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Mini-Review of Knowledge Gaps in Salt Tolerance of Plants Applied to Willows and Poplars

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Salt tolerance of agricultural crops has been studied since the 1940, but knowledge regarding salt tolerance of woody crops is still in its initial phase. Salt tolerance of agricultural crops has been expressed as the yield decrease due to a certain salt concentration within the root zone as compared to a non-saline control. The most well-known plant response curve to salinity has been a piece-wise linear regression relating crop yield to root zone salinity. This method used the hypothesis that crops tolerate salt up to a threshold after which their yield decreases approximately linearly. Critique to this method included its lack of sensitivity to dynamic factors such as weather conditions. As a result, other classification indices have been developed, but none is as well accepted as the threshold-slope model. In addition to a mini-review of the key salt tolerance studies, our objective was to classify salt tolerance levels of poplars and willows. Initial classification showed that salt tolerance of these genera ranged from sensitive to moderately tolerant.

Keywords: electrical conductivity, intensive forestry, *Populus*, phytoremediation, *Salix*, stress

Introduction

Salt stress has been widely studied in agricultural crops for many years, and irrigated agriculture has become more and more dependent on low quality saline water during the past three decades (Ayers and Westcot 1994; Katerji *et al.* 2003; Maas and Hoffman 1977). If no precautions are taken, salts will accumulate in the soil of the root zone over time. Salt accumulation depends on several factors; the amount and timing of precipitation and irrigation water quality are the most important factors. In areas that lack major precipitation events, irrigation with volumes above crop water requirements can cause salts to leach out of the root zone before they build up to levels that may negatively affect yields. Knowledge of crop salt tolerance levels is very important. A well accepted model is that agricultural crops tolerate root zone salinity up to a threshold level after which their yields decrease approximately linearly (Maas and Hoffman 1977). The greatest challenge, however, is that salt tolerance not only differs at the species level but also among cultivars within the same species (Katerji *et al.* 1992).

Initially salt research for agricultural crops focused on physical indicators such as growth and yield (Maas and Hoffman 1977), but more recently the focus has been shifted to physiological traits and to studies that combined both physical and physiological stress indicators (Isla, Aragüés and Royo 1998; Katerji *et al.* 2003; Katerji *et al.* 1992). Common physiological indicators include canopy temperature, pre-dawn leaf water potential, carbon isotope discrimination, evapotranspiration, and stomatal conductance (Isla *et al.* 1998; Jackson *et al.* 1981; Katerji *et al.* 2003). The combination of root zone salinity (electrical conductivity), physical stress indicators and physiological measurements within the same study will lead to better understanding of salt tolerance in crops.

For example, a salt tolerance classification that relates root zone salinity to crop yield would have more practical applications than one based on pre-dawn leaf water potential, but both classifications are needed for a better understanding of the salinity effect on crops (Katerji *et al.* 2003). Currently, for some agricultural crops the relative salt tolerance is known well enough to be used as a general guideline (Ayers and Westcot 1994), but for others information is still lacking (Shannon and Grieve 1999). Well-replicated studies that include an adequate range of salinities are required to gain useful salt tolerance data. These studies should report data on environmental conditions, growth stage and data related to water and salinity status of the root zone.

In recent years the phytoremediation potentials of willows and poplars have been studied (Mirck *et al.* 2005). Mitigation of saline wastewaters through the use of willows and poplars has been of special interest (Dimitriou, Aronsson and Weih 2006; Zalesny *et al.* 2007). Therefore it is of great importance to improve our knowledge of salt tolerance of short rotation woody crops (SRWC) relative to most other economically important species.

Because salt tolerance differs both at the species and at the cultivar level clonally propagated SRWC may represent

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a perfect model species. Both willows and poplars can easily be propagated from un-rooted or rooted cuttings that are genetically identical to the parent organism. Clonally replicated growth tests provide tremendous opportunities for developing relationships between growth and yield parameters and root zone salinity, as well as quantifying the degree of within species genetic variation in salt tolerance as a basis for clonal selection and breeding.

In this paper we summarize key research on salt tolerance of agricultural crops and initial research on salt tolerance of SRWC. The objectives for this mini-review were to develop a list of essential data that should be reported for salt studies and to classify the salt tolerance of SRWC.

