Tolerance of Wheat to Soil Sodicity Can Be Better Detected through an Incremental Crop Tolerance Approach and Ascertained through Multiple Sowing Times

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Abstract: Soil sodicity is a significant crop production constraint around the world. Inherited tolerance is a precursor to pre-breeding and breeding tolerant cultivars. However, high yield per se and seasonal variability are potential limitations to identify real tolerance rather than escape correctly. To minimise this risk, we generated yield, yield components and supporting data at two times of sowing (TOS) of 15 lines representing four quadrants of a biplot from a sodic- vs. non-sodic yield dataset of 112 wheat lines trialled in the previous year. Data from sodic and non-sodic sites were investigated using three analytical approaches namely, simple ratio of yield (REI), ratio of genotypic effects (TI) after excluding site effects, and the incremental crop tolerance (ICT) reflected as deviation from regression. REI and TI produced similar results showing ninelines to be tolerant, but only four lines namely, Scepter, Condo, WA345, and WA134 passed the ICT test. The tolerance comparison at the two TOSs differentiated lines tolerant at either or both TOSs. Association of Yield-ICT with leaf tissue mineral analysis and ICT for morphological traits was genotype specific, thus not usable invariably for detection of tolerant germplasm. Hence, we conclude that (i) focussing on yield rather than yield components or tissue tests, (ii) following the ICT approach, and (iii) evaluation at multiple sowing times will provide an accurate and rigorous test for identifying inherited tolerance that breeders and physiologists can reliably use. We anticipate our suggested approach to be applicable globally across crops.

Keywords: wheat; sodicity tolerance; sodic soil; incremental crop tolerance; tolerance indices; sodicity stress; yield potential

1. Introduction

Wheat is one of the most important crops for global food security, providing 20 percent of protein and calories for more than 4.5 billion people [1]. Based on the last ten years, wheat occupies the largest area (220 million hectares) among all crops and produces around 719 million metric tons [2]. In Australia, wheat is the predominant export grain commodity grown under rain-fed conditions [3,4]. The Australian average wheat yield is only 1.87 t/ha compared to a world average of 3.24 t/ha over the last ten years. In Australia, wheat yields are below the water-limited potential due to insufficient use of growing season available water [5,6].

Abiotic stresses reduce crop production by more than 50% compared to non-limiting growth environments [7]. Along with heat, drought, and frost, dryland salinity is also a major problem in Australia, valued at over $250 million a year in lost crop production or quality [8]. Australasia has the widest distribution of salt-affected soils with 357.6 million hectares, of which 340 million hectares is sodic [9]. Water stress due to drought and salinity is the single most common growth-limiting factor for crop production in the USA [10]. High salt concentration in the soil also causes water stress in plants by reducing osmotic...
potential and thus the total soil water potential [11,12], whereas sodicity (additionally) damages crops through adverse soil physical and chemical properties [13,14].

Sodic soils are characterised by high sodium (Na) concentration, with an exchangeable sodium percentage (ESP) threshold at 15 and high alkalinity with pH greater than 8.5 [15], but in Australia soils with ESP greater than six are also considered sodic [16]. High Na concentration relative to other cations results in aggregate dispersion and poor soil structure, which causes increased runoff due to low permeability and water-logging as it rains, and surface crusting and high soil strength as it dries [17]. High-strength soils adversely affect root penetration and seedling emergence, while both water-logging and surface crusting create anoxic conditions leading to plant death [8,14]. Furthermore, changes in the soil redox potential, pH and altered soil solution composition due to high Na concentration cause a nutrient imbalance in plants in terms of both deficiency and toxicity of specific elements [18–21], and these ultimately affect plant growth and development by altering morpho-physiological processes [17].

Yield loss under sodicity varies with the extent of the increase in pH and ESP [22]. Choudhary et al. (1996) [23] reported a significant reduction of root and shoot growth and grain yield in wheat, but deterioration is known to vary with cultivar and growth stage [24]. Wheat grown under sodic soil conditions can be adversely affected by waterlogging during winter due to water accumulating in the topsoil as rainfall exceeds evapotranspiration. In addition, plants often experience additional setbacks during grain filling in spring because of insufficient water in the subsoil or restricted root growth [25] due to physical (high soil strength) and/or elemental toxicity. Many studies have demonstrated soil management and plant breeding to be complementary in raising crop productivity for saline and sodic soils [26,27]. However, genetic solutions may provide a permanent tangible solution by developing better adapted cultivars capable of overcoming both surface and subsoil sodicity-related constraints [28].

Progress in developing salinity/sodicity tolerant cultivars is slow [27,29–32] most likely due to the physiological complexity of tolerance, polygenic control and low heritability of traits, difficulty in phenotyping, lack of reliable and rapid screening assays, and the narrow genetic base among modern cultivars [33–37]. Variable degree of the impact of sub-soil constraints on crop growth due to differences in seasonal rainfall pattern [38] and spatial variability of sub-soil constraints like boron toxicity, even over very small distances in the paddock [39], also leads to confusing and misleading results. The lack of effective selection indices further hinders the success of breeding programs under such conditions [40]. Therefore, improving the tolerance to sodicity requires access to new genetic diversity, efficient screening techniques and selection criteria to identify tolerant germplasm and understand mechanisms of tolerance.

This paper is aimed at identifying tolerant lines of wheat from a set of field experiments conducted over two different times of sowing in a sodic and non-sodic soil, with the idea that only the lines with real tolerance to sodicity factors (rather than simply escape due to phenology matched favourable seasonal conditions) would exhibit tolerance at both times of sowing. To identify sodicity tolerance, we focused on the concept of Incremental Crop Tolerance (ICT) rather than relative yield because selection based on other methods may reflect yield potential per se and not the real tolerance [41]. We also examined several morpho-physiological traits in order to identify those associated with tolerance in the identified lines.

2. Materials and Methods

2.1. Site Description

Both the sodic (−31.499, 118.216) and non-sodic (−31.489, 118.216) sites used here were located at Dryland Research Institute, Department of Primary Industries and Regional Development (DPIRD), Merredin, Western Australia and used in 2018 and 2019. Broadly the soil type of sodic site and non-sodic site belong to clays & shallow loamy duplexes and the Deep sandy duplexes groups, respectively. Table 1 shows the soil properties of both the...
sodic and non-sodic soil sites, which were approximately 1 km apart. Soil properties were analysed from pooled samples, at 0–70 cm depth, collected from five random locations at each site. Daily meteorological data were obtained from the nearest weather station of DPIRD (Table S1). The sodic soil site had not only high ESP and pH, but also had high boron, exchangeable Ca and Mg, and high calcium carbonate.

