Kernel Distributions in Main Spikes of Salt-Stressed Wheat: A Probabilistic Modeling Approach

Scott M. Lesch,* Catherine M. Grieve, Eugene V. Maas, and Leland E. Francois

ABSTRACT

Grain development in wheat (Triticum aestivum L.) is a complex process that responds to interactions among primary genotypic factors and the environment. This study was conducted to determine the effects of salinity stress on kernel occurrence and kernel mass distributions within the main spike. Mexican semidwarf wheat cultivars Yecora Rojo and Anza were grown in sand tanks in the greenhouse with saline and nonsaline nutrient solutions. At harvest, each spikelet position and grain position was identified and the weight of every kernel was determined. Hierarchical multiple linear regression models were derived and fit to the kernel mass patterns. In a similar manner, logistic regression models were derived and fit to the kernel occurrence patterns. Kernel mass was shown to be highly dependent on spikelet location along the spike, kernel position within the spikelet, and salinity stress. Results from the logistic regression models confirm that these same factors affect kernel occurrence. Both types of statistical analysis are advantageous, since the changes in kernel occurrence and kernel mass distributions due to each of the above factors can be easily detected and studied.

GRain development in wheat is a complex process that responds to interactions among many primary genotypic factors and the environment. Two important yield components, the number and mass of individual kernels, may be reduced by adverse conditions through effects on floret development and fertilization, as well as on the size and partitioning of the assimilate pool. Interactions among florets at the time of anthesis and competition between the developing kernels for photosynthates influence the number and size of the kernels that are ultimately formed. Patterns of kernel set and growth in wheat spikes have been studied by removal of competing sink sites and/or by reduction of carbohydrate supplies through defoliation and shading (e.g., Rawson and Evans, 1970; Brenner and Rawson, 1978; Pinthus and Millet, 1978; Fischer and HilleRisLambers, 1978; Simmons et al., 1982; McMaster et al., 1987). Evans et al. (1972) suggested that the mechanisms involved in inhibition of kernel setting in the more distal florets and spikelets are more likely to be controlled by hormones than by competition for assimilates. Conversely, kernel development is determined by the availability of assimilates, the growth potential of the kernel and the resistance within the phloem to the movement of assimilates to the kernel (Brenner and Rawson, 1978). Proper analysis of yield component parameters is critical for the correct interpretation and understanding of the anatomical factors involved. Analysis of these yield parameters is complicated by the physical geometry of the spike; the potential occurrence and final mass of a kernel will be influenced by both the position of the spikelet along the spike and the position of the kernel within the spikelet. A further complication arises because of the stochastic nature of the spike development process. Not all spikes under the same environmental conditions will produce the same number of spikelets, and different spikelets within the same spike can exhibit quite different kernel set and kernel mass patterns.

In this paper, kernel occurrence and kernel mass distributions in mature spikes of two Mexican hard red spring wheat cultivars (Yecora Rojo and Anza) are determined. Distribution patterns and interactions among the kernels in the nonsaline control spikes are compared with salt-stressed spikes. To facilitate these comparisons, a series of empirically based, statistical models are developed and fit to the yield component data. Through the use of such models, formal tests concerning changes in the distribution patterns caused by salinity stress can be carried out.

The development of the models and the test results concerning salinity-induced changes in kernel occurrence and kernel mass distribution patterns are presented. Additionally, we discuss the motivation behind the model parameterization, as well as an anatomical interpretation of the parameter estimates and test results.

MATERIALS AND METHODS

Plant Culture

Yecora Rojo and Anza wheat were grown in six sand tanks in the greenhouse in Riverside, CA, during January through May 1989. Details of the growth conditions are given in a companion paper (Grieve et al., 1992). Three tanks of nonsaline control plants were irrigated with a modified Hoagland’s nutrient solution that had an osmotic potential ($\psi_o$) of -0.05 MPa and an electrical conductivity (EC$_{iw}$) of 2.0 dS m$^{-1}$. In the second set of three tanks, plants were salinized with nutrient solution that contained NaCl and CaCl$_2$ (2:1 molar ratio). The $\psi_o$ of this solution was -0.65 MPa; EC$_{iw}$ = 14.3 dS m$^{-1}$.

