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THE EARLY STAGES OF DEVELOPMENT IN THE RYE SPIKE

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INTRODUCTION

For the working method of various breeding programs, it should be of importance when the stages in the development of cereals could be indicated by symbols. In breeding work involving early-ripening varieties, it may be useful to know the course of development. For example, in the case of two varieties ripening at the same time, it is possible that in one of them the first stages proceed rapidly, whereas the later stages pass rather slowly. In the other variety the reverse may be the case. When we know this, the desired result may be expected from intercrossing them. Also it should be useful, for instance in the case of rye, to determine the right moment of colchicine treatment. It has appeared that colchicine treatment has only a slight effect, or no effect at all, when the reproductive phase has started (BREMER-REINDERS and BREMER, 1952). For determining the right stage of sensitivity to growth substances, which are used in weed control (ANDERSEN, 1952), it may be also of importance.

In most publications describing the developmental morphology of the inflorescence of grasses, no symbols are used for the successive stages. As a rule only a short description is given. FEEKES (1941), however, uses figures, but these chiefly refer to later stages, such as shooting, flowering and ripening. Other investigators, e.g. Blaauw and coworkers, used symbols for the description of the development of bulbs. The developmental morphology during transition from the vegetative to the reproductive phase is divided in stages which are indicated by Roman figures, so that by using a certain figure the stage of flower development can be indicated with sufficient exactness. However, difficulties arise when the development of the tulip (MULDER-LUYTEN, 1928) has to be compared with that of a more complex inflorescence as, for example, that of the hyacinth (BLAAUW, 1920). So in later years the indication by Roman figures has been abandoned, and only terms as final growing point, flower primordium, etc., are used. In 1942 BEYER, in order to arrive at greater uniformity, proposed to use symbols of general value, but he maintained the stages I and II introduced by BLAAUW. Stadium I means, in all crops, that the growing point is still vegetative. Stadium II begins when flower initiation has started, which is recognizable by a sudden elongation of the growing point. The following principal stages are the initiation of perianth, anthers and pistil. To indicate these stages in various bulb species in a corresponding way, BEYER uses the initials of the latin name of the organ that becomes visible.

The aim of this article is to give a description of the normal course of development of the rye plant, in particular the first beginning of flower initiation and the further stages of development of the young ear. The developmental stages will be indicated by a symbol, for which I have used the abbreviations of the latin names of the flower structures, following therefore the idea of BEYER.

DESCRIPTION OF THE GROWTH DEVELOPMENT

The development of winter rye will be described in this paper following the observations which for the greater part were made in the years 1941–1944. When rye is sown at the normal time, about the middle of October, the plantlets emerge from the soil about ten days later. Soon after the coleoptile has appeared, it splits and the first leaf comes out. After some weeks, about half December, three leaves are visible, the third still being partly covered by the leaf sheaths of the two preceding leaves.

When examining the young plant in this stage, in the axils of the first and the second leaf tiller buds are found, which are not yet visible externally. After the first three leaves have been removed, the younger leaves enclosed in their sheaths become visible. In this stage the growing point is short, having a length of about 500–600 μ. The sixth leaf primordium encloses the growing point collar-shaped; the seventh leaf initial is the basal one. Some younger leaf primordia initiate acropetally as laterally alternating ridges.

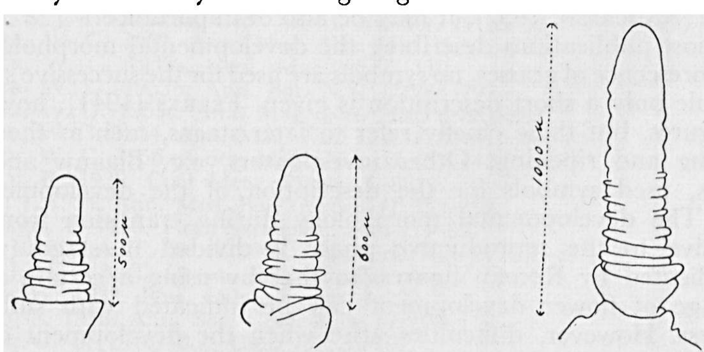

Fig. 1. Stadium I. Growing point vegetative. Length 500 μ, length 600 μ. Stadium II. Growing point elongated; initiation of the reproductive phase. Length 1000 μ.

