European Journal of Agronomy 99 (2018) 51–61

Contents lists available at ScienceDirect

European Journal of Agronomy

journal homepage: www.elsevier.com/locate/eja

Crop-weed interactions in saline environments

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ARTICLE INFO

Keywords:
Salinity
Weeds
Abiotic stress
Crop management
Salt stress

ABSTRACT

Soil salinization is one of the most critical environmental factors affecting crop yield. It is estimated that 20% of cultivated land and 33% of irrigated agricultural land are affected by salinity. In the last decades, considerable effort to manage saline agro-ecosystems has focused on 1) controlling soil salinity to minimize/reduce the accumulation of salts in the root zone and 2) improving plants ability to cope with osmotic and ionic stress. Less attention has been given to other components of the agro-ecosystem including weed populations, which also react and adapt to soil salinization and indirectly affect plant growth and yield. Weeds represent an increasing challenge for crop systems since they have high genetic resilience and adaptation ability to adverse environmental conditions such as soil salinization. In this review, we assess current knowledge on salinity tolerance of weeds in agricultural contexts and discuss critical components of crop-weed interactions that may increase weeds competitiveness under salinity. Compared to crop species, weeds generally exhibit greater salt tolerance due to high intraspecific variability, associated with diverse physiological adaptation mechanisms (e.g. phenotipic plasticity, seed heteromorphism, allelopathy). Weed competitiveness in saline soils may be enhanced by their earlier emergence, faster growth rates and synergies occurring between soil salts and allelochemicals released by weeds. In the future, a better understanding of crop-weed relationships and molecular, physiological and agronomic stress responses under salinity is essential to design efficient strategies to achieve weed control under altered climatic and environmental conditions.

1. Introduction

Soil salinization is one of the most critical environmental factors affecting crop yield. Salinization of agricultural land is a consequence of climate change, competition for natural resources due to an increasing world population, and inadequate irrigation management (Rengasamy, 2006; Godfray et al., 2010). It is estimated that 20% of cultivated land and 33% of irrigated agricultural land are affected by salinity, a phenomenon that is expanding at an annual rate of 10% (Shrivastava and Kumar, 2015). This problem has been observed not only in the driest areas of the world but also in temperate regions, where there is increasing concern for secondary salinization due to seawater intrusion and consequent use of brackish waters for irrigation. Improving crop management under limited resources and environmental constraints is a primary target of agriculture specialists who need to respond to an increasing demand for food (FAO, 2009). Problems associated with soil salinization include, at the soil level, a reduction in water infiltration and soil hydraulic conductivity, surface crusting, soil structure degradation and overall loss of arable lands (Warrence et al., 2002). At the plant level salinity causes osmotic stress due to high salt concentration in the soil water surrounding the root zone, followed by ionic stress due to the accumulation of Na^+ and Cl^- in plant tissues, leading to decreased growth and yield (Munns and Tester, 2008). In recent decades, management of saline agro-ecosystems has focused on 1) controlling soil salinity to minimize/reduce the accumulation of salts in the root zone (Shrivastava and Kumar, 2015) and 2) improving plants ability to cope with osmotic and ionic stress (Jamil et al., 2011). Less attention has been given to other components of the agro-ecosystem such as the soil microbiome (de Souza Silva and Fay, 2012; Canfora et al., 2017), soil mesofauna (Thakur et al., 2014; Pereira et al., 2015), and weed populations (Li et al., 2011; Hakim et al., 2011; Ma et al., 2014), which also respond to soil salinization and indirectly affect plant growth and yield. Among these, weeds play a central role. Weed control contributes for around 10% of cultivation costs in agriculture, but this cost can vary greatly depending on weed species, cultivation systems and locations (Bastiaans et al., 2000; Zimdahl, 2004). Weeds represent an increasing challenge for crop systems because, compared to cultivated crops, they have conserved higher genetic resilience and adaptation ability to adverse environmental conditions (Clements et al., 2004; Chen et al., 2015; Mitchell et al., 2016; Lu et al., 2016). The genetic diversity that

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https://doi.org/10.1016/j.eja.2018.06.009
Received 29 January 2018; Received in revised form 10 May 2018; Accepted 26 June 2018

differentiates *high yielding* performant cultivated crops from wild weed species has already been shown to increase the competitiveness of the latter in several agricultural contexts (Patterson, 1995; Concenço et al., 2012). Moreover, the consequences of climate change, including the decline in quality and abundance of natural resources, may further alter crop-weed relationships and consequently affect crop yield (Peters et al., 2014).

