

ORIGINAL ARTICLE

Nonlinear Allometric Equation for Crop Response to Soil Salinity

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Crop response to soil salinity has been extensively studied, from empirical works to modelling approach, being described by different equations, first as a piecewise linear model. The equation employed can differ with actual response, causing miscalculation in practical situations, particularly at the higher extremes of the curve. The aim of this work is to propose a new equation, which allows determining the full response to salinity of plant species and to provide a verification using different experimental data sets. A new nonlinear equation is exposed supported by the allometric approach, in which the allometric exponent is salinity-dependent and decreases with the increase in relative salinity. A conversion procedure of parameters of the threshold-slope model is presented; also, a simple procedure for estimating the maximum salinity (zero-yield point) when data sets are incomplete is exposed. The equation was tested in a wide range of experimental situations, using data sets from published works, as well as new measurements on seed germination. The statistical indicators of quality (R^2 , absolute sum of squares and standard deviation of residuals) showed that the equation accurately fits the tested empirical results. The new equation for determining crop response to soil salinity is able to follow the response curve of any crop with remarkable accuracy and flexibility. Remarkable characteristics are: a maximum at minimum salinity, a maximum salinity point can be found (zero-yield) depending on the data sets, and a meaningful inflection point, as well as the two points at which the slope of the curve equals unity, can be found.

Key words: crop modelling, salinity tolerance, allometry, crop stress, soil salinity

S_t	Maximum salinity tolerated by a crop without yield reduction (Maas and Hoffman 1977)	B_s	Biomass under saline condition
c_{50}	Salinity at which the yield is reduced by 50% of van Genuchten (1983)	B_x	Maximum total biomass production without saline restriction
Y	Any structural and functional variables of organisms as height or growth rate	S	Salinity in soil under actual growing conditions
m	Corporal mass	S_x	Maximum salinity tolerated by the crop (or measured).
Y_0	Allometric constant	b_s	Allometric exponent of salinity to biomass/yield relationship
b	Allometric exponent	b_s'	Allometric constant of the salinity-dependent b_s
M	Mineral nutrient accumulated by a crop	b_{sd}	Exponent of the salinity-dependent b_s
M_T	Total nutrient accumulated in the total biomass	a	Allometric constant of the salinity response curve
B	Crop biomass	c	Constant fixing the starting point of the salinity curve
B_T	Total crop biomass	R^2	Coefficient of determination
M_0	Allometric constant for the specific M to B relationship	$Sy.x$	Standard deviation of residuals
		CV	Coefficient of variation
		n	Number of points/sample

Among concerns in agricultural sciences soil salinization has long been identified as a major problem (Alam, 1999). It has been estimated that about 10% of the total land surface of the world have salt affected soils, a magnitude close to one billion hectares, and one third of all agricultural lands are also becoming saline (Pessarakli and Szablocs, 1999; Sen *et al.*, 2002). Globally, about 20% of the irrigated land is salt affected (FAO, 2014). Thus, salinity response in plants has been considered of main importance and it is the core of the study on this agricultural problem.

The quantitative approach to the salinity response was first focused as a piecewise linear function by Maas and Hoffman (1977). This function established an extremely practical method, since it is determined by just two independent parameters: the soil salinity threshold, S_i (maximum salinity tolerated by a crop without yield reduction compared to the same crop under non-saline conditions) and the slope that determines the yield reduction per unit of salinity increase. In the next decade van Genuchten (1983) introduced a non-linear equation in a study which included various mathematical expressions, while van Genuchten and Gupta (1993) exposed the weaknesses of the linear approach, showing evidence of the strength of the s-shaped asymptotic function of van Genuchten (1983). In this equation he added the c_{50} parameter, the salinity at which the yield is reduced by 50%.

On the other hand, Misle (2013) supported that the allometric approach is a synthetic but powerful tool

in crop ecophysiology. Although allometric theory is debated among scientists (West *et al.*, 1997; Enquist, 2002), well-founded reasons sustain to include allometric relationships in a systemic approach to practical applications as crop mineral nutrition under stress (Misle and Garrido, 2008).

Hence in this work we hypothesize, supported by the allometric approach, that salinity in soil can interfere the acquiring of resources such as water, mineral nutrients and oxygen, so that a power equation can describe the crop response in growth or other measure. Thus, the aim of this study was to propose a new equation, which allows determining the full response to salinity of plant species and to provide a verification using different experimental data sets.

