THE AGRICULTURAL VALUE OF AWNS IN CEREALS [1]

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SUMMARY

1. Many investigators mention the positive influence of awns on the yield of cereal varieties. Only a few negative results are recorded. These may have been caused by sampling errors or by linkage of the factor for awns with negative yield-factors.

2. The remarkable difference in habit noticed earlier between bearded and awnless wheat types was confirmed. The bearded plants are on an average more robust than the awnless ones. The difference appears to be caused by an inexact separation of heterozygously bearded plants and homozygously awnless plants with short tips on the glumes. Robust awnless plants are on an average inclined to be classified as heterozygously bearded, weak heterozygously bearded plants being sometimes taken for awnless. When the awnless and heterozygously bearded plants are combined in one group no differences in habit from the group of bearded plants are discernable. By comparing the average yield per plant or per culm of the combined group with that of the bearded group a reliable impression of the production value of the awns can be obtained.

3. Under the experimental conditions the contribution of the awns to the yield was about 10 % for spring-barley, 3–5 % for winter-wheat and less than 2 % for winter-rye.

4. The increase in yield caused by the awns can be ascribed to their assimilatory activity. The extra yield consists mainly of dry matter low in protein, probably starch.

5. Examination of segregating strains can be used to determine the production value of other characteristics.

6. The better adaptation of bearded wheats to dry and warm climates can be ascribed to the fact that the awns have xeromorphous characteristics, their most productive stage in addition co-inciding with the period of the most rapid seed development.

1 INTRODUCTION

The presence or absence of awns is a striking characteristic of cereal varieties and for a long time breeders have been wondering whether awns have a positive or a negative value.

Awns can be a source of great inconvenience to the reapers, though this impediment is gradually decreasing since the introduction of mechanical harvesting. Awns can impair the food value of straw and chaff, especially when they have sharp teeth, as is the case with most bearded varieties. In wheat the awns now and then impede ear emergence. This is nearly always caused by the sheath of the uppermost leaf being twisted just below the juncture of the blade, owing to wind or for other reasons, at the moment when the awns are there, in the sheath. The awns are then caught in the bend and the ear is usually compelled to break from the sheath sideways. In most cases the awns do not become unstuck until the ear stalk and the ear are considerably deformed.

On the other hand, awns can be useful in restricting the damage caused by birds, because it is more difficult for them to secure the seeds in the bearded ears. This advantage is, however, only of local interest. Only if awns positively contribute to the yield of a cereal variety, attention can be given justifiably to the selection of bearded types of cereals.

2 REVIEW OF LITERATURE

a *The awns as a yield factor*

Already as far back as 1892 ZOEBL and MIKOSCH published their researches regarding the favourable influence of the awn on the size of the kernel of

