148. Studies on the Right- and Left-Handedness of Spikelets in Einkorn Wheats.¹⁾ 1.

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The stereo-isomeric dimorphism of the first leaf of certain *Gramineae* which finds its expression in the direction—right or left—in which this leaf is folded, attracted the attention of a few geneticists in the earlier days of Mendelism. The first attempt in this line was made by Compton (1910) who studied the proportion of right- and left-handed seedlings in barley and maize. Compton showed in two-rowed barley that right- or left-handedness of an individual is not inherited, but the ratio of right- and left-handed seedlings remains constant, namely $Rh/Lh = 1.4$.

Although Compton found that *Rh*- and *Lh*-seedlings in maize occur in equal numbers, he obtained different ratios when the kernels were collected separately from the odd and the even rows. Namely, kernels from odd rows gave an excess of left-handed seedlings, while those from the even rows produced an excess of the opposite kind.

Recently Kihara (1950) published a short review on right- and left-handedness in plants with regard to the arrangement of right- and left-handed spikelets in several varieties of Einkorn wheats (*Triticum monococcum* L.).

The designations used by Kihara are as follows:

1. Right (*R*)- and left (*L*)-handed seedlings are such whose first leaf is folded in the manner showed in Figs. 1a and 1b, respectively. Compton used the same designations in the opposite sense.
2. The *R*- or *L*-handedness of a spikelet is determined by the position of the first floret in the spikelet. The spikelet will be *R*-handed when—viewed from its dorsal side—the first floret is toward the right hand of the observer, *L*-handed when it is toward his left hand (Fig. 2).
3. The spikelets are designated by successive numbers from the lowest first upwards, beginning with 1. In this way one of the two rows will receive the odd numbers and will be called the odd row (*O*), while the opposite row, having the even numbers, will be the even row (*E*).

Kihara examined 108 ears of *T. monococcum* and arrived at the following conclusions:

1. The ratio of right- and left-handed spikelets is approximately 1:1.
2. The ratio is quite different, if we take into consideration the *R/L*-character of the first spikelet in the row. Namely, the row which begins with a right-

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handed spikelet showed considerably more such spikelets than left-handed ones; correspondingly, a row whose first spikelet was left-handed showed an excess of left-handed spikelets. The ratios $R:L$ in both cases were 1.6 and 0.58, respectively.

Fig. 2. Right- and left-handed spikelets.

Fig. 1a and b. Right- and left-handed seedlings.

3. The regularity in the successive alternation of right- and left-handed spikelets is most apparent near the third spikelet (88%). It becomes less and less definite in the upper part of the ear.

4. Of the seedlings obtained from the first florets of the R -handed spikelets 60% were right-handed. Among the corresponding seedlings from the L -handed spikelets 60% were left-handed.

5. The first leaf of the seedlings obtained from the second florets tends to hold in the opposite direction to that of the seedlings from the first florets.

Fig. 3. Examples of OL - and OR - ears.

The present paper deals with statistical studies of the R/L -character of spikelets in *Triticum monococcum* var. *flavescens*.

If we take the flag-leaf as the starting point of observation, we will find a regular alternation of R - and L -handed leaves downwards¹⁾ and R - and L -handed spikelets upwards. If the flag-leaf is R -handed, right-handed spikelets will prevail in the odd row; has the flag-leaf the opposite character, L -handed spikelets will prevail in the odd row (OL -ears and OR -ears, respectively/ Fig. 3/).

From the examination of 821 ears, 411 OL -ears and 398 OR -ears were obtained. The remaining 12 ears could not be classified because their spikelets were rudimentary. From these results it may be assumed that the proportion of OR - and OL -ears in the

1) The folding of the sheath coincides with that of the blade. However, there are some exceptions.

population is 1:1 ($\chi^2 = 0.209$, $D.F. = 1$, $0.5 < P < 0.7$). In order to make clear the R/L -relationship between flag-leaf and spikelet and between different spikelets, Figs. 4a and 4b were constructed from 400 ears with R -handed flag-leaves and 378 ears with L -handed flag-leaves, respectively. Of 400 ears with R -handed flag-leaves (Fig. 4a)

Fig. 4a.

Fig. 4b.

Figs. 4a and 4b. Diagrams of the distribution in the examined ears of the R/L -handed flag-leaves and spikelets.