THEORY

Allometry in biological sciences is the study of size correlated variations in organic form and process (Niklas, 1994). It was first applied by Pearsall (1927) to plants. However, the modern terminology was adopted by Huxley and Teissier (1936). Currently, it has been sustained that in many structural and functional variables of organisms as height or growth rate, Y , a power relationship with the corporal mass, m , or with measures as length or diameter can be found:

$$Y = Y_0 m^b \quad [1]$$

where Y_0 is a constant associated to the variable and organism type and b is the allometric exponent (Niklas, 1994; West *et al.*, 1997; Enquist, 2002). In similar terms, Misle (2006, 2013) has proposed that mineral nutrients accumulation is allometrically related

with the total biomass in crops:

$$\frac{M}{M_T} = M_0 \left(\frac{B}{B_T} \right)^b \quad [2]$$

where M is the nutrient accumulated at any time associated to a biomass, B ; M_T is the total nutrient in the total biomass, B_T , both accumulated by the crop at the end of the growing period; M_0 is a normalization constant usually expected to be equal to unity.

West *et al.* (1997) and Enquist (2002) have explained the basis of allometry, which are particularly relevant when functional relationships are considered. They have been supporting for long that the occurrence of allometric relationships constitutes the condition for “*maximizing the scaling of surfaces where resources are exchanged with the environment (e.g. roots area, leaf area, lungs or gut surfaces)*”. If “*physiological rates must match the ability of vascular networks to obtain and deliver resources*” it is plausible that salinity in soil can interfere the acquiring of resources as water, mineral nutrients and oxygen in such a way that a power relationship can describe the response in growth or other measure. In fact, it is well known that abiotic stress modulates plant root development (Sánchez-Calderón *et al.*, 2013). Moreover, an oxygen deficient soil environment can interfere with nutrient uptake and translocation of water and ions (Hodge *et al.*, 2009).

Kahlaoui *et al.* (2011) studied the response of three tomato cultivars to water regime using saline water (6.57 dS m⁻¹) and found that mineral nutrients decrease as water levels decrease, while Na⁺ and Cl⁻ increase. It is well-known that salinity inhibits water uptake due to osmotic effect, also disturbs the normal

metabolism caused by high Na⁺ concentration in plant tissues and inhibits the absorption of other essential cations (Alam, 1999); furthermore, soil aeration is diminished due to deterioration in the physical structure of soils (Yadav *et al.*, 2011). Thus, conversely to the relationship of any mineral nutrient to the biomass in Eq. 2 and taking into account the reduction in biomass caused by the salinity increase, the following expression was proposed by Misle and Garrido (2008):

$$1 - \frac{B_s}{B_x} = \left[\frac{S}{S_x} \right]^{b_s} \quad [3]$$

where S is the salinity of the soil under actual conditions between 0 - S_x , B_x is the maximum total biomass production without saline restriction and B_s is the estimate of biomass under saline condition S , usually the unknown quantity. S_x is the maximum salinity tolerated by the crop (measured) or ideally, the zero-yield point.

Eq. 3 is a simple and sound hypothesis, functional enough, which is easy to couple with the other components in the simulation work of Misle and Garrido (2008), but it is not realistic enough. To illustrate this point, in Fig. 1 a linear fit and the power equation (Eq. 3) are compared to a more realistic s-shaped curve. As can be observed, a power equation first underestimates and then overestimates compared to the s-shaped curve, as well as the linear fit.

While considering the above arguments it can be questioned whether any additional effect is needed to take into account in the allometric equation that

makes this response a non-linear allometry. If something like this can be postulated for the salinity response, some evidence should be presented for the new proposed b_s . Here, an example is useful. When a simple allometric relationship is considered, the plot of the allometric exponent against the variable selected to be set on the abscise axis (i.e. leaf width, biomass, etc.) results in an almost constant value, with some experimental variability around a mean value (Fig. 2a). But when the hypothetical b_s is calculated from empirical data on the salinity response as $b_s = \ln(1 - B/B_x) / \ln(S/S_x)$ a power-like shaped curve is obtained (Fig. 2b).

Therefore, a new hypothesis is plausible: the allometric exponent b_s is also salinity-dependent and should decrease with the increase in the relative salinity (S/S_x) by a power function with a negative allometric exponent, b_{sd} (decreasing rate):

$$b_s = b'_s \left(\frac{S}{S_x} + c \right)^{b_{sd}} \quad [4]$$

b'_s is the constant of this allometric relationship associated to the intercept on the y-axis (maximum b_s). So that this new equation is proposed:

$$\frac{B_s}{B_x} = 1 - a \left[\frac{S}{S_x} + c \right]^{b'_s \left(\frac{S}{S_x} + c \right)^{b_{sd}}} \quad [5]$$

The constant c , locates the starting point of the curve. The constant a is associated to the strength of the decline of the curve with the increase in relative salinity, whose meaning refers to salinity tolerance.

