MEETING OF THE LONDON SECTION, HELD AT THE IMPERIAL HOTEL, RUSSELL SQUARE, ON MONDAY, OCTOBER 11TH, 1920.

Mr. WALTER A. RILEY, Junr., in the Chair.

The following paper was read and discussed :—

The Development of the Flower and Grain of Barley.

By WINIFRED E. BRENCHLEY, D.Sc. (Rothamsted Experimental Station).

THE value of barley for malting and brewing purposes is so closely associated with the developmental history of the grain, and particularly of the endosperm, that much attention and research have been devoted to the subject. A great deal of detailed work has been done, bearing chiefly on the later stages of development and on the structure of the mature grain; the earlier stages seem to have been less exhaustively treated. It may prove of interest, therefore, to attempt to gather together some of the scattered information relating to the flower and immature grain of barley in order to present a more complete picture of the course of events, without, however, going into much detail on cytological points.

Barley has been cultivated from prehistoric times, and is among the most ancient of our food plants.* The only form now found wild (in parts of Asia and Eastern Europe) is the two-rowed barley (*Hordeum distichon*), though, according to De Candolle (*Origin of Cultivated Plants*, 1884, pp. 367—370), the four-rowed (*H. vulgare*) and six-rowed (*H. hexastichon*) were originally wild, but have become extinct as such since the beginning of the historical epoch. The hypothesis is drawn that the four- and six-rowed barleys were derived from the two-rowed in the remote past. All three types are still in cultivation, modified in various ways by the progress of plant breeding in modern times.

Inflorescence or ear.—A mature barley plant consists of a number of stalks or tillers, each bearing several long, narrow leaves, sheathing at the base, from within which rises a stem bearing the ear, which is the

* An old coin by Aristoxenos, dated *circa* 320—300 B.C. (now in the possession of the Rothamsted Experimental Station), shows a head of Demeter bound with a corn (barley?) wreath, and on the obverse a perfect representation of an ear of two-rowed barley, which might easily pass for a modern ear.

flowering and fruiting part of the plant. The floral organs of barley, as of other grasses, are different from those of ordinary flowering plants, though the essential sexual parts are the same. The unit of the inflorescence is the spikelet, which may contain only one flower, as in barley, or several, as in wheat. A large number of spikelets are grouped together in a definite way to form the ear, which thus consists of a central axis or rachis, on which clusters of individual spikelets are systematically arranged. The rachis of the barley ear is not smooth or straight, but is jointed, and projects into small cushions placed alternately up its length, each cushion bearing a group of three spikelets. The spikelets vary in their manner of development, and so give rise to the different types of barley met with under cultivation. In six-rowed barleys all the spikelets develop grains, which are regularly arranged, so that the ear possesses six straight longitudinal rows of grains, placed at equal distances from one another round the rachis. In four-rowed barleys, as bere or bigg, all the spikelets again develop, but, while the central grains of each triplet form two regular rows on opposite sides of the rachis, the lateral grains form one irregular double row on either side, making the whole ear apparently four-rowed. In the two-rowed barleys, as the Goldthorpe and Chevallier types, only the middle spikelet of each three produces a grain, the two outer ones remaining abortive, two rows of grains being thus produced.

FIG. 1. Barley Rachis.

In the majority of barleys each fertile spikelet is provided with a long bristle or awn, which is of considerable importance and will be discussed later in the paper.

Fully developed spikelet.—The single flower of the spikelet is partially enclosed by two long narrow sheaths known as "empty glumes," which do not get larger as development takes place, and which can still be seen on the outer side at the base of each grain of a mature ear. Each of these empty glumes is prolonged at the tip into a small awn. Within these are two broad membranous sheaths, which completely enclose all the vital parts of the flower, and are known as "flowering glumes" or "paleæ." The outer palea, which is on the side of the flower furthest away from the axis, is much expanded, and folds right round the flower. It is also drawn out at the tip into a very long awn, often several inches in length. The inner palea, nearest to the axis, is narrower, and only comes halfway round the flower; the tip is more or less truncate, and no awn is present. Just within the base of the outer flowering glume are two small scale-like structures fringed with long hairs, known as "lodicules," which play an important part in the opening and closing of the flower.

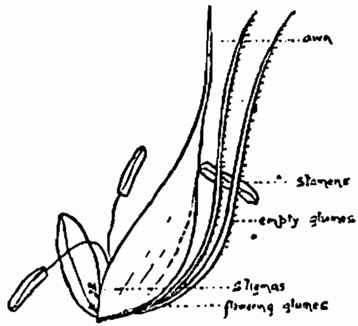

Fig. 2.—Spikelet of Wild Barley.