Approximately 10 plants of each cultivar were randomly selected from each tank. Mainstem leaves were identified as they developed and were tagged with distinctively colored wire rings. Plants were harvested at maturity; main spikes were dissected and examined in detail. Each developed kernel was identified by both its spikelet position and grain position within the spikelet. Spikelets were numbered acropetally, with spikelet position No. 1 being defined as the first visible node of the rachis. Within each spikelet, the basal floret (and the kernel therein) was designated as grain position 1, the second floret was designed as position 2, the third 3, etc. The recorded data consisted of whether or not a kernel occurred (developed) within each spikelet and grain position, and the weight of each developed kernel.

Since $<$1% of all the developed kernels occurred at or beyond Grain Position 4, we limit our investigation of ker-

Abbreviations: EC$_{iw}$, electrical conductivity of irrigation water; $\psi_o$, osmotic potential; iid, independently and identically; KMDP, kernel mass distribution potential; LDP, logistic difference probability; $\psi_o$, osmotic potential.
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Fig. 1. Geometric representation of a spike, showing how spikelet positions can be scaled into spikelet locations. The total number of spikelets produced on the spike was considered a stochastic nuisance parameter, and was removed through the scaling procedure before comparing spikes with different spikelet counts.

Spikelet Position Scaling

Statistical analyses of mainstem components based on the position of the individual kernels along the spike are complicated by the fact that, even within a given treatment, not all main spikes have the same number of spikelets. Therefore, a scaling procedure was used to facilitate the comparison of both mass and occurrence data from all the tagged plants in each treatment. Each spikelet position number was divided by 1.0 plus the total number of spikelets for that spike. Every spikelet position number was thereby converted to a spikelet location value contained within the (0,1) interval. This scaling procedure allowed for simultaneous comparison of all the yield data within a given treatment. This scaling approach is illustrated in Fig. 1. The example spike in this diagram has a total of 20 spikelets and five potential grain positions. These spikelet positions can be converted to 20 spikelet locations by dividing each spikelet position number by 21. After such a scaling, the mass of the kernels within each grain position could be plotted (along the 0,1 spikelet location axis) and directly compared with the kernel mass data from another spike having a different number of spikelets. The histogram to the right of the example spike in Fig. 1 shows the frequency count of total number occurring spikelets per spike for Yecora Rojo in the control treatment. Note that if we had limited our analysis to only those spikes with 21 spikelets (the most common spikelet occurrence rate), we would have had to discard almost one-half of the total available data from this treatment.

Statistical Methodology and Model Parameterization

As previously implied, any statistical model used to describe either the kernel mass or occurrence data should account for both spikelet location and grain position effects. However, differences between individual spikes within a given treatment can also be quite pronounced, and should be accounted for when possible. This is especially true when modeling the kernel mass data, since specific kernel mass features can vary considerably from spike to spike. Figures 2a and 2b highlight two important artifacts that consistently appeared in the data. In Fig. 2a, the observed kernel mass patterns within the basal grain position have been plotted for three spikes from the Yecora Rojo control treatment. Note that the relationship between kernel mass and spikelet location tends to be fairly consistent from spike to spike; i.e., the mass of the kernels in each spike tends to follow the same type of curved pattern across the spikelet locations. However, these patterns also appear to be shifted up or down the kernel mass axis. This shifting occurs because different spikes will tend to produce kernels of different mass, even under similar environmental conditions. In this paper we refer to such a change in the kernel mass distributions as a change in the spike's kernel mass distribution potential, and we develop models that can account for these KMDP differences.

