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Breeding for Seed Retention in Orchardgrass (*Dactylis Glomerata* L.)[1]

M. Falcinelli[2]

ABSTRACT

Loss of seed from maturing inflorescence (seed shattering) is common in grasses and constitutes a serious economic problem in many species. Seed shattering was studied in two orchardgrass cultivars which showed high and low shattering ('Hallmark' and 'Marta', respectively) and in their progenies with the aim of improving seed retention in 'Hallmark'.

Morphology and histology of individual spikelets of both cultivars were examined in 1986 to determine the mechanism of seed shattering.

It was observed that shattering is a two-stage process, involving disarticulation of the rachilla, followed by subsequent release of seed from the glumes. No clear-cut morphological and histological differences in spikelet structure were observed between high and low-shattering cultivars. The major differences were found in the development of the two abscission layers: the primary below the caryopsis and the secondary just above the glumes. In Hallmark these layers were identifiable and more evident at an earlier stage of seed development.

Twenty plants of Hallmark were selfed and crossed with a Marta counterpart and the same was done for 20 plants of Marta. Parents and progenies of plants from the two cultivars obtained by selfing or crossing were evaluated for seed shattering as spaced plants in the field. Fifty days after the anthesis date, plants were visually scored for seed shattering. Hallmark and Hallmark selfed had very high seed shattering scores (8.02 and 8.52, respectively), while Marta and Marta selfed had low seed shattering scores (2.53 and 2.04, respectively). The two F1 populations from reciprocal crosses had the same scores (6.60). There was a large difference in seed retention between Hallmark and Marta and the genetic control of this character seems to be simple and well fixed in the two populations.

Italian genotypes such as Marta have genetic resistance to shattering. Combining this resistance to seed shattering has great potential to improve seed yield characteristic of new forage cultivars.

Additional index words: **shattering, cocksfoot, abscission.**

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INTRODUCTION

Orchardgrass is one of the grazing plants of the temperate zones. It is taxonomically classified in the genus *Dactylis*, which is a small genus in the tribe *Festuceae* of the grass family. The best-known species in the genus is *Dactylis glomerata* L., orchardgrass or cocksfoot. The common name 'cocksfoot', which is especially used in the British Isles, comes from the characteristic shape of its inflorescence. Orchardgrass reproduces sexually by seed formation and asexually by tiller formation. The inflorescence of orchardgrass differentiates at the base of the plant and moves upward by elongation of internodes. Flowering culms grow from 60 cm to 200 cm in height, depending on climatic conditions, but are generally 100-130 cm high. These culms bear few leaves, but there are many basal leaves associated with the plant. The inflorescence of orchardgrass is a panicle and is composed of spikelets that bear two to five florets. The lowermost branches of the inflorescence are larger and more branching than ones near the top (Jung and Baker, 1985).

As is well known, in this species seeds do not mature and ripen uniformly and early maturing seeds frequently shatter before the late developing ones mature. Usually commercial cultivars of orchardgrass achieve maximum yields of germinable seeds at the cream cheese stage (Pegler, 1976) or at 44% moisture content (Klein and Harmond, 1971). Early harvesting can result in overproduction of light seeds which are removed during seed cleaning, whereas delayed harvesting may result in high losses through seed shattering. Losses of up to 24% have been reported by Nellist and Rees (1963) in orchardgrass seed crops due to delayed harvesting.

Several strategies are employed by seed producers to minimize seed losses, but the additional costs involved have limited their adoption. For example in the Pacific Northwest region of the United States, most grass grown for seed is swathed, allowed to cure in the windrow, then harvested with a combine (Youngberg, 1980). The most effective solution to the problem is selection for non-shattering genotypes that retain all seed at the full maturity stage (McWilliam and Gibbon, 1981; Falcinelli et al., 1984).

Previous papers (Falcinelli et al, 1983; 1984) have reported that many populations of *D. glomerata* from Southern Italy and some populations from Central Italy showed no seed shattering even at the full maturity stage; seed shattering is delayed until late autumn (Falcinelli et al., 1985). In general, natural populations of the species appear to show a wide degree of variability for seed retention. Strong rachillae and densely packed panicles and spikelets appear to be the main causes of this high degree of seed retention (Falcinelli et al., 1984).

Because of the importance of *D. glomerata* as a perennial grass for sown pastures, a breeding program has been undertaken to improve seed retention in a commercial cultivar. To provide a basis for this program, a study was made of the variation for seed retention within the species (Falcinelli et al., 1984), and the nature of its genetic control. Attempts were also made to identify particular features of the inflorescence to assist in selection.

MATERIALS AND METHODS

This study was carried out using two contrasting cultivars for seed shattering Marta and Hallmark and their progenies. Hallmark is the most popular cultivar in the southern part of the region of orchardgrass adaptation (Jung and Baker, 1985). Seed shattering occurs at the cream cheese stage. Marta is an Italian cultivar with high seed retention, and was obtained from the Plant Breeding Institute, University of Perugia.

Anatomical Study

Material for this study was obtained from 20 different genotypes chosen at random from each cultivar, Hallmark and Marta, and grown in pots under greenhouse conditions in 1986 in Perugia (Italy).

Histological development of the abscission zones in panicles of Hallmark and Marta spikelets was followed. Panicles, selected at random, were tagged at the peak of anthesis, as indicated by the exsertion of anthers in the middle portion of the panicle.

A single panicle from each genotype was sampled for anatomical study. Samples of the spikelets were taken from the middle portion of each panicle four and five weeks after peak anthesis. At least 20 Hallmark and Marta spikelets were observed for each sample. Observations were made to determine the dispersal mechanism using the scanning electron microscopy laboratory of the University of Perugia. Materials were coated with gold to about 20 nm thickness with a Polaron E-5000 coating unit.

