THE DEVELOPMENT OF THE OAT PANICLE 1

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INTRODUCTION

Oats (Avena sativa L.) differs from the other commonly grown small grains by having an inflorescence in the form of a panicle, while the inflorescences of wheat, barley, and rye are spikes. The panicle consists of a main axis with subdivided branches grouped in clusters (half whorls) at the nodes of the main axis. The arrangement of the clusters or half whorls is alternate and the spikelets are pediceled. On the other hand, the spike is an unbranched inflorescence in which the spikelets are sessile on the main axis.

A panicle differs from a spike in the plan of differentiation and development, as well as in form. However, it is not the purpose of this paper to compare or contrast the development of the panicle with the development of the spike, but to illustrate and describe the principal stages in the formation of the oat panicle and flower.

Few descriptions of the development of the oat panicle have been published. Cannon (4) 2 studied the spikelet development of Avena fatua L., describing and illustrating various stages in the development of the flower and flower parts. He also studied the formation of the male and female gametophytes, fertilization, and the subsequent development of the Caryopsis. The description of the development of the oat panicle given by Noguchi (6) is brief and the paper contains only three figures. In addition to other grasses, Arber (1) has discussed the morphology of several forms of Avena.

MATERIALS AND METHODS

The methods used in taking the photomicrographs in this article are similar to those already described (2, 3).

Plants were grown in the field and greenhouse. They were sampled from time to time to obtain successively advanced stages of development. The panicles were dissected for study and photographing.

DESCRIPTION OF PANICLE DEVELOPMENT

The oat stem, like that of barley and wheat (2, 3) passes through two stages in its development. In the first stage the growing point remains short, the leaf initials differentiate, leaves grow, and tiller buds develop in the axils of the leaves at the base of the stem. During the second stage the internodes of the stem elongate, and the branches, spikelets, and flower parts differentiate and develop.

Two growing points (pl. 1, A and B), show the first stage in the differentiation and development of an oat stem. The growing point in plate 1, A was removed from the stem of a plant showing two leaves.

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2 Reference is made by number (italic) to Literature Cited, p. 982.
These two leaves and the third leaf initial have been removed to show the growing point and the position and size of the remaining leaf initials. The fourth leaf initial partly encloses the growing point, the fifth leaf initial is seen as a ridge across the growing point, and the growing point itself appears as a smooth, rounded projection above the fifth leaf initial (pl. 1, A, I, 5, and gp).

A more advanced stage in the development of a leaf initial is presented in plate 1, B, L. The growing point with the fourth leaf initial appearing as a ridge across it, can be seen through the slit between the leaf margins. As growth continues one leaf margin laps over the other, and the blade becomes rolled.

An oat panicle, as above defined, is a many-branched determinate inflorescence consisting of a main axis from which arise lateral axillary branches which are grouped on alternate sides of the main axis at its nodes. The main axis and each of the lateral branches terminate in a single apical spikelet. The main axis is therefore a determinate inflorescence. The branches have been designated as branches of the first, second, or third order depending upon their point of origin, i.e., whether they arise from the main axis (first order) or from the lateral branches (second or third order).

Previous to the differentiation of the branches of the panicle, the growing point elongates, but the elongation is not so marked as in barley or wheat. This difference between oats and barley or wheat lies, probably, in the difference in the number of nodes on the main axis of the inflorescence. The average number of half whorls of branches on the panicle of some oat varieties, according to Fore and Woodworth (5), may range from 5 to 7, while a wheat or barley spike may have from 7 to 20 or more nodes. The averages mentioned vary according to variety and growth conditions.

Panicle formation is first indicated by the appearance of single, lateral, alternate projections (pl. 1, C, and D, B) arising in the axils of leaf initials (pl. 1, C and D, I) beneath the apex of the growing point (pl. 1, C and D, t). At first one, two, and later, several projections can be seen (pl. 1, D). These are the primordia of the branches of the first order.

The sequence of differentiation of the branch primordia of the different orders can be traced in plate 1, C to F, inclusive. The differentiation of the branches of the first order has just been described. As the branch primordia of the first order increase in size at those nodes where many lateral branches are found, branch primordia of the

EXPLANATORY LEGEND FOR PLATE 1.

A. Leaf initials and growing point of an oat plant in the two-leaf stage: li, Fourth leaf initial; 5, fifth leaf initial; gp, growing point. *X 40.