Salt Tolerance Background

Soil and Water Salinity Measurements

Salt-affected soils result from a wide variety of factors such as soil type, slope, drainage, fertilizer application, climate and irrigation. The soil water salinity (EC_{sw}) is the average root zone salinity to which the plant is exposed, but because this is difficult to measure salinity measurements are normally done on a saturation extract and referred to as soil salinity (EC_e). This method is repeatable in the laboratory at a constant temperature of 25°C (Steppuhn, Genuchten and Grieve 2005). Although salts in solution will vary with how much dilution water is used, the EC_e is directly related to the concentration of soluble salts in the soil solution and for many soils the soluble salt concentration of the soil solution at field capacity is about twice that at saturation (Table 1; Ayers and Westcot 1994). Both the salinity of the soil water and that of the saturation extract are related to that of the water applied as well; if a leaching factor between 15 and 20% is used, then the soil water salinity (EC_{sw}) will be approximately 3 times that of the water applied (EC_w).

On most agricultural lands that require irrigation, irrigation water quality is the most critical and variable factor for plant growth. Irrigation water quality affects soil physical conditions that likely influence crop yield. A salinity problem exists when salts in the crop root zone reduce the water availability to the crop so yield is affected (Ayers and Westcot 1994). In addition, ion toxicities and/or deficiencies may result from high concentrations of certain ions and/or competition among specific cations or anions (Shannon and Grieve 1999). Although all dissolved solids contribute ions to the total concentration, the focus has been on the following constituents: calcium, magnesium, sodium, carbonate, bicarbonate, chloride, sulfate, nitrate, ammonium, phosphate, potassium and boron (Ayers and Westcot 1994).

Table 1. Relative values of salinity measurements (adapted from Ayers and Westcot 1994).

Salinity Measurement	Relative Value
Water salinity (EC_w)	1
Soil salinity (EC_e)	1.5
Soil-water salinity (EC_{sw})	3

The Food and Agricultural Organization (FAO) has developed a management tool consisting of four generalized criteria to assist in the classification of irrigation water quality (Table 2; Ayers and Westcot 1994; Bauder *et al.* 1994). The *first criterion* is the assessment of salinity hazard, which is measured as electrical conductivity of the water (EC_w) or total dissolved solids (TDS). The *second criterion* is to assess potential impacts on infiltration; the application of water with high Na to Ca and Mg content can decrease crop yield due to a decrease in infiltration, especially if salinity is low relative to sodium adsorption ratio (**SAR**) (Table 2). The imbalance between these ions can be quantified using the SAR:

$$SAR = \frac{[Na^+]}{\sqrt{([Ca^{2+}] + [Mg^{2+}])}} \quad (1)$$

Where Na^+, Ca^{2+} and Mg^{2+} are the concentrations of the respective ions in the soil solution, and [] refers to their concentration expressed in mmols L^{-1} (Sposito and Mattigod 1977). The decrease in permeability of low EC_w water is greater than that of high EC_w water. Therefore, a more accurate evaluation of the infiltration requires the concurrent use of EC_w and SAR (Table 2). Soil particle size will affect infiltration as well; soils with more than 30% expansive (smectite) clay content are most likely to show decreased infiltration at elevated SAR. The *third criterion* quantifies the acidity/basicity of the irrigation water through pH measurements; the normal pH range for irrigation water is between 6.5 and 8.4 (Ayers and Westcot 1994). Low pH values may limit availability of plant nutrients (Hoeft *et al.* 2000; Jones and Jacobsen 2005). Values of pH above 8.5 are often caused by high HCO_3 and carbonate (CO_3) concentrations. High carbonates cause Mg and Ca to become insoluble, which could intensify the impact of high SAR water (Bauder *et al.* 1994).