### Table 1. Soil properties at different layers of the sodic and non-sodic site used to characterize wheat lines.

| Properties                      | Unit    | Site         | Sodic 0–30 cm | Sodic 30–70 cm | Non-Sodic 0–30 cm | Non-Sodic 30–70 cm |
|---------------------------------|---------|--------------|---------------|----------------|-------------------|-------------------|
| Texture                         |         |              | 3.375         | 3.5            | 2.5               | 2.5               |
| ESP Exchangeable                | %       |              | 11.75         | 25.625         | 2.3               | 4.15              |
| pH Level (CaCl<sub>2</sub>)     |         |              | 6.725         | 8.05           | 5                 | 5.45              |
| pH Level (H<sub>2</sub>O)       |         |              | 7.75          | 9.15           | 6                 | 6.05              |
| Ammonium Nitrogen               | mg/kg   |              | 9.75          | 1.5            | 5                 | 1                 |
| Nitrate Nitrogen                | mg/kg   |              | 16.25         | 13.5           | 15.5              | 8                 |
| Phosphorus Colwell              | mg/kg   |              | 21.25         | 28             | 4                 |                   |
| Potassium Colwell               | mg/kg   |              | 256.5         | 277.25         | 87.5              | 49                |
| Sulfur                          | mg/kg   |              | 11.725        | 56.85          | 5.5               | 42.4              |
| Organic Carbon                  | %       |              | 0.4425        | 0.115          | 0.44              | 0.12              |
| Conductivity                    | dS/m    |              | 0.16825       | 0.456          | 0.0455            | 0.069             |
| DTPA Copper                     | mg/kg   |              | 0.865         | 0.915          | 0.57              | 0.07              |
| DTPA Iron                       | mg/kg   |              | 20.365        | 11.3375        | 21.41             | 6.455             |
| DTPA Manganese                  | mg/kg   |              | 17.315        | 3.8775         | 8.015             | 0.86              |
| DTPA Zinc                       | mg/kg   |              | 0.5575        | 0.1725         | 0.42              | 0.71              |
| Exc. Aluminium                  | meq/100 g|              | 0.168          | 0.17375        | 0.232             | 0.2125            |
| Exc. Calcium                    | meq/100 g|              | 7.5025        | 7.6475         | 2.045             | 2.29              |
| Exc. Magnesium                  | meq/100 g|              | 4.7725        | 7.7575         | 0.37              | 1.03              |
| Exc. Potassium                  | meq/100 g|              | 0.645         | 0.7125         | 0.19              | 0.09              |
| Exc. Sodium                     | meq/100 g|              | 1.8125        | 5.5875         | 0.065             | 0.15              |
| Boron Hot CaCl<sub>2</sub>      | mg/kg   |              | 4.505         | 17.915         | 0.685             | 0.94              |
| Calcium Carbonate               | %       |              | 0.8225        | 8.38           | 0.25              | 0.28              |
| Dispersion Index                |         |              | 10.25         | 11             | 0                 |                   |
| Prewash exch. Ca                | meq/100 g|              | 6.35          | 9.155          | 1.555             | 1.95              |
| Prewash exch. K                 | meq/100 g|              | 0.5775        | 0.5475         | 0.12              | 0.065             |
| Prewash exch. Mg                | meq/100 g|              | 4.3225        | 6.4575         | 0.285             | 0.77              |
| Prewash exch. Na                | meq/100 g|              | 0.8475        | 1.87           | 0.1               | 0.1               |

#### 2.2. Plant Materials

The 2018 field trial included 20 released Australian cultivars and 92 FIGS (Focused Identification of Germplasm for Specific Traits) lines. The FIGS lines were from a salinity tolerant collection of international cultivars obtained from ICARDA and bulked in Western Australia. The 2019 field trial included fifteen of these earlier screened lines, including ten salinity FIGS lines and five Australian cultivars (Table S2). These 15 lines were chosen to represent all four quarters of the 2018 scatter plot for relative grain yield under sodic vs. non-sodic site.

#### 2.3. Experiment Design and Layout

The 15 lines selected for detailed analyses in 2019 were planted under sodic and non-sodic conditions at two different sowing times, on 7 June 2019 (TOS1) and 8 July 2019 (TOS2), with different randomizations prepared for each experiment. The TOS1 experiments at both sites comprised two adjacent blocks, with a partially replicated layout of FIGS lines and three Australian cultivars as checks sown alongside three replicates of paired plots of 20 Australian cultivars sown using an RCB layout with additional replicates of some cultivars. The TOS2 experiments were laid out in arrays of 5 ranges × 12 rows and
comprised four replicate blocks of 15 genotypes. The plot sizes in 2018 were 4.4 m × 1.7 m (5 rows each) with 22 cm row spacing in 2019 they were 4 m × 1.9 m (7 rows each).

Experimental design in the previous year where lines were shortlisted for experiment presented in this paper had 2–4 replications of 112 genotypes (20 Australian cultivars and 92 FIGS collection) laid out following a randomized complete block (RCB) design.

2.4. Field Phenotypic Data

Data on grain yield, plants/m², heads/m², 1000 kernel weight, plant height, and biomass at anthesis and maturity were collected from all field plots. The anthesis date was recorded when 50% of heads in a plot had reached anthesis. Data on leaf number, flag leaf length and width, and tiller number were recorded on three tagged plants in each plot. Leaf growth data were collected at two-week intervals. Data on tiller numbers, spike length, spikelet number and grain number per spike were also recorded on the same tagged plants after maturity.

2.5. Leaf Tissue Analyses

At anthesis, about 50 youngest fully mature flag leaves (YML) were collected randomly from each plot, dried at 40 °C for 48 h followed by Inductively Coupled Plasma analysis at the Australian Precision Ag Laboratory (APAL) at Perth (Western Australia).

2.6. Analysis of Sodicity Tolerance

The sodic and non-sodic experiments sown at the same time were analysed jointly, with separate combined analyses for the TOS1 2019 trials, TOS2 2019 trials, and 2018 trials. A linear mixed model was fitted for grain yield using the approach described in Lemerle and Smith, 2006 [42], which fits the overall means for the sodic and non-sodic environments as fixed effects and the genotypic effects for the sodic and non-sodic environments as random effects. Terms were included in the model to allow for heterogeneous genetic variances at each site and to estimate the genetic correlation between the sodic and non-sodic environments. Additional terms were included in the random structure to describe the layout and blocking structures of the experiments. Separate spatial models were fitted for each environment using the methods of Gilmour et al., 1997 [43]. Genotypic effects were derived for the sodic and non-sodic environments as empirical best linear unbiased predictors.