In Fig. 2b, the individual kernel weights within Grain Positions 1 and 2 have been plotted for these same three spikes. Note that the correlation between the mass of these neighboring kernels is quite high. This type of correlation structure can be exploited during the modeling stage by developing hierarchical equations that relate the mass of an
The model describing kernel mass within the third grain position is:

\[ Y_{3k} = B_{02} + B_{12}[x] + B_{22}[x^2] \]

where \( x \) represents the spikelet location during the remainder of this paper. The kernel mass within the \( k \)th spike, and \( E(Y_{1k}) = B_{01} + B_{11}[x] + B_{21}[x^2] \)

Given the above considerations, grain position specific kernel mass distributions can be developed from logistic regression equations. For a given wheat variety and salinity stress level, define \( z_x,j,k \) as:

\[ z_x,j,k = \begin{cases} 1 & \text{if kernel mass distribution potentials}\newline \text{within the basal grain position, and mass of a kernel occurring in the} \\
\text{xth spikelet location and jth grain position of the} \\
\text{first two grain positions for the three spikes illustrated} \\
\text{expected mass of the Y}_{2k} \text{ kernel within the } k \text{th spike becomes:} \\
\text{mass distribution potentials across stress levels, independently of other factors. The full} \\
\text{expected mass of the Y}_{2k} \text{ kernel within the } k \text{th spike, given the observed weight of the } Y_{lk} \text{ kernel, is:}\newline\end{cases} \]

\[ E(Y_{2k} | Y_{lk}) = B_{02} + B_{12}[x] + B_{22}[x^2] + C_2[U_{2k} - U_{1k}] + I_2[z] + e_3 \]

\( e_3 \sim iid N(0, \sigma^2_3) \), and \( z \) again represents an indicator variable where \( z = 1 \) if \( Y_{2k} \) exists, or \( z = 0 \) if no kernel occurs at \( Y_{2k} \) and we replace \( Y_{lk} \) with \( Y_{2k} \) in the equation. The expected \( Y_{2k} \) kernel mass averaged across all \( k \) spikes from changes in salinity stress levels can then be defined to be \( E(Y_{2k}) = \sum_{k=1}^{nk} E(Y_{2k}) \)

Each of the models defined above relates the expected kernel mass to three factors: the spikelet location, grain position, and individual spike attributes. In Eq. \([1.0]\), the relationship between the kernel mass distributions and the spikelet location is constant across the spikes, while individual spike characteristics are accounted for through the \( C_2 \) and \( C_3 \) correlation parameters. By allowing for individual intercept estimates and the spikelet location is again specified to be constant across the spikes, while individual spike characteristics are accounted for through the \( C_2 \) and \( C_3 \) correlation parameters. The expected \( Y_{2k} \) kernel mass within the \( k \)th spike becomes:

\[ E(Y_{2k} | Y_{lk}) = B_{02} + B_{12}[x] + B_{22}[x^2] + C_2[U_{2k} - U_{1k}] + I_2[z] + e_3 \]

\( e_3 \sim iid N(0, \sigma^2_3) \), and \( z \) again represents an indicator variable where \( z = 1 \) if \( Y_{2k} \) exists, or \( z = 0 \) if no kernel occurs at \( Y_{2k} \) and we replace \( Y_{lk} \) with \( Y_{2k} \) in the equation. The expected \( Y_{2k} \) kernel mass averaged across all \( k \) spikes from changes in salinity stress levels can then be defined to be \( E(Y_{2k}) = \sum_{k=1}^{nk} E(Y_{2k}) \)

