausible fits irrespective of annual differences in yield, this method enables the estimation of a universal set of salt tolerance parameters associated to a specific cultivar.

3.6.2. Yield differences

While the method disentangles cultivar-specific yields from cultivarspecific salt tolerance parameters, which is a significant asset, the annual yield differences remain. This is inherent to field experimentation, and, in addition, it is a reality to the farmers, too. Fig. 10 shows the annually varying estimates of the zero-observed effect yields (*Y0*). Simultaneous estimation leads to slightly different values in each year as compared to separate estimation. This slight shift makes the sum of squares for that particular year worse, but it creates room for adjustment of the other parameters such that an acceptable fit is obtained for all years together.

The choice of the model (vanGenuchten-Hoffman or Maas-Hoffman), or the hypothesis (multiplicative or minimum) has little effect on the tuber yield estimates. Tuber yields can be up to 60 tons ha⁻¹, not much different from what is obtained in commercial production in The Netherlands.

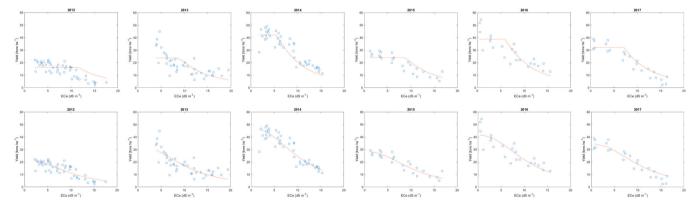


Fig. 8. Fits for joint single parameter sets over multiple years. Miss Mignonne. Upper row: multiplicative hypothesis; Lower row: minimum rule hypothesis.

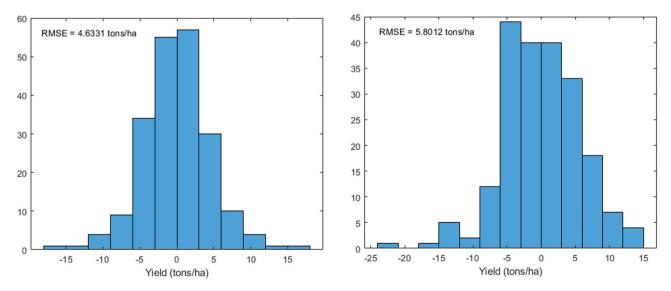


Fig. 9. Histogram of residual error over all years. Miss Mignonne. Left: multiplicative hypothesis; Right: minimum rule hypothesis.

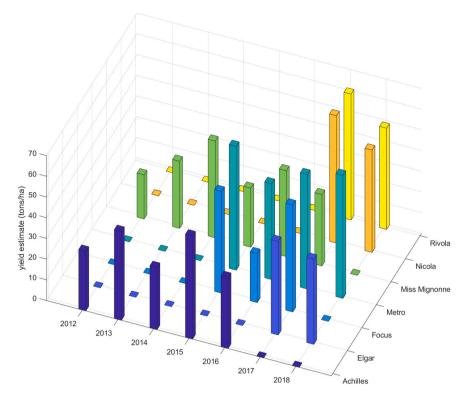


Fig. 10. Estimates of the annually varying yield per cultivar in the absence of salinity stress under simultaneous estimation (model vanGenuchten-Hoffman, multiplicative rule).

3.6.3. Joint uncertainty region

As expected, the uncertainty range of the simultaneous estimation is narrower than the uncertainty range of the estimates for individual years, as shown in Fig. 11 for Miss Mignonne.

The individual uncertainty contours for the years 2013 and 2016 are unreliable, but they are shown here because these data are nevertheless incorporated in the joint estimation, as they are real data (cf. Fig. 8). It may seem strange that some individual year contours are outside the joint contour (e.g. 2012), but it should be kept in mind that the individual year contours shown are cross sections at the actual estimated yield in that single year. The estimated Y0 in 2012 is 18.3 tons ha⁻¹,

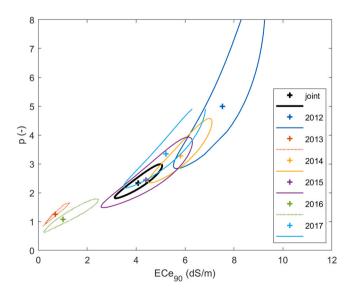


Fig. 11. Joint estimation over 2012–2017 (thick line). Miss Mignonne. Multiplicative rule. Also shown are the uncertainty regions for the individual years under separate estimation.

whereas the fit in the joint estimate for that year is $21.3 \text{ tons ha}^{-1}$, and hence in view of the correlation shown in Fig. 4, the salt tolerance cross section of the 3-D uncertainty space at these new values shifts to the left.