As long as the growing point is vegetative, producing leaves only, the plant is in Stadium I of its development. During the winter months growth is going on slowly. In the course of January, depending on the weather, the third leaf has emerged completely, while in most plants the fourth leaf appears already. The seventh leaf primordium now overarches the growing point collar-shaped. At the time when the plant in the field shows the third or fourth green leaf, the initiation of leaves on the main axis has practically come to an end. Tillering now becomes visible externally in many cases the tiller bud in the axil of the first leaf and in favourable cases also that in the axil of the second leaf already show a green leaf extending from its prophyl Also in the axil of the third leaf a tiller bud is produced.

When sowing takes place somewhat earlier, tillering has progressed a little further. In that case most of the plants show three or four tillers. The differentiation stage of the growing point of the main axis, however, is the same. If growth conditions are favourable, so if spacing is sufficient and food supply is satisfactory, some more tillers are produced during further development. A few of them are still branches of the first order, but for the greater part they are branches of the second or higher order, that is tiller buds are produced in the axils of leaves of the older side branches.

After the development of leaves and side branches, the plant passes into the reproductive phase, that of spike differentiation. This turning-point comes rather suddenly, by the end of February or the beginning of March, more or less influenced by the weather conditions during winter and also slightly dependent on the date of sowing. According to NOGUCHI (1929) the transition from vegetative to reproductive phase takes place about 60 days before heading. At that time the main axis shows 5 or 6 green leaves. In most cases the coleoptile cannot be recognized any more. The 8th leaf now encloses the growing point collar-shaped; the 9th leaf initial is the basal one. PURVIS (1934) states that spike differentiation as a rule begins after 9 leaves have been produced.

In preparation for spike differentiation the growing point begins to elongate, the length increasing rapidly to about 1 mm and the shape becoming more cylindrical. Stadium II of the development has started (Fig. 1). The elongation of the growing point may be compared with the corresponding phenomenon in other plant species where the apex of the growing point more or less suddenly becomes hemispherical. Often there is a short time during which the formation of new leaves at the base of the elongated growing point is continued, while in the upper middle region flower differentiation starts. This stage is marked by the occurrence of double ridges, especially in the basal region, instead of the single ridges during leaf initiation only. The upper ridge of each pair, properly representing the interbracteal space, may produce all the spikelet structures, the lower one in some cases developing into a leaf. This can also be concluded from the measurements given by SCHOUTE (1910, Tables pp. 80–83). From these figures we see that the first eight leaves possess a rather short leaf sheath, while the 9th and following leaves have a much longer leaf sheath, being stem-enveloping leaves initiated at a moment when spike differentiation and elongation of the stem internodes already have begun. According to SCHOUTE the number of leaves on the main axis may vary from 12 to 15 for Petkus rye.

The differentiation of the spikelet primordia begins with a swelling of the interbracteal space (Fig. 2). This takes place more or less simultaneously over the whole length of the elongated growing point, except at the top and at the base. The lower ridge of each pair of ridges representing the bract primordium is not or but slightly developed over the greater part of the length of the young ear. With a spike length of slightly more than 1 mm, there are 5 or 6 spikelet

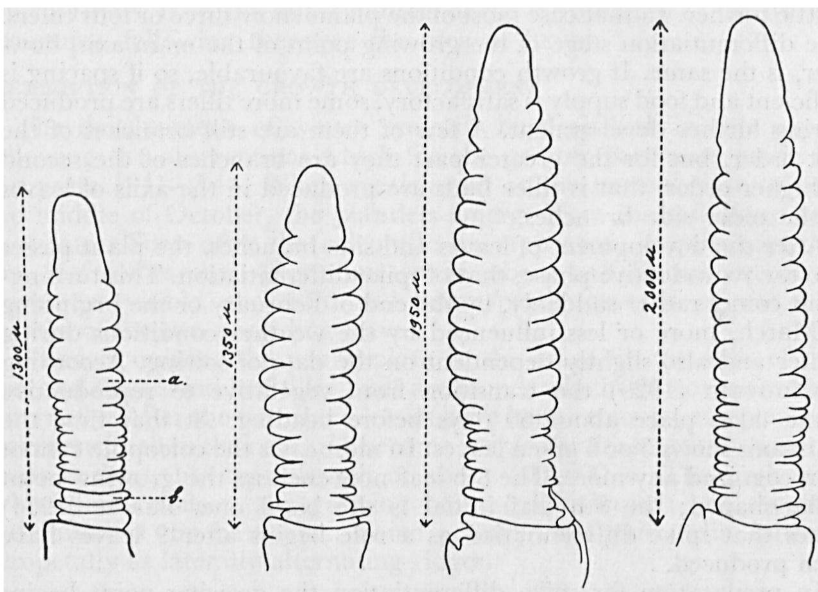

Fig. 2. Stadium Spi. Spikelet primordia initiated. a. Spikelet primordium. b. Leaf primordium. Length of young spike: 1300, 1350, 1950, 2000 μ.