B. Leaf initial nearly enclosing the growing point: L, Third leaf initial. *X 40.

C. First stage of panicle development: li, Leaf initial; bi, branch initial, first order; t, tip of main axis. *X 35.

D. First stage of panicle formation, showing several branch initials: li, Leaf initial; bi, branch initial, first order; 5, tip of main axis. *X 35.

E. A panicle at the beginning of the formation of branches of the second order: li, Leaf initial; bi, branch initial, second order; t, tip of main axis. *X 35.

F. A panicle at the beginning of the formation of branches of the third order: bi, Branch initial, third order; li, Leaf initial; bi, branch initial, second order; t, tip of main axis. *X 35.

G. A panicle at the beginning of spikelet differentiation: e, Empty glume; g, lemma; 51 and 52, initials of the second and third flowers. *X 35.

H. The apical spikelet of the central axis, very much enlarged: e, Empty glume; g, lemma; an, anther; 51 and 52, initials of the second and third flowers. *X 55.

I. A panicle showing the relative stages of spikelet development. Empty glumes partly enclose the spikelets: e, Collar; e, empty glumes. *X 20.

J. A panicle showing part of the spikelets enclosed by the empty glumes. The empty glumes have been removed from the apical spikelet of the main axis: c, Collar; e, empty glumes; 51 to 56, first to fifth flowers. *X 20.
FOR EXPLANATORY LEGEND SEE OPPOSITE PAGE.
PLATE 2

FOR EXPLANATORY LEGEND SEE OPPOSITE PAGE.
second order appear beneath the apex and on alternate sides of the first (pl. 1, E, b). In turn and in the same manner, primordia of the branches of the third order arise from the second (pl. 1, F, b).

All the primordia of the lateral branches of the various orders arise in the axils of leaf initials (pl. 1, C, D, and E, l). The leaf initials can be clearly seen at the basal nodes of the main axis (pl. 1, D, and E, l). The leaf initials become successively less distinct from the base of the main axis upward to the tip, and likewise, they are less distinct on the branches of the second order.

It should be noted that all branch primordia arise beneath the apex of the parent axis (pl. 1, C to F). The apex of the branch primordium is the region from which the spikelets differentiate; therefore, new branches arise subapically from the parent axis. Branches elongate between the spikelet and their attachment to the parent axis.

Spikelet differentiation begins first with the spikelet at the tip of the central axis (pl. 1, F, t) and proceeds basally in succession at the tips of the primordia of the branches of the first order. At the nodes the sequence of spikelet differentiation is (1) branches of the first order, (2) branches of the second order, and (3) branches of the third order. To generalize, those branch primordia that differentiate first are the first to show the differentiation of spikelets.

The beginning of the sequence of spikelet differentiation can be seen in plate 1, G, by noting the more advanced stage of differentiation of the spikelet at the tip of the panicle in comparison with that of the two just below it. The branches at the base of the panicle have not yet shown any evidence of spikelet differentiation. Decidescence occurs in the same order as indicated for spikelet differentiation.

Differentiation of the empty glumes is the first indication of spikelet development (pl. 1, F and G, e). The pair of empty glume initials first appear as prominent ridges, one slightly above the other and each half encircling the branch primordium just beneath the apex (pl. 1, F, e). The meristem from which flower initials are formed is irregular in outline and extends above the empty glume initials. The empty glumes grow and enclose the developing flowers (pl. 1, I and J, e).

Within the spikelet the flowers differentiate acropetally. The flowers are alternate and attached to a short rachilla (pl. 1, H, J, and pl. 2, F). Flower primordia first appear as protuberances beneath the apex of the growing point above the empty glume initials (pl. 1, F, f designate). The more basal flower is always more advanced in its development than those above it.

In oats the basal flower and the next one above it are usually fertile, but the third flower does not often produce a kernel. While stamens and pistils differentiate in nearly all the flowers, those stamens

EXPLANATORY LEGEND FOR PLATE 2.

A. An early stage of pistil and anther development: p, Pistil; an, anther. × 50.
B. Anthers and an oat pistil at the beginning of the differentiation of the styles: s, Style initial. × 50.
C. A pistil of oats at the beginning of the elongation of the styles: o, Ovary; s, style. × 35.
D. A later stage of pistil development: o, Lodicles; o, ovary; s, style. × 35.
E. A pistil of oats showing elongation of the styles and enlargement of the ovary: o, Ovary; s, style. × 40.
F. A spikelet of oats, empty glumes removed, to show the position and development of the flowers and awn on the first flower; f1 to f4, First to fourth flowers; a, awn; gp, growing point. × 20.
G. An oat flower, one anther removed, with the styles covered with papillae, the primordia of the stigmatic branches: o, Lodicles; o, ovary; s, style; an, anther. × 40.
H. An oat flower, one anther removed, showing the development of the lodicules and stigmatic branches: a, Lodicles; s, stigma; an, anther. × 20.
I. A fully developed oat flower; o, Lodicules; s, filament; st, stigma; an, anthers. × 15.
J. Unfertilized oat flowers which have opened for pollination: st, Stigma. × 1½.
K. Sterile flowers: f1 to f5, First to third flowers. × 8.
and pistils in all the flowers above the second flower (pl. 1, J, fl; and fl;), and pl. 2, F, fl to fl;), usually remain small and rudimentary. In plate 2, K, fl; the rudiment of the third flower is shown. The remainder of the infertile flowers can be found in the folds of the lemma of the third flower.