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barley. Also VON PROSKOWETZ (1893) mentioned the importance of the awn for the plant. SCHMID (1898) proved that removal of the awns can cause a decrease of the kernel-weight. Of the tested barley-varieties this decrease amounted to 0–13%; it was 1½–7% for emmer, and ½–2% for spelt. In respect of rye the influence was not so clear; a few times it was even in favour of de-awning. PERLITIUS (1904) also registered the harmful consequences of removal of the awns of barley and wheat. The decrease of the yield was greater as the removal was effected earlier. ZALESKI (1910) compared awned and awnless plants in progenies of individual plants of some *Triticum* forms. The awned plants had heavier ears and a higher kernel-weight than the awnless plants. TEDIN (1916) collected barley ears after a severe storm. Ears which had lost part of the awns proved to have a kernel-weight which was, dependent on the variety, from 3 to even 24.2% less than that of undamaged ears. GRANTHAM's (1918) experiments showed an average yield much in favour of bearded varieties as compared with beardless ones. HARLAN & ANTHONY (1920) found that grains of awned spikelets of barley contained, when ripe, considerably more dry matter than grains from de-awned spikelets. HAYES (1923) stated that seeds of bearded plants and of bearded strains of wheat were longer, plumper and heavier than seeds from awnless plants. MEISTER, SCHECHURDIN & PLOTNIKOW (1927) could hardly see any difference between the development of the seed of awned and de-awned plants of wheat, the de-awning, according to TULAIKOV and PISAREVSKI (1927), who examined the same material chemically, being neither reflected in the composition of the seed. A close examination of their figures shows, however, that also in this case the removal of the awns has presumably resulted in some loss in the yield. CLARK, FLORELL & HOOKER (1928) noticed, in crosses between bearded and awnless varieties of wheat, a slight inclination to higher yields in case of longer awns. CLARK & QUISENBERRY (1929) noticed, in contradistinction with the majority of investigators in this field, a difference in yield in favour of awnless wheat varieties, though part of this difference had to be accounted for by the larger shattering occurring in bearded types. GOULDEN & NEATBY (1929) found higher yields in bearded than in awnless wheat types. MOSKALENKO (1930) examined the relation between awns and the size of the kernels in segregating progenies. The relation was not always the same and statistically non-significant. In the majority of cases, however, the bearded plants had the greatest kernel-weight. AAMODT & TORRIE (1934) studied segregating progenies of crosses between bearded and awnless varieties of spring-wheat. The differences noticed were not significant. ROSENQUIST (1936) compared the size of the seeds in the upper part and the lower part of individual ears. For awnless ears the ratio was on an average 967 : 1000. For ears which were heterozygous for the factor of awnedness and which bear awns on the spikelets of the upper part of the ear, the ratio was 981 : 1000. The difference is 1.4% in favour of the awned spikelets, whereby is to be taken into account that the awns of heterozygously bearded plants remain shorter than those of homozygous fully bearded plants. LAMB (1937) obtained indications that the presence of awns might give small increases of yield, but he considered these insufficient to justify the perpetuation of bearded selections in a program of improvement. BAYLES & SUNESON (1940) noticed that bearded lines of wheat often have a greater kernel-weight and a greater volume-weight than the awnless. The superiority in yield of the bearded strains was, however, less frequent. ISENBECK & VON ROSENSTIEL (1944) mention that at the Breeding Station at Müncheberg a certain relation between awns and increased yield was noticed. MILLER, GAUCH & GRIES (1944) made de-awning experiments with winter-wheat varieties. The decrease registered in yield was from 50 to 80% due to a lower kernel-weight, the remaining part was attributable to the fact that, owing to the treatment, a slightly smaller number of seeds developed. SUNESON, BAYLES & FIFIELD (1948) bred, by repeated back-crosses, pairs of wheat varieties which were as much as possible equal in their characteristics, such as chemical composition, milling and baking quality, but which differed genetically only by the presence or absence of awns. On an average the bearded types were more productive than the awnless, the greater kernel-weight being the chief determining factor. KRAMER, POST & WILTEN (1952) proved that removal of the awns of spring-barley lowered the yield by 10%.

By far the greater majority of the investigators therefore come to the conclusion that awns favourably influence the yield of cereal varieties. Some negative results may have been caused by sampling errors, or by linkage when only one or very few crosses were tested.

b *The physiological activity of the awns*

The favourable influence of awns on the yield, as arrived at experimentally, has led to studies of their physiological activity. ZOEBL & MIKOSCH (1892) experienced that awned barley-ears evaporate 4 to 5 times as much water as de-awned ears. The transpiration rate of awned ears may be as high as one half of the transpiration of the whole plant. SCHMID's (1898) transpiration experiments substantiated these findings. The evaporation capacity of the de-awned ears is to be put on a par with that of awnless ears. According to PERLITIUS (1904) the perspiration-rate of the ears is the greatest in the stage of the rapid filling of the grain. GAUCH & MILLER (1940) followed the course of the perspiration of bearded and de-awned wheat varieties from flowering till full maturity. The awns are not responsible for more than 1–5% of the loss of water of the whole plant. SCHMID (1898) experimented on the assimilation function of barley awns. Different varieties showed a divergence of assimilation capacity, which amounted to 2–4 times the capacity of the de-awned ears. The assimilation capacity of the awns was sometimes up to 1/6th of that of the whole plant.