Derivatives: The equation for the allometric exponent (Eq. 4) can easily be derived, taking S/S_x as

the independent variable, to get:

$$\frac{db_s}{d(S/S_x)} = b'_s \cdot b_{sd} \cdot \left(\frac{S}{S_x} + c \right)^{b_{sd}-1} \quad [6]$$

Experimental data can be analyzed to compare the data sets by discrete intervals as Δb_s with the equation [6]. In Fig. 3 yield response data from McElgunn and Lawrence (1973) were transformed to be compared with the fit of the derivative Eq. 6. Similarly, Eq. 5 can be derived to get:

$$\frac{d(B_s/B_x)}{d(S/S_x)} = -a \cdot \left[\frac{S}{S_x} + c \right]^{b'_s \left(\frac{S}{S_x} + c \right)^{b_{sd}}} \cdot \left[b'_s \cdot b_{sd} \cdot \left(\frac{S}{S_x} + c \right)^{b_{sd}-1} \cdot \ln \left(\frac{S}{S_x} + c \right) + b'_s \cdot \left(\frac{S}{S_x} + c \right)^{b_{sd}-1} \right] \quad [7]$$

$\Delta(Y/Y_x)$ points (as approximation to the derivative of B_s/B_x) were calculated from data of McElgunn and Lawrence (1973) in bromegrass and plotted in Fig. 3 with the regression curve of the fit of the derivative Eq. 7.

The insets in Figs. 3a and 3b show the theoretical shapes of both derivatives. Thus consistency is presented for Eq. 5 regarding its logical coherence. In addition, Eq. 7 can be used to obtain the inflection point of the curve, which can be a much more meaningful point than the classical S_i or c_{50} at the time of comparing species and cultivars. The minimum in Fig. 3b reveals the inflection point. Two additional points can also be considered as characteristics: the two points at which the slope of the response curve (first derivative) equals unity. In general, the first of these points occurring when growth/yield response begin to diminish at increasing salinity will indicate the point from which the next unity of salinity increase causes a decrease of growth/yield in more than the previous unity, indicating the salinity from which

growth/yield is more seriously affected and may be not convenient for cash crops. Thus, this point is a more refined criteria for defining a S_i . In the dataset of alfalfa (Fig 4 b) for instance, these two points occur approximately at 45.9 mM (0.092 as S/S_x) and 286.4 mM (0.574 as S/S_x). The interval between these points is the mostly linear part of the curve.

APPLICABILITY OF THE NEW EQUATION PROPOSED

Examples of fit quality in different crops

Eq. 5 has been tested with different experimental results, covering published works and new data sets from the authors. Regarding our own datasets three species were selected: tomato, muskmelon and quinoa. Emergency until full cotyledon expansion, in pots with quartz sand inside a controlled temperature and light chamber was recorded for tomato and muskmelon, while the emergency in pots under greenhouse conditions was recorded for quinoa. The treatments were defined by irrigating the pots with NaCl solutions at different electrical conductivities: 2 to 16 dS m^{-1} in tomato and muskmelon and 0 to 45 dS m^{-1} in quinoa.

In Fig. 4a we fitted experimental results on wheat (Rengasamy, 2010) to Eq. 5 (see Table 1) while the estimated points for the response curves of six different species published in a review by Munns and Tester (2008) are shown in Fig. 4b. Notably, curves full overlap with the simulated points and exhibit the accuracy and flexibility of Eq. 5.

For additional verification the equation was tested in a wider range of crops. In Table 1 parameters of Eq. 5 for different species are listed. The indicators of

fit quality (R^2 , absolute sum of squares and standard deviation of residues) showed that the equation related properly to the tested results (Table 1). However, when considering published results we handled only a single pool of data. As apparent benefit high R^2 was obtained due to the smooth s-shape in the series of points with 6 or more salinity treatments. But Rengasamy (2010) published a table with all replicates, enabling us for additional demand to Eq. 5 which resulted in accurate fits also (Table 1, Figure 4a). Conversely, in our results with muskmelon and tomato, regressions did not score the high R^2 of the first examples due to the space limitation inside the growth chamber, which restricted treatments to only 5 electrical conductivities, despite having 4 and 5 replicates (Fig. 4).

In general, this new equation fits similarly to van Genuchten equation as shown in Figure 5 using other known dataset from Steppuhn and Wall (1997) but has the advantages early exposed.

Conversion of parameters from the piecewise linear method

Data available in tables that summarize the parameters (S_i and the slope) in the piecewise linear method for different crops can be easily converted to the allometric equation presented here. It is just needed to create a data set in relative magnitudes using the two parameters of the linear method and adding points between the S_i and the zero-yield point; then this data set can be fit to the allometric Eq. 5. This way, a crop with $S_i = 2.5$ and slope = 0.08, similar to *Solanum* or cucurbit species (Ayers and Westcot, 1985, Grieve *et al.*, 2012) will result in a

conversion with $R^2 = 0.9988$ using the following parameters of Eq. 5: $a = 0.9840$, $b_s' = 4.211e-008$, $c = 1.041$ and $b_{sd} = -0.3333$.