An important benefit derived from using these models is that is affecting the expected kernel mass can be tested from changes in salinity stress levels. This can be done by adjusting for the position-to-position correlation structure will help account for the differences in kernel mass incurred from spikelet location and/or grain position effects.
Next, separate the Zx,j,k data points into nonoverlapping sub-
parameter estimate is found to be statistically significant.
nominal term that can be fit to the data, such that the
where the superscript t represents the highest order poly-
qth interval. The following logistic regression model(s) can
resent these kernel occurrence frequer/~ies and m,~ rep~'esent
frequency by averaging across the Zx, k data. Let pq j rep-
and the mean spikelet location value associated with this
subset represents a specific spikelet location interval con-
section.
For a more detailed discussion on logistic regression model
building and testing, the reader is referred to Hosmer and
spikelet location axis will be presented in the discussion
determining where these differences are occurring along the
individual kernel mass deviations through both the
second and third grain-position models can respond to
kernel mass (identified in Fig. 3 by the letter A). The
viate too far from the general curve, such as the first
cannot respond to individual kernel weights that de-
mg). However, the model for this first grain position
tential (the KMDP estimate for this spike was 23.87
for this spike's particular kernel mass distribution po-
quadratic curve, as dictated by Eq. [1.0]. Fitting a
unique intercept estimate allowed this curve to adjust
error estimates were usually --10.0 mg, suggesting
that the mass of an individual kernel could generally
accounted for, since the data points are based on treatment
specific stress level to two factors: the spikelet location and
3. All the general F-tests concerning spikelet location
distributions across treatment levels are given in Table
mass estimate.

The advantage of working with averaged data is that
9 out of the 12 fitted models explaining between 78
and 88% of the observed variability. The mean-square
deviance residuals indicates only that differences between
and reduced models, to an appropriate chi-square distri-
... (0.90,0.98). (Spikelet location values never fell
below 0.02 or above 0.98.) The total number of spi-
developed, it was necessary to average the Z,,,i,k data.
The full data set consisted of 4960 kernels from 118 spikes; however,
99.8% of all the developed kernels occurred within
the total spikelet location axis; the subset bounds were
into 12 nonoverlapping subsets based on the spikelet
location values. Each subset covered exactly 8% of
the corresponding mean spikelet location values within the
subset.

Before the kernel occurrence models could be de-
veloped, it was necessary to average the Z,,,i,k data.

This pattern was not evident in the Anza cultivar.

There is also some evidence within the Yecora
453

Methods

RESULTS AND DISCUSSION

The kernel mass equation parameter estimates and
indicator variables, t-test statistics revealed that all pa-
summary statistics, found with the SAS (1985) GLM

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indicator variables, t-test statistics revealed that all pa-
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Table 2. Parameter estimates: Kernel mass equations for two wheat cultivars. (All parameter estimates are significant at the 0.01 level, unless otherwise noted.)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Yecora Rojo</th>
<th>Anza</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grain osmotic potential (MPa)</td>
<td>0.05</td>
<td>0.65</td>
</tr>
<tr>
<td>$E_{B0}$</td>
<td>30.26</td>
<td>37.25</td>
</tr>
<tr>
<td>$E_{B1}$</td>
<td>50.82</td>
<td>58.64</td>
</tr>
<tr>
<td>$E_{B2}$</td>
<td>29.30</td>
<td>30.70</td>
</tr>
<tr>
<td>$E_{B3}$</td>
<td>18.60</td>
<td>1.160</td>
</tr>
<tr>
<td>$E_{C2}$</td>
<td>0.872</td>
<td>0.773</td>
</tr>
<tr>
<td>$E_{C3}$</td>
<td>0.809</td>
<td>0.631</td>
</tr>
<tr>
<td>$E_{R2}$</td>
<td>0.867</td>
<td>0.779</td>
</tr>
<tr>
<td>MSE (mg)</td>
<td>11.14</td>
<td>7.74</td>
</tr>
</tbody>
</table>

* Significant at the 0.05 and 0.02 levels, respectively.

All individual intercept estimates are significant at the 0.01 level.

The decision to split the $Z_{x,j,k}$ data into exactly 12 subsets was not made arbitrarily. It was decided a priori that each of the $E_{C}$ estimates should be based on $\geq 50$ potential kernel occurrence counts. Partitioning the data into 12 subsets generally achieved this goal.