Three male organs or stamens are present, each consisting of a long slender stalk or filament, and a two-lobed anther containing the pollen. In the middle of the flower, practically filling up the space between the flowering glumes, is the female organ or ovary, which eventually develops into the barley grain. The ovary is crowned by two feathery stigmas, which serve to collect the pollen when it is set free from the anthers.

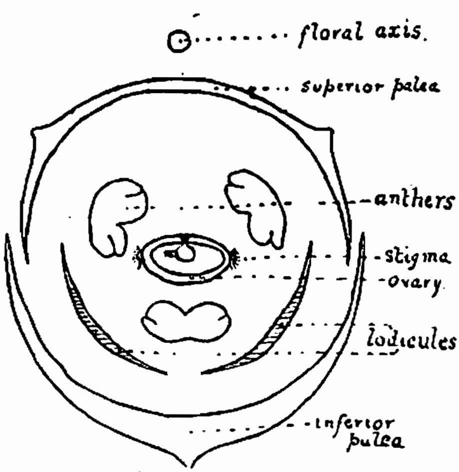

Fig. 3.—Transverse Section of Barley Flower (Diagrammatic).

In the lateral spikelets of two-rowed barley the ovary remains undeveloped, though traces of it are usually present, but in most cases the stamens develop to a greater or less extent.

The course of development of the barley flower can be traced by examining the ear at different stages of growth. The following account is drawn up from observations on a two-rowed barley, the four- and six-rowed varieties not being available :—

(a) *Very young ear* (*¼ inch long*).—The early stages of growth of the ear takes place within the shelter of the sheathing leaves of the plant, which wrap round the young ear until it is almost ready for pollination. The ear terminates the axis of the shoot, and, when once it begins to be formed, no more leaves can be produced by that particular shoot. By the time the young ear is ¼ inch long, all the parts are laid down, and most are sufficiently clear to be recognisable with a low magnification. Even at this time the course of events is clearly marked out, and, in the two-rowed barley, the middle flower of each triplet is much more developed than the lateral ones. The empty glumes are much larger in comparison with the rest of the flower than they are later on, and the soft and flexible awns of the empty and flowering glumes seem to be out of all proportion to the other structures in size and length. The inner palea, nearest the axis, is quite short, and only reaches halfway up the flower, so leaving the sexual organs somewhat exposed. At this stage the filaments are so short that the anthers appear almost sessile. The ovary is less advanced than the stamens and appears externally as a small mass of tissue, with a slight depression at the top which indicates the division between the future stigmas. The lodicules are very undeveloped and need considerable magnification to render them visible.

Towards the top of the ear the character of the central flowers of the spikelets changes almost abruptly, the upper flowers being much less advanced and possessing practically no awns. The transition is so sudden that it is obviously significant, and examination of older ears show that these upper flowers never develop, but die off and give the barley ear its characteristic truncated appearance.

At this very early stage the empty glumes and the flowering glumes constitute all that can be seen of the lateral spikelets with low magnification, and no awns are apparent on the outer flowering glumes.

(b) *Intermediate stage of development.*—By the time the ear, independent of the awns, is about an inch long, all the floral organs are well developed and the structure of the lateral flowers is more apparent.

In the central spikelets the empty glumes are less in evidence, as they have not increased in size in the same proportion as the others. The outer palea, with its very long awn, wraps completely round the flower, while the inner palea is still short and narrow, only reaching halfway up the ovary and halfway round the flower. The lodicules are clearly shown as two small masses of tissue just within the outer palea, and the stamens and ovary appear much as before, except that they are larger and the depression in the ovary is far more marked, indicating the stigmas quite clearly.

The failure of the upper flowers to develop is now quite evident, for the ovaries are very small and show little or no increase in the depth of the depression, while the awns are absent, making the flowers resemble in external appearance the undeveloped lateral spikelets throughout the ear. In the lateral spikelets themselves the outer palea still possesses no awn, and the inner palea is small, enclosing three very undeveloped stamens.

Blooming and pollination of barley flower.—In order that the ovary may develop into a normal grain of barley, it is essential that fusion shall occur between certain nuclei of the pollen grain and ovary, thus effecting fertilisation. Before this can take place, it is necessary that the pollen grains shall be deposited on the stigma, whence access to the ovary is easy. This act of deposition is known as pollination and occurs at the time that the flower is in blossom.

