THE DEVELOPMENT OF THE INFLORESCENCE
OF AVENA SATIVA, L.*

(Communicated by Professor R. D. Watt.)
(With seven text-figures.)

(Read before the Royal Society of New South Wales, Aug. 7, 1929.)

Introduction.

Very little investigational work of a detailed microscopic nature has been done with oats, the greater importance of wheat having eclipsed the other cereals, with perhaps the exception of barley, which, owing to its malting qualities, has received a great deal of study, especially in connection with the grain. Cannon (2) made a very complete study of the development of the flower and embryo of Avena, fatua, but paid no special attention to the development of the inflorescence as a whole.

While a detailed description of the mature panicle of oats is deemed unnecessary, for the sake of completeness, some reference must be made to those special features which have a definite morphological bearing on the developmental work that follows.

The main axis or rachis of the inflorescence is a continuation of the stem of the plant, and is normally straight or only slightly undulating. Each half whorl of branches arises from a node in the rachis similar to the nodes of

* The morphological work included in this paper is a small section of a dissertation (Callaghan (1)) presented at Oxford for the degree of Doctor of Philosophy, and as yet unpublished.
the lower unspecialised portions of the culm. The branching of the main axis is racemose, that of the side branches, cymose.

A scheme of branching is indicated in Figure (1), which according to Zade (11) was propounded by Fernekeess (8). From this and from figures (6 and 7) it will be seen that
the branches decrease in length from those of the lowest node, which are the longest, to those of higher origin on the rachis.

The spikelet represents the unit of inflorescence and consists of a short axis, the rachilla, bearing one to four flowers, one, two, or three of which may develop, the upper flowers, or flower, remaining rudimentary and imperfect.

In sharp contrast to one another are the equilateral, or spreading panicle, and the unilateral, or one-sided panicle. The branches of the latter remain almost erect and closely adpressed to the rachis, whilst twisted growth completes the apparent one-sidedness.

Attention is drawn to the nature of the branching from the lowest node of the unilateral panicle. The branching from the first node of the rachis in this case is morphologically the same as in the equilateral panicle, but the secondary branching is delayed somewhat, so that variously long intervals occur between the node, or point of initial branching, and the actual point of isolation of the secondary branches, and in some instances a false node is the result.

Denaiffe and Sirodot (4, loc. cit. p. 40) have described and figured abnormal nodes of unilateral panicles. Etheridge (5) and Marquand (10) regard the false node phenomenon as varietal, and both use it in their classifications for purposes of distinguishing between certain varieties of *Avena sativa orientalis*.

Figure (2) shows the nature of the branching from the first node of various forms. A represents that of an equilateral panicle showing the branches isolated at a level corresponding to that of the "collar". B is of the unilateral type, and in this there is a short interval between the level of the "collar" and the actual point of isolation
of the branches. In the abnormal unilateral forms, the condition shown in B is extenuated still further, and the branches are consolidated for some distance above the actual node, not only with themselves, but together with the rachis. The false node thus formed is illustrated in A, D, and E of figure (2). The faint suture there shown is usually quite distinct along the rachis, between the false node and the true node below. Intermediate expressions are commonly met with in the same variety.

The nature of the "collar" is similarly very variable. In D the latter extends from the level of the node to the point of isolation of the branches; in C it is only partially extended in this way; while in E, it is not extended but remains near the node, as in the normal panicle. This "collar" is present in all oat inflorescences, and in the -equilateral panicles of two recently evolved Australian varieties, (Boppy and Kiah), it has been observed as a distinct bract extended into a leaf-like flange.

Developmental Phases.

Several very important changes take place in the development of the plant between the time of the unfolding of the first foliage leaf and that of the fifth. Briefly these may be stated as, (1) the initiation of adventitious root development, (2) the beginning of internode elongation, resulting in the so-called "shooting" of the stems, (3) the establishment of tiller buds in the axils of the coleoptile and of the first three or four leaves, and (4) differentiation of the inflorescence primordium at the apex of the primary shoot. The first three of these important changes develop simultaneously, but the rudiments of the inflorescence do not appear until the tillering process is under way, and after its origination no further leaf rudiments appear, and all the tillering buds that are to be formed as direct off-shoots of the main axis are already differentiated.

Fig. 2.

Showing variations in the manner of branching from the lowest node of the rachis. A, that of an equilateral panicle; B, C, D, and E, various forms of the unilateral Panicle, c, "collar" or vestigial bract; s, suture. ×3.

E—August 7, 1929.
of the branches. In the abnormal unilateral forms, the condition shown in B is extenuated still further, and the branches are consolidated for some distance above the actual node, not only with themselves, but together with the rachis. The false node thus formed is illustrated in C, D, and E of figure (2). The faint suture there shown is usually quite distinct along the rachis, between the false node and the true node below. Intermediate expressions are commonly met with in the same variety.