372 proved to have *R*-handed first spikelets (*R*), while only the remaining 28 had *L*-handed first spikelets (*L*). Thus, flag-leaf and first spikelet show a very strong tendency toward a similar conformation of the *R/L*-character. On the other hand, the second spikelet shows a strong tendency in the opposite direction from that of the first one, while the third spikelet repeats the *R/L*-character of the first one. This means that a strong *R/L*-antidromy controls the symmetry conditions of the Einkorn ear. The regularity, however, diminishes with the ascending position of the spikelets. In general, the *R*- or *L*-handedness of any spikelet in the odd row will mostly coincide with that of the flagleaf, while in the even row the tendency will be reversed.

If this pattern is maintained, we can call the relationship "concordant"; then, the designation "discordant" will be applied to the exceptions of the rule.

The situation will be clearer, if we use the percentage of normal sequences to express the proportion of concordance. Let us take as example the second spikelet in Fig. 4a. The spikelet in this position should be *L*-handed, according to the above mentioned norm. Therefore, the proportion of concordance (*C*) can be calculated by $(362+20)/400$ ($= 95.5\%$). For all the 778 *RO*- and *LO*-ears *C* can be calculated by $(362+20+343+18)/778$ ($= 95.5\%$).

Assuming that the determination of right- and left-handedness is controlled by the threshold reaction, which is the result of the external influences and the specific potency, the relative value of the potency denoted by *Y* will be calculated by finding the "probit" of concordance proportion (*C*) from Fisher and Yates' "Statistical Tables" (1949), subtracting 5. Here we assume that the external influences are represented by a random variable which distributes normally.

Computing the potencies of determination (*Y*) from the proportions of concordance (*C*) in the 809 samples of ears and plotting the values upwards in serial order (solid line in Fig. 6), one will see the gradual increase and decrease of the values of *Y*, with the highest point at the third spikelet.

We guess therefore that continuous gradients of the potencies of determination must be there in the ears before the right-and left-handedness of the spikelets is determined.

From the analysis of the curves in Fig. 6, we found that the rate of decrease in the potency at any point of the ear will be approximately proportional to the magnitude of the potency at that point with addition of small quantities (β) characteristic of the given species. This relation will be expressed by the formula:

Fig. 5. Curves showing the relation between the percentage of concordance (ordinate) and the position of the spikelet on the ear (abscissa).

$$(1) \quad -\frac{dY_x}{dx} = \alpha Y_x + \beta$$

In this formula, x represents the position where the x th spikelet appears and Y_x is the value of Y in that position, while α and β are constants which are characteristic of the given genotype. For *T. monococcum flavescens* examined in 1949, the values of α and β were about 0.20 and 0.01 respectively. This formula, though it can not be applied in the apical or basal part of the ear, will give some clues for a study on the mode of gradient formation.

Determination of the right- and left-handedness in any spikelets is not independent of that of the spikelets in its vicinity.

This will be demonstrated as follows.

Let $Y_{\bullet x}$, $Y_{\circ x}$, $Y_{\circ\circ x}$, ... etc. respectively be the values of Y in the x th spikelet if the spikelet immediately below it ($(x-2)$ th), the second one below ($(x-4)$ th), the third one below ($(x-6)$ th) and so on are discordant. Then it will be found that:

$$(2) \quad Y_{\bullet x} < Y_{\circ x} < Y_{\circ\circ x} < \dots \leq Y_x$$

Namely, the more distant the discordant spikelet, the smaller

is its effect on decreasing the value of Y_x . In Fig. 6 the curves for Y_x , $Y_{\bullet x}$, and $Y_{\circ x}$ are shown.

Effects produced by the discordant spikelet immediately below and belonging to the opposite row ($(x-1)$ th spikelet) will be described in the next paper.

Fig. 6. Curves showing the distribution of relative values of the potencies for the determination of the *R/L*-handedness in the ear. Abscissa: position of the spikelet on the ear. Ordinate: relative value of potency.

From the above analysis it seems that the determination of right- and left-handedness starts in the vicinity of the third spikelet where the potency is at the highest, and then proceeds upwards and downwards as the differentiation of the ear goes on.

The adequacy of this hypothesis will be judged by a precise examination of developmental processes in the primordial ears.

References.

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