Procedure for estimating a zero-yield point when data sets are incomplete

Frequently available good experimental results do not test crop responses at extreme salinity, close to the zero-yield point. This makes desirable to have additional points because sometimes regressions could not converge to estimate the parameters or the fit is ambiguous.

In these cases we propose to perform a linear regression for estimating a zero-yield point prior to the

regression with Eq. 5. For performing this procedure the experimental points at the lower salinity treatments should be eliminated in order to consider just the descending part as in the linear method. Then, an estimative zero-yield point can be added to the data set to proceed with the fit of Eq. 5.

Divisions for classifying crop tolerance to salinity using the allometric method

The classification of crop salinity tolerance is usually graphed by the piecewise linear method (Maas and Hoffman, 1977). Similar divisions can be made by the method exposed here (Fig. 6).

Table 1: Estimated parameters and goodness of fit using the allometric Eq. 5 in 16 different cases. Maximum used for relative S were: 27.9; 20.0; 39.6; 18.0; 14; 44.2; n/a; n/a; n/a; n/a; n/a; n/a; 14.1; 16.0; 16.0 and 45.0 dS m^{-1} , respectively.

Species	Author(s)	Parameter				R^2	Absolute Sum of Squares	Sy.x	n^*
		a	c	b_s'	b_{sd}				
Tomato	Osawa (1965)	0.9820	-0.02518	0.2479	-0.4965	0.9809	0.01288	0.080	6
Barley	Saini (1972)	0.8687	0.44200	0.7451	-2.6570	0.9993	0.00074	0.012	9
Bromegrass	McElgunn and Lawrence (1973)	0.8153	0.42710	1.5760	-2.8990	0.9990	0.00257	0.013	19
Cabbage (in sand)	Paliwal and Maliwal (1975)	0.6869	0.15100	1.3400	-0.2125	0.9959	0.001863	0.031	6
Wheat	Steppuhn and Wall (1997)	0.9421	0.04257	0.3575	-0.9252	0.9885	0.01536	0.047	11
Wheat in Hoagland solution	Rengasamy (2010)	0.6958	0.35050	2.4880	-3.0790	0.9974	0.007707	0.020	24
Alfalfa	Munns and Tester (2008)	0.514	0.64210	3.4840	-1.9300	0.9991	0.001202	0.012	24
Barley	Munns and Tester (2008)	1.520	0.01947	0.6384	-0.2107	0.9994	0.000629	0.009	(13)
Bread wheat	Munns and Tester (2008)	1.675	0.004791	0.6766	-0.1279	0.9994	0.00043	0.012	(11)
Rice	Munns and Tester (2008)	2.217	0.02209	0.4120	-0.3588	0.9980	0.001599	0.023	(7)
Saltbush	Munns and Tester (2008)	0.6369	-0.05013	0.9178	-0.4063	0.9367	0.02837	0.098	(7)
Tall wheatgrass	Munns and Tester (2008)	0.7841	0.05881	0.2165	-0.7456	0.9988	0.000632	0.011	(7)
<i>Jatropha curcas</i>	Díaz-López <i>et al.</i> (2012)	0.8311	-0.09418	0.3951	-0.6770	0.9985	0.00079	0.020	(9)
Tomato emergency biomass	Misle <i>et al.</i> (unpublished)	0.9723	1.755E-06	0.5433	-1.0270	0.7038	1.95500	0.274	6
Muskmelon emergency biomass	Misle <i>et al.</i> (unpublished)	1.0030	1.191E-06	0.2468	-0.7491	0.8465	0.69490	0.186	25
Quinoa emergency %	Misle <i>et al.</i> (unpublished)	0.9523	0.3133	0.5467	-4.090	0.9526	0,1751	0,091	20

* : numbers in brackets means that original data were not available and points were selected from the curve.