The nature of the "collar" is similarly very variable. In D the latter extends from the level of the node to the point of isolation of the branches; in C it is only partially extended in this way; while in E, it is not extended but remains near the node, as in the normal panicle. This "collar" is present in all oat inflorescences, and in the equilateral panicles of two recently evolved Australian varieties, (Hoppy and Kiah), it has been observed as a distinct bract extended into a leaf-like flange.

**Developmental Phases.**

Several very important changes take place in the development of the plant between the time of the unfolding of the first foliage leaf and that of the fifth. Briefly these may be stated as, (1) the initiation of adventitious root development, (2) the beginning of internode elongation, resulting in the so-called "shooting" of the stems, (3) the establishment of tiller buds in the axils of the coleoptile and of the first three or four leaves, and (4) differentiation of the inflorescence primordium at the apex of the primary shoot. The first three of these important changes develop simultaneously, but the rudiments of the inflorescence do not appear until the tillering process is under way, and after its origination no further leaf rudiments appear, and all the tillering buds that are to be formed as direct off-shoots of the main axis are already differentiated.
It is evident, therefore, that the rudiments of the mature plant, excepting accidents, are established by about the time of the unfolding of the fifth leaf, those of the main axis by the commencement of the fourth leaf-stage, and subsequent growth is concerned with the development of the inflorescences and the elongation of the internodes of both main and lateral axes, the latter synchronizing for the most part with the unfolding of the successive leaves of the plant.

* Accidents to the plant such as fungus or insect attack, or destruction by grazing animals.

---

Fig. 3.

Diagram to show the state of development of the young plant at the close of the fourth leaf-stage. The main axis is represented by 1 and successive leaves of that axis, commencing with the coleoptile, as \( \frac{1}{4}, \frac{2}{4} \) etc. and the shoots as 11, 12 etc. \( r \), roots, and \( p \), rudiments of the inflorescence. \( \times 12 \).
It is evident, therefore, that the rudiments of the mature plant, excepting accidents,* are established by about the time of the unfolding of the fifth leaf, those of the main axis by the commencement of the fourth leaf-stage, and subsequent growth is concerned with the development of the inflorescences and the elongation of the internodes of both main and lateral axes, the latter synchronizing for the most part with the unfolding of the successive leaves of the plant.

* Accidents to the plant such as fungus or insect attack, or destruction by grazing animals.
The state of development of the young plant at the close of the fourth leaf-stage, when the folded tip of the fifth leaf is just peeping, is represented diagrammatically in figure 3, and the relation and orientation of the axes and leaves is shown in figure 4.

Development of the Inflorescence.

The foregoing remarks make it clear that the development of the inflorescence commences very early in the life of the plant after all the leaf rudiments have formed. The first signs of development are evident at the close of the third leaf-stage (see figure 5, A). Two low, primary ridges of tissue, similar in origin and continuing the alternate arrangement of the foliage leaves, make their appearance around the periphery, and at the base of the merismatic apex (figure 5, C1 and C2 of all drawings). These flanges mark the positions of the first and second nodes of the rachis, and they persist as vestigial structures in the mature inflorescence, referred to previously as the "collars."

The meristem above these nodes then elongates and at the same time bulges of tissue originate throughout its length (see figure 5, E), each extending partially around the primordium. These subsequently develop into the branches of the higher nodes. Thus in the eighth drawing of figure 6, the initial of branch a, is accompanied by the alternate branch b at a lower level on the rachis, represented in sections 7 and 6; and similarly down the rachis (Ax) the alternate branches d, e, and / originate in that sequence, as the remaining sections of figure 6 show. For some time the chief development of the inflorescence is concerned with the higher-placed branches, followed later by an elongation of the internode between the lower nodes, and branching from the axils of the vestigial bracts.

Median longitudinal sections of the developing inflorescence. A, at the close of third leaf stage; B, fourth leaf stage; C, fifth leaf stage; D and E, sixth leaf stage, and F, close of sixth leaf stage. c1 and c2, collar or vertigial bract of lowest and second lowest node of the rachis. ×83.
The state of development of the young plant at the close of the fourth leaf-stage, when the folded tip of the fifth leaf is just peeping, is represented diagrammatically in figure 3, and the relation and orientation of the axes and leaves is shown in figure 4.

Development of the Inflorescence.

The foregoing remarks make it clear that the development of the inflorescence commences very early in the life of the plant after all the leaf rudiments have formed. The first signs of development are evident at the close of the third leaf-stage (see figure 5, A).