Finally, the *fourth criterion* is specific ion toxicity. Specific ions such as Cl, Na, B and NO_3 should be tested (Table 2; Ayers and Westcot 1994). Both Cl and Na are the primary ions that can be absorbed through the leaves and cause leaf burn. In addition, Cl is a mobile anion and moves with the soil-water, which is taken up by the crops. Within the crops it will accumulate in the leaves. Symptoms of Cl toxicity are necrosis of the leaves and early leaf drop (Ayers and Westcot 1994). Sodium often reaches a toxic concentration before other ions do, possibly because it uses binding sites for K in enzymes for cellular functions (Palmer 1937). Symptoms of Na toxicity (especially for woody species) include leaf burn and dead tissue at the outside edges of leaves. Symptoms first appear on the older leaves, starting at the outer edges. Boron toxicity is a risk for some well and groundwater, especially near geothermal areas and earthquake faults (Ayers and Westcot 1994). If wastewaters such as landfill leachate are used, then B toxicity can be an issue as well (Zalesny and Bauer 2007; Zalesny *et al.* 2008). High NO_3 concentrations can also potentially be harmful, with effects such as excessive vegetative growth, lodging and delayed crop maturity, but can be prevented through proper

Table 2. Guidelines for interpretation of irrigation water quality (Adapted from Ayers and Westcot 1994; Bauder 1994).

Irrigation Criterion	Measurement		Limitations for Use		
			None	Slight to Moderate	Severe
1) Salinity hazard (affects crop water availability)					
	EC_w (dS m^{-1})		<0.7	0.70–3.0	>3.0
	TDS (mg L^{-1})		<450	450–2000	>2000
2) Sodium hazard (affects water infiltration into the soil; SAR and EC_w evaluated together)					
SAR:	0-3	EC_w (dS m^{-1}):	>0.7	0.7–0.2	<0.2
	3-6		>1.2	1.2–0.3	<0.3
	6-12		>1.9	1.9–0.5	<0.5
	12-20		>2.9	2.9–1.3	<1.3
	20-40		>5.0	5.0–2.9	<2.9
3) Acidity/basicity (affects nutrient availability)					
	pH		Normal range 6.5 - 8.4		
	HCO_3 (mg L^{-1})		<90	90–500	>500
4) Specific Ion Toxicity (species dependent) (affects plant health)					
	Cl (mg L^{-1})		<100	175–700	>350
	Na (mg L^{-1})		<46	46–460	>460
	B (mg L^{-1})		<0.7	0.7–3.0	>3.0
	NO_3 (mg L^{-1})		<5	5–30	>30

fertilization and irrigation management. Water quality problems are complex and a combination of problems may affect crop production more severely than a single problem. If multiple problems are encountered, they will be easier understood when considered individually.

The relative effect of specific ions in the root zone solution in comparison with decreasing osmotic potential or increasing electrical conductivity has been debated. One of the concerns is related to the anion dominance. A previous study concluded that Na_2SO_4 caused more injury to cereals than $MgSO_4$, but less than NaCl (Magistad *et al.* 1943), but another study found little difference in yields of garden beets, wax beans, or carrots when Cl and SO_4 salts were converted to osmotic pressures (Warne *et al.* 1990). In addition, *Chenopodium rubrum* L. plants showed greater growth when subjected to Cl solutions as compared to plants that received SO_4 treatments (Warne *et al.* 1990).

Salinity Management

Salts present in the irrigation water are likely to build-up in the soil over time; crops remove the majority of the applied water, but leave most of the salt behind in the shrinking volume of soil water. To prevent yield decreases of the crop the salt can be leached from the root zone through over irrigation. The fraction of applied water that passes through the root zone and percolates below is called the leaching fraction (LF). The concentration of salts in the soil decreases with increased leaching fraction and increases with depth in the root zone (Ayers and Westcot 1994).

Salt varies from approximately that of the irrigation water near the surface to many times that of the applied water at the bottom of the rooting zone. It takes time for salts to accumulate in the root zone. If good quality irrigation water is used it can be as much as two years before salt concentrations reach damaging concentrations. In addition, the later in the growing season salts reach critical concentration the lesser crop yields will be affected. Therefore it is expected that if salts are leached out during the dormant season through rainfall and/or pre-planting irrigation, little to no leaching would be required during the growing season.

Many salinity problems are also associated with shallow ground water tables (within two meters of the surface). Salts accumulate in this water table and move to the surface through capillarity. Adequate drainage of shallow water tables will make salinity manageable (Ayers and Westcot 1994). Maintaining adequate soil-water availability and drainage are equally important for long-term salinity control.