The logistic regression models were fit to these data by using the SAS CATMOD procedure (SAS, 1985); the resulting maximum-likelihood parameter estimates for each model are shown in Table 4. All the parameter estimates were significant through the second degree well below the $\alpha = 0.01$ level, indicating that a very strong relationship existed between the average kernel occurrence rate and spikelet location.

The cumulative deviance values (and corresponding $\chi^2$ probabilities) are given at the bottom of Table 4. These goodness-of-fit statistics suggest that the logistic regression models fitted to the Anza kernel occurrence rates were sufficient in explaining all of the observed occurrence rate variability. This was not the case for three of the six logistic regression models to fit to the Yecora Rojo data.

The predicted vs. observed kernel occurrence rates for the Anza data at -0.05 MPa are shown in Fig. 4 for the first three grain positions. In these plots, predicted vs. observed kernel masses for grain positions 1, 2, and 3 at each spikelet location in a Yecora Rojo control spike. "A": unusually low kernel mass in position 1; "B": the correct prediction of low kernel mass in position 2, based on the knowledge of the low kernel mass in position 1; "C": a correct upward adjustment in the prediction of the kernel mass in position 3, based on the knowledge of no kernel development in position 2.
Table 3. General F-tests: Kernel mass equations for wheat.

<table>
<thead>
<tr>
<th>Grain position</th>
<th>RSS</th>
<th>df</th>
<th>RSS</th>
<th>df</th>
<th>Hypothesis</th>
<th>F-value</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yecora Rojo</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1, 2, 3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>8307.89</td>
<td>868</td>
<td>8629.88</td>
<td>870</td>
<td>(B111, B211)</td>
<td>16.23</td>
<td>0.0001</td>
</tr>
<tr>
<td>2</td>
<td>8176.90</td>
<td>815</td>
<td>27787.8</td>
<td>818</td>
<td>(B021, B121, B221)</td>
<td>651.5</td>
<td>0.0001</td>
</tr>
<tr>
<td>3</td>
<td>5755.98</td>
<td>439</td>
<td>13333.0</td>
<td>442</td>
<td>(B031, B131, B231)</td>
<td>192.6</td>
<td>0.0001</td>
</tr>
<tr>
<td>2</td>
<td>7720.45</td>
<td>966</td>
<td>23942.2</td>
<td>969</td>
<td>(B022, B122, B222)</td>
<td>676.6</td>
<td>0.0001</td>
</tr>
<tr>
<td>3</td>
<td>6687.10</td>
<td>579</td>
<td>13904.5</td>
<td>582</td>
<td>(B032, B132, B232)</td>
<td>208.3</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

Residual sum of squares. Equations given in Appendix.

The observed average rates within each grain position appear to be well described by the fitted equations for this cultivar and treatment level.

The general X² test statistics, computed from the difference of the deviance scores, are shown in Table 5. All of the X² statistics were significant well below the α = 0.01 level, suggesting that the observed kernel occurrence distributions within both cultivars were influenced by the increased salinity.

Salinity-Induced Changes in the Kernel Mass Distributions

As indicated in Table 3, all of the general F-tests concerning spikelet location parameters revealed that significant changes in these estimates were occurring across the treatments. Therefore, understanding how these changes affect the estimated kernel mass becomes important.

Changes in observed kernel mass averages across treatments were discussed in detail in Grieve et al. (1992). Here we concentrate instead on how and where changes occur in the estimated maximum kernel mass. The fitted response equations were used to determine for each grain position the spikelet location yielding the maximum kernel mass and the estimated kernel mass for that location. In Table 6, the predicted kernel mass at the maximum kernel mass location is given for each grain position within both cultivars and treatment levels. Increases in the estimated maximum kernel mass ranged between 22 and 29%; all increases were statistically significant. Additionally, the largest kernel mass always occurred in Grain Position 2, the next largest in Position 1, and the smallest in Position 3. These results are similar to those found by Grieve et al. (1992) concerning changes in the average kernel mass across treatment levels.