As the time for blooming approaches, an elongation of the main stem below the spike takes place, pushing the ear out beyond the protecting leaves. By this time the awns have stiffened up considerably and are tough and springy instead of being soft and flaccid. The fertile spikelets are conspicuous on account of their size and large awns, which are often 5 or 6 inches long, flattened towards the base where they join the glume, and provided on the edges with numerous short spines, which give the awns their characteristic roughness.

Fruwirth ("Das Blühen der Gerste," *Fühling's Landswirtschaftliche Zeitung*, 1906, **55**, 544—553) has made detailed observations on the blossoming of various types of barley, and states that flowering takes place in a regular progression. All the flowers do not mature simultaneously, but those of the first formed tillers are the first to be ready for pollination; in any ear, the flowers just above the middle of the centre row are the first to reach that state, the progression then being upwards and downwards, though occasional irregularities occur. In some cases the flowers open for a time by the separation of the flowering glumes, due to the lodicules becoming turgid and forcing the glumes apart; in other cases the flowers do not open at all, but pollination occurs within the closed glumes. The method of flowering is to a large extent characteristic of the type of barley, but it also depends upon the rapidity with which the ear is pushed out of the sheathing leaves just before flowering time. In two-rowed nodding barley and in four-rowed barley open flowering is the rule, unless growth is so slow that the time for blooming arrives before the ear has emerged from the sheathing leaves. In two-rowed upright barley and in six-rowed barley blooming nearly always occurs with closed glumes, the failure of the flowers to open in these cases being due to the small size and weakness of the lodicules, which are therefore unable to force the glumes apart.

If the temperature is sufficiently high, open flowering begins at 5.30 to 6.0 A.M. and goes on freely till about 8 o'clock; after this there is a cessation till the afternoon, when a few more flowers may open between 3 and 5 P.M. It is difficult to trace the course of events where closed blooming takes place, but it probably takes 3—4 days for all the flowers on an ear to bloom, and from 7—9 days for all the ears on a plant to complete the process. When the anthers are ripe they open or dehisce by means of a short slit at one end, through which the pollen emerges. Dehiscence usually begins before the glumes separate, so that the stigmas are nearly always covered with pollen before the flower actually opens. When the glumes separate the filaments stretch and push the anthers out into the air, where they sway about in the breeze and scatter the remaining pollen. The stigmas do not protrude at all, and after 20 to 30 minutes the lodicules become flaccid again and the glumes shut together. The filaments elongate even with closed flowering, but in this case they crumple up within the flower; the anthers are not pushed out, and so all the pollen is confined to the one blossom. It is thus seen that with both open and closed flowering self-pollination is secured. Occasional cross-pollination (*i.e.*, deposition of pollen from one flower on the stigma of another) may occur with open flowers, but as the glumes are only slightly separated for a short period of time, foreign pollen is by no means certain to find its way in, and as, in addition, the stigmas do not protrude and self-pollination has nearly always occurred previously, relatively few authenticated cases of cross-pollination occur (W. W. Robbins, *The Botany of Crop Plants*, 1917, p. 139). The possibility of crossing naturally varies with the behaviour of the type of barley. It is interesting to note that the types in which cross-fertilisation may occur—the open-flowering forms—are those in which infection of the ear by fungus spores, as smut and ergot, is most probable.

The closed flowering types do not lend themselves so readily to infection.

Fertilisation of the barley ovule.—The ovary or undeveloped grain of barley encloses a single ovule or undeveloped seed. At the time of flowering this ovule is covered with two integuments or coats which surround a mass of tissue—the nucellus—built up of numerous thin-walled cells. The integuments are so arranged as to leave a small channel at the lower end communicating with the nucellus. Within the latter is one much larger cell—the embryo sac—which at this time contains at least eight nuclei, probably more (W. Johannsen, *Développement et constitution de l'endosperme de l'orge*, Laboratoire de Carlsberg, 1884, p. 62). One end of the embryo sac approaches near to the base of the channel or micropyle through the integuments, and at this end are found three nuclei, one being the essential ovum or egg cell, which eventually gives rise to the young plant, the other two being called synergidæ. Two more nuclei are present in the middle of the embryo sac, and several others—the antipodal nuclei—at the further end.

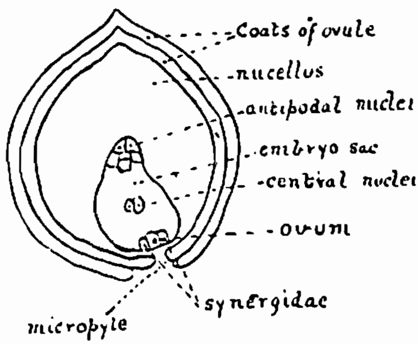

FIG. 4.—Ovule of Barley.