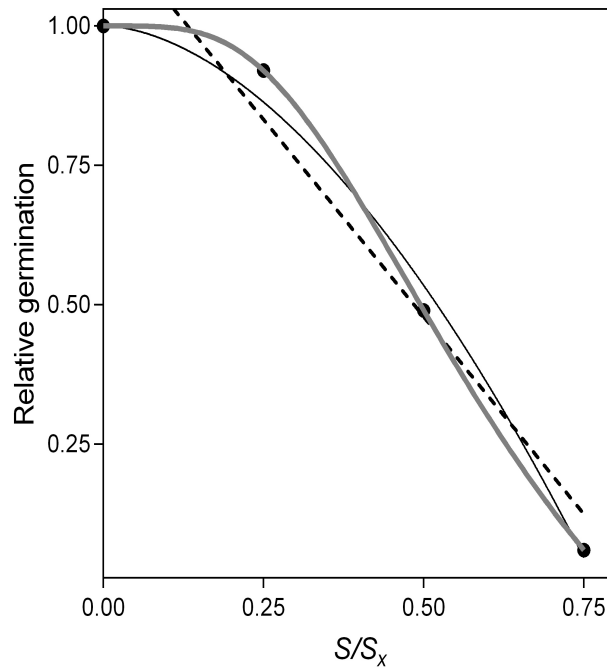


Figure 1: General shapes for hypothetical salinity response curves, linear, sigmoid (in grey) and power (Eq. 3) shapes. R^2 for power equation: 0.991. Original data of germination percentage at 20°C from Belaqqiz *et al.* 2009 (0.75 = 150 mM NaCl).

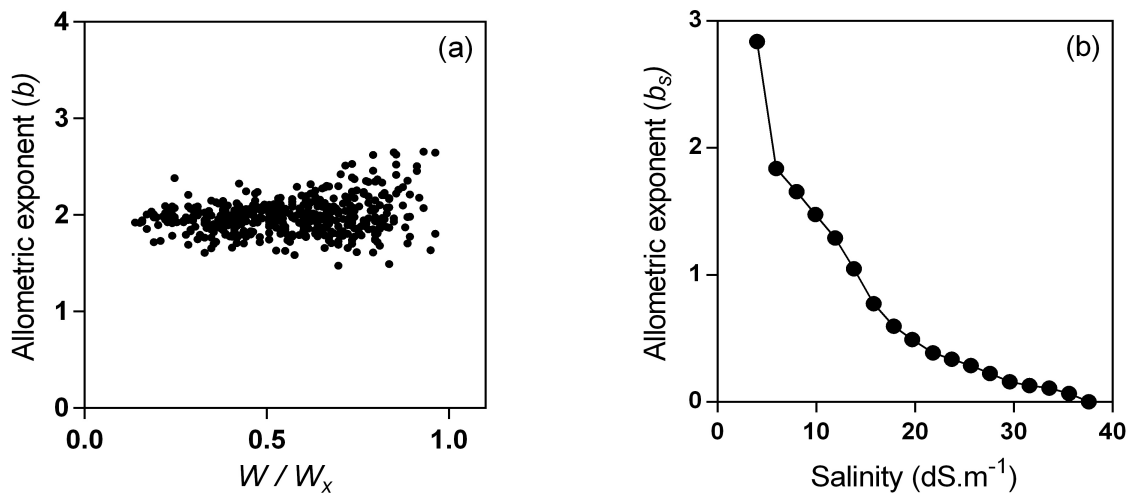


Figure 2: Plot of calculated (a) allometric exponent b in the relationship between leaf width and leaf area of muskmelon (elaborated from data of Misle *et al.* 2013) and (b) the hypothetical allometric exponent b_s in the relationship between biomass and salinity reveals a non-linear allometry (elaborated from salinity response data of McElgunn and Lawrence, 1973 in bromegrass).

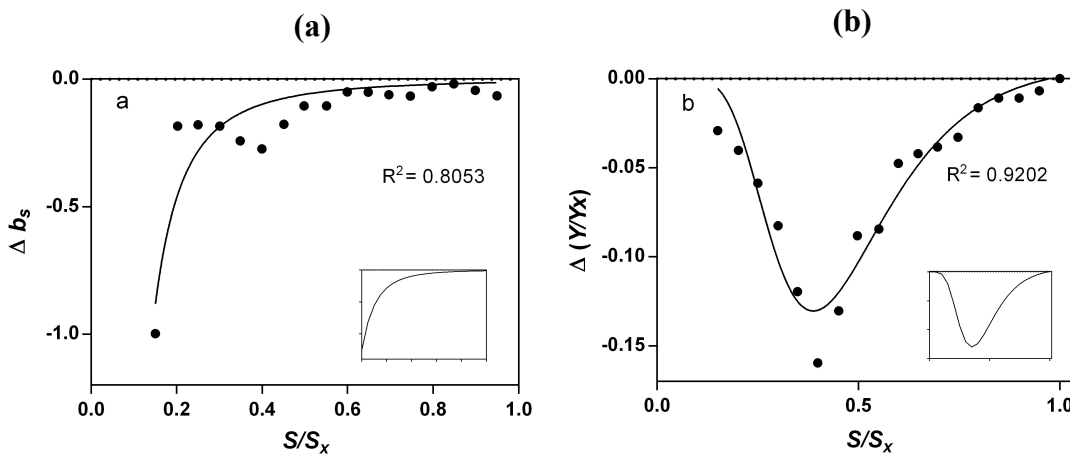


Figure 3: Derivatives of (a) the equation of the hypothetical allometric exponent b_s fitted (curve) to the calculated points Δb_s by Eq. 6 and (b) Eq. 5 fitted (curve) to the $\Delta(Y/Y_x)$ points by Eq. 7. The insets show the theoretical shapes of both derivatives. Original data of salinity response in bromegrass, from McElgunn and Lawrence (1973).