Salt Tolerance Classification

Crops respond differently to salts; there is an 8 to 10-fold range in salt tolerance of agricultural crops. Currently, general salt tolerance guidelines are available for most agricultural crops (Ayers and Westcot 1994). When it comes to soil salinity, traditionally crop salt tolerance has been expressed as the yield decrease for a given level of soluble salts in the root medium as compared to non-saline controls. When specific ion toxicities are not considered growth reduction is primarily related to osmotic potential of the soil solution in the root zone (Maas and Hoffman 1977). The most common plant response function to salinity has been a piece-wise linear regression (threshold-slope model) relating yields to root zone salinity (Ayers and Westcot 1994; Maas and Hoffman 1977). For this threshold-slope model two parameters are essential for the expression of salt tolerance: 1) the maximum allowable soil salinity without yield reduction, and 2) the percentage decrease per unit salinity yield increase. Relative yield (Y_r), after the soil salinity exceeds the threshold (t), $EC_e > t$, can be calculated according

to the following equation:

$$Y_r = 100 - s(EC_e) - t \quad (2)$$

Where t is the salinity threshold, in dS m^{-1}, s is the% yield decrease per unit salinity increase and EC_e is the saturation extract in dS m^{-1} (Maas and Hoffman 1977). Division boundaries for salt tolerance ratings are shown in Figure 1. Standard soil salinity is measured in EC_e or EC_{sw}. If only the Cl concentration of a solution is known it can be converted into EC_{sw} according to the following equation:

$$ln\,EC_{sw} = 0.824 ln\,Cl - 1.42 \quad (3)$$

This equation converts Cl (in mmol L^{-1}) into EC_{sw} (dS m^{-1}), which can be divided by two for conversion into EC_e (Van Hoorn *et al.* 1993), assuming that EC_{sw} is twice EC_e (Ayers and Westcot 1994).

Before the introduction of the threshold-slope function by Maas and Hoffman (1977) the general practice was to use C_{50}, defined as the electrical conductivity of the root zone salinity resulting in a relative yield of 50% (Steppuhn *et al.* 2005). Many factors, e.g. temperature and soil type, influence the yield of crops in addition to the response to increasing root zone salinity. Therefore, the single-value C_{50} would seem insufficient. The shape of the yield response before reaching 50% of the relative yield can be of interest as well, therefore C_{50} can be enhanced with a term that dictates this shape for an improved Salinity Tolerance Index (STIndex):

$$ST\ Index = C_{50}(1 + s) \quad (4)$$

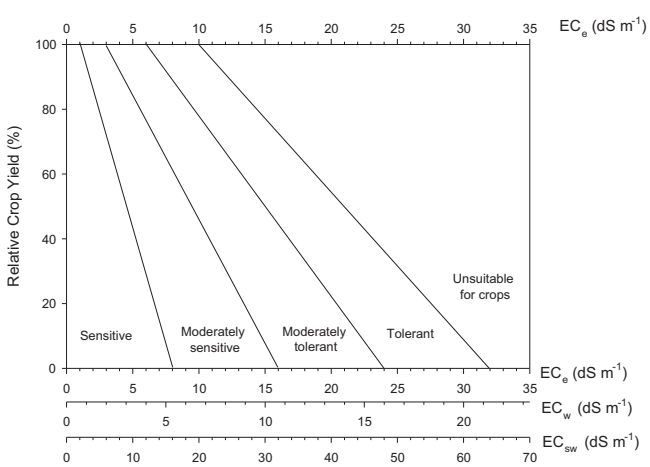

Fig. 1. Divisions for classifying plant tolerance to salinity, based on a comparison of yield at elevated salinity compared to low salinity controls. On the x-axis soil salinity (EC_e), water salinity (EC_w) and soil-water salinity (EC_{sw}) are used to improve compatibility with previously published salt tolerance literature (Adapted from Maas and Hoffman 1977).

Where C_{50} is the EC_e at relative yield 50%, and s represent the steepness of the slope. Both components can be calculated as regression constants (Steppuhn *et al.* 2005).