In this review we assess current knowledge on salinity tolerance of weeds and discuss critical components of crop-weed interactions that may increase weeds competitiveness and spread under salinity. The ultimate goal was to highlight functional traits and responses which could allow us to better understand how increasing salinity may affect crop-weed competition and how weed management should best evolve to cope with these constraints in the future.

2. Salinity tolerance of weeds and crops

Plant responses to salinity can be assessed based on different criteria depending on the specific research and agronomic objectives. For instance, plant survival vs. adaptation to high root-zone salinity implies different physiological mechanisms and consequent effects on crop yield (Rodriguez et al., 2010; Ali and Yun, 2017). Also, the relevance of stress adaptation responses will depend on agricultural contexts and/or transitory (seasonal) vs. long-term salinization (Maggio et al., 2004; De Pascale et al., 2012). A growth model to describe the yield response of plants to increasing salinity of the root zone has been proposed by Maas and Hoffman in 1977 and, despite some limitations (Maggio et al., 2002; Steppuhn et al., 2005), it remains useful for a *first level assessment* of the relative tolerance of different species to salinity. The model is based on two parameters that can be defined by plotting the relative yield as a continuous function of root zone salinity (Fig. 1). At low soil salinity concentrations, yields are generally not affected or, in some cases, even enhanced by salinity. In contrast, increases of soil salinity beyond a certain threshold” will cause a slow decrease in yield. This response is typically described by two intersecting linear regions. The first is a tolerance plateau with zero slope (yield response at low salt concentration), whereas the second linear region is concentration-dependent with a characteristic ‘slope’ which defines the yield reduction per unit increase in salinity. The intersecting point of the two lines identifies a characteristic ‘threshold’ that is the maximum soil salinity that does not reduce yield below that obtained under non-saline conditions (Maggio et al., 2001; Jalali et al., 2017). This model has been used to rank crop species with respect to their salinity tolerance (Tanji and Kielen, 2002). Using the same approach, we did a metadata analysis to categorize the most common weeds and compare them with cultivated plants. In Table 1, 43 weed species are listed with an indication of specific salinity tolerance threshold (Th), slope (Sl) and category of tolerance based on Maas and Hoffman (1977). A first comparison of the data in Table 1 with the relevant literature for crop salt tolerance indicates that weeds, with respect to germination and growth parameters (fresh, dry weight biomass or shoot length), are generally more tolerant than most crops (44% of the species in Table 1 is classified as T or ET and 76% as MT, T or ET). At germination, a critical stage in crop-weed interactions, characteristic stress tolerance parameters vary substantially among weeds. Mean values of thresholds and slopes were 5.29 dS m^{-1} and 6.76% per dS m^{-1}, respectively, ranging from extremely tolerant species such as *Kochia scoparia* with Th = 18.18 dS m^{-1} and Sl = 1.07% per dS m^{-1} to very sensitive species such as *Orobanche cernua* with Th = 0.94 dS m^{-1} and Sl = 16.9% per dS m^{-1}. To better visualize the relative crop-weed salinity tolerance, we used the two characteristic parameters (threshold, Th and slope, Sl) to calculate the Electrical Conductivity (EC) level at which each species had a 50% reduction (EC_{50}) in dry weight biomass compared to non-salinized controls (Figs. 1 and 2) (Steppuhn et al., 2005). The average EC_{50} for the 18 most common weed species worldwide shown in Fig. 2 was 16.4 dS m^{-1}, while the average EC_{50} for 35 common crop species (Tanji and Kielen, 2002) was 10.6 dS m^{-1}, further indicating that weeds are more tolerant to root-zone salinity than crops. Specific response functions for some common crops and associated weed species revealed important differences in terms of salinity tolerance threshold (Th) and responses to increasing soil salinity after Th (Sl) (Fig. 3). Corn and soybean are more sensitive than their associated weed species. With respect to corn (Fig. 3A), *Cynodon dactylon, Echinochloa crus-galli* and *Setaria italica* have higher Th, while *Digitaria sanguinalis* and *Setaria italica* present lower Sl. As for soybean (Fig. 3B), *Sorghum halepense* has higher Th whereas *Echinochloa crus-galli, Xanthium strumarium* and *Portulaca oleracea* manifest both higher Th and lower Sl (Essa, 2002). In contrast, wheat (Fig. 3C) shows similar tolerance to *Lolium perenne,* higher tolerance than *Bromus tectorum* (only for Th) and higher tolerance compared to *Avena fatua* only in terms of Th, yet lower tolerance in terms of Sl. Rice (Fig. 3D) tolerates salinity better than *Echinochloa colona, Oryza sativa* (weedy species) and *Cyperus iria* in terms of Th, whereas it shows a remarkable decline in yield (Sl) compared to these weeds, at salinity higher than their specific tolerance thresholds (Aslam et al., 1993). Rice is much more sensitive than *Echinochloa crus-galli* in terms of both Th and Sl, indicating an important interspecific variability (compare *E. colona* vs. *E. crus-galli*). The salinity tolerance difference between cultivated rice and its relative wild species is consistent with a significant loss of competitiveness vs. weeds that has occurred during the selection of cultivated varieties. Finally, sugar beet shows higher salinity tolerance compared to *Xanthium strumarium*, *Avena fatua* and *Sorghum halepense* in terms of slope (Sl), whereas it has a slightly reduced threshold compared to those weeds (Fig. 2E).