primordia on each side. In the basal region double structures are still visible. The spikelet primordia reach fairly large proportions before their differentiation is continued; the young ear, which originally is cylindrical, becomes more elliptical in transverse section. We shall indicate this stage with the symbol Spi (spicula = spikelet). A young spike of 1.5 mm length in the stage Spi contains, for instance, 9 spikelet primordia on one side and 10 spikelet primordia on the other side. These spikelet primordia are largest in the central region of the young ear, diminuating in size towards top and base.

During these preliminary processes of the reproductive phase shooting has started, becoming visible with the beginning of internode elongation of the stem. This elongation of the internodes of the stem is continued during all further stages of the reproductive phase.

Meanwhile differentiation continues, the first structures becoming visible in the spikelets in the central portion of the young spike, which now has reached a length of about 2 mm. The empty glume (bracteola) is the first structure of the spikelet to differentiate. It appears as a transverse ridge on both sides of the spikelet initial. This stage may be indicated by the symbol Gl (gluma = glume), see Fig. 3.

The differentiation of the first flower primordia follows immediately. During this process the number of spikelets still increases. Until the moment that the spike has reached a length of about 2 mm, the number of spikelets varies from 10 to 15 on one side of a spike. This number increases to about 20. In countings e.g. 17 spikelets were found on one side and 18 on the other side of the spike, in another case this number was 21 and 22 resp. on both sides of the spike. The ultimate number of spikelets of an adult spike is reached when the young spike has a length of about 4 to 5 mm. The activity of the meristematic tissue at the top of the spike, however, continues during the period of spike development. It stops when flowering begins and the last initiated spikelets never complete their development.

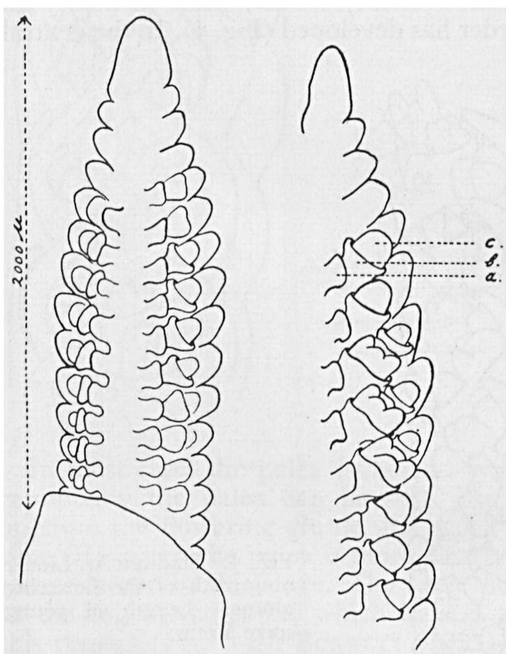

Fig. 3. (left). Stadium Pr. Flower primordia initiating. Length of young spike 2000 μ.

Fig. 3. (right). Stadium An. Primordia of anthers initiating in flowers of the first order. Flower primordia of the second order developing in the spikelets of the central region.

a. Empty glume. b. Flowering glume (palea inferior). c. Flower primordium.

When differentiation of flower primordia begins, so when the young ear has still a length of about 2 mm, a new stage sets in, to which is given the symbol Pr (primordium). In the axils of the glumes the flower primordia soon become distinct by the flowering glume (palea inferior) surrounding as a semicircular zone a hemispherical meristem from which the remaining organs will originate (Fig. 3). By some authors (BONNETT, SHARMAN) the flowering glume is called lemma; also in "Grassen en Granen" (Grasses and Cereals) (1951) this term is used by JANSEN.