When pollination has occurred the pollen grains deposited on the stigma begin to germinate and send out slender tubes, which penetrate the tissues of the stigma and one of which eventually makes its way right down the stigma, and round the ovule to the micropyle, through which it enters the nucellus till it reaches the embryo sac. The nuclei of the pollen grain pass down this tube and enter the embryo sac, where one unites with the ovum or egg cell, thus effecting fertilisation. After this the nuclei divide rapidly, the embryo being produced from the fertilised ovum, while the central nuclei give rise to the endosperm, which is the all-important part of the barley grain to the brewer and maltster.

Development of the barley grain.—With the division of the nuclei the embryo sac increases rapidly in size, partly at the expense of the surrounding tissues. As time goes on the greater part of the nucellus and ovary walls is used up as food material for the developing plant, so that in the mature grain these structures are much reduced, though they can still be traced to some extent. The absorption of the nucellus occurs almost directly after fertilisation and is practically complete, but the outer layer persists and its cells become thickened, probably aiding in the formation of the semi-permeable membrane which exercises a selective function with regard to the admission of liquids into the grain (A. J. Brown, "On the existence of a semi-permeable membrane enclosing the seeds of some of the Gramineæ," *Ann. Bot.*, 1907, **21**, 86; this Journal, 1907, **13**, 384).

The fertilised ovum divides rapidly, cell walls are produced round the nuclei, and the embryo is marked out at the lower end of the grain, ultimately consisting of a plumule or shoot, and radicle or young root, together with a sheathing cotyledon or scutellum which serves as an absorbing organ. The plumule is made up of several rudimentary leaves surrounded by a plumule sheath which serves to protect the delicate leaves when they are forcing their way up through the soil at the time of germination. The radicle, with its root cap, is embedded in a substantial sheath, and rudiments of several secondary roots can be seen, eight being the full number. The scutellum covers the whole embryo like a shield on the side adjoining the endosperm, and, to quote Brown and Morris (*Journ. Chem. Soc.*, 1890, **57**, 463), "It serves as a special organ of absorption through which, during germination, the nutritive matter stored in the endosperm must pass on its way to the growing portions of the embryo."

Pari-passu with the growth of the embryo the endosperm is laid down within the embryo sac, originating from the central nuclei and ultimately occupying the bulk of the grain. Its development has been fully delineated by Johannsen (*loc. cit.*, pp. 62—68), and it will suffice to say here that in the mature grain the endosperm consists of a mass of large thin walled cells packed full of starch grains of various sizes, bounded by a triple layer of rather irregularly arranged cells, with thick cellulose walls, which contain no starch, but are full of aleurone grains and fatty matters. This aleurone layer is not developed across the face of the scutellum, which abuts directly on the starch-containing cells. Some of the latter in this region are emptied and crushed during development.

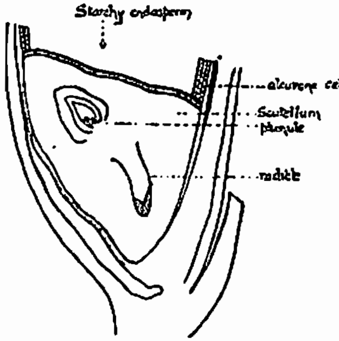

FIG. 5.—Section of Barley Embryo.

The starch grains vary considerably in size from tiny rudimentary granules to large fully-developed grains. Vine ("Observations on some characters of hard and tender barleys," Part I, this Journal, 1913, **19**, 444) considered that the presence of an excessive proportion of minute starch granules is the main feature of "starch hardness" as distinguished from "steeliness," and showed that the ratio of rudimentary starch granules is much higher in hard than in tender barleys, the small granules being much more resistant to enzyme action, moisture and temperature than are the mature granules of normal size.