The F-tests shown in Table 3 also suggest that a change in the kernel-to-kernel correlation structure may have occurred within the Yecora Rojo cultivar across treatment levels. However, the variability associated with the Yecora Rojo KMDP estimates decreased substantially when the -0.65 MPa stress level was applied, from 51.64 mg down to 11.25 mg. This in turn implies that the range in which an individual kernel mass could occur was reduced by half. Such a reduction is bound to lower the correlation estimate, since the strength of the kernel-to-kernel correlation will be directly related to the range of the kernel mass data.

Therefore, it seems more likely that the application of salinity stress caused the average kernel mass between spikes to behave more uniformly, rather than changing the correlation structure within the spike itself. This conclusion is supported by the lack of any significant

Table 4. Parameter estimates: Kernel occurrence equations for two wheat cultivars. All parameter estimates are significant at the 0.01 level, unless otherwise noted.

<table>
<thead>
<tr>
<th>Grain position</th>
<th>Osmotic potential</th>
<th>Parameter</th>
<th>Yecora Rojo</th>
<th>Anza</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td></td>
<td>B01</td>
<td>-4.388</td>
<td>10.03</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>B11</td>
<td>45.56</td>
<td>112.9</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>B21</td>
<td>-76.19</td>
<td>-324.4</td>
</tr>
<tr>
<td>1</td>
<td></td>
<td>B31</td>
<td>35.28</td>
<td>379.6</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>B41</td>
<td>NS</td>
<td>-157.0</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>B02</td>
<td>-4.450</td>
<td>-6.067</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>B12</td>
<td>34.66</td>
<td>47.01</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>B22</td>
<td>-36.22</td>
<td>-65.15</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>B32</td>
<td>NS</td>
<td>25.01</td>
</tr>
<tr>
<td>1</td>
<td></td>
<td>B03</td>
<td>-7.527</td>
<td>-15.21</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>B13</td>
<td>43.20</td>
<td>78.16</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>B23</td>
<td>-50.58</td>
<td>-79.95</td>
</tr>
<tr>
<td>1</td>
<td>Deviance</td>
<td>8.96</td>
<td>14.30</td>
<td>11.64</td>
</tr>
<tr>
<td>2</td>
<td>Deviance</td>
<td>23.21</td>
<td>17.03</td>
<td>13.56</td>
</tr>
<tr>
<td>3</td>
<td>Deviance</td>
<td>10.88</td>
<td>4.98</td>
<td>14.72</td>
</tr>
</tbody>
</table>

(Probability) (0.346) (0.046) (0.235) (0.261)

(Probability) (0.006) (0.030) (0.139) (0.879)

(Probability) (0.284) (0.836) (0.099) (0.610)

*,~ Significant at the 0.05 and 0.02 levels, respectively.

Parameter was not statistically significant, and hence was not included during the final model estimation process.
Hypothesis: The fitted logistic regression parameter estimates do not change between the -0.05 MPa and -0.65 MPa treatments.

Changes in the correlation parameter estimates for Anza (where the corresponding reduction in the variability of the KMDP estimates was much less severe).

The effect on a kernel’s mass when the kernel in the previous position fails to develop can be seen directly in Table 2. The estimates associated with the indicator variables imply that, in this case, the average mass of a kernel increased anywhere from 1.4 to 8.2 mg. These results indicate that the loss of a kernel within a spikelet may be partially compensated for by an increase in the mass of the adjacent kernel. Previous work (Rawson and Evans, 1970; Bremner and Rawson, 1978; Pinthus and Millet, 1978) has shown that removal of sink sites by sterilization of neighboring (adjacent) florets, particularly those in the central spikelets, leads to increased growth of the remaining kernels. This response may be the result of reduced competition for supplies of assimilates, minerals, and internal growth substances. Alternatively, this response may be due to the removal of an inhibitory effect, perhaps one of a hormonal nature.