The Maas-Hoffman model and the C_{50} have been useful for a first level ranking of crop salt tolerance. It is common knowledge that plants are exposed to multiple stresses at the same time. For example, drought, heat and salt stress often happen simultaneously. Therefore, it is questionable whether the correlation between whole plant response and root zone salinity is appropriate as a salt tolerance classification method, because growth is affected by climatic and soil factors as well. Past experiments have shown the sensitivity of the threshold value to weather conditions; periods of warm dry weather resulted in higher crop sensitivity to salinity in broad bean (Katerji *et al.* 2003), and the threshold value based on the root zone salinity increased by 92% due to a 7°C temperature increase to the root temperature, when a model that did take environmental factors into account was invariant (Dalton, Maggio and Piccinni 1997).

A model that is less sensitive to these environmental variables and includes physiological measurements would improve our understanding of physiological processes that play a role in plant salt tolerance (Dalton *et al.* 1997; Maggio *et al.* 2011). The basic requirements of an effective dynamic salinity stress index (SSI) are that: 1) it correlates with plant response in a saline environment; and 2) it is quantitatively coupled to the dynamic processes that take place in the plant-soil-air continuum (Dalton *et al.* 1997). The dynamic index might be composed of two components: an expression for the transport of the dominant salinizing ion to the shoot and a measure of shoot growth rate. While a dynamic SSI might be superior to a static root zone classification, the latter is more straightforward and practical and no complete classification of crops according to the dynamic SSI has been made.

Crop salt tolerance has been studied using physiological indicators as well. Rarely though have studies combined the use of physical (growth and yield) and physiological indicators. Common physiological indicators are pre-dawn leaf water potential, stomatal conductance and canopy temperature (Katerji *et al.* 1992). The concurrent use of physical and physiological indicators is expected to result in more reliable salt tolerance knowledge. For example, Katerji *et al.* (2003) used both pre-dawn water potential and root zone soil salinity to classify salt tolerance of ten crops.

Increased salinity reduces the availability of water to the plant, which is reflected by the leaf water potential. The concept of the Water Stress Day Index (WSDI) is that it quantifies the stress imposed on a crop during the growing season (Katerji *et al.* 2000). They found that because pre-dawn water potential excludes the effects of evaporative demand, this would classify the crops as if they were grown under the same climatological circumstances. In practice the use of the WSDI remains limited, due to the lack of a simple and sufficiently sensitive method.

The next breakthrough in standardizing salinity research was the introduction of the plant model systems that linked physiological observations of plant salt tolerance and genetics (Maggio *et al.* 2011). Current knowledge, gained through model species such as *Arabidopsis thaliana*, indicates that

Table 3. Support information required as part of salt tolerance experiments. Information was compiled from Ayers and Westcot 1994; Grattan and Grieve 1999; Katerji *et al.* 1992; Maas 1993; Shannon and Grieve 1999; Shelhevet *et al.* 1994; Steppuhn *et al.* 2005.

Component	Environmental Interactions	Notes
Soil:	• Fertility	At greater soil fertility larger (relative) yield reduction
	• Structure/texture	Influence extrapolation of salt tolerance data to field condition (EC_{sw}:EC_e)#####
		Influence infiltration, water holding capacity, water content at saturation versus at field capacity
	• Soil water elements and pH	Soil water elements vary in time and space (depth)
Water:	• Irrigation water elements, pH	Realistic ion ratios and their availability are important (Na^+, Ca^{2+}, Mg^{2+}, Cl^-, SO_4^{2-}, HCO_3^-)
	• Leaching factor	What leaching is required to sustain growth?
	• Irrigation method, frequency, time of day	Irrigation can affect oxygen rate
	• Water table	Shallow water tables affect root growth and salt distribution
Climate:	• Temperature	High temperatures increase crop stress levels
	• Relative humidity	High relative humidity may decrease crop stress levels
	• Precipitation	Precipitation has no direct effect on salt stress, but increases leaching
Plant:	• Growth stage	Seedling stage is often more sensitive to salinity
	• Root distribution	Where is the maximum water uptake?
	• Salinity distribution within root zone	Mean salinity within rooting depth can be used as approximation

genetic variation defining salt tolerance levels control four major processes: 1) water/ion homeostasis; 2) hormone regulation and metabolic adjustment; 3) growth control; and 4) injury control (Bressan, Bohnert and Zhu 2009).