3.6.4. Which cultivars are significantly more salt tolerant? - Revisited

Applying the models under the multiplicative rule, finally gives rise to the united salt tolerance parameters and their uncertainty for the various cultivars. The estimates for the vanGenuchten-Hoffman model and the associated true uncertainty regions, enclosed by the contours of equal sum of squares, for all thirteen cultivars with multiple year data are shown in Fig. 12 for the standard parameterization (*ECe*₅₀), and for the alternate parameter *ECe*₉₀ in Fig. 13.

The characteristic salinities with the vanGenuchten-Hoffman model vary from ECe_{50} 9.5–13, ECe_{90} 4–8 dS m⁻¹, and for the Maas-Hoffman

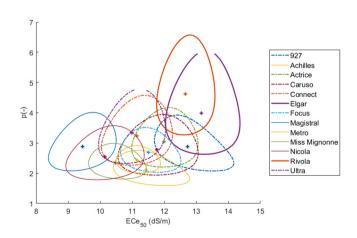


Fig. 12. Salt tolerance parameters (cross hairs) and uncertainty regions (contours) from simultaneous estimation over multiple years under the multiplicative limitation hypothesis showing significant differences between potato varieties. Standard vanGenuchten-Hoffman parameters.

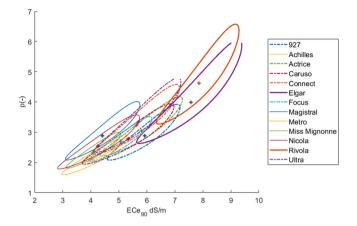


Fig. 13. Salt tolerance parameters (cross hairs) and uncertainty regions (contours) from simultaneous estimation over multiple years under the multiplicative limitation hypothesis showing significant differences between potato varieties. Alternate vanGenuchten-Hoffman parameter.

model (not shown) from ECe_{thr} 1.5–6 dS m⁻¹, ECe_{90} 3–8 dS m⁻¹. The slope parameter is quite similar across cultivars except for Rivola and to a lesser extent Elgar. Rivola is clearly distinct from the other varieties. It has a high characteristic salinity, about twice as high as, for instance, Achilles, but also a steeper slope. It has also a good yield (50–60 tons ha⁻¹). Other good candidates for salt affected soils are Elgar and '927'; although the observed yields are somewhat lower (40–45 tons ha⁻¹ and 45–50 tons ha⁻¹, respectively). The lower sensitivity to high salinities by virtue of less steep slope can be an advantage. In terms of ECe_{90} the ranking of the tested cultivars is {Achilles, Miss Mignonne, Nicola, Magistral, Metro} with an ECe_{90} between 4 and 4.5 dS m⁻¹, followed by {Focus, Caruso, Connect, Ultra, Actrice, '927'} with an ECe_{90} between 5 and 6 dS m⁻¹, and finally {Elgar, Rivola) with an ECe_{90} above 7.5 dS m⁻¹.

4. Discussion

4.1. Estimation procedure and data

Each parameter estimation endeavor hinges on the quality of the data. Field data are notoriously subject to variability. In the field trials underlying our data, elaborate control on salinity and water dynamics during the growing season favored the analysis, which otherwise would have been extremely difficult or impossible. This is because without such control the seasonal mean salinity would not be representative for the entire root zone at all times. Even with these precautions, tuber yield showed wide variability between replicates with seemingly equal salinity treatment. We coped with this by taking all data into account in a formal parameter estimation procedure.

Our procedure provides cultivar-specific estimates of crop salt tolerance and their associated uncertainties. We found that the vanGenuchten-Hoffman model generally provides an adequate description, although the difference with the Maas-Hoffman model is not decisive, and other descriptions might also be possible. Differences between models in yield prediction at salinities where yield reduction is already considerable are less important for agricultural practice, but lack of yield data or very noisy data reduces the robustness of the predictions at low salinities in any model. Experiments with a restricted number of salinities that focus on traits as a proxy of the yield as advocated for fast in vitro screening (e.g. Morpurgo (1991); Naik and Widholm (1993); Ekanayake and Dodds (1993); Zhang and Donnelly (1997)), - while perhaps adequate to isolate promising accessions -, do not provide sufficient information for the prediction of yield reduction by salinity in the field.