In spite of these unequivocal results for a long time there was no clear picture of the mechanism of the influence of the awn on the yield.

3 EXPERIMENTAL PART

Experiments made in 1923 and 1933 upon the influence of the awn on the yield have already been circumstantially reported on (VERVELDE, 1946).

The effect of de-awning wheat, rye and barley was checked in 1923. De-awning caused some decrease of the number of grains developed in the de-awned spikelets. This is also mentioned by MILLER, GAUCH & GRIES (1944). De-awning of the whole plant made the weight of the grain drop. The decrease was c. 6% for wheat and rye, and c. 12% for barley. Where the spikelets were alternately de-awned this caused a decrease of the kernel-weight, amounting to 4–6% for wheat, 1–2½% for rye, and 2–5% for barley.

In 1933 extensive comparisons were made between bearded and awnless plants of F_2-generations of crosses between an awnless and a number of bearded varieties of wheat. It was considered that one cross only would leave too much uncertainty about the genetical equivalence of the two groups of F_2-plants in consequence of a possible linkage of productivity-genes with the gene or genes which determine awnedness. Therefore 8 different crosses were examined. The results were not in agreement with the expectations that the kernel weight of the bearded plants would be greater than that of the awnless plants. On an average of the 8 crosses the bearded plants had exactly the same kernel weight as the awnless ones. It was, however, remarkable that the bearded plants contained an average of 5.74% more grains than the awnless ones, the former having on an average also a greater number of earbearing culms per plant. Thus the average grain yield of the bearded plants was 8.47% greater than that of the awnless plants. Though the greater average yield of the bearded plants may be partly due to a direct influence of the awns upon the productivity, the greater number of seeds per plant may have contributed as well. As it is hardly conceivable that the awns could influence the number of grains per ear and the number of ear-bearing culms per plant, it seemed advisable to further clarify this phenomenon.

To this end a number of crosses was made between two awnless and some bearded varieties of winter-wheat. During the season 1946/1947 F_2-generations of 16 crosses were grown. The seed was sown grain by grain at regular intervals. Of the 16 populations 4 failed owing to the severe winter. The others were used for examination of various characters when winter had passed. Each plant was studied individually. In this way it was possible to state later, as soon as the difference between awnless, bearded and intermediately bearded plants was noticeable, whether possible differences in habit during the early stages of development were related with awnedness. Again, at maturity the bearded plants showed more grains per ear and more culms per plant than the awnless plants, as is shown in table 1. This table also shows averages for some other characteristics for the three classes of awnedness. It appears that the groups of the bearded and awnless plants show some differences in habit, other than those already mentioned. Thus the bearded plants have in the tillering-stage more tillers, in the stage of shooting more culms shooting up

Table 1. Average characteristics of bearded, awnless and intermediately bearded plants from the F_2 obtained from a wheat-cross.

	Bearded	Awnless	Intermediately bearded	Awnless + intermediately bearded
Number of plants	982	983	1916	
Number of tillers in the tillering stage	4.82	4.72	4.91	4.87
Number of shooting up culms	5.64	5.26	5.67	5.55
Length during shooting in cm	71.9	70.9	72.2	71.9
Number of culms at maturity	5.47	5.16	5.58	5.47
Length of the longest culm at maturity in cm	120.0	120.2	121.1	120.9
Number of spikelets per ear	23.86	23.85	23.87	23.86
Weight of the plant in g	28.32	25.87	28.65	27.88
Weight of the seed per plant in g	8.934	7.956	8.952	8.675
Number of grains per plant	208.7	195.7	218.9	212.5
Weight of 1000 grains in g	42.60	40.49	40.81	40.69
Weight of the seed per culm in g	1.601	1.511	1.576	1.555
Number of grains per culm	37.55	37.28	38.58	38.20

and also longer culms; when ripe they have a greater plant weight and a greater number of grains per plant. Everything points to the bearded plants being on an average somewhat more robust than the awnless ones.