Essential Support Information

Crops have been tested for salt tolerance under many physical and environmental conditions, which makes comparative analyses of results challenging. Many of these factors affect crop tolerance to salinity, but unfortunately in many experiments proper documentations of these factors is lacking. Salt experiments can be carried out in greenhouses, lysimeters and the field with a variety of "substrates", ranging from sand to heavy clay to hydroponic solutions. If a soil substrate is used it can range from a marginal to a fertile soil. Environmental conditions can vary greatly as well; experimental locations can range from cold and humid climates to hot and dry. Testing for crop salt tolerance involves the separation of above mentioned factors from the salinity treatment. This is commonly done by comparing the salt treatments to a non-saline control resulting in a relative yield, but the control might be nutrient deficient causing unrealistic data (Grattan and Grieve 1999). Methods of accounting for such differences have been used (Flowers 2004; Zalesny *et al.* 2007). In order to improve the comparability and reliability of various salt tolerance experiments the reporting of support information is required (Table 3). This is especially important if the Maas-Hoffman model is used for classification as the root zone salinity measurements do not account for environmental factors. A combination of standard physical (crop growth and yield) and physiological measurements should be collected as well; physiological measures tend to have faster responses and may be better predictors of stress (Table 4).

Salt Classification of Woody Crops

Although salt tolerance has been evaluated extensively for many food crops (Ayers and Westcot 1994; Grattan and Grieve 1999; Maas 1993), few studies have classified the salt tolerance of woody crops. Studies that assessed woody crop salt tolerance show a similar lack of support information as their agricultural counterparts (Table 5). For example, nursery soil was used in two cases, but no fertility information was listed and none of the studies listed pH values of the substrate or the irrigation water. In addition, information was lacking

Table 4. Common growth, yield, and physiological measurements that are carried out during salt tolerance experiments with agricultural crops (Fung *et al.* 1998; Katerji *et al.* 1992; Katerji *et al.* 2003; Mirck and Volk 2010; Van Hoorn *et al.* 1993).

Measurement	Type of Measurement	Response Time
Yield, biomass	Growth and yield	Slow
Leaf area, leaf biomass	Growth and yield	Intermediate
Pre-dawn leaf-water potential	Physiology	Fast
Stomatal conductance	Physiology	Fast

Table 5. Support information from six salt tolerance experiments during which both poplar and willow were tested.

Characteristic	Measure	Steppuhn *et al.* 2008	Hangs *et al.* 2011	Shannon *et al.* 1999	Chen *et al.* 2003	Chen *et al.* 2002	Fung *et al.* 1998
Soil	Fertility		NO_3, P, K, SO_4, Ca, Mg, Na, Cl, SAR, pH		Na, Cl	Na, Cl	
	Structure	Sand	Loam	Sand	Nursery soil	Nursery soil	Sand
	Volumetric Water Content	31%		34%			
	Control		non-saline				
	Treatment		slightly saline, moderately saline, severely saline				
Water	Type	Fertilizer	Tap water?	Fertilizer	Fertilizer	Fertilizer	Fertilizer
	Elements	known		known	known	known	known
	Control	50% Hoagland's + Ca, Mg		Hoagland's	Hoagland's	Hoagland's	Hoagland's
	Treatment	50% Hoagland's + $CaCl_2$, $MgSO_4$, Na_2SO_4, NaCl		Hoagland's + $MgCl_2$ (main salt) and Ca, Na	Hoagland's + 2 steps: 100 mM NaCl; 200 mM NaCl	Hoagland's + 300 mM NaCl	Hoagland's + 86 or 172 mmol L-1 NaCl
	Extra treatment			3 levels B, 3 levels Se			
	Irrigation	5 per d	1 per d	1 per d	1 per wk	1 per wk	1 per wk
Climate	Temp (N:D)	14:23°C	18:22°C	16:30°C	20:30°C	20:30°C	
	Radiation	7.9 kJ m^{-2} min^{-1}	400 μmol m^{-2} s^{-1}		100-800 μmol m^{-2} s^{-1}	100-1000 μmol m^{-2} s^{-1}	450-1600 mmol m^{-2} s^{-1}
	Relative Humidity		70%		50-90%		
Plant	Material	Cuttings	Cuttings	Cuttings	Rooted ex-plants	Seedlings/ cuttings 1 yr	Cuttings
	Initial growth	40 d	0 d	91 d	3 months	2 months	3 months
	Treatment phase	49 d	60 d	30 d	20 d	30 d	21 d
	Species/ # Cultivars	Poplar/ 4	Willow/ 37	Poplar/ 8	Poplar/ 2	Poplar/ 3	Poplar/ 3
Type of Study		Greenhouse	Growth chamber	Outdoor lysimeters	Greenhouse	Greenhouse	Open greenhouse

Table 6A. Treatment information and measurements from six salt tolerance experiments during which both poplar and willow were tested.