In assessing salt tolerance models, single year experiments are

insufficient in view of the unavoidable variability between years. A major contribution to reducing uncertainties is our approach to evaluate the salt tolerance jointly over multiple years. While evaluation over individual years separately already narrows down the set of possible salt tolerance estimates, it is the subsequent joint estimation of salt tolerance that substantially reduces the uncertainties.

Further reduction of uncertainties might be achieved if unequivocal and independent information on the zero-observed effect yield would be available. Note that the supremum of *YO* over all years is the lower bound of the potential yield; the potential yield itself cannot be estimated from these kind of field trials. In view of the unavoidable environmental variability in the field, an exact value of *YO* in any particular year would require experimentation in the complete absence of soils salinity, which is virtually impossible in the field. It must be noted that even if *YO* would be known exactly, estimation of salt tolerance parameters directly from the relative yield, as is common practice, is allowed under the multiplicative rule only. In this respect our findings that this rule gives much better results than the minimum rule is reassuring.

4.2. Joint multiple year estimation

If salt tolerance is a cultivar specific property, one single parameter set per cultivar set should characterize it. It could be that there are cultivars with time varying salt tolerance, but current methods including ours cannot detect it, and such cultivars will not be suitable for cropping on salt affected land anyway.

We tested several approaches of joining the estimation results over multiple years to obtain a single parameter set. The simplest approach involved calculating a weighted mean from the individual year estimates, inversely proportional to the estimated uncertainty ranges, thus giving more weight to years with less data variability. Even though the correlation between estimates is ignored, a preliminary ranking of cultivars is obtained, but the procedure remains somewhat arbitrary.

A better approach is to consider the joint estimation for all years together. This, however, requires a suitable model formulation on how yield reduction by salinity and yield reduction by other factors interact. Our findings are that, in contrast to the minimum rule, the multiplicative rule is able to produce quite acceptable fits across all years. The unification of seemingly different year is possible due to the fact that the knowledge on each individual year serves as a prior for the estimation of the other years. Said differently, the possibility that the true parameter for a particular year is anywhere within the individual year uncertainty contour is restricted by the measurements of the other years, thus narrowing down the parameters to the most likely ones.

We acknowledge that the multiplicative rule may not apply to all types of simultaneous limitations. In particular, the interaction between salinity and water availability may be more complex, see, for instance, Homaee et al. (2002a, 2002b). The continuous irrigation at the Texel experiments was designed to avoid simultaneous water limitations, thus giving confidence in our results, but the downside is that with the current data water interaction cannot be studied.

4.3. Yield variation and yield limiting factors

The necessity to introduce another yield limiting factor (g_k) in our study is brought about by the year-to-year yield variations. Not only does yield vary in practice, but unsuccessful attempts to provide explanations with the current state of knowledge as expressed in models underline that more work is needed in this area (Fleisher et al., 2017; Kadaja and Tooming, 2004; Yin and Struik, 2010).

What can be the possible sources of the unknown factor that is limiting yield? One possibility is that crops grown on the plots in previous years, being different among the plots within a treatment group of the current year, influenced the soil microbiology and phytopathology (Geels and Schippers, 1983; Larkin and Honeycutt, 2006). In addition, the weather may vary from year to year, but in that case yields of cultivars tested in the same year would likely be correlated, which appears not to be the case in our study (cf. Fig. 10). The same holds for differences in nutrient availability between years. Water limitation, possibly in interaction with air humidity (Backhausen et al., 2005), may be possible, but only gives yield differences between cultivars if each cultivar responds to these factors in a cultivar specific way.

There are reasons to assume that indeed tuber formation depends in cultivar specific ways on the actual dynamics of soil and weather conditions. The sequence of events, such as rainfall, day-time and night-time temperatures, although the same for all cultivars, may have a different effect on the tuber formation per accession. There are various accounts on the interrelationship between genetics and emergent properties, one of the first being the work of Ewing about the interaction with heat stress (Ewing, 1981). It is known that there are 'early' and 'late' potatoes, also showing the interaction between genetics and environmental conditions. The need for greater understanding of the response to a changing environment is even larger in the light of global warming (Dahal et al., 2019; George et al., 2017; Levy and Veilleux, 2007). While these studies are phenomenological, the ultimate dream is to be able to provide a molecular genetic basis (Khan et al., 2019; Yin and Struik, 2010). However, none of these publications explicitly addresses the effect on final yield of environmental dynamics during growth, except to some extent Levy (1992) who studied the effect of the start of the saline treatment.