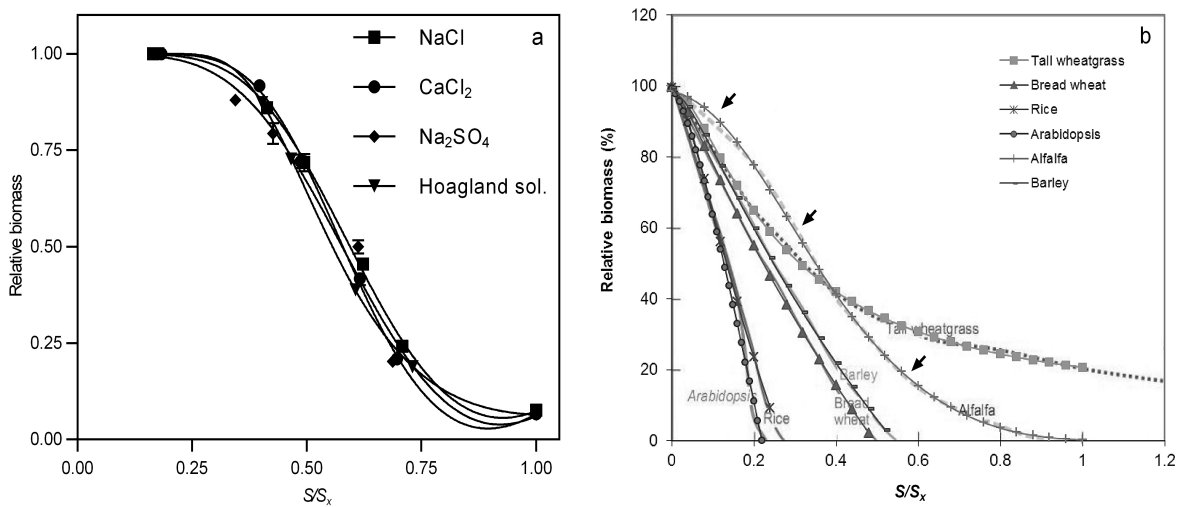


Figure 4: Salinity response curves of relative biomass in (a) wheat plants grown in pots irrigated with different solutions (Rengasamy, 2010; the curve is the fit of Eq. 5, vertical bars indicate the standard error using 4 replicates) and (b) an overlapping of Fig. 1 in Munns and Tester (2008) with our plot of the estimated points by Eq. 5 (Two species were not included to avoid the excess of curves). Arrows along the curve of alfalfa indicate the approximate location of the inflection point (central arrow) and points at which the slope equals unity.

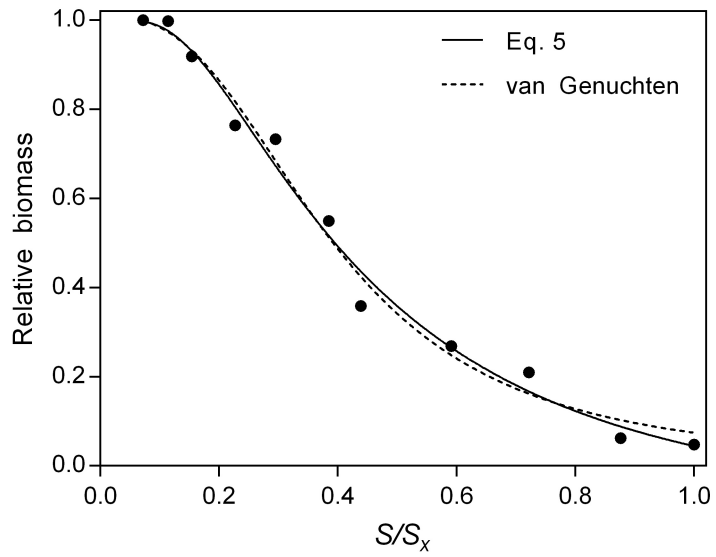
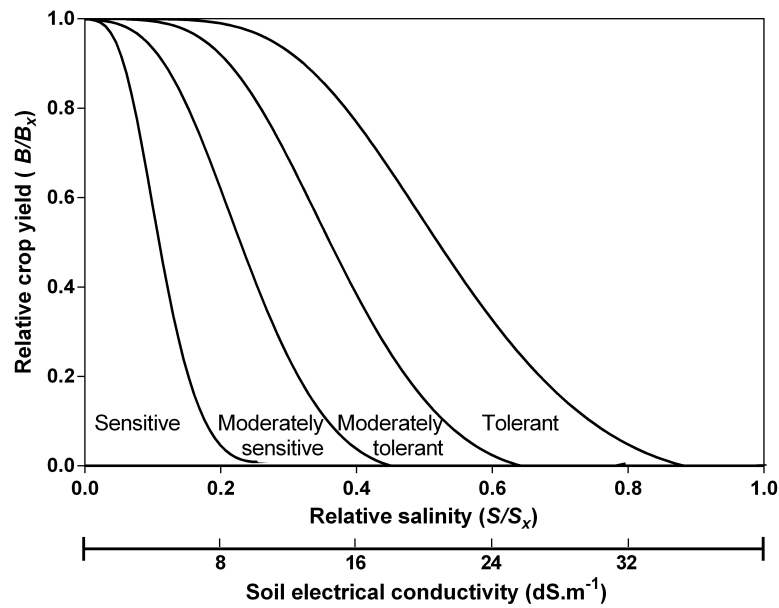