For a further analysis of this phenomenon it is necessary to include also the group of intermediately bearded plants in these considerations. Contrary to the self-evident expectation that this group will keep an intermediate position between the group of the bearded and the group of the awnless plants, the intermediately bearded plants appear to be still more robust than the two other groups. This is shown by the number of sprouts in the tillering stage, by the number of shooting culms, by the length, by the number of culms at maturity, by the weight per plant and the number of grains per plant. When (as shown in table 1) the group of the awnless and the group of the intermediately bearded plants are united into one group, this combined group is in most characteristics practically equal to the group of bearded plants. It looks as if within the combined group of awnless and heterozygously bearded plants the more robust plants belong preferably to the heterozygously bearded group. There is no genetic basis for this preference and the cause must therefore lie elsewhere. The explanation can be found in the rather slight phenotypic difference between the awnless and the intermediately bearded plants. Usually also the awnless plants have short tips at the uppermost spikelets of the ear. Owing to the variation from plant to plant within the two groups specimens occur in both groups, of which it is uncertain to say to which class they belong, so that they are sometimes placed in the wrong group. This was also noticed by CLARK & QUISENBERRY (1929). Usually the robust awnless plants are the ones tending to be classified as intermediately bearded, on the other hand the very weak, intermediately bearded plants stand a fair chance of being considered awnless owing to their short awns. The intermediately bearded group will consequently seem on an average to consist of more robust plants than the awnless group. The fully bearded plants can be correctly classified without any difficulty. In the case of one of the 12 crosses involved in the test, the classification of the F_2-plants was verified by means of the F_3-strains. Of the 65 F_2-plants considered to be awnless 8 plants, bearing 28 culms and 1044 grains, proved to be heterozygously bearded; of the 136 F_2-plants considered to be intermediately bearded 7, bearing 57 culms and 2428 grains, proved to be homozygously awnless. The classification of the other crosses was not considered, as the cultivation and examination of the F_3-strains would involve a considerable amount of work whereas the influence of the awns also can be deducted from a comparison of the group of bearded plants with the combined group of the intermediately bearded and the awnless plants.

This comparison shows that the bearded plants have a grain-weight which is 104.7 % of that of the other plants. They also surpass the other plants with a yield which is on an average 103.0 % per plant and per culm also 103.0 % of the yield of the latter. As in the intermediately bearded plants probably some influence of the short awns will be present, the difference in yield between the fully bearded and the awnless plants may be a little more than 3 %.

The de-awning experiments of 1923 were repeated in 1943 on spring-barley and winter-wheat, sown normally in rows. In the barley a number of culms were selected which were equivalent as far as possible. Part of them were left untreated, another part was completely de-awned and the third lot was de-awned at alternate spikelets along both sides of the ear. Of the wheat, plants with two culms were selected. These plants were divided into three groups, two of which were likewise completely de-awned or de-awned at alternate spikelets. The kernel weights obtained are given in table 2.

Table 2. Weight of 1000 grains of cereal plants with and without awns.