Let $Y_{NS}$ and $Y_S$ denote the site grain yield means for the non-sodic and sodic environments at a particular time of sowing, respectively, $v_i$ denote the genotypic effect associated with grain yield for the $i$th genotype, $s_{NS}^2$ denote the estimated genetic variance for the non-sodic site, and $s_{NS,S}^2$ denote the estimated genetic covariance between the non-sodic and sodic sites. Predicted grain yields were calculated as $(Y_i)_{NS} = Y_{NS} + (v_i)_{NS}$ for the non-sodic environment and $(Y_i)_S = Y_S + (v_i)_S$ for the sodic environment.

Three analytical approaches were used to calculate sodicity tolerance:

- Ratio of relative predicted yields (REI) = $(Y_i)_{NS} / (Y_i)_S$
- TI = $(v_i)_S - (v_i)_{NS}$ This is an implementation of the TOL index [45] using genotypic effects which corrects for the difference in site mean grain yields.
- Yield-ICT = $(v_i)_S - \beta (v_i)_{NS}$ where $\beta = s_{NS,S}^2 / s_{NS}^2$ The ICT for other traits were calculated similarly to Yield-ICT.

2.7. Changes in Leaf Counts through Time

Changes in leaf counts through time were modelled for the selected 15 lines via a multi-environment analysis using a random regression approach implemented in a linear mixed model framework [46]. Each field experiment conducted in 2019 represented a soil type by the time of sowing combination and was treated as a distinct environment. The overall relationship between leaf count and log-transformed days since sowing was fitted
for each environment as fixed effects, with the genotype-specific variation simultaneously modelled as random deviations around the overall fixed environment profile. Terms were included to model covariance between random intercept and slope terms. Intercept and slope values for curves describing each genotype by environment combination were determined by combining the estimates of the environment-specific responses, derived from the model as empirical best linear unbiased estimators, with the genotype-specific random intercept and slope effects, derived as empirical best linear unbiased predictors.

All analyses were conducted in the R statistical computing environment [47]. Tolerance index and leaf count through time analyses were implemented using the ASReml-R package [48], with variance components estimated using REML [46]. The biplot was created using the R ggbplot2 package [49]. The correlation plot was created using the R corrplot package [50].

3. Results

3.1. Soil Conditions

The soil type in the sodic and non-sodic site used here was a typical clay loam and grey sand, respectively. Averaged of 0–70 cm, the sodic site had high higher pH and nearly six times higher ESP (18.7) compared to the non-sodic site (3.2; Table 1). Soil test data showed that the sodic site had higher concentrations of nitrogen, potassium, manganese, magnesium, and sulphur compared to the non-sodic site (Table 1). Among potentially detrimental elements, the sodic site had high concentrations of boron (11.2 mg/kg) and sodium (3.7 meq/100 g) but not so for aluminum (0.17 meq/100 g) [51].

3.2. Grain Yields and Genotypic Tolerance to Sodicity

The relative predicted grain yields for all 112 lines screened in 2018 in sodic and non-sodic soil are shown in Figure 1, with the 15 lines selected for further detailed analyses in 2019 trials shown with green circles.

![Figure 1. Relative grain yields of 112 wheat lines in sodic and non-sodic soil in 2018. The green circles represent selected lines used for detailed studies presented here.](image)

Predicted grain yields (t/ha) for the 15 lines examined in detail here are presented in Table 2. This compares data from the original field trial in 2018 and the subsequent field trials at two times of sowing in 2019. In 2019, the mean predicted grain yield for the two times of sowing were 1.466 t/ha and 1.497 t/ha at the sodic site and 1.198 t/ha and 1.184 t/ha, respectively at the non-sodic site (Table 2). The cultivar Scepter was consistently the highest yielding over both sites and time of sowings, followed by Ninja at TOS1 at both sites and TOS2 at the non-sodic site (Table 2). Line WA332 followed by WA005 was the lowest yielding genotype over both sites and sowing dates (Table 2).
Table 2. Predicted mean grain yields (t/ha) and sodicity tolerance analyses based on Ratio of relative predicted grain yields, Yield Tolerance Index (TI), and Yield Incremental Crop Tolerance (Yield-ICT). Data are for 15 wheat lines screened in 2018 and 2019; in 2019 at two times of sowing (TOS1 and TOS2). The ratio of relative predicted yields is calculated by the line yield/site mean yield for each site (see Methods). Bold text represents the top two highest values in each column.

| Line/Trial | 2018 | 2019 TOS1 | 2019 TOS2 | 2018 | 2019 TOS1 | 2019 TOS2 | 2018 | 2019 TOS1 | 2019 TOS2 | 2018 | 2019 TOS1 | 2019 TOS2 | 2018 | 2019 TOS1 | 2019 TOS2 | 2018 | 2019 TOS1 | 2019 TOS2 |
|------------|------|-----------|-----------|------|-----------|-----------|------|-----------|-----------|------|-----------|-----------|------|-----------|-----------|------|-----------|-----------|
| Condo      | 1.832| 1.802     | 1.954     | 1.576| 1.388     | 1.458     | 1.125| 1.120     | 1.060     | 0.211| 0.269     | 0.184     | 0.204| 0.034     | 0.045     |
| Krichauff  | 1.683| 1.789     | 1.731     | 1.368| 1.437     | 1.326     | 1.191| 1.074     | 1.033     | 0.271| 0.207     | 0.093     | 0.271| −0.054    | 0.021     |
| Magenta    | 1.333| 1.476     | 1.781     | 1.459| 1.095     | 1.405     | 0.884| 1.164     | 1.003     | −0.170| 0.237     | 0.064     | −0.174| 0.159     | −0.049     |
| Ninja      | 1.892| 1.991     | 1.864     | 1.834| 1.357     | 1.482     | 0.998| 1.103     | 0.995     | 0.013| 0.289     | 0.070     | −0.003| −0.036    | −0.081     |
| Scepter    | 2.089| 2.208     | 2.028     | 1.966| 1.639     | 1.487     | 1.028| 1.163     | 1.079     | 0.079| 0.425     | 0.229     | 0.059| 0.056     | 0.075     |
| WA005      | 0.909| 0.707     | 0.919     | 1.081| 0.738     | 0.780     | 0.814| 0.827     | 0.931     | −0.216| −0.175    | −0.174    | −0.207| −0.063    | 0.031     |
| WA034w     | 1.106| 1.105     | 1.545     | 1.237| 0.863     | 1.175     | 0.865| 1.105     | 1.039     | −0.176| 0.098     | 0.057     | −0.172| 0.143     | 0.061     |
| WA134      | 1.969| 1.897     | 1.676     | 1.613| 1.452     | 1.303     | 1.181| 1.128     | 1.017     | 0.311| 0.301     | 0.060     | 0.303| 0.031     | 0.000     |
| WA143      | 1.599| 1.547     | 1.102     | 1.708| 1.248     | 0.966     | 0.906| 1.071     | 0.902     | −0.154| 0.156     | −0.176    | −0.166| −0.004    | −0.066     |
| WA194      | 1.362| 1.525     | 1.461     | 1.157| 1.255     | 1.141     | 1.139| 1.049     | 1.013     | 0.161| 0.126     | 0.007     | 0.167| −0.038    | 0.029     |
| WA250      | 1.669| 1.536     | 1.711     | 1.498| 1.210     | 1.332     | 1.078| 1.096     | 1.016     | 0.127| 0.182     | 0.067     | 0.122| 0.042     | −0.008     |
| WA325      | 1.562| 1.641     | 1.763     | 1.478| 1.410     | 1.371     | 1.023| 1.004     | 1.017     | 0.040| 0.087     | 0.080     | 0.035| −0.160    | −0.015     |
| WA332      | 0.830| 0.155     | 0.301     | 0.988| 0.392     | 0.439     | 0.812| 0.341     | 0.543     | −0.203| −0.381    | −0.450    | −0.191| −0.084    | −0.073     |
| WA345      | 1.662| 1.449     | 1.440     | 1.469| 1.149     | 1.102     | 1.095| 1.089     | 1.034     | 0.149| 0.156     | 0.025     | 0.145| 0.049     | 0.067     |
| WA377      | 1.215| 1.168     | 1.174     | 1.423| 1.145     | 0.995     | 0.826| 0.881     | 0.933     | −0.252| −0.121    | −0.134    | −0.255| −0.226    | −0.038     |