Figure 5: Fit of Eq. 5 and van Genuchten equation to results obtained by Steppuhn and Wall (1997) in Biggar spring wheat.



Parameter	Border curve by crop category			
	Sensitive	Moderately sensitive	Moderately tolerant	Tolerant
<i>a</i>	0.8713	0.4922	0.3433	0.2432
<i>c</i>	0.8315	0.7729	0.6899	0.5942
<i>b'_s</i>	4.2970	8.2930	8.7970	8.4230
<i>b_{sd}</i>	-12.270	-4.262	-2.995	-2.162

Figure 6: Divisions for classifying crops tolerance to salinity using the allometric Eq. 5 and according to Maas and Hoffman (1977). The table below the figure contains the fit values for the parameters required to define the border curve by crop category. Each curve in the graph was drawn by these parameters.

DISCUSSION

The piecewise linear method continues to be a very useful way to easily characterize crop response to salinity (Grieve *et al.*, 2012). But as research is focusing in a wider range of the response curve in plants, the tailing phenomenon analyzed by van Genuchten and Gupta (1993) becomes more important since, in their words, this part of the curve cannot be described with the linear threshold-slope model. In other terms, the region of validity of this model ends in the descendent quasi-linear part of the curve. The situation is comparable with the temperature response function in biological processes, a subject in which the degree-day method (linear) has coexisted with non-linear models for decades. The minimum of biological activity in poikilotherms by the linear method is the zero-point of the regression line on the x-axis, being so called the "base temperature" (Bonhomme, 2000). But physiological activity continues even at lower temperatures (Sharpe and DeMichele, 1977). This way, the linear method is still used for practical purposes but it is widely accepted that the nature of the biological response is non-linear (Sharpe and DeMichele, 1977; Yan and Hunt, 1999). As regards to salinity response at high salinities a comparable situation has been accepted from the work of van Genuchten (1983). However, in this equation an arbitrary criterion is needed for defining a zero-yield point since the curve is asymptotic regarding the salinity axis. Mathematically, in our equation a true zero point can be found, depending on the data sets. Each time an hypothetically true S_x at zero-

yield/growth ($B_y/B_x = 0$) is taken, obviously $S/S_x = 1$; but when experimental data are used directly for regression a $B_y/B_x > 0$ is obtained for $S/S_x = 1$ (Figure 3a); however the curve can be extrapolated to zero at a point $S/S_x > 1$, meaning that a non-true zero-yield point was formerly used as S_x . For illustrating the relevance of this aspect we analysed three works in which different cultivars were considered: Khan *et al.* (1997) in nine cultivars of rice; Essa (2002) in three cultivars of soybean and Chilo *et al.* (2009) in two cultivars of quinoa. The coefficient of variation (CV) among cultivars for the lowest and the highest salinity used was calculated for 4, 3 and 6 plant parameters, respectively. The mean CV for the lowest salinities was 9.4% while the mean CV for the highest salinities was 46.9%. This clearly highlights the importance of taking into account the final part of the curve when comparing cultivars, since their differences are accentuated. Of course, against our proposal is the need of just two parameters additionally to the maximum yield/growth in the earlier equations (Maas and Hoffman, 1977; van Genuchten, 1983) while we require four, but currently processing regressions for equations with two or more constants does not make a difference in time. As can be observed in Figs. 4 to 6 valuable aspects of Eq. 5 are i) that a maximum salinity point can be found (zero-yield) depending on the data sets ii) mathematically the curve will always have a maximum (or 100%) at minimum salinity (expected $c = 0$), when using relative salinity response, and iii) there is a meaningful inflection point. Some doubt regarding how to compare different datasets (species, cultivars) can emerge when offering figures

in relative magnitudes (S/S_x) but this was done for the analytical convenience of this proposal and when including the equation in any programmed media, even a spreadsheet, results can be directly calculated according to S_x .