Characteristic	Measure	Units	Steppuhn *et al.* 2008						Hangs *et al.* 2011				Shannon *et al.* 1999						
Treatment	EC_e	dS m^{-1}	1.0	2.0	4.0	7.0	11.0	15.5	0.8	3.6	5.0	8.0	0.8	1.8	2.8	3.8	5.1	6.0	7.0
	EC_w	dS m^{-1}	0.7	1.3	2.7	4.7	7.3	10.3	0.5	2.4	3.3	5.3	0.6	1.2	1.8	2.6	3.4	4.0	4.7
	EC_{sw}	dS m^{-1}	2.0	4.0	8.0	14.0	22.0	31.0	1.6	7.2	10.0	16.0	1.7	3.6	5.5	7.7	10.2	12.0	14.1
Measurement	Growth and Yield	cm	Height						Height										
		g	New shoot biomass						Biomass (leaf, shoot, root)				Biomass (leaf, shoot, root)						
		cm^2 cm^{-2}							Leaf area										
	Physiological	μg cm^{-2} s^{-1}																	
		Mpa																	
		μmol m^{-2} s^{-1}																	
		s cm^{-1}																	
Threshold	EC_e	dS m^{-1}	2.3–4.2						3.6–5.0				2.8–3.8						
C_{50}	EC_e	dS m^{-1}	3.3–5.9						5.0–7.0				3.9–5.3						

Table 6B. Treatment information and measurements from six salt tolerance experiments during which both poplar and willow were tested.

Characteristic	Measure	Units	Chen *et al.* 2003				Chen *et al.* 2002				Fung *et al.* 1998		
Treatment	EC_e	dS m^{-1}	0.1	1.8	2.8	0.2	3.8	5.8	7.3	8.7	0.0	2.4	4.8
	EC_w	dS m^{-1}	0.1	1.1	1.8	0.1	2.5	3.9	4.9	5.8	0.0	1.6	3.2
	EC_{sw}	dS m^{-1}	0.2	3.5	5.3	0.3	7.6	11.6	14.6	17.4	0.0	4.8	9.6
Measurement	Growth and Yield	cm						Height				Stem height	
		g						Biomass (leaf, shoot, root)					
		$cm^2\ cm^{-2}$						Leaf area				Leaf area	
		mm										Diameter	
	Physiological	$\mu g\ cm^{-2}\ s^{-1}$						Transpiration					
		Mpa										Pre-dawn water potential	
		$\mu mol\ m^{-2}\ s^{-1}$										Net photosynthesis	
		s cm^{-1}										Stomatal resistance	
Threshold	EC_e	dS m^{-1}						4.1				<2.4	
C_{50}	EC_e	dS m^{-1}						5.0–5.8				>4.8	

Table 7. Support and treatment information to test productivity constraints of willow to saline landfill leachate.

Characteristic	Measure	Units	Stephens *et al.* 2000						
Soil	Type		Sandy loam						
	Elements								
	Volumetric Water Content								
	Control								
	Treatment								
Water	Type		Water						
	Elements		Cl, Na, Mg, K, Ca						
	Control		Water						
	Treatment		Cl, Na, Mg, K, Ca (422, 352, 282, 211, 141, 70 mmol Cl L^{-1} (added at beginning)						
	Irrigation		1 per d (precipitation as well)						
Climate	Temp (N:D)								
	Radiation								
	Relative Humidity								
Plant	Material		rooted cuttings						
	Initial growth		3 months						
	Treatment phase		21 d						
	Species/ # Cultivars		willow/ 1						
Type of Study						Outside pots			
Treatment	EC_e	dS m^{-1}	0.0	4.0	7.2	10.0	12.7	15.2	17.6
	EC_w	dS m^{-1}	0.0	2.7	4.8	6.6	8.4	10.1	11.7
	EC_{sw}	dS m^{-1}	0.0	8.0	14.3	19.9	25.3	30.3	35.2
Measurement	Growth and Yield	cm							
		g	Biomass (leaf, shoot, root)						
		cm^2 cm^{-2}							
	Physiological	μg cm^{-2} s^{-1}	Transpiration						
		Mpa							
		μmol m^{-2} s^{-1}							
		s cm^{-1}							
Threshold	EC_e	dS m^{-1}	<4.0						
C_{50}	EC_e	dS m^{-1}	10–12.7						