Site Mean | 1.51 ± 0.14 | 1.47 ± 0.19 | 1.5 ± 0.17 | 1.46 ± 0.12 | 1.2 ± 0.12 | 1.18 ± 0.11
Three types of approaches were used to evaluate sodicity tolerance: (1) the ratio of relative predicted grain yields (calculated from Table 2; see Methods), (2) the Yield Tolerance Index (TI), and (3) the Yield Incremental Crop Tolerance (Yield-ICT) (Table 2; see Methods). The correlations between these analyses of sodicity tolerance are shown in Figure 2. For the large dataset of 112 lines used in 2018, there were high correlations of the relative predicted grain yield (RY18) with either the Tolerance Index (TI18) or the Incremental Crop Tolerance measurement (ICT18, r = 0.99 in both cases, Figure 2). There were also generally higher correlations between trials using RT or TI than ICT (Figure 2).

The discrimination of individual lines based on different methods used to evaluate sodicity tolerance is shown in Figures 3 and 4. The genetic effects for yields at the sodic site were plotted against those at the non-sodic site for both TOS, and a regression was fitted to visualize Yield-ICT (Figure 3a,b). The Yield-ICT value is represented by the vertical distance between the wheat line and the regression line.

Scepter, followed by WA134, were consistently the top two lines across all field trials for the three methods used to evaluate sodicity tolerance (bold values in Table 2); in contrast, WA332 was the least tolerant. In the TOS1 vs. TOS2 plot, lines were spread over all four quarters for Yield-ICT (Figure 3a), but they tended to cluster in the top right quadrant if tolerance was gauged simply as a plot of the TI (Figure 3b). Considering both TI and ICT analyses, Magenta, Condo, WA250, WA345 and WA34w were also tolerant lines at TOS1 of which Magenta, and WA250 dropped at TOS2 because of ICT or TI was &lt; 0. Instead, Krichauff, a known sodic soil tolerant line, appeared in this quadrant. Notably, although Ninja had a high yield in non-sodic soil, it had a negative ICT value at both TOSs (Figure 3a and Table 2). WA005 showed a positive ICT in TOS2 only while WA377 and WA332 were always positioned in the bottom left quadrant, indicating a low yield potential and low tolerance to sodic soil.
Figure 3. Yield-ICT (a), TI (b) and REI (c) comparison in the TOS2 vs. TOS1 matrix (the difference in scale is not meaningful. Data were taken from the 2019 field trial in sodic and noon-sodic soil. Considering both TOSs, only Scepter, Condo, WA034w and WA345 were tolerant to sodic soil (Figure 3a). On the other hand, WA332, WA377, WA325, WA143 and Ninja showed intolerance to sodic soil at both TOSs (Figure 3a).

Magenta WA250, WA194, WA005 and Krichauff showed inconsistent Yield-ICT values over TOSs (Figure 4a,b; Table 2). Magenta showed the largest decline in ICT from TOS1 to TOS2, while the highest Yield-ICT gains occurred for Krichauff and WA005. Yield-ICT not only varied over sowing times but there were also variations in magnitude and rank of Yield-ICT calculated from 2018 data (Table 2).

3.3. Relation of Yield-ICT with Other Trait Values

A principal component analysis (PCA) was restricted to TOS1 as datasets for TOS2 were incomplete. With all variables included, approximately 70% of the variation was explained by the first two principal components, and Yield-ICT was slightly correlated with grain number ICT and spike length ICT. Heading time ICT was negatively correlated with grain number ICT and spikelet length ICT (Figure 5). The intolerant lines WA332 and WA377 had high values in the direction of high heading time ICT. Yield-ICT was not related to tiller number/plant ICT (TN) or heads/m² ICT (heads/m²; “Heads” in Figure 5). WA325 and WA250 which had a high number of heads/m² and WA134 which had a high TN were not in the high Yield-ICT group.
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Figure 4. Plots of genetic effects from the sodic environment against genetic effects from the non-sodic environment in (a) TOS1 and (b) TOS2. Yield-ICT is the vertical distance between the point and the dashed regression line.

Figure 5. PCA biplot with lines clustered based on Yield-ICT and other traits-ICT. Data are from 2019 TOS1 trial. The “other traits-ICT” include tiller number ICT (TN), grain number ICT (GN) and heads/m² ICT (Heads).

Table 3. Lines with simultaneous positive values of yield-ICT and other yield components-ICT at two times of sowing in 2019 at Merredin.
Condo, Scepter, WA034w, WA345, and Magenta identified as tolerant at TOS1 (Table 2 and Figure 5) grouped together in the direction of increasing Yield-ICT in this biplot suggesting a similar role of yield components in building tolerance.