Very soon, first once more in the spikelets of the central region, three small protuberances appear upon the meristem which at first is hemispherically shaped. These protuberances are the primordia of the anthers (Fig. 3). This stage is marked by the symbol An (androecium). During this stage the margin of the flowering glume grows vigorously at its basal side. This outgrowth is the beginning of the development of the awn. At the same time a flower of the second order becomes visible.

When the young spike has reached a length of 5 mm, it looks like Fig. 4. This development from the first elongation of the growing point, thus from the beginning of Stadium II, till the moment at which the spike is 5 mm long, proceeds very rapidly. It takes place in two to three weeks, as a rule from the middle of March (about March 20) to early in April (about April 10).

On all spikelets, except the youngest at the top and the base of the spike, the anthers and the undifferentiated pistil meristem of the flowers of first order are now clearly visible, while in nearly all spikelets a flower of second order has developed (Fig. 4). In the central

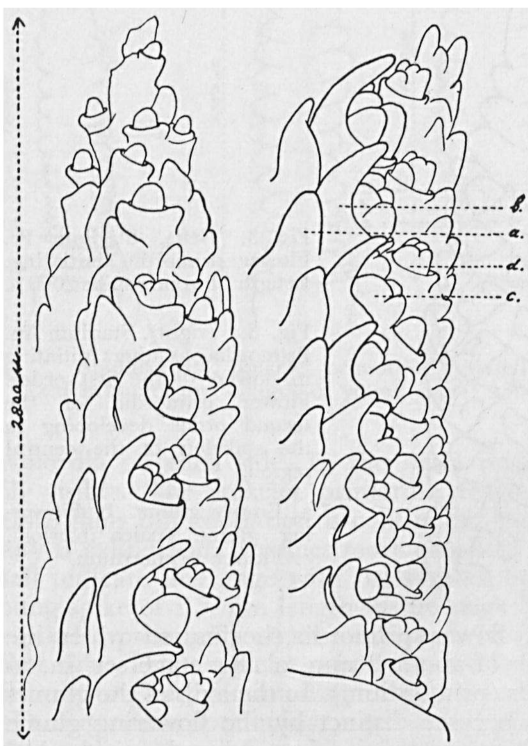

Fig. 4. Stadium Ar. Linear outgrowth of the flowering glume. Length of young spike 5 mm.

a. Empty glume. b. Flowering glume (palea inferior). c. Flower of the first order. d. Flower of the second order.

region of the spike the flower primordia of the second order already show the anthers, initiating in the hemispherical meristem. The characteristic feature in this stage is the enormous linear outgrowth of the flowering glume. This outgrowth is already recognizable as the future awn of the adult spike. This stadium has been indicated with the symbol Ar (arista = awn).

The differentiation of the palea, as it is mostly called instead of palea superior, cannot be followed, since it is hidden by the flower parts of the spikelet below.

During further growth, when the young spike has reached a length of about 8 mm, the anthers show a longitudinal partition (Fig. 5). This stadium has been indicated by the symbol Th (theca = pollen sac).

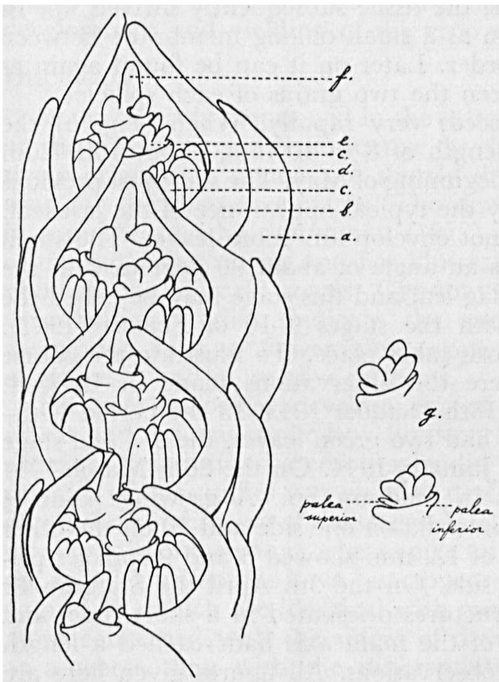

Fig. 5. Stadium Th. Anthers lobed; the anthers are divided into two pollen sacs. Length of young spike 8 mm. Side view.

a. Empty glume. b. Flowering glume. c. Anthers lobed. d. Central meristem of flower of the first order. e. Flower of the second order. f. Apex of the spikelet axis.

g. Flower of the second order, showing flowering glume (palea inferior), palea (superior), three anther primordia and the central meristem.