Two low, primary ridges of tissue, similar in origin and continuing the alternate arrangement of the foliage leaves, make their appearance around the periphery, and at the base of the merismatic apex (figure 5, c₁ and c₂ of all drawings). These flanges mark the positions of the first and second nodes of the rachis, and they persist as vestigial structures in the mature inflorescence, referred to previously as the "collars".

The meristem above these nodes then elongates and at the same time bulges of tissue originate throughout its length (see figure 5, E), each extending partially around the primordium. These subsequently develop into the branches of the higher nodes. Thus in the eighth drawing of figure 6, the initial of branch a, is accompanied by the alternate branch b at a lower level on the rachis, represented in sections 7 and 6; and similarly down the rachis (Ax) the alternate branches d, e, and f originate in that sequence, as the remaining sections of figure 6 show.

For some time the chief development of the inflorescence is concerned with the higher-placed branches, followed later by an elongation of the internode between the lower nodes, and branching from the axils of the vestigial bracts.
Successive stages in the development are shown in the drawing of figure 5, representing median longitudinal sections of the developing inflorescence. The leaf-stage is recorded in each case by way of correlating vegetative development with that of the inflorescence. By reference to figure 5, it is evident that until the sixth leaf of the

axis has unfolded no very marked advance is made in inflorescence growth. During the sixth leaf-stage, however, the full complement of branch primordia are established, the last of which to appear being that from the axis of the lower flange or vestigial bract. This phase may be followed by reference to the transverse sections of figure 6,
where the lowest branch primordium is represented as a bulge of tissue, \( f \), in the axis of the vestigial bract \( c_1 \); whilst in alternate arrangement with the latter, the next lowest branch \( e \), in the axis of a second vestigial bract \( c_2 \), has already reached the stage of rebranching, as the two portions marked \( e \) in the third drawing of the same figure indicate. Further progress in the growth and rebranching of the lower branches \( f \) and \( e \) are traced in the successive drawings of figure 7. These drawings are transverse representatives of the median longitudinal section shown in figure 5, F.

Each branch primordium that arises undergoes rapid elongation accompanied by a similar growth in length of the rachis between them. Spikelet primordia develop at the apex of each branch, whilst others arise sympodially along the axis of the branches. The spikelet terminating the rachis is the first of the panicle to develop. Spikelet development, however, does not come within the province of this paper. Figure 6 shows a series of transverse sections through a developing inflorescence at the same stage as that depicted longitudinally in figure 5, E, and in this, marked ts, the first evidence of spikelet formation at the apex of the rachis is shown. Further, it will be seen that although the terminal spikelet is at this advanced state of development, branching has only just begun at the lowest node. This figure also shows the regular alternate manner of branching throughout the inflorescence.

**Significant Relationships.**

The early stages above described, during which the foundations of the plants' yielding capabilities are being laid down in the form of inflorescence and spikelet primordia, mark the first, and probably the most important, critical period of its existence. It is during this period
that the plant decides, as it were, on the production possible, from the cultural material available.

The phenomenon described by practical workers with oats as "bolting", results in very poor panicle develop-

Fig. 7.
Series of transverse sections through the two lowest nodes of the rachis of an inflorescence at the same stage of development as F in figure 4. The indications are the same as those in figure 6. Note the spikelets of f in various stages of development. \( \times 78 \).

ment. Two papers by Elliott (6, 7) deal with the specific problem of Oat Blast and Sterility in Oats; in these the fact is established that these lesions are non-pathogenic, and that they are most probably of a physiological nature.
"Bolting" differs to some extent from Oat Blast described by Elliott (6, 7), in that many sterile spikelets may appear on otherwise fully developed panicles; nevertheless, the conditions seem to be related in certain cases. Oat Blast, as Elliott (6, 7) points out, is probably controlled by weather conditions at the time of panicle exsertion. This latter period is without doubt the second crucial stage in the life of the plant, and cultural conditions then materially affect the ultimate yield of each inflorescence.

In plants that have "bolted" the two lower nodes, or even more, fail to develop branches, and the panicle may only produce five to ten spikelets, or as occasionally happens, only the terminal spikelet. The conditions of culture as controlled by soil and weather, and the time of sowing are intimately connected with the development of the panicle. If the equilibrium of growth is interfered with at the time of development of inflorescence primordia, shooting of the culms may progress rapidly following on more favourable conditions, allowing only time for the establishment of the upper branches and spikelets of the panicle. In all cases of poorly developed panicles, however, the two vestigial bracts demarking the lower nodes of the inflorescence are clearly defined; this is to be expected from the order of development of the inflorescence parts.