The increase in size of the ovary begins immediately after fertilisation, growth at first being so rapid that the increase in length can easily be measured at 12-hour intervals (A. Mann and H. V. Harlan, "Morphology of the Barley Grain with reference to its Enzyme-Secreting Areas," *U.S. Dept. Agric. Bull.*, 1915, 183; H. V. Harlan, "Daily Development of Hannchen Barley from Flowering to Maturity at Aberdeen, Idaho," *Journ. Agric. Res.*, 1920, **19**, 393—429). After about a week growth in length practically ceases, the grain begins to swell and continues to get broader and thicker almost until maturity. At first the young barley grain is quite separate from the flowering glumes (as in wheat), but after about ten days a sticky substance is secreted which fastens the glumes to the young fruit or kernel, so that a mature barley grain consists of the combined kernel and glumes. From the time of flowering a steady influx of food material takes place into the grain. Water, nitrogen and ash constituents pass in together, and increasing quantities of carbohydrates, chiefly starch, are laid down (W. E. Brenchley, "The Development of the Grain of Barley," *Ann. Bot.*, 1912, **26**, 903—927). About two or three weeks before the barley is fit to cut, the quantity of nitrogen and ash reach their maximum, and then remain fairly constant. At the same time a definite loss of water occurs, causing desiccation, maturation changes set in and the barley ripens off. When desiccation takes place the green cells of the grain begin to lose their colour and turn brown, the awns remaining green longer than the grain itself. Hardening of the grain and awns is associated with the loss of water, so that by harvest time the grain is very firm, and the awns are so brittle that they easily snap off.

One other point may perhaps be mentioned here, as it is of interest from the point of view of identifying different types of barley. On the outside of the grain, but lying inside the furrow formed during development, is a bristle-like structure called the *rachilla*, springing from the base of the grain. This is really a continuation of the short lateral stem on which the barley spikelet is borne, and though it is of no importance to the grain itself, it varies in type in different barleys, and serves as a means of separating one type from another in the threshed state.

Functions of the awns.—The awns attract considerable attention as they are usually so long and rough that they make the crop unpleasant to handle and give extra trouble at threshing time. In addition they are apt to cause sore mouths when barley hay or straw is fed to stock. It has been proved, however, that they are no mere ornamental excrescences, but play an important part in the nutrition and development of the grain.

The importance of the awns is suggested by the developmental history of the grain already sketched out. In the perfect flowers the awns are strongly marked at a very early date, but in the imperfect lateral spikelets and in the abortive flowers at the apex of the spike the awns do not appear at any stage, suggesting that possibly some vital connection exists between these structures and the sexual organs in typically awned varieties. In every barley ear the largest and heaviest grains are in the middle of the ear, and the longest awns occur on these grains, indicating some correlation between these two facts.

According to Zoebl and Mikosch (*Sitzungsber. kgl. Akad. Wissensch. Wien.*, 1892, CI. Abs. in *Ann. Agron.*, 1895, **21**, No. 3, 143, 144), Perlitius ("Einfluss der Begrannung auf die Wasserverdungstung der Aehren und die Kornqualität," *Mitt. Landw. Inst. Univ. Breslau*, 1903,

2, No. 2, 305—381, Abs. in *Deut. Landw. Presse*, **30**, No. 50, 450, 451) and Schultze (*Mitt. Landw. Lehrkanz. k.k. Hochsch. Bodenkul. Wien.*, 1913, **1**, No. 3, 285—308), the beards are essentially transpiring organs and large amounts of water pass through them, the quantity increasing with their length. The awn is built up of green chlorophyll-containing tissue, traversed by numerous intercellular spaces communicating with the outer air by stomates—essentially the structure of an organ of transpiration. Experiments by Zoebl and Mikosch showed that much of the water lost by the ear escapes through the awns, four or five times as much often passing off from normal ears as from others from which the awns have been artificially removed.

Transpiration is most active during the development of the spike and grains, rising to a maximum just about the time the grains reach the milk stage. Perlitius states that the length of awns and the vegetative period of the spike are inversely proportional to one another, and that under normal weather conditions awned varieties tend to ripen earlier than awnless. The conclusion is drawn that the awns have a decided influence on the volume and weight of the barley kernels, as a rapid transpiration current implies that a large amount of food material is brought from other parts of the plant to the ear, there to be elaborated and laid down as reserves in the grain. Perlitius also claims that chemical analyses indicate that the grain of awned varieties is richer in starch and ash and lower in nitrogen than that of awnless sorts, and suggests that the extra amount of ash indicates that awned varieties are capable of utilising mineral fertilisers to the best advantage.