The final tuber yield is the result of the integration of growth rate and root-shoot partitioning over time. In principle, dynamic models describing these processes have the potential to cope with dynamic variations. We believe that our results are valuable in the further development of dynamic crop models. Genetic differences between varieties may be expressed as differences in process parameters (Spitters and Schapendonk, 1990; Yin and van Laar, 2005), and the actual variation in environmental and soil conditions will then be responsible for differences in final yield. It is, however, almost impossible to calibrate such models from final yields alone. The minimum that should be done is to follow some easily detectable traits, such as above ground biomass, leaf area index, plant height, and possibly others during the growing season, in combination with the final tuber yield. It goes without saying that such experimentation would require extensive resources. In the light of all this, our approach of an empirical additional limiting factor is perhaps a gross simplification of reality, but it does provide a significant and practical means of uniting the results of several years of experimentation, as testified by our results.

Our results highlight that differences in salt tolerance exist among potato cultivars. Some of the differences we observed would not have been picked up when testing at just a single salinity level as is sometimes done in fast screening. While estimation of the entire salt tolerance curve is more labor intensive and time consuming, we are convinced that the entire curve is essential in dynamic crop models. The characteristic salinity parameter serves as an indication of the effect of the average salinity over the season, while the slope is relevant to cope with the seasonal dynamics.

The salt tolerance of certain potato cultivars, as found in our field trials, is substantially higher than reported by FAO. Thus, potatoes may be grown at more brackish/salt affected conditions than believed previously, which may have important implications for global food production. A final word of caution is, however, in place regarding such extrapolation of our results to other situations. The results in this study were obtained in sandy soil, and for crops that till emergence did not receive saline water. As pointed out by Levy and Veilleux (2007), high yield cultivars may have adapted to the conditions of moderate climate zones. Reversing the argument, it remains to be seen how well cultivars that are relatively salt tolerant in our experiment perform under other climate and soil conditions.

5. Conclusions

essential to have cultivar-specific parameters. The proposed method alleviates the difficulty of seemingly annually varying parameters. Our study shows that the characterization of crop salt tolerance by characteristic parameters cannot be done by determining the response at one or two salinities only but requires the acquisition of the entire salt tolerance curve. Moreover, single year experimentation is not enough to obtain a reliable picture of salt tolerance of a particular cultivar. Thanks to assessing the uncertainties of parameter estimates and the joint estimation over multiple years, we could prove that there are significant differences in salt tolerance among potato cultivars. These differences do exist and can be considerable. In this study, the cultivars Rivola, Elgar and '927' were found to be more tolerant than other cultivars on sandy soils. Analysis of two possible models for describing the interaction of another, unknown, limiting factor with salt limitation revealed that the multiplicative rule performs better than the minimum rule and can provide acceptable fits for all tested years. In combination, our work positively identifies high yielding potato cultivars that have potential for salt affected agriculture.

Funding

This work was partly supported by the Salt Farm Foundation, Den Burg, The Netherlands.

Declaration of Competing Interest

None.

Acknowledgements

We like to thank Edwin van Straten for the technical assistance during the field tests.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agwat.2021.106902.