In most cases the palea (superior) is not visible at this stage. Exceptionally the palea can be seen just at the base of the anthers opposite the flowering glume, the palea being a small organ at this time. However, the palea is more clearly shown in the flowers of the second order in this stage. The same holds for the younger flowers at the top of the spike, which have a more favourable position in this respect (Fig. 5 g). Bonnett (1935) also says that the initiation and the development of the palea, soon following that of the flowering glume, is very difficult to observe, because it is hidden by the other spikelet structures. This is confirmed by Sharman (1945), who mentions that it is very difficult to determine when the palea is actually initiated.

The pistil meristem in the centre is still undifferentiated. It will be formed from the central portion of the meristem located between the anthers, but this occurs considerably later than the initiation of the anther primordia. According to Bonnett (1935) the differentiation of the pistil into ovary, style and stigma cannot be observed.

After the differentiation of the flower parts the further elongation proceeds rapidly. During this process the activity of the meristematic tissue at the top of the main axis and at the top of the spikelet axis is continued. The number of flowers per spikelet, however, is limited in the case of rye. In Fig. 5 the initiation of as much as five flower primordia can be observed. Only two of them will come to full development; exceptionally three flowers may develop. As soon as pollination in a spikelet begins, the activity of the meristematic tissue stops and the tip degenerates, the tissue subsequently shrivels up. In the adult spike it can be seen as a small oblong membrane between the two flowers of the first order. Later on it can be found again as a brush-shaped thread between the two grains of each spikelet.

Further development proceeds very rapidly. When (Fig. 5) the young spike has reached a length of 8 to 10 mm, about 10th–20th April, heading follows in the beginning of May. The stage just previous to heading is distinguished by the typical appearance of the last leaf. The sheath of this leaf does not envelop any more leaves. The small lamina of this last leaf makes an angle of about 90 degrees with the stem. This leaf is called the flag leaf and this stage may be called the flag stage. It corresponds with the stages 9–10 of Feekes (1941).

During this flag stage meiosis takes place. To illustrate the course of events I will describe here the observations made in 1943/44. Petkus rye was sown on the 18th October 1943. In the period 15th–26th November the plantlets had two green leaves, the 3–4 leaf-stage was reached on the 2nd–4th January 1944. On the 26th March 1944 the reproductive phase was in Stadium Spi. A growing point of 1.5 mm showed 9 spikelet primordia on one side and 10 on the other side. Another growing point of 1.2 mm showed 8 and 9 spikelet primordia respectively on each side. On the 5th April the Stadium Pr was reached, more flower structures originated in a short time, and on the 13th April the spike of the main axis had reached a length of 5.3 mm, as a mean of 5 observations. All figures given here are the mean value of 5 observations on five different spikes. On the 21th April this spike length amounted to 16.0 mm, on the 28th April to 27.0 mm. On the 5th May spike length had increased to 85.0 mm; tetrads had not yet developed at this time. On the 12th May the late flag stage was reached; the plants were almost heading now. The spike length was now 109.0 mm; pollen grains had developed, and the shape of the tetrad was still distinguishable. In a somewhat younger spike of 95.0 mm still large groups of tetrads were connected together. In a somewhat older spike of 117.0 mm the surface of the pollen grains had become more smooth; the original shape of the tetrads is still more or less recognizable. On the 19th May the mean spike length amounted to 110 mm, on the 26th May it had the same length. Pollination began on the 30th May. The spike did not elongate any more; the mean of weekly measurements, continued till in July, lay between 110 and 120 mm (resp. 120–113–110–118–116 mm).

After heading has started, which normally takes place in the beginning of May, rapid extension of the ear follows, and the crop is fully headed a week to about ten days later. A few days later the stage of flowering already begins; five to ten days after full heading, flowering is general. This usually happens in the last week of May or early in June.

In order to distinguish the stages between heading and ripeness of the grain, it is recommended to use Feekes' method. Each figure of this scale indicates a certain morphological stage of development. The grain is ripe about six weeks after full flowering. With the last phase, the dry-ripeness of the grain, the rye plant has completed its development and yielding of the crop can soon follow now.