Recent work by Harlan and Anthony ("Development of Barley Kernels in Normal and Clipped Spikes and the Limitations of Awnless and Hooded Varieties," *Journ. Agric. Res.*, 1920, **19**, 431—472) has corroborated these earlier results and brought additional facts to light. Clipping the awns of bearded barley lowers the yield, chiefly by reducing the quantity of starch laid down. Typical hooded and awnless barleys normally give a lower yield than bearded sorts, and their ears have a tendency to shatter. With regard to this last point analyses show that the intake of mineral matter is much the same whether the ears are bearded or awnless. When awns are absent the amount of ash constituents deposited in the rachis of the ear is excessive and the latter becomes very brittle and shatters easily. When awns are present a large proportion of this mineral matter is transferred to them, thus rendering the rachis less brittle. As much as 30 per cent. of ash may be present in mature awns, and the rachises of clipped spikes may contain as much as 25 per cent. more ash than the rachises of normal spikes. The ash-content of the ear is thus of great importance in breeding experiments which aim at producing awnless varieties of good yield which will not shatter badly.

The above sketch of the development of the barley flower and grain gives but the merest outline of the course of events. At almost every point in the later history of the grain extensive research has been undertaken and detailed information can be obtained by reference to the literature quoted. Some of the earlier stages, however, have been less fully worked out, especially with regard to their morphological development, and these might offer a promising field for investigation.

Glossary of Terms.

Awn or *Beard.*—A bristle-like prolongation of the glume in grass flowers, which in barley is several inches long.

Bract.—A leaf on the flowering stem between the flower and the first ordinary foliage leaf. The bracts are often very different from the ordinary leaves in appearance and structure.

Caryopsis.—A fruit in which the pericarp is united to the testa of the single enclosed seed. The characteristic fruit of cereals and grasses.

Empty Glumes.—Two glumes at the base of a grass spikelet which do not contain any other floral organs, but which more or less enclose all the flowers of the spikelet.

Flowering Glumes.—The two glumes of a grass flower which enclose the male and female organs (see *Palea*).

Glumes.—Membranous or chaffy leaves, which form part of the flowers of grasses and cereals, enclosing the male and female floral organs when the latter are present.

Inflorescence.—The entire head or cluster of flowers, *e.g.*, the unripe ear in cereals.

Lemma.—Another name for the inferior palea.

Lodicule.—A small scale between the stamens and the flowering glumes in the flower of grasses.

Ovary.—The immature fruit, consisting of an outer wall enclosing one or more ovules.

Ovule.—The undeveloped immature seed.

Pale or *Palea.*—Another name for the flowering glume.

The *inferior palea* is the outer of the two flowering glumes and faces the rachis of the ear.

The *superior palea* is the inner flowering glume and is next to the rachis.

Pericarp.—The wall of the ripened ovary or fruit.

Pistil.—The female organ of a flower, consisting of ovary, style, and stigma.

Rachis.—The axis of the inflorescence of a grass, on which the spikelets are arranged.

Seed.—The ripened ovule, consisting of the embryo or young plant, with, in many cases, the addition of endosperm or reserve food material.

Spikelet.—The unit of inflorescence in grasses, consisting of one or more flowers enclosed within two empty glumes.

Stamen.—The male organ of a flower, consisting of a slender stalk or *filament* bearing an *anther* containing numerous *pollen grains.*

Style.—A projection from the tip of the ovary, which bears the stigma.

Stigma.—The enlarged or modified tip of the style, which serves to catch the pollen grains.

Testa.—The outer covering of the seed.

Discussion.