regarding elements in the irrigation water or associated pH values (Hangs *et al.* 2011). One or multiple weather variables were lacking as well; most experiments did have information regarding temperatures, but relative humidity data were often lacking.

Salt treatment levels, the way the treatments are induced, and measurement methods to identify salt tolerance often vary among experiments. The six studies that tested salt tolerance of poplars (*Populus* spp.) and willows (*Salix* spp.) had two to seven treatment levels (Table 6A/B). Five of these treatments were induced by adding irrigation water with different salinity levels, and one consisted of different salinity soils. All six studies used growth and yield measurements to identify salt tolerance levels and three studies also included physiological measurements. Like agricultural crops, woody crops differ in their tolerance to salts. Therefore relative yield can be correlated to soil salinity in a similar fashion. Five of the six studies focused on poplars and one on willow, for all of them threshold values could be calculated and for five estimations of C_{50} were possible as well (Table 6A/B). The threshold values all ranged between 2.3 and 4.1 for poplar and between 3.6 and 5.0 for willow, which would mean that both poplars and willows are either moderately sensitive or moderately tolerant to salts (Figure 1). When considering the C_{50} values the range for poplars was 3.3 to 5.9, which would categorize them sensitive to moderately sensitive and for willows this was 5.0 to 7.0, which would categorize them moderately sensitive.

One of the applications for knowledge of salt tolerance of woody crops is for their use as vegetation filters to treat saline waste waters. Many studies have been carried out to test the tolerance of woody crops to waste waters such as landfill leachate (Cureton, Groenevelt and McBride 1991; Ettala 1988; Stephens, Tyrrel and Tiberghien 2000). Unlike the studies described in the previous paragraph, most of these studies are carried out in the field and often even on top of landfills. As a result it is more difficult to control all factors that affect salt tolerance. Usually the main objective is not to test the woody crops for their salt tolerance, but to solve a pollution problem in a more sustainable fashion. Many wastewater studies often have the objective to reduce the volume of leachate due to evapotranspiration aided by woody crops and commonly use tap water as a control. This tap water control commonly lacks required macro- and micro nutrients. Due to the fact that the control treatment in these experiments does not contain optimum concentrations of all nutrients higher-than-actual salt tolerances may be observed (Table 7). This makes it difficult to use these studies as a reliable guideline for salt tolerance of woody crops.

Conclusion

The comparison of studies that assessed salt tolerance among either agricultural or woody crops can be facilitated through improved similarity of the study facilities. This mini-review article reveals that the majority of salt tolerance studies take place under different environmental conditions, measure a variety of growth and yield measurements and sometimes included plant physiological effects of salt stress as well. In addition to various conditions, information that would be required to adequately compare different studies is often lacking. Therefore, one objective of this mini-review was the development of a list with standard support information and an additional table with commonly used growth and physiological measurements (Tables 3, 4).

When compared to agricultural crops, very little research has been done to test salt tolerances of woody crops. This review summarized the data from poplar and willow salt studies that used nutrients in optimum concentrations for the trees as the control treatments. This revealed that both woody crops have salt tolerances that range from sensitive to moderately tolerant. While this can be a rough guideline for future studies, a minimal number of cultivars were tested. From agricultural crops we know that not only species, but also cultivars differ in their tolerance to salts (Katerji *et al.* 1992). While this can be seen as a challenge it can be considered an opportunity as well, as the wide genetic variation among poplars, but especially among willows can result in the discovery of more salt tolerant woody crops.

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