Discussion

As was already mentioned in the introduction, in most publications on the vegetative and reproductive development of grasses, the successively originating organs are shortly described, but no symbols are used for the successive stages. The development of rye is described in a publication by Schneider (1912). He gives a short description of the successive stages, and has illustrated his paper by some microphotographs of early stages. Gregory and Purvis (1937) in their vernalisation studies, indicate the successive stages with a short description, such as "flower initials appear", "anthers lobed", "growth of glumes", and more of such terms.

The morphological development of the inflorescence of barley, wheat and oat was studied by Bonnett (1935, 1936, 1937). He gives an exact description based on splendid microphotographs. However, the aim of this studies was more to describe the development than to give a short indication of the stages. Van de Sande Bakhuyzen (1942) gives graphs of the young wheat spike up to a length of 2 mm, at which the spikelet primordia have just appeared. Though he uses the terms 1a and 1b, which are identical with our Stadia I and II, his study is more concerned with the stages of development of the wheat plant as a whole than with the differentiation of the flower structures. For his purpose he used Feekes' classification.

A confirmation of our experience that colchicine treatment gives the best results when it is applied to very young seedlings, is found in a paper by Sharman (1945). Sharman mainly studied, by means of serial sections, the developmental anatomy of the growing point and the young inflorescence of Gramineae. The origin of the buds has a special significance in cereal and grass breeding techniques involving the use of colchicine to obtain chromosome doubling. From his work it becomes evident that generative cells, female as well as male, originate in the hypodermic layer. In Gramineae the ovule is not derived from the carpel wall but from the rest of the axis on which the palea, stamens and carpel are borne. He emphasises that in the case of colchicine treatment this has to be applied at an early stage in the development of the seedling.

SUMMARY

In this paper a description is given of the normal course of development of the rye plant. Symbols are used to indicate the successive stages of development. In agreement with Blaauw and co-workers the indications Stadium I (vegetative phase) and Stadium II (beginning of reproductive phase) are maintained. To distinguish the earlier stages of the reproductive phase, use is made of abbrevations

of the botanical name of the organs whose development in a certain stage is characteristic for what one observes.

Stadium I: Growing point vegetative; only leaf initials present.
Stadium II: Elongation of the growing point; beginning of the reproductive phase. Spike length $\pm$ 1 mm.
Stadium Spi: Spikelet primordia developing.
Stadium Gl: Initiation of the empty glumes on both sides of spikelet primordia.
Stadium Pr: First flower primordia become visible. Spike length $\pm$ 2 mm.
Stadium An: Primordia of anthers become visible.
Stadium Ar: Rapid elongation of the awn on the flowering glume of flowers of the first order. Flower primordia of higher order become visible. Spike length $\pm$ 5 mm.
Stadium Th: Anther primordia of flowers of the first order are divided into two thecae. Spike length $\pm$ 8 mm.

For older stages it is recommended to use the classification of FEEKES (1941).

REFERENCES

ANDERSEN, S. 1952. Physiol. Plant. *5*:199.
BAKHUYSEN, H. L. VAN DE SANDE. 1943. Landbouwk. Tijdschr. *55*:533.
BEYER, J. J. 1942. Med. L. H. S. 46, verh. *5*:1.
BLAAUW, A. H. 1920. Med. L. H. S. *18*:1.
BONNETT, O. T. 1935. Journ. Agric. Res. *51*:451.
BONNETT, O. T. 1936. Journ. Agric. Res. *53*:445.
BONNETT, O. T. 1937. Journ. Agric. Res. *54*:927.
BREMER-REINDERS, D. E. and G. BREMER. 1952. Euphytica *1*:87.
FEEKES, W. 1941. Versl. techn. tarwe Commissie. *17*:525.
GREGORY, F. G. and O. N. PURVIS. 1937. Ann. of Bot. N.S. *1*:569.
MULDER, R. and I. LUYTEN. 1928. Verh. Kon. Akad. Wetensch. Amsterdam 26 no. *3*:1.
NOGUCHI, Y. 1929. Journ. Coll. Agric. Imp. Univ. Tokyo *10*:247.
SCHNEIDER, E. 1912. Beitr. z. Pflanzenzucht *2*:129.
SCHOUTE, J. C. 1910. Verh. Kon. Akad. Wetensch. Amsterdam 15 no. *2*:1.
SHARMAN, B. C. 1945. Bot. Gaz. *106*:269.
SOEST, J. L. VAN e.a. 1951. Grassen en Granen. Tjeenk Willink Zwolle.