It is suggested that the recently evolved science of photoperiodicity may have a significant bearing on the above problem, for late sowings appear to result in a higher percentage of bolters, or panicles bearing sterile spikelets. The length of day may determine the phase of rapid growth that results in reproduction at a time when the plant is physiologically unprepared.

From figure 3, it will be seen that prior to the elongation of the internodes, the inflorescence and four or five of the higher internodes are crowded together at the apex of each.
stem. It is at this stage (i.e., the fourth or fifth leaf-stage) according to Cunliffe, Fryer and Gibson (3) that the plant is most liable to Frit Fly attack. From the foregoing developmental description several reasons for the noticeably high mortality of plants at this specific stage present themselves.

(1) The three or four highest nodes of the plant are crowded together and surmounted by the developing inflorescence, as yet very small, thus the larva passing down between the folded leaves and leaf-sheaths at this stage is very soon brought into contact with the most actively-growing regions of the plant, and is more liable to destroy the shoot while the inflorescence is so small and accessible.

(2) The concentration of sugars in the region of the developing inflorescence and the unelongated internodes is probably at its highest during the life of the plant at this period prior to active elongation of the stems and panicle formation.

(3) As the larva is small, a certain amount of leverage gained from the tightly folded young leaves and leaf-sheaths at this stage may facilitate its entry, and at the same time direct it to the growing apex of the plant.

The first of these points must, it seems, have a significant influence upon the mortality of the plants. Once the internodes commence to elongate, the nodes become more widely separated and the inflorescence is carried higher, thus the chance of the plant surviving an attack should increase accordingly. Further, there is a decided strengthening and thickening of the stem and leaf-sheath tissues after the initial elongation of each internode.

1. Frit Fly (Oscinella frit) fortunately is unknown in Australia, but in Great Britain and Europe generally, it is by far the most troublesome and destructive pest attacking oats.
From observations and measurements of the internodes of two widely different varieties up to the fifth-leaf stage, little difference in the rate of internode growth was observed, though the varieties showed constant differences in internode length. Whether there is a varietal difference between the rate of internode growth after the fifth leaf-stage, which is the critical period from the point of view of Frit Fly attack, remains undecided, but it is a point worthy of careful study. Differences in such rate of elongation may have some bearing upon the higher susceptibility of some varieties over others.

The most likely reason, however, for the extreme susceptibility of the plant at the fourth and fifth leaf-stages, is that concerned with the nature of the cell sap at that period. Should the concentration of sugars be the controlling factor in attack, it becomes a difficult and well-nigh impossible task to find an index to explain the comparative resistance of certain varieties.

Recently Finnell (9) published data indicating different results from the grazing of wheat at various stages in its early growth. Oats now take their place as a grazing proposition in Australia and undoubtedly the correct time to graze is of basic importance. It is suggested that the latter problem is closely concerned with the development of the inflorescence.

From Finnell's (9) work with wheat it seems that his remarks may be equally true for oats, i.e., "that while sound plants are reduced in total production by late grazing, their response in numbers of replacement shoots formed is in respect to the degree of partial or entire replacement required."

Late grazing, and the consequent complete destruction of already differentiated panicles, necessitating complete
replacement by the growth of secondary tillers, appears to have a doubtful advantage over an early grazing, whereby a high percentage of initiated panicles may escape destruction, and only partial replacement be necessitated.

**SUMMARY.**

1. A relative description of the mature inflorescence is given, special attention being paid to the false node of some unilateral panicles.

2. Growth phases synchronising with inflorescence development are briefly related.

3. The development of the inflorescence, as studied in the variety Abundance, of the species *Avena sativa*, L., is described and figured.

4. The following problems appear to be significantly related to the development of the inflorescence:

   (a) The phenomenon known as "bolting" in oats.

   (b) Frit Fly attack.

   (c) The correct time to graze a young crop of oats.

**LITERATURE CITED.**


(See ZADE, “Der Hafer,” *l.c.* pp. 58-9.)


View This Item Online: https://www.biodiversitylibrary.org/item/173933
DOI: https://doi.org/10.5962/p.359988
Permalink: https://www.biodiversitylibrary.org/partpdf/359988

Holding Institution
Smithsonian Libraries

Sponsored by
Biodiversity Heritage Library

Copyright & Reuse
Copyright Status: In Copyright. Digitized with the permission of the rights holder
Rights Holder: Royal Society of New South Wales
License: http://creativecommons.org/licenses/by-nc-sa/3.0/
Rights: https://www.biodiversitylibrary.org/permissions/

This document was created from content at the Biodiversity Heritage Library, the world’s largest open access digital library for biodiversity literature and archives. Visit BHL at https://www.biodiversitylibrary.org.

This file was generated 27 June 2023 at 09:05 UTC