The parts of the flower differentiate acropetally. First the lemma and then the palea appear as transverse ridges across the flower initial (pl. 1, G, g, and H, g). Soon the anther initials appear as small papillae above the glume initials (pl. 1, H, an) and finally the pistil differentiates from the meristem between the anthers at the apex of the growing point.

Anthers first appear as papillae upon the meristem above the flowering glume initials. Very early in the development of the anther the four chambers or locules can be identified. Even before the stage shown in plate 2, A; the anthers have separated from the meristem beneath them and filaments have formed. From this stage, as far as external appearances indicate, little change occurs in the anthers except an increase in size.

At the time the three papillae or anther initials appear, a fourth papilla, the pistil initial, can also be seen. At first the pistil shows no change except an increase in size.

Differentiation of the pistil begins with the formation of a ridge (pl. 2, A, p). The ridge does not at first completely encircle the pistil initial and is more prominent on the side next to the lemma. A papilla, the primordium of the ovule, can be seen in the opening between the ends of the crescent-shaped ridge.

Pistil development is continued by the extension of the ridge entirely around the growing point, enclosing the ovule initial. The margins of the ridge on either side, opposite the laterally placed anthers grow more rapidly than any other portions of the ridge. These two rapidly growing points are the style initials (pl. 2, B, s).

Increases in the length of the style initials, in the size of the ovary, and the closing of the opening above the ovule are shown in plate 2, C, D, and E. The differentiation and development of the ovule cannot be followed in these illustrations, but the various stages of ovule development have been adequately described by Percival (7) for wheat.

The stigmatic branches are the last of the parts of the pistil to differentiate. They first make their appearance upon the styles as papillae (pl. 2, G), increase in length (pl. 2, H, st), finally attain full size and are covered throughout their length with projections which function as lodging points for pollen grains (pl. 2, I, st).

Some of the stages in the development of the lodicules are shown, beginning with plate 2, D, lo. In the specimens shown in the photomicrographs of the earlier stages of flower development (pl. 2, A, B, C) the lodicules were destroyed when the lemma was removed to expose the pistil. The lodicules first appear as blunt projections located on either side of the flower at the inner margins of the palea. They increase in size and become rounded at the base and pointed at the tip as shown in plate 2, H, lo, after which there is very little change.

The chief function of the lodicules is to force the lemma and palea apart and open the flower at anthesis by becoming turgid and thus increasing in size. This function is illustrated in plate 2, J, which is a spikelet taken from a plant grown in the greenhouse. Many times
under certain greenhouse conditions viable pollen is not produced and unfertilized flowers open day after day over a considerable period of time.

SUMMARY

A study of the morphological development of the oat panicle was made by dissecting the growing points and panicles from stems in different stages of development. The principal stages of development are shown in photomicrographs.

An oat stem passes through two stages of development. In the first stage leaves and tillers are produced and in the second stage the internodes of the stem elongate and the panicle and its parts differentiate and develop.

Panicle formation is first indicated by the appearance of single, lateral, alternate projections arising in the axils of leaf initials beneath the apex of the growing point. These projections are the primordia of the branches of the first order.

Branches of the second and third order are produced from the parent axes in the same manner that the branches of the first order are produced from the main axis.

Spikelets differentiate from the tips of the branch primordia. Spikelet differentiation begins first at the apex of the main axis and proceeds basally on the branches of the first order and in sequence on the branches of the second and third orders.

The empty glumes are the first of the spikelet parts to differentiate. The flowers of a spikelet differentiate acropetally.

Flower parts differentiate in the following order: Lemma, anthers, palea, lodicules, and pistil.

Ovary, styles, and stigmas is the order of differentiation of the parts of the pistil.

Since the main axis and all branches terminate in spikelets, a panicle can be called a determinate inflorescence.

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