Cereal varieties	Untreated		Spikelets alternately de-awned				Completely de-awned	
			Non-de-awned spikelets		De-awned spikelets			
	In g	In %	In g	In %	In g	In %	In g	In %
Spring barley („Mansholts 2-rijïge")	58.52	100	57.00	97.4	54.99	94.0	52.21	89.2
Wheat („Kruisingsangel")	51.66	100	51.83	100.3	50.01	96.8	51.35	99.4
Wheat („Nieuwe Angeltarwe") ..	58.45	100	56.85	97.3	56.16	96.1	55.29	94.6

Because of some statistical imperfections the experiment with wheat was repeated in 1946. Sets of 3 equivalent plants each with 2 ear-bearing culms and standing closely together, were marked for the experiment. The first plant of each set remained untreated, the second was completely de-awned and of the third each alternate spikelet was de-awned. Care was taken that in this third way of treatment the de-awned and the untreated spikelets were given, on an average, equivalent positions on the ear. The results for the longest culm and for the second culm were determined separately as is shown in table 3.

Table 3. Weight of 1000 grains of wheat-plants with and without awns.

Cereal varieties		Untreated		Spikelets alternately de-awned				Completely de-awned	
				Non-de-awned spikelets		De-awned spikelets			
		In g	In %	In g	In %	In g	In %	In g	In %
Variety	1st ear ..	45.41	100	46.01	101.3	43.54	95.9	42.60	93.8
„Kruisingsangel"	2nd ear ..	43.90	100	43.01	98.0	41.01	93.4	40.52	92.3
Variety	1st ear ..	51.13	100	50.83	99.4	48.73	95.3	48.67	95.2
„Nieuwe Angeltarwe"	2nd ear ..	48.46	100	49.00	101.1	47.29	97.6	47.49	98.0

Taken as a whole the tests mentioned here justify the conclusion that the awns account for c. 4% of the yielding capacity of bearded wheat under the circumstances prevalent in the tests. For spring-barley this percentage is c. 10%.

To complete the de-awning tests of 1943 and 1946 some chemical determinations were also made on samples of seed derived from the different tests.

The figures of 1943 showed that in general the protein contents of the untreated grain were somewhat lower. The figures can, however, not be reproduced as they were lost during the war. The protein content in the seed from the 1946 de-awning experiment gave the same picture, as is shown in table 4.

Table 4. Protein percentage in wheat-grains of plants with and without awns.

Cereal varieties		Untreated	Spikelets alternately de-awned		Completely de-awned
			Non-de-awned spikelets	De-awned spikelets	
Variety	1st ear ..	10.7	11.5	11.1	11.4
„Kruisingsangel"	2nd ear ..	10.2	10.9	11.1	10.8
Variety	1st ear ..	10.4	10.4	10.9	11.0
„Nieuwe Angeltarwe"	2nd ear ..	10.2	10.4	10.8	10.8

The ash content of the different treatments varied but little and showed no relation to the method of treatment, as also PERLITIUS (1904) experienced.

The lower protein content of the seed of the untreated plants indicates the contribution of the awns to the yield to consist of dry matter low in protein, the main constituent probably being starch. The dry matter added by the awns dilutes the protein in the seed and causes a lower protein content than where the awns are absent.

DISCUSSION

The influence of the awns is shown in a higher kernel weight and not in a noticeable alteration of the other yield-characteristics such as the number of ears per plant or the number of grains per ear. This indicates that the activity of the awns does not become operative before the number of ears per plant and the number of seeds per ear have been fixed, that is, not before flowering. This is in agreement with the results obtained by HARLAN & ANTHONY (1920). Not before a number of days after flowering did they observe differences occurring in the rate of development of the grains of awned and de-awned ears of barley. This moment co-incided with the beginning of the rapid accumulation of starch in the grains. This confirms that the awns are indeed suppliers of starch. A similar conclusion can be drawn from the lower percentage of nitrogen where awns are present, as was observed by PERLITIUS (1904) and HARLAN & ANTHONY (1920) and also in our experiments.