References

- Backhausen, J.E., Klein, M., Klocke, M., Jung, S., Scheibe, R., 2005. Salt tolerance of potato (Solanum tuberosum L. var. Desirée) plants depends on light intensity and air humidity. Plant Sci. 169, 229–237.
- Bernstein, L., Ayers, A.D., Wadleigh, C.H., 1951. The salt tolerance of White Rose potatoes. Proc. Am. Soc. Hortic. Sci. 57, 231, 236.
- Dahal, K., Li, X.Q., Tai, H., Creelman, A., Bizimungu, B., 2019. Improving potato stress tolerance and tuber yield under a climate change scenario – a current overview. Front. Plant Sci. 10.
- De Vos, A., Bruning, B., van Straten, G., Oosterbaan, R., Rozema, J., van Bodegom, P., 2016. Crop Salt Tolerance Under Controlled Field Conditions in The Netherlands, Based on Trials Conducted at Salt Farm Texel. Salt Farm Texel, Den Hoorn, Texel.
- Draper, N.R., Smith, H., 1966. Applied Regression Analysis. John Wiley & Sons, New York, London, Sydney.
- Ekanayake, I.J., Dodds, J.H., 1993. In-vitro testing for the effects of salt stress on growth and survival of sweet potato. Sci. Hortic. 55, 239–248.
- Elkhatib, H.A., Elkhatib, E.A., Khalaf-Allah, A.M., El-Sharkawy, A.M., 2005. Salt tolerance of four potato cultivars. J. Plant Nutr. 27, 1575–1583.
- Ewing, E.E., 1981. Heat stress and the tuberization stimulus. Am. Potato J. 58, 31–49. Fleisher, D.H., Condori, B., Quiroz, R., Alva, A., Asseng, S., Barreda, C., Bindi, M.,
- Boote, K.J., Ferrise, R., Franke, A.C., Govindakrishnan, P.M., Harahagazwe, D., Hoogenboom, G., Naresh Kumar, S., Merante, P., Nendel, C., Olesen, J.E., Parker, P. S., Raes, D., Raymundo, R., Ruane, A.C., Stockle, C., Supit, I., Vanuytrecht, E., Wolf, J., Woli, P., 2017. A potato model intercomparison across varying climates and productivity levels. Glob. Change Biol. 23, 1258–1281.
- Geels, F.P., Schippers, B., 1983. Reduction of yield depressions in high frequency potato cropping soil after seed tuber treatments with antagonistic fluorescent Pseudomonas spp. J. Phytopathol. 108, 207–214.
- George, T.S., Taylor, M.A., Dodd, I.C., White, P.J., 2017. Climate change and consequences for potato production: a review of tolerance to emerging abiotic stress. Potato Res. 60, 239–268.

Homaee, M., Feddes, R.A., Dirksen, C., 2002a. A macroscopic water extraction model for nonuniform transient salinity and water stress. Soil Sci. Soc. Am. J. 66, 1764–1772.

Homaee, M., Feddes, R.A., Dirksen, C., 2002b. Simulation of root water uptake: III. Nonuniform transient combined salinity and water stress. Agric. Water Manag. 57, 127–144.

To incorporate salt limitation functions in crop yield models it is

G. van Straten et al.

- Jaarsma, R., de Vries, R.S.M., de Boer, A.H., 2013. Effect of salt stress on growth, Na+ accumulation and proline metabolism in potato (Solanum tuberosum) cultivars. PLoS One 8, e60183.
- Kadaja, J., Tooming, H., 2004. Potato production model based on principle of maximum plant productivity. Agric. For. Meteorol. 127, 17–33.
- Katerji, N., Van Hoorn, J.W., Hamdy, A., Mastrorilli, M., 2000. Salt tolerance classification of crops according to soil salinity and to water stress day index. Agric. Water Manag. 43, 99–109.
- Khan, M.S., Yin, X., van der Putten, P.E.L., Jansen, H.J., van Eck, H.J., van Eeuwijk, F.A., Struik, P.C., 2019. A model-based approach to analyse genetic variation in potato using standard cultivars and a segregating population. II. Tuber bulking and resource use efficiency. Field Crops Res. 242, 107582.
- Khenifi, M.L., Boudjeniba, M., Kameli, A., 2011. Effects of salt stress on micropropagation of potato (Solanum tuberosum L.). Afr. J. Biotechnol. 10, 7840–7845.
- Khrais, T., Leclerc, Y., Donnelly, D.J., 1998. Relative salinity tolerance of potato cultivars assessed by in vitro screening. Am. J. Potato Res. 75, 207–210.
- Larkin, R.P., Honeycutt, C.W., 2006. Effects of different 3-year cropping systems on soil microbial communities and rhizoctonia diseases of potato. Phytopathology 96, 68–79.
- Levy, D., 1992. The response of potatoes (Solunum tuberosum L.) to salinity: plant growth and tuber yields in the arid desert of Israel. Ann. Appl. Biol. 120, 547–555.
- Levy, D., Veilleux, R.E., 2007. Adaptation of potato to high temperatures and salinity a review. Am. J. Potato Res. 84, 487–506.
- Levy, D., Fogelman, E., Itzhak, Y., 1988. The effect of water salinity on potatoes (Solanum tuberosum L.): physiological indices and yielding capacity. Potato Res. 31, 601–610.
- Maas, E.V., 1993. Testing Crops for Salinity Tolerance. In: Manville, B.V.B.J.W., Duncan, R.R., Yohe, J.M. (Eds.). INSTORMIL, University of Nevada, Lincoln, NE, USA, pp. 234–247.
- Maas, E.V., Hoffman, G.J., 1977. Crop salt tolerance current assessment. ASCE J. Irrig. Drain. Div. 103, 115–134.
- Morpurgo, R., 1991. Correlation between potato clones grown in vivo and in vitro under sodium chloride stress conditions. Plant Breed. 107, 80–82.
- Munns, R., Husain, S., Rivelli, A.R., James, R.A., Condon, A.G., Lindsay, M.P., Lagudah, E.S., Schachtman, D.P., Hare, R.A., 2002. Avenues for increasing salt tolerance of crops, and the role of physiologically based selection traits. Plant and Soil 247, 93–105.
- Nadler, A., Heuer, B., 1995. Effect of saline irrigation and water deficit on tuber quality. Potato Res. 38, 119–123.