3.4. Relation of Yield-ICT with Yield Components-ICT Values

There was no strong correlation observed between Yield-ICTs and yield contributing parameters or other morphological traits with relationships summarised in Table 3. However, there were strong line and TOS associations. High Yield-ICTs of Scepter, WA345 and WA34w were associated with high Head/m²-ICT at TOS2 but not for any line at TOS1. Lines WA250 and WA325 had high Head/m²-ICT at both TOSs but had low Yield-ICT for yield at both TOSs. Likewise, Plant height-ICT seemed associated with Yield-ICT, although associations were more prominent at TOS2 (data not presented). Scepter and WA034w had clearly high Plant height-ICT as well as Yield-ICT at both TOSs. Magenta had a shorter plant height at the sodic site at both TOSs (low Plant height-ICT) but showed low Yield-ICT at TOS2 only (data not presented).

Table 3. Lines with simultaneous positive values of yield-ICT and other yield components-ICT at two times of sowing in 2019 at Merredin.

| Line     | Head/m² | Days to Heading | Flag Leaf Length | Plant Height | 1000 Kernels wt | Final Leaf Number | Peduncle Length | Grain Number | Grain Weight | Spike Length | Spikelet No | Tiller No |
|----------|---------|-----------------|------------------|--------------|----------------|-------------------|----------------|--------------|-------------|--------------|-------------|-----------|
| TOS:     | 1 2 1 2 | 1 2 1 2 1 2 1 2 | 1 2 1 2 1 2 1 2 | 1 1 1 1 1 1 1 1 | 1 1 1 1 1 1 1 1 | 1 1 1 1 1 1 1 1 | 1 1 1 1 1 1 1 1 | 1 1 1 1 1 1 1 1 | 1 1 1 1 1 1 1 1 | 1 1 1 1 1 1 1 1 | 1 1 1 1 1 1 1 1 |
| Condo    | +       | + +             | + +             | + +          | +             | + +               | + +           | + +           | + +          | + +          | + +        | + +       |
| Krichauff|         |                 |                 |              |               |                   |               |               |              |             |            |           |
| Magenta  | +       | + +             | + +             | + +          | +             | + +               | + +           | + +           | + +          | + +          | + +        | + +       |
| Ninja    |         |                 |                 |              |               |                   |               |               |              |             |            |           |
| Scepter  | +       | + +             | + +             | + +          | +             | + +               | + +           | + +           | + +          | + +          | + +        | + +       |
| WA005    |         |                 |                 |              |               |                   |               |               |              |             |            |           |
| WA034w   | +       | + +             | + +             | + +          | +             | + +               | + +           | + +           | + +          | + +          | + +        | + +       |
| WA134    | +       | + +             | + +             | + +          | +             | + +               | + +           | + +           | + +          | + +          | + +        | + +       |
| WA143    | +       | + +             | + +             | + +          | +             | + +               | + +           | + +           | + +          | + +          | + +        | + +       |
| WA194    | +       | + +             | + +             | + +          | +             | + +               | + +           | + +           | + +          | + +          | + +        | + +       |
| WA250    | +       | + +             | + +             | + +          | +             | + +               | + +           | + +           | + +          | + +          | + +        | + +       |
| WA325    | +       | + +             | + +             | + +          | +             | + +               | + +           | + +           | + +          | + +          | + +        | + +       |
| WA332    | +       | + +             | + +             | + +          | +             | + +               | + +           | + +           | + +          | + +          | + +        | + +       |
| WA345    | +       | + +             | + +             | + +          | +             | + +               | + +           | + +           | + +          | + +          | + +        | + +       |
| WA377    | +       | + +             | + +             | + +          | +             | + +               | + +           | + +           | + +          | + +          | + +        | + +       |

Days to heading-ICT did not show any relationship with Yield-ICT (data not presented).

High Flag leaf length-ICT for WA345, Condo and Magenta were associated with high Yield-ICT at TOS1 but only for WA345 at TOS2. The relationship between Grain weight-ICT and Yield-ICT appeared negative. None of the high Yield-ICT lines had high values for grain weight at TOS2. At TOS1, Magenta and WA034, the topmost Yield-ICT lines had below average Grain weight-ICT; at TOS2, Yield-ICT for Magenta was low, but its Grain weight-ICT was above average. Similarly, Scepter and WA134 swapped ranks for Yield-ICT and Grain weight-ICT over the TOSs. WA134, WA143 and WA194 had high 1000 grain weight-ICT for in both TOSs. WA345, WA134 and Scepter had a positive correlation with Yield-ICT in TOS1, while WA194 and WA005 had a positive correlation with Yield-ICT at TOS2.

3.5. Leaf Mineral Concentration Relations with Yield

Tissue test data were available only for the TOS1 2019 trial. Released cultivars included in the trial tended to have higher concentrations of potentially toxic elements (Al and B) in comparison to the FIGS lines (WA005-WA377) at both sites. However, differences were smaller, yet significant, at the sodic site (Table S3).

Aluminum (Al) concentrations of leaf material of plants grown in the sodic site were generally higher (up to 197%) than the non-sodic site. However, line-specific increase was statistically significant for only WA005, which had 88 mg/kg higher Al concentration.
This is one of the lines identified with a low Yield-ICT (Table 2). Scepter, one of the high Yield-ICT lines, clearly had a low increase of Al accumulation with only 1.94% more Al in sodic soil (Table 4).

Table 4. Changes of the leaf mineral accumulation (%) from non-sodic to sodic environment.