Two physiological functions of the awns have been studied in order to explain their influence on the yield; transpiration and assimilation. It is certain that the awns are responsible for a considerable proportion of the transpiration of the ear. Yet, elsewhere (VERVELDE, 1946) it was already pointed out that the greater flow of water caused by the awns towards the ear can affect the transport of assimilates towards the developing seed only under conditions of extremely rapid evaporation. There is also little reason to expect that the presence of awns will increase the water consumption of a cereal crop under field conditions, as one might be inclined to conclude from laboratory-tests with separate plants or ears, the water consumption by a closed vegetation being preponderantly controlled by atmospheric conditions and hardly dependent on the structure of the plant-cover (PENMAN, 1949). As a greater part of the evaporated water of bearded plants is led through the ear, this will result in a smaller transpiration by the other parts of the plant. The transpiration of the awns will therefore not have such a vital consequence for the plants as to explain the generally observed influence of awns on yield.

The assimilation of the awns has not been further tested since the experiments by SCHMID (1898). His tests, however, prove convincingly that the assimilation capacity of the awn is great. Thus he observed that the awned ear of barley assimilated during a few hours in broad daylight 2–4 times as much as the de-awned ear. The assimilation capacity of the awns sometimes amounted to 1/6th of the total assimilation capacity of the plant. BOONSTRA's (1936) tests make the influence of the awns easy to understand. He proved that the carbohydrates, required for filling the wheat-grain are formed during the growth of the seed and are not present beforehand by way of reserve. Only those organs of the plant which are capable of assimilation during the growth period of the grain, covering about 5 weeks, contribute directly to the seed-production. BOONSTRA also, by shading or removal of certain organs, succeeded in determining the share of the various organs in the production process. The ear contributed 30 % of the dry matter required for the filling of the grain, the ear-stalk 10 %, the stem and the sheaths 35 %, and the leaf blades 25 %. The winter-wheat used for the tests was awnless. An increase of the assimilation capacity of the ear due to the presence of awns must have a noticeable influence on the seed formation, though the share the awns have in seed-formation is not equal to their assimilation-capacity since the awns also have an intensive respiration.

It seems plausible to suppose that the influence of the awns will be closely connected with their length. This explains to a certain extent why the contribution of the awns to the seed-production of the various cereals is different and amounts to 10 % and more for barley, 3,5 % for ordinary bread-wheat and probably less than 2 % for rye.

The question whether awns are of value to increased yield can therefore, at least for barley and wheat, be answered in the affirmative. The question arises as to whether in respect of other easily identifiable characteristics of cereals research into their yield-function would be desirable. This could give important indications for their value in breeding. Of some negative yield-factors (susceptibility to frost, diseases and pests; inclination to lodging or shattering, chlorophyll deficiencies) the influence on the yield is firmly established, but this can hardly be said of any positive yield-factor. An examination of segregating progenies of crosses could be an important expedient, provided care be taken against statistical errors. A reason for the scarcity of such investigations is undoubtedly the fact that many characteristics are of a quantitative nature and also strongly modifiable. This makes it extremely difficult to divide a population with some degree of certainty into genotypes without a very elaborate progeny test.

An important question is why, in the warmer and drier areas, the bearded wheats especially predominate, whereas in a temperate climate, for instance in N.W. Europe, awnless wheats are almost exclusively cultivated. Apparently the advantage of awns is relatively greater in the former areas than elsewhere. This would suggest that the awns are better adapted to production under warm and dry conditions than some other organs of the plant which contribute to grain-filling. Physiological reasons can be advanced for this presumption. In the first place the awn is a young organ which is in its most productive stage during the period of seed development ("anabolic stage" according to VAN DE SANDE BAKHUYZEN, 1937) and therefore more able to stand up against unfavourable circumstances, which could upset metabolism. In the second place the consecutively appearing organs of the wheat-plant show an increasing degree of xeromorphism (VAN DE SANDE BAKHUYZEN, 1937), which characteristic therefore must be expected to be present to a considerable extent in the awns. The awns are indeed strongly reduced leaf blades, of which little more than the mid-vein remains. By such reductions many xerophytes attain a favourable water-supply of the assimilating tissues.

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