- Nagaz, K., Masmoudi, M.M., Mechlia, N.B., 2007. Soil salinity and yield of drip-irrigated potato under different irrigation regimes with saline water in arid conditions of Southern Tunisia. J. Agron. 6, 324–330.
- Naik, P.S., Widholm, J.M., 1993. Comparison of tissue culture and whole plant responses to salinity in potato. Plant Cell Tissue Organ Cult. 33, 273–280.
- Plaut, Z., Edelstein, M., Ben-Hur, M., 2013. Overcoming salinity barriers to crop production using traditional methods. Crit. Rev. Plant Sci. 32, 250–291.
- Pradel, W., Gatto, M., Hareau, G., Pandey, S.K., Bhardway, V., 2019. Adoption of potato varieties and their role for climate change adaptation in India. Clim. Risk Manag. 23, 114–123.
- Shannon, M.C., Grieve, C.M., 1999. Tolerance of vegetable crops to salinity. Sci. Hortic. 78, 5–38.
- Spitters, C.J.T., Schapendonk, A.H.C.M., 1990. Evaluation of breeding strategies for drought tolerance in potato by means of crop growth simulation. Plant Soil 123, 193–203.
- Tanji, K.K., Kielen, N.C., 2002. Agricultural drainage water management in arid and semi-arid areas. In: FAO Irrigation and Drainage Paper Series 61. FAO, Rome.
- Van Der Ploeg, R.R., Böhm, W., Kirkham, M.B., 1999. On the origin of the theory of mineral nutrition of plants and the Law of the Minimum. Soil Sci. Soc. Am. J. 63, 1055–1062.
- van Genuchten, M.T., Gupta, S.K., 1993. A reassessment of the crop tolerance response function. J. Indian Soc. Soil Sci. 41, 730–737.
- Van Genuchten, M.T., Hoffman, G., 1984. Analysis of crop salt tolerance data. In: Shainberg, I., Shalhevet, J. (Eds.), Soil Salinity Under Irrigation - Process and Management. Springer Verlag, Berlin, pp. 258–271 (Vol. Ecological Studies).
- van Straten, G., de Vos, A.C., Rozema, J., Bruning, B., van Bodegom, P.M., 2019. An improved methodology to evaluate crop salt tolerance from field trials. Agric. Water Manag. 213, 375–387.
- Velásquez, B., Balzarini, M., Taleisnik, E., 2005. Salt tolerance variability amongst Argentine Andean potatoes (Solanum tuberosum L. subsp. andigena). Potato Res. 48, 59–67.
- Yin, X., Struik, P.C., 2010. Modelling the crop: from system dynamics to systems biology. J. Exp. Bot. 61, 2171–2183.
- Yin, X., van Laar, H.H., 2005. Crop Systems Dynamics: An Ecophysiological Simulation Model for Genotype-by-Environment Interactions. Wageningen Academic Publishers, Wageningen.
- Zhang, Y., Donnelly, D.J., 1997. In vitro bioassays for salinity tolerance screening of potato. Potato Res. 40, 285–295.