| LINE    | Al   | Ca   | K    | Na   | Mg   | P    | S    | B    | Zn   | Cu   | Mn   | Fe   |
|---------|------|------|------|------|------|------|------|------|------|------|------|------|
| Condo   | 16.50| -27.91| -4.84| -3.03| 16.92| 1.41 | -1.10| 620.72| -16.39| 32.52| 31.69| 6.82 |
| Krichauff| -5.71| -8.57| -6.40| -15.15| 6.38 | 0.00 | -4.71| 199.58| -19.23| 16.55| 44.88| -5.71|
| Magenta | 18.81| -13.58| 0.83 | -37.50| 9.80 | -6.85| 8.14 | 341.35| -8.62 | 61.79| 94.74| 6.45 |
| Ninja   | 38.18| -43.59| 12.09| 4.76 | 8.47 | 1.52 | 7.69 | 1460.44| -16.00| 29.64| 52.84| 9.09 |
| Scepter | 1.94 | -23.68| 0.24 | -19.61| 17.76| 2.22 | 9.14 | 231.62| -16.00| 29.64| 52.84| 9.09 |
| WA005   | 197.01| -41.43| 7.07 | -5.00| -4.35| 14.89| 8.14 | 341.35| -2.08 | 68.18| 94.74| 6.45 |
| WA034w  | 28.68| -31.69| 22.31| 29.41| 9.80 | -6.85| 8.14 | 341.35| -2.08 | 68.18| 94.74| 6.45 |
| WA134   | -1.44| -47.22| 11.11| 10.00| -14.06| 6.12 | -15.29| 1559.57| -4.88 | 72.45| 13.25| -4.28|
| WA143   | 15.85| -35.87| -8.79| -10.71| -8.93| -15.37| -12.00| 1037.17| -28.07| 91.25| 22.03| 29.91|
| WA194   | 47.40| -31.78| -3.51| -25.00| 6.78 | -2.04| 12.20 | 1037.17| -28.07| 91.25| 22.03| 29.91|
| WA250   | -35.52| -42.45| 6.95 | 29.17 | -12.33| 0.00 | -8.24 | 470.65 | -23.53| 66.67| 3.88 | -17.42|
| WA132   | 17.96| -32.85| 19.74| -8.33| -20.00| 0.00 | -11.11| 549.72 | -5.56 | 76.47| 41.50| 0.75 |
| WA332   | 8.37 | -50.00| 8.28 | 36.36 | -13.04| 5.56 | -18.07| 720.51 | -16.67| 55.08| -26.25| 2.22 |
| WA345   | 33.33| 23.02 | -23.18| 60.98| 29.33 | -24.07| -7.61 | 336.78 | -45.00| 46.73| 131.64| 44.03|
| WA377   | 14.39| -33.85| -3.81| 28.85 | -10.00| 11.11 | -9.88 | 567.83 | -16.33| 113.04| 48.65| 4.78 |

Boron (B) concentrations of leaf tissue were significantly higher at the sodic site \((p < 0.001)\) with Ninja showing the highest concentration (142 mg/kg). The increase of Boron accumulation was low for the high Yield-ICT lines Scepter (231%) and WA345 (337%) but not so for Condo (621%). The low Yield-ICT lines had inconsistent boron concentrations, e.g., WA377 (568%), WA325 (550%), WA332 (721; Table 4).

Iron concentration did not align at all with yield-ICT. For example, the low Yield-ICT lines WA325, WA332 and WA377 did not have higher iron on sodic soil, and the high Yield-ICT lines WA034w and WA345 had higher iron concentrations on the sodic site.

Most lines accumulated higher concentrations of nutrient elements (N, P, K) at the sodic site, presumably given a higher inherent nutrient value of clay (Table 1). The comparison of absolute levels or ranks between sites was not conclusive for any nutrient. For example, P in plants at the sodic site was lower for WA143 and WA345 but only the former is in the low Yield-ICT group. Element ratios except K/Na ratio were also inconsistent. The K/Na ratio was higher at the sodic site for Magenta and Scepter, two of the high Yield-ICT lines, but not for all. Other elements were inconsistent between lines in sodic and non-sodic sites (Table 4).

3.6. Leaf Counts

Lines behaved differently between sodic and non-sodic sites regarding leaf development, but the differences were not significant. Overall, WA345 produced the lowest number of leaves under both sodic and non-sodic trial at both TOSs, and thereby had the lowest leaf appearance rate compared to others (data not presented).

4. Discussion

4.1. The Sodic and Non-Sodic Soil Sites Used Here

Rengasamy [52] has identified at least six types of sodic soils being saline-sodic soils that are either acidic (pH < 6), neutral (pH 6–8) or alkaline (pH > 8), and non-saline sodic soils that are either acidic, neutral or alkaline. The sodic soil used here had an ESP of 18.7 and a pH (water) of 8.45, i.e., the site used here is a saline-sodic soil with alkaline pH.
This category of sodic soil represents the largest land area (23.6%) of salt-affected soils in Australia [52]. The sodic soil used here also had high boron, high calcium and magnesium, and high calcium carbonate (Table 1). In contrast, the non-sodic soil used here had an ESP of 3.2 (non-sodic) and a pH (water) of 6.03 (Table 1).

The mean yield of lines at the sodic soil site was equal or significantly higher than the mean yield of non-sodic sites at both TOS (Table 2) despite high ESP and pH values in the sodic site (Table 1). This likely occurred because pH was not extremely high in the topsoil, and the soil was richer in nutrients (N and K) at the sodic site (Table 1). As all the trials described here were in the low rainfall zone of Western Australia, the low water and nutrient holding capacity of the sandy soil at the non-sodic site might also be a cause behind lower yields in the non-sodic site.

4.2. Genetic Diversity for Grain Yield in Sodic Soil

The 15 selected lines were chosen from a much larger group of 112 lines screened for sodicity tolerance in national trials across Australia. Data from the full set of lines will be included in other publications. The 15 selected lines included five released cultivars and ten lines from an international FIGS nursery (Methods) and represented lines with high genetic diversity for their country of origin (Table S1). Therefore, it could be assumed that these lines would exhibit different types and levels of tolerance based on their sodicity class of soil and stresses developed.

These lines also represented a 4-fold genetic diversity for grain yield in the sodic and non-sodic soil used in trials described here (Figure 1). Across all three sodic soil trials there was a 2.5 to 14.2-fold difference in the predicted grain yields for the 15 wheat lines (calculated from Table 2). These results clearly demonstrate major genetic diversity for grain yield for lines in sodic soil.

4.3. Methods Used to Evaluate Sodicity Tolerance of Wheat Based on a Stressed and Non-Stressed Field Site

Three methods were used here to evaluate sodicity tolerance based on grain yields in a stressed (sodic) and non-stressed (non-sodic) soil: (1) Predicted relative grain yields (also referred to as Relative efficiency index; REI), (2) Tolerance Index (TI), and (3) Incremental Crop Tolerance (Yield-ICT; see Methods). Sodicity tolerance indices are quantitative measures derived to compare the response of lines exposed to a sodic relative to non-sodic environment. They offer a means by which lines can be ranked according to some inferred quality reflecting tolerance, but the most appropriate index in any application will depend on the reason motivating the comparison. Where maximising profit and avoiding risk are the objectives, an index which identifies lines which can maintain yield in both sodic and non-sodic soils, and which favours higher-yielding lines, is likely to be relevant. Where the focus is on identifying the mechanisms, which allow lines to cope with the stress imposed by a sodic environment, the differential performance compared to other lines tested under similar conditions rather than high yield may be a preferred measure to identify lines with adaptive traits.