Mr. E. S. Beaven said he had been extremely interested in the paper which Dr. Brenchley had read. He had been more or less acquainted with the very valuable work which Dr. Brenchley had done at Rothamsted for a great number of years; and she had very kindly from time to time given him some assistance in his own investigations. He believed that this was the first time they had had the development of the ear of barley from its very early stages put before the Institute; and they owed so much as an Industry to the barley plant that it was a good thing they should have those stages made clear to them. He was particularly interested from the point of view of some of his own researches on the later development of barley in what Dr. Brenchley had said with regard to the function of the awn. There was no doubt that the most important factor in the quantity of grain which they were able to obtain on any area of ground, whether it was a square yard or an acre, or a thousand acres, was that process which Dr. Brenchley had herself done so much in her former papers to elucidate. He meant the migration of the food materials which were accumulated in the stem and leaves of the plant into the grain. As he had pointed out in a paper to the British Association in Australia in 1914, with barley the proportion of the total dry matter of the plant which was ultimately accumulated in the grain was very high. In his own cultivations it frequently reached 50 per cent., that was to say, the grain contained 50 per cent. of the total dry matter of the plant. He thought that was probably a proportion which was not reached with either of the other cereals, and he did not know that it was reached in any other plant. That process of migration of the reserve materials from their original location in the leaves and in the stem of the plant obviously could not be carried on in the absence of a transpiration current. The material moved in a fluid or semi-fluid form, and this uplift of tons of carbohydrates and other matter of the plant was one of the marvels of Nature, upon which, perhaps, the human race depended for its nutrition more than upon any other natural process. Dr. Brenchley had just told them about a factor of importance, which he did not think had been sufficiently studied, viz., the function of the awn. It was very interesting from more than one point of view. If the awn was one of the main transpiring organs of the plant, then it helped them to account for the uplift of material which they got. He had a number of awnless barleys in his own collection, and it was quite true that they were useless from the point of view of yield of grain, whether they were furnished, as they sometimes were, with a kind of trifurcate appendage, which took the place of the awn, or quite awnless. There was only one absolutely awnless barley, so far as he knew, and that was a hybrid barley, which occurred in a cross made by Rimpau, of Schlansted, the breeder of the giant German rye, which they heard a good deal about at one time. That barley certainly produced a very thin husky poor grain, which would be useless for malting purposes. He saw no prospect at all, and his attempts at cross fertilisation showed no indication, that they could dispense with the awn, however inconvenient it might be in cattle feeding. There was another point which occurred to him, and upon which he would be glad to have Dr. Brenchley's view. If the awn served the purpose of a transpiring organ, then, since through the later stages of growth of the endosperm the connection between the flowering glume or the outer palea was maintained, although there were varieties of barley in which there was no connection, "naked" barleys, in which the paleæ did not adhere to the pericarp, it would be very interesting to know whether she thought that transpiration took place to any extent through the endosperm into the outer palea and thence to the awn. That was an important point on which he would be very glad to have her opinion, because he knew she had made a prolonged research on the movements of matter in the cereal plants.

Mr. COOK said he did not think he had anything to say except as a country brewer who happened to be in London and came along to hear the Paper. He had very much appreciated listening to Dr. Brenchley. He had always taken an interest in that part of the subject because he thought, as a brewer, one should know the history of one's main material right from the very beginning. He had in his possession a paper which he had often read of Dr. Horace Brown's which Dr. Brown had read before that Society. It had been added to later by Dr. Morris.

Mr. HULTON said he would like to ask Dr. Brenchley whether the absence of the awn in wheat made any difference to the yield. Since this appendage appeared to be so important in barley, one would imagine it should be equally valuable in the case of wheat; but wheat seemed to get on very well without the awn.

Mr. HIND said Dr. Brenchley spoke of the paleæ as flowering glumes and compared them to petals; were they not more often compared to bract and bracteole? He was very interested in the description of the function of the lodicules, which he thought represented a perianth. He would like to know what part of the flower Dr. Brenchley associated them with. Another thing that struck him was the mention made by Dr. Brenchley of four-rowed barley. It seemed rather unorthodox to speak of a barley as four-rowed, as the spikelets were developed in threes on the rachis. Many Continental farmers had told him that the barley they grew was certainly four-rowed, but it was really only an apparent four-rowed arrangement. The frequent occurrence of open flowering in nodding barleys mentioned by Dr. Brenchley was very curious, inasmuch as it would appear that nodding barleys were just the sort that could not be cross-fertilised, on account of the protection of the flower by its inverted position.

Dr. BRENCHLEY (in reply) said she was afraid that her use of the word "petals" may have misled someone. She had no intention of drawing any real comparison between the outer coats of an ordinary flower and the glumes and lodicules of barley. The whole matter was so controversial that, personally, she preferred to keep outside it. But one view certainly was that the lodicules represent the perianth, and another that they have no representative in the ordinary flower. It was purely a matter of drawing their attention to the fact that the two types of flower were so different, without in the slightest degree suggesting that the glumes and lodicules could be made to fit in with the sepals and petals of an ordinary flower. With regard to the cross fertilisation, it was quite a useful idea that in the nodding barley it was prevented by the position of the ear. But that would not apply, would it, in the case of six-rowed barley in which open flowering occurred? It might be mere accident. It was also very difficult to draw any comparison between wheat and barley. Certainly wheat had no awn, and the two structures were so different, owing to the fact that the glumes did not join up, that it was almost impossible to say what would happen if they had an awn in the wheat flower. Again, with regard to cross fertilisation, she had not realised, until Mr. Hulton had pointed it out, that where cross fertilisation obtained, they got inferior products. She was not a plant breeder herself; and was not aware that cross fertilisation was regarded as being bad, except in so far as a mixed product was introduced into their crop, and it certainly was not wise to introduce a mixed strain in that. Concerning the transpiration current, she did not see how food could pass either through the paleæ to the endosperm, or *vice versa*, because the fusion between the glumes and fruit was purely a "sticky" fusion. It was not organic in the sense that a water-conducting structure was formed. The barley did not form morphological "struts," as one might call them, *i.e.*, vessels passing through the grain into the paleæ, when that fusion of the paleæ and the grain took place. What she, personally, thought was, that the fact that they had got a big transpiring centre in the near neighbourhood of the grain, brought up a large quantity of food from the soil into that region, and the grain was in such a condition that it was prepared to divert an extra amount of that food into its cells instead of letting it all go into the awn.