Salinity-Induced Changes in the Kernel Occurrence Distributions

The X² test statistics in Table 5 confirm that the kernel occurrence distributions were also changing across treatment levels. As shown in Table 7, raising the salinity level tended to raise the overall average kernel occurrence rate within each grain position (with the exception of the first grain position in Anza); however, to understand how these kernel occurrence rates change along the spikelet location axis, direct comparisons of the fitted logistic regressions should be made.

One way to make such a comparison would be to plot the logistic curves predicted under both treatments on the same graph and look for where they differ. A natural extension of this approach would be to subtract one curve from the other; i.e., subtract the predicted kernel occurrence rates under the -0.65 MPa treatment from the predicted rates under the -0.05 MPa treatment at every point along the spikelet location axis. The resulting curve would represent the difference between the predicted probabilities, and hence the change in the kernel occurrence rate subject to a change in the spikelet location.

These types of plots, referred to in this paper as logistic difference probability plots, are shown for each cultivar and grain position in Fig. 5. There are some striking similarities between the LDP plots. For example, within the first quarter of the spike, the kernel
environmental conditions during the growth of the plant.

To individual spike characteristics and the prevailing position of spikelet position (location) is also clearly subject to occur more toward the terminal end of the spike, are salinity treatment. These increases, which tended to exceed the rates in the salinity treatments anywhere occurrence rates in the control treatments tended to increase more strongly up toward the spike apex. The kernel production potential in both cultivars seemed to have drop slightly near the spike base, but then again be related to the actual amount of available assimilates, which would explain the consistent increase in yield and mass. The results found in this study indicate that salinity stress can have a strong effect on the final kernel occurrence and kernel mass distributions within the spikes.

The cumulative effect of salinity stress on kernel growth in response to changing environmental conditions, such as temperature, available light and nutrient supply, and salinity, among others. Kernel production and mass are also influenced by environmental conditions, such as temperature, available light and nutrient supply, and salinity, among others. Kernel production and mass are influenced by fac-
tors unique to each spikelet, in addition to spikelet location and grain position effects. These factors could be interpreted as (nor can they take the place of) empirically based statistical models, which should not include assumptions on pathway resistance to assimilates, which would explain the consistent increase in yield and mass.

The degree of correlation between adjacent kernels found in this study seems to support such assumptions. The magnitude of the correlation parameter estimates within the models suggest that the mass and density of assimilates along the rachis. However, this parallel linkage of assimilates, which is linked in parallel to the source of assimilates, is strongly influenced by the potential for kernel production and the ultimate movements and biochemical response functions. In this manner, the maximum amount of information contained within the experimental data can be extracted and used in the formulation and/or testing of models based on anatomically based models. However, proper formulation and testing of models based on anatomically based models. However, proper formulation and testing of models based on anatomically based models. However, proper formulation and testing of models based on anatomically based models. However, proper formulation and testing of models based on anatomically based models. However, proper formulation and testing of models based on anatomically based models. However, proper formulation and testing of models based on anatomically based models.
wO = 1, w1 = x, w2 = x^2, vO = 0, v1 = x, v2 = x^2.

For data from the —0.65 MPa level, define wO = 0, w1 = 0, w2 = 0, vO = 1, v1 = x, v2 = x^2.

The full model is parameterized as:

\[ A \] \quad E(y_{kl}) = 501 k1 wO + 501 k2 vO + 5111 w1 + 5211 w2 + 5112 v1 + 5212 v2

The reduced model is parameterized as:

\[ B \] \quad E(y_{kl}) = 501 k1 wO + 501 k2 vO + Bu x + 521 x^2

The computed F-value represents a formal test of the hypothesis \( H_0 : (5111, 5211) = (5112, 5212) \).

Rejection of this test implies that the spikelet location (linear and quadratic) parameter estimates are changing across the treatment levels.