Genotypic effects derived from fitting a linear mixed model describe the performance of the genotypes relative to each other. Some proportion of the genotypic effect will be inherent to the genotype and can be expected to manifest in both the sodic and non-sodic environments, but some proportion will reflect an interaction with the environment. The two TOS experiments sown in 2019 reflected an attempt to control any interaction between the genotype and any seasonal conditions by having trials located as close as feasibly possible and sowing them at the same time. We, therefore, anticipate that any interaction effect will primarily be due to the different soil types. Soil type cannot be randomised in a field trial, however, and this is unavoidably confounded with the blocking structure of the trials.

The first method used here to evaluate sodicity tolerance (REI) is based on the relative yield of lines in sodic and non-sodic environments, respectively, scaled by the inverse of the ratio of the trial mean yields (Methods). In the particular context of these trials, the
non-sodic sites had sandy soils, which were lower yielding than the loamy soils of sodic sites. The scaling factor corrects the relative yields for the difference in mean yield caused by the different soil types, so that a line with average yield performance at both locations will have an REI of 1, while a line performing consistently better or worse than average in both environments, measured by the percentage of site mean yield, will also have an REI of 1. REI different from 1 indicates differential performance with respect to the percent of the respective mean site yields.

The TI is a similar measure to REI, but the focus here is on the predicted additional yield in tonnes per hectare rather than the multiplicative aspect of the percentage of the site mean yield. TI is calculated as the difference in the genotypic effects for a line between sodic and non-sodic environments, so when TI = 0 this indicates that the genotypic contribution to yield is equal in both environments; a positive TI reflects that the genotypic contribution is greater in the sodic site than the non-sodic site; while a negative TI reflects that the genotypic contribution to yield is lower in the sodic site compared to the non-sodic site. The TI can be visualised by plotting sodic random effects against non-sodic random effects and calculating the vertical distance from a diagonal line with a zero intercept. Where higher yields are observed on average in sodic compared with non-sodic environments, it is evident that the vertical distance from the diagonal line will increase as the magnitude of the random effects increase, indicating that TI will be correlated with yield. A positive TI will therefore indicate that the line maintains yield in a sodic environment, but higher-yielding lines will rank higher than lower-yielding lines. An index of this nature may identify the most profitable lines for sowing in a sodic environment, but this selection criteria method may reflect yield potential rather than the possession of traits that reflect actual tolerance [42].

For the purposes of identifying physiological aspects that influence adaptation to a sodic environment, deviation from the expected performance may be more relevant. The ICT approach was originally proposed by Lemerle et al. in 2006 [42] in the context of assessing the true competitive ability of lines in the presence of weeds. ICT has also been used to characterise crops for drought tolerance [53–55]. ICT is calculated as a difference of random effects, but with the random effect reflecting performance in the unstressed environment first multiplied by a coefficient calculated from a ratio of the estimated shared genotypic covariance between the sodic and non-sodic blocks and the genetic variance at the non-sodic environment. The ICT can be visualised in a similar way to the TI as the vertical distance from a regression line, but with a slope reflecting the correlation between the sodic and non-sodic random effects. The Yield-ICT therefore reflects the deviation (in yield) from the average performance of all lines exposed to the same stressed and unstressed environments, identifying differential performance independent of yield. This approach does not seek to identify the best prospects for maximising profit in a sodic environment, but it may identify those lines which express a tolerance response when subjected to sodic soils and may warrant further investigation to understand the underlying mechanisms employed by the lines.

The analysis of sodicity tolerance by the three different analytical methods here showed that different results often occurred for each method. The benefit of Yield-ICT over the relative predicted grain yields and TI for evaluating sodicity tolerance is that it is more discriminating; this can be seen by a comparison of data in Table 2. For example in the 2019 trial in TOSI, the relative predicted grain yields indicate that 14 out of 15 lines would be tolerant, i.e., they have a relative predicted grain yield of >1 for lines grown in sodic relative to non-sodic soil. However, the Yield-ICT score indicates that only 7 lines are “tolerant,” i.e., that they have a positive (not negative) score (Table 2). Yield-ICT values also indicate that the only lines with consistently positive scores in 2018 and at both times of sowing in 2019 are: Condo, Scepter, WA134 and WA345. When evaluating individual lines, the data presented here indicate that Condo and Scepter are both often the highest yielding in sodic soil sites, making Condo and Scepter ideal for on-farm selection, with WA134 and WA345 good for further research for genetic improvement of wheat on sodic soils.
Where the top two lines for each trial site are selected across all methods used to evaluate sodicity tolerance (bold figures in Table 2), some consistencies occur. The ranking of lines with the highest sodicity tolerance based on the sum of top two values for all methods are: Scepter (5 top scores), WA134 (4), Krichaff (3), Condo and Magenta (2), and WA034w and W345 (1); the remaining lines were never one of the top two lines in any of the three methods (Table 2).

4.4. Methods Used to Valuate Sodicity Tolerance of Wheat Based on a Single Field Site

The relationship ($r^2$) of grain yields in a stressed environment (e.g., sodic soil) relative to grain yields in non-stressed environment (e.g., non-sodic soil) is often used to estimate tolerance [45,56,57] One concern of all such methods involving a comparison of a sodic and a non-sodic site, whether it involves using REI, TI or Yield-ICT as used here, is that these approaches assume that the non-stressed environment has simply removed the physiological constraint(s) in the stressed environment, and that there are no additional stresses associated with the non-stressed environment. The latter criteria may not have been met in the sodic and non-sodic soil sites used here.

Originally, the screening of 112 lines in non-sodic and sodic soil was done so that sites were as close as possible (in this case, within 1 km) to eliminate any major environmental factors that may have occurred. While temperature, irradiance, day length and rainfall were consistent between the sodic and non-sodic soil sites used in experiments described here (data not presented), there were additional constraints in the non-sodic soil site that were not present in the sodic soil site. This is demonstrated by mean site grain yields in the non-sodic soil site that are equal or less than the mean site grain yields in the (stressed) sodic sites for 2018 and for 2019 at both TOSs. (Table 2).

One method to eliminate potentially questionable comparisons between different stressed and non-stressed sites could be to select sodic soil sites and then ameliorate soil sodicity in replicated plots in the same site so as to maintain a similar soil composition (particle size) and nutrition but only eliminate or minimise the stress (soil sodicity).