Salinity affects plants in different ways such as osmotic effects, specific-ion toxicity and nutritional disorders (Lauchli and Epstein, 1990). The extent by which one mechanism affects plants over the others depends upon many factors including the species, genotypes, plant age, ionic strength and composition of the salinizing solution. When considering the characteristic curve, the response at low salinities decreases at increasing rates while salinity is increased until the inflection point, probably due to the increasing osmotic effect. As well known, the effect of salinity at low to moderate concentrations is due to the osmotic effect (Yadav *et al.*, 2011). Despite this effect continues progressively with higher salinity, the specific ionic effect would become relevant from the inflection point, causing the response curve to decrease exponentially with new increases in salinity, but as the growth is lesser, additional increase in ionic concentrations could be slowed down, giving an apparent relief to the increasing damages, until the death of plants. Munns (2004) highlighted that when relative growth rate is decreased, the ion concentration in shoot increases and whenever the ion uptake rate is decreased the ion concentration in shoot can decrease. Experiments using NaCl and PEG or mannitol at the same osmotic potential have demonstrated the higher harmful effects of saline treatments, revealing the ionic effect (Bernstein, 1975;

Shabala, 2000; Zhang *et al.*, 2012). Indeed, Munns and Tester (2008) summarized the characteristics of the osmotic and ionic effects, being the former fast and involved in the decrease of new growth, while the latter is slow and leads to the senescence of older leaves; according to them, at high salinity levels the ionic effect dominates over the osmotic effect. Moreover, Shabala (2000) concluded that the perception of the ionic and osmotic components of salt stress is probably associated to different ionic mechanisms. Recently, Zhang *et al.* (2012) confirmed these observations in a study on barley germination by which they determined in general that at low salinities the osmotic effect is mainly involved; at medium salinities the two effects act together, while at high salinities the ionic effect dominates the harmful action on the germination process. This sequence of observations indicates the gradual change from osmotic to ionic-dominated effects which should match, turning at the inflection point. Thus, evidence in the literature supports us in our proposition on the meaning and utility of the inflection point.

Despite the fascinating parallelism of the c_{50} (van Genuchten 1983) ($B/B_x=0.5$) with the inflection point criteria in some results such as in McElgunn and Lawrence (1973) where symmetry is evidenced by relativizing measures, in other cases such as the curve of alfalfa in Munns and Tester (2008) the inflection point occurs at $B_s/B_x \approx 0.6$. As analyzed in detail by Munns and Tester (2008), variations in osmotic tolerance and ionic tolerance can produce different patterns in the growth response to salinity stress. Thus, the inflection point criteria can have

more applicability in crop breeding as well as in crop management compared to the c_{50} . Some works have exposed the convenience of the c_{50} being more useful for the comparison between genotypes than the linear approach (Royo *et al.*, 2000; Steppuhn *et al.*, 2005). But the c_{50} is arbitrary, while the inflection point is a characteristic mathematical point of the curve, suggesting us that the same utility of c_{50} can be better fulfilled by our proposal.

The parameters of Eq. 5 can be subject of further study to test their dependence from external factors. The same species and cultivar has frequently been studied under different environmental conditions as soil or temperature (Paliwal and Maliwal, 1975; El-Dardiry, 2007; Gorai and Neffati, 2007; Belaqziz *et al.*, 2009). Usually apparent changes in the curve are revealed in these studies but it is necessary to separate the differing yield/growth observed at the lower salinities (different B_x 's) from the changes in the coefficients a , c , b_s ' and b_{sd} itself. For instance, two cultivars differing in salinity tolerance may differ mainly in a , while two different species differing in salinity tolerance may differ mainly in c . For determining such differences, salinity treatments should be increased (6 or more) in order to have reliable curves. This kind of studies can help to understand the relationships of the parameters in the Eq. 5 with the underlying mechanisms.

CONCLUSION

A new equation for determining the salinity response in crops was proposed sustained by the allometric approach. The function overpasses the linear allometry found in Misle and Garrido (2008) as

our analysis showed that if an allometric exponent exists, it is also salinity-dependent. Remarkable characteristics are: a maximum at minimum salinity, a maximum salinity point can be found (zero-yield) depending on the data sets and a meaningful inflection point, as well as the two points at which the slope of the curve equals unity. Thus, we propose a function able to follow the response curve of any crop with remarkable accuracy and flexibility. Our verification covered 16 examples of good fit; however, additional research is needed for further validation and inquiry on the physiological meaning of the parameters of Eq. 5.

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