Mr. BEAVEN stated that it would be only water that would go through the awn.

Dr. BRENCHLEY said that only water passed through it, but of course the undeveloped mineral matters came up. She had omitted one material fact in her paper, which was that where they had typical awned barleys, the latter tended to ripen earlier than those in which the awns were, either naturally or artificially, absent. That meant that the presence of the awns hastened ripening. She had noticed that the awns were the last part of the barley grain to ripen—that the grain became brown and ripe long before the last traces of green colour went from the awns, which looked to her as though the grain was working in its awns laying down food right to the end. She did not know whether that fact had been noticed, but it was probable that it had. Although many of the ears showed brown and brittle awns, others, although the grain was perfectly ripe, showed green awns. Then, with regard to the amount of transpiration, it had been shown that the awns were as effective transpiring organs as the foliage leaves. There was as much transpiration by way of the awns in the case of a typical barley as went on through the leaves. In other words, as much as 50 per cent. of water passed through the awns, which compared with the 50 per cent. of dry matter found in the grain by Mr. Beavan.

Mr. FIELD, in proposing a vote of thanks, said he hoped that the work of the Research Fund Sub-Committee would result in brewers generally taking more interest in the most important of all the cereals with which they were concerned. When this interesting and important paper appeared in the Journal it would be read by all the members of the Institute with as much pleasure as it had given to those present. He thanked Dr. Brenchley on behalf of the London Section for her very great kindness in coming there. As the Chairman had said, she was the first lady who had honoured them, but they all sincerely hoped she would not be the last.

Mr. HARMAN wrote that he would like to have Dr. Brenchley's opinion on the following points, which seemed of rather special interest. The first point is the curious "disregard" of the barley plant for what has been regarded for so many years as of prime importance to the plant, namely, the value of cross fertilisation. For not only does the barley plant *discourage* the development of organs—the lodicules which Dr. Brenchley tells us are specially adapted organs for bringing about cross fertilisation—but in cases where cross fertilisation is allowed to proceed, there is actually produced a weaker plant, more susceptible to mould and other diseases. He would like to ask if this is found only in the cultivated, and not wild, barley, and if so, whether the same tendency is found in other plants which are highly cultivated? Dr. Brenchley is, no doubt, aware that Dr. Horace Brown was of opinion that the lodicules were rudimentary or vestigial and of no use to the plant. The second question is with reference to the interesting account Dr. Brenchley gave of the function of the awn, and he understood that this was believed to be not only an organ of transpiration—that is, regulating the water content of the grain—but at the same time an excretory organ in which the water acts as a carrier for salts in solution, which are in excess of the plant's requirements. He should like to have asked if such an organ is known, or at all common, in other plants, more particularly having regard to the excretion of presumably *useful* material in the form of salts which the awn thus disposes of. The third point which occurred to him was in relation to the aleurone layer. He thought Dr. Brenchley said this might be four cells thick, and as it is usually supposed to be three, and he had never found more in sections he had examined, he should like to know if four is abnormal or fairly common?

Dr. BRENCHLEY replied that (1) The lodicules are hardly "specially adapted organs for bringing about cross fertilisation," but they seem to be the agents whereby the glumes are forced apart for a short time, thereby rendering it *possible*, but not *inevitable*, that foreign pollen can enter and so effect cross pollination. Further, he did not wish to convey the impression that cross fertilisation necessarily gives a weaker plant, but simply that when the flowers open, *i.e.*, when cross pollination is possible—there is more opportunity for fungus spores to gain access to the grain and set up disease. (2) It is difficult to give an exact parallel to the awn with regard to its excretory functions, if we are justified in so calling them. Various plants are able to store up waste products as crystals in the cells of various parts, thereby removing them out of harm's way. It is quite possible that some parallel could be found if analytical data were examined with that idea in view. (3) The aleurone layer is typically three cells thick, though by occasional irregularity here and there it may be four.