Grain Position 2

For kernel mass data from the —0.05 MPa level define wO = 1, w1 = x, w2 = x^2, vO = 0, v1 = 0, v2 = 0, and r1 = \( y_{lk} - u \), z1 = 0 (if the kernel in Position 1 occurs) or r1 = \( u_{lk} - u \), z1 = 1 (if the kernel in Position 1 does not occur), r2 = 0, and z2 = 0. For data from the —0.65 MPa level define wO = 0, w1 = 0, w2 = 0, vO = 1, v1 = x, v2 = x^2, r1 = 0, z1 = 0, and r2 = \( y_{lk} - \frac{u_1 + \ldots + u_{k-1}}{u_k} \), z2 = 0 (if the kernel in Position 2 occurs), or r2 = \( \frac{u_1 + \ldots + u_{k-1}}{u_k} \), z2 = 1 (if the kernel in Position 2 does not occur).

The full model is parameterized as:

\[ A \] \quad E(y_{lk}) = 5021 wO + 5022 vO + 5121 w1 + 5122 w2 + 5221 v1 + 5222 v2 + C21 r1 + C22 r2 + 721 z1 + 722 z2

The reduced model which is used to test for equivalent spikelet location parameter estimates across treatment levels is:

\[ B \] \quad E(y_{lk}) = 502 + 512 x + 522 x^2 + C21 r1 + C22 r2 + 721 z1 + 722 z2

The formal hypothesis being tested is:

\( H_0 : (5021, 5121, 5221) = (5022, 5122, 5222) \)

The reduced model which can be used to test for an equivalent correlation parameter estimate is:

\[ C \] \quad E(y_{lk}) = 5021 wO + 5022 vO + 5121 w1 + 5122 w2 + 5221 v1 + 5222 v2 + C31 r1 + C32 r2 + 731 z1 + 732 z2

The formal hypothesis being tested through this equation is:

\( H_0 : (C31) = (C32) \).

Grain Position 3

For kernel mass data from the —0.05 MPa level define wO = 1, w1 = x, w2 = x^2, vO = 0, v1 = 0, v2 = 0, and r1 = \( y_{lk} - u \), z1 = 0 (if the kernel in Position 1 occurs), or r1 = \( u_{lk} - u \), z1 = 1 (if the kernel in Position 1 does not occur), r2 = 0, and z2 = 0. For data from the —0.65 MPa level define wO = 0, w1 = 0, w2 = 0, vO = 1, v1 = x, v2 = x^2, r1 = 0, z1 = 0, and r2 = \( y_{lk} - \frac{u_1 + \ldots + u_{k-1}}{u_k} \), z2 = 0 (if the kernel in Position 2 occurs), or r2 = \( \frac{u_1 + \ldots + u_{k-1}}{u_k} \), z2 = 1 (if the kernel in Position 2 does not occur).

The full model is parameterized as:

\[ A \] \quad E(y_{lk}) = 5031 wO + 5032 vO + 5131 w1 + 5132 w2 + 5231 v1 + 5232 v2 + C31 r1 + C32 r2 + 731 z1 + 732 z2

The reduced model which is used to test for equivalent spikelet location parameter estimates across treatment levels is:

\[ B \] \quad E(y_{lk}) = 503 + 513 x + 523 x^2 + C31 r1 + C32 r2 + 731 z1 + 732 z2

The formal hypothesis being tested is:

\( H_0 : (5031, 5131, 5231) = (5032, 5132, 5232) \)

The reduced model which can be used to test for an equivalent correlation parameter estimate is:

\[ C \] \quad E(y_{lk}) = 5031 wO + 5032 vO + 5131 w1 + 5132 w2 + 5231 v1 + 5232 v2 + C3 y_{2k} - u^2, z1 + 731 z1 + 732 z2

The formal hypothesis being tested through this equation is:

\( H_0 : (C31) = (C32) \).