A second strategy was used here by evaluating (i) “sodicity tolerance” based on grain yields only in the sodic soil, and (ii) quantifying the potential for escape due to differences in phenology. Comparing lines over different times of sowing at the same location in the same season is likely to reveal real tolerance to sodic soils and the possibility of escape enabled through phenology. The caveat to this approach is that there must be a demonstration of differences in the variety specific yield stability (sodicity contrast) over all the times of sowing—this did occur in 2019 where the site mean grain yields in TOS2 relative to TOS1 were similar (calculated from Table 2), but the varieties exhibited differences in yield -ICT i.e., escape is clearly indicated by the differences in the mean grain yield of the lines over different times of sowing. What this means is that “escape” can potentially be evaluated in an individual line where a substantial change in grain yield occurs in TOS2 relative to TOS1. Accordingly, the desirable lines with “sodicity tolerance” should have (1) high grain yields in the sodic soil accompanied, with (2) high yield stability over different sowing times in the sodic soil. This approach, using the single sodic soil, indicated that lines Condo, Krichaff, Ninja and Scepter were high yielding at both TOS (>1.7 t/ha), and they had <8% increases in predicted grain yield between TOS2 and TOS1 (calculated from Table 2). In contrast, lines like WA005, WA034w and WA332 were all low yielding (<1.5 t/ha), and they had 30–94% increases in grain yield between TOS2 and TOS1 (calculated from Table 2).

The water-limited grain yield (WLGY) potentials were 2.49 t/ha and 2.14 t/ha (calculated based on seasonal rainfall flowing formula adopted from Sharma and Anderson 2014 [58]) in 2018 and 2019, respectively. It appeared that apart from Scepter in 2019 at the sodic site, none of the lines could meet the WLGY potential threshold in any of the trials. While this generally low WLGY suggests scope for improving yield per se, our results demonstrate an opportunity of protecting the realisable potential by improving the accuracy of breeding for tolerance to soil stresses.
4.5. Physiological Traits Associated with Sodicity Tolerance

Final yield is defined by all the successful events from plant establishment to grain filling, and all the yield-contributing traits have a complementary role in the final yield. In wheat, sodicity has been reported to limit plant growth and development through poor germination, reduced tillering and flag leaf area, leaf appearance rate, decreased root and shoot growth, early senescence, and finally, lower grain yield [23,59–62]. In this study, overall no strong correlation could be demonstrated between Yield-ICT and ICT for any of the measured traits. However, different lines showed high tolerance for different traits. The tolerant lines showed tolerance to more numbers of agronomic traits as well as maintaining low leaf concentrations of some potentially toxic minerals like Al and B (Table 4). Lines that did not show the positive association of yield-ICT with ICT of any of the agronomic traits in fact were the most intolerant lines at both TOS (e.g., WA377, WA332, WA325 and Ninja).

As sodicity produces complex nature of stress including chemical, physical and physiological stresses, plants combine a suite of responses including a number of physiological and biochemical responses at the molecular, cellular, and whole plant level [63–66], which indicates that different lines might have evolved different survival mechanisms against these multiple stresses. This interpretation is also supported by the fact that the lines exhibiting positive tolerance at both times of sowing often showed tolerance against yield-building traits, while many of the intolerant lines were intolerant against all tested traits. Hence, we conclude that the sodicity tolerance in fact, comprises cumulative effects of multiple tolerances manifested through multiple yield building traits.

Maintaining grain and spike-related traits along with plant height were observed as the most important traits for a higher yield for lines growing in sodic soil since there were positive associations in the tolerant lines and negative in the intolerant lines. Plant height is an important trait that supports grain filling under stress conditions utilizing stored soluble carbohydrates when the plant senesces early due to stress [67]. Whether such relationships are the cause or the result of tolerance to sodic soil requires further research.

Sodicity tolerance of the genotypes was not correlated with any of the leaf mineral concentrations usually associated with sodic soils [27]; and this contrasts with several previous studies which reported a significant correlation of sodicity tolerance with high Na\(^+\) concentration, low K\(^+\) and K/Na ratio [68,69]. Since plants tend to adopt avoidance (exclusion) or osmotic adjustment (tissue tolerance) mechanisms for surviving in stress environments, we understand that in many soils it may be difficult if not impossible to correlate tolerance with tissue mineral content and use these criteria for selecting and breeding new cultivars unless exact mechanism have been identified and precisely marked. Another simple interpretation of these findings is that different sodic soils have different stresses, and there is a need to pyramid genes for multiple tolerance.

4.6. Conclusions

Good genetic diversity exists for grain yield on a natural sodic soil evaluated here. The tolerance screening methods evaluated here support that Yield-ICT is the best “tolerance” index compared to REI and TI as it is aimed at providing the most accurate measurement of tolerance, while other indices are confounded with yield potential. By utilizing ICT approach this study successfully identified four tolerant and four intolerant lines over both seasons and year. The TOS comparison of ICT demonstrated that germplasm screening following multiple sowing times in a season at the same location can further shortlist tolerance by distinguishing lines that are likely to have soil related tolerance rather than season related escape mechanisms. It is anticipated that the application of Yield-ICT criterion coupled with multiple sowing times will merit the identification of true tolerance to other soil stresses as well as other crops. These results should be used cautiously because the criteria for any comparisons between sites needs be validated, i.e., the non-stressed site should only have the targeted stress(es) reduced or eliminated, not have its own unique stresses. However, this is not always possible under natural conditions because soil gradients in a landscape seldom provide such plus minus contrasts.
Poor correlation of yield-ICT with the agronomic traits and physiological factors suggest that different lines have evolved survival mechanism as sodicity arises due to a range of multiple stresses (pH, ECe, B toxicity, carbonate toxicity, etc.). Hence, the identified tolerant lines at different TOSs should be subjected to further investigation to identify the mechanism of their tolerance with physiological and biochemical responses at a molecular and cellular level. The identified tolerant lines having high yield could readily be used by the farmers while the low yielding tolerant lines could potentially be utilized in the pre-breeding and breeding of cultivars for sodic soil. The likelihood of “sodicity tolerance” being tolerant to multiple stresses is also supported by the fact that the soil used here is only one of six major types of sodic sols ranging in salinity and pH (Section 4.1). The diversity of sodicity tolerance could also be confirmed with genetic studies from multi-locational sites relating genes for specific stress tolerance to grain yields of lines in sodic soils. Results presented here support that there is good genetic diversity for tolerance, and this supports further research on a diverse range of sodic soils (multiple sites at multiple times of sowing) to identify and develop genotypes tolerant to the wide range of stresses found in sodic soils.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/agronomy11081571/s1. Table S1: Monthly average weather conditions in the trial sites during the seasons 2018 and 2019 at Merredin, Table S2: Country of origin, AUS and IG No, and pedigree of wheat lines used, Table S3: Yield and leave tissue mineral concentrations in the lines grown at the sodic and non-sodic site in TOS1.

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