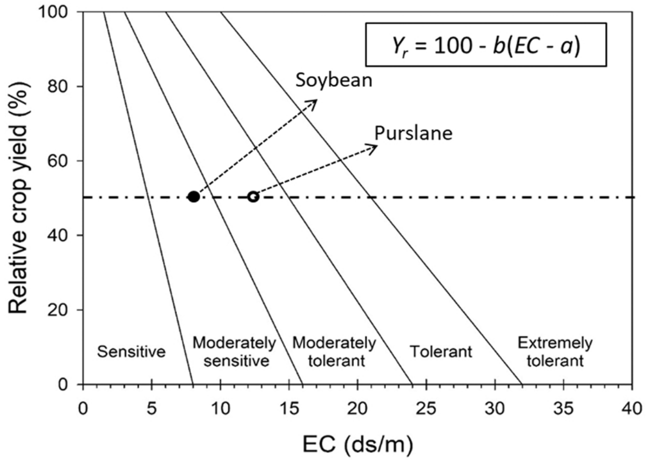

Fig. 1. Boundaries of salinity tolerance categories, from sensitive to extremely tolerant, obtained based on the Maas and Hoffman relationship (1977) (Tanji and Kielen, 2002). Classification of soybean and purslane, based on data from Fig. 2, are reported as an example. The inset shows the Maas and Hoffman relationship: $Y_r = 100 - b\,(EC_e - a)$ where a = the salinity threshold expressed in dS/m; b = the slope expressed in percent per dS/m; and EC_e = the mean electrical conductivity of a saturated paste taken from the root zone.

While a first level assessment demonstrates that weeds may cope better than crops with increasing salinization, it is also important to unravel the *bio-functional* basis for weed competitiveness and invasion. In the following sections we review the multiple determinants that may enhance weeds competitiveness and spread as these may serve as leverage points to elaborate adequate control strategies in saline environments.

3. Competitive advantage of weeds in saline soils

Plant tolerance to Na^+ and Cl^- ions varies widely, from very sensitive glycophytes such as chickpea to tolerant halophytic species like stem-succulent Tecticornia species (English and Colmer, 2013; Flowers and Colmer, 2015). Although there is still a debate on the tolerance