Field Experiment

Morphological characters of the panicle and seed retention were evaluated in Hallmark, Marta and in their selfed and crossed progenies. The selfed seed was obtained from the selfing of 20 different genotypes chosen at random in each variety in 1984. Seed was also obtained in 1984 crossing in both directions pairs of plants of Hallmark and Marta which were obtained from the same genotypes utilized in selfing.

Two hundred seeds of each population (Hallmark, Marta, Hallmark selfed, Marta selfed and F_1, included reciprocals) were sown in boxes in the autumn of 1984. Sixty-four genotypes of each population were chosen at random and planted in the University of Perugia experimental field (43°05'N) in March of 1985.

Seedlings were space planted 60 cm apart in a randomized complete block design with two replications. Plots consisted of two rows of 32 plants for each entry.

Observations were recorded on 30 plants per plot, with plants at either end of the rows excluded from the experiment to avoid bias due to border effects.

Plots received, in kg ha^{-2}, 100 N, 100 P, 100 K at establishment, and subsequently 50 N in the spring of 1986.

Two inflorescences of each genotype were selected for uniformity of size and flowering date.

Twenty-eight days after anthesis commenced, one inflorescence was removed and the following characters were evaluated: panicle length, 1st, 2nd, and 3rd internode length, 1st, 2nd, and 3rd branch length (Fig. 1), spikelet length, glume length and width, caryopsis length (Fig. 2), caryopsis per spikelet.

To estimate seed shattering, the remaining inflorescence was used fifty days after anthesis date. Although laborious quantitative measures of seed retention were employed in our study (unpublished data), visual assessment of seed retention was also effective in screening initial orchardgrass populations. Sixty plants per population were visually scored for seed shattering after striking the panicle on a white cardboard. They were then scored on a scale from 1 (less than 5 seeds shattered), to 9 (all seeds shattered).

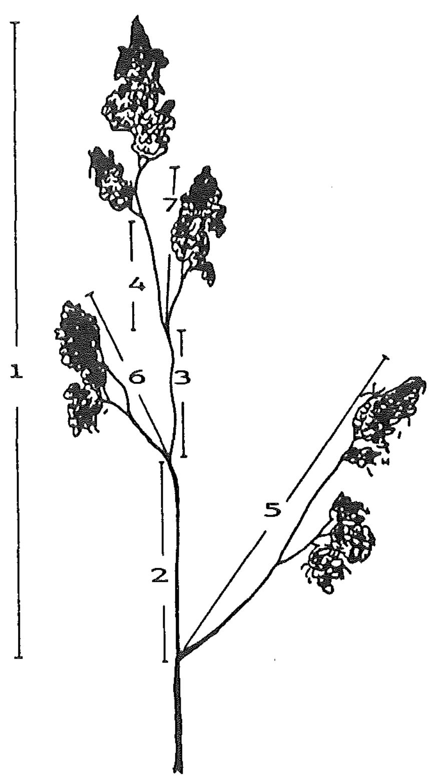

Figure 1. Infloṟescence of *D. glomerata* L.:
1 = total length
2-3-4 = 1st, 2nd, and 3rd internode length
5-6-7 = 1st, 2nd, and 3rd branch length.

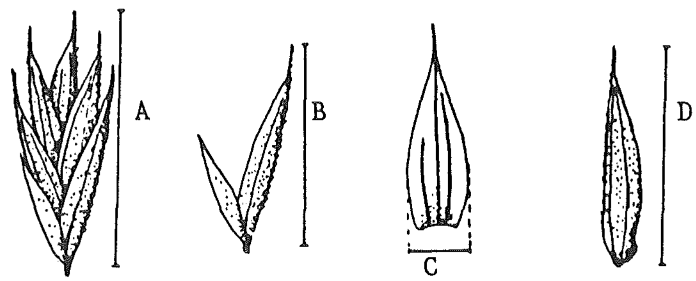

Figure 2. A = Spikelet length, B = Glume length, C = Glume width, D = Caryopsis length.

RESULTS

Anatomical Study

Sequential histogenesis of the abscission zones in both cultivars showed that abscissions occurred between the junction of the caryopsis and the tip of the rachilla (primary abscission = pa) or just above the glumes (secondary abscission = sa) as indicated by the arrows in Fig. 3; H1, M1. In Hallmark, shatter began approximately 28 days following anthesis (Fig. 3, H2). In three dimensional view, the abscission zone on the tip of the rachilla was a circular trough of small, thin-walled cells and large, thick-walled cells surrounding the vascular bundle (Fig. 3, H3).

At the same period (28 days after anthesis) Marta showed a strong rachilla with the caryopsis very well attached (Fig. 3; M2); Figure 3, M3, shows the tip cells of the rachilla when the caryopsis was torn; the shattering began about 50 days after anthesis (Fig. 3, M4) and continued very slowly in the panicle for a long period (1-2 months).

In both cultivars separation occurred by cell lysis, probably by hydrolytic enzymes, as suggested by the remaining jagged cell walls Hallmark (Fig. 3, H3).

In conclusion histological development of the zone pa began early in Hallmark and late in Marta. The sa zone was not studied in detail. Conclusive evidence of the above can be obtained from anatomical studies at more frequent and periodic intervals.

Field experiment

A good stand was developed for all populations. Morphological characters of the panicle in Hallmark, Marta and in their selfed and crossed progenies are reported (Tables 1 and 2).

Hallmark had higher values than Marta for all panicle traits (Table 1), this is particularly evident for total panicle length (28.7 cm vs 22.7 cm), for 1st branch length (14.1 cm vs 12.1 cm), for 2nd branch length (9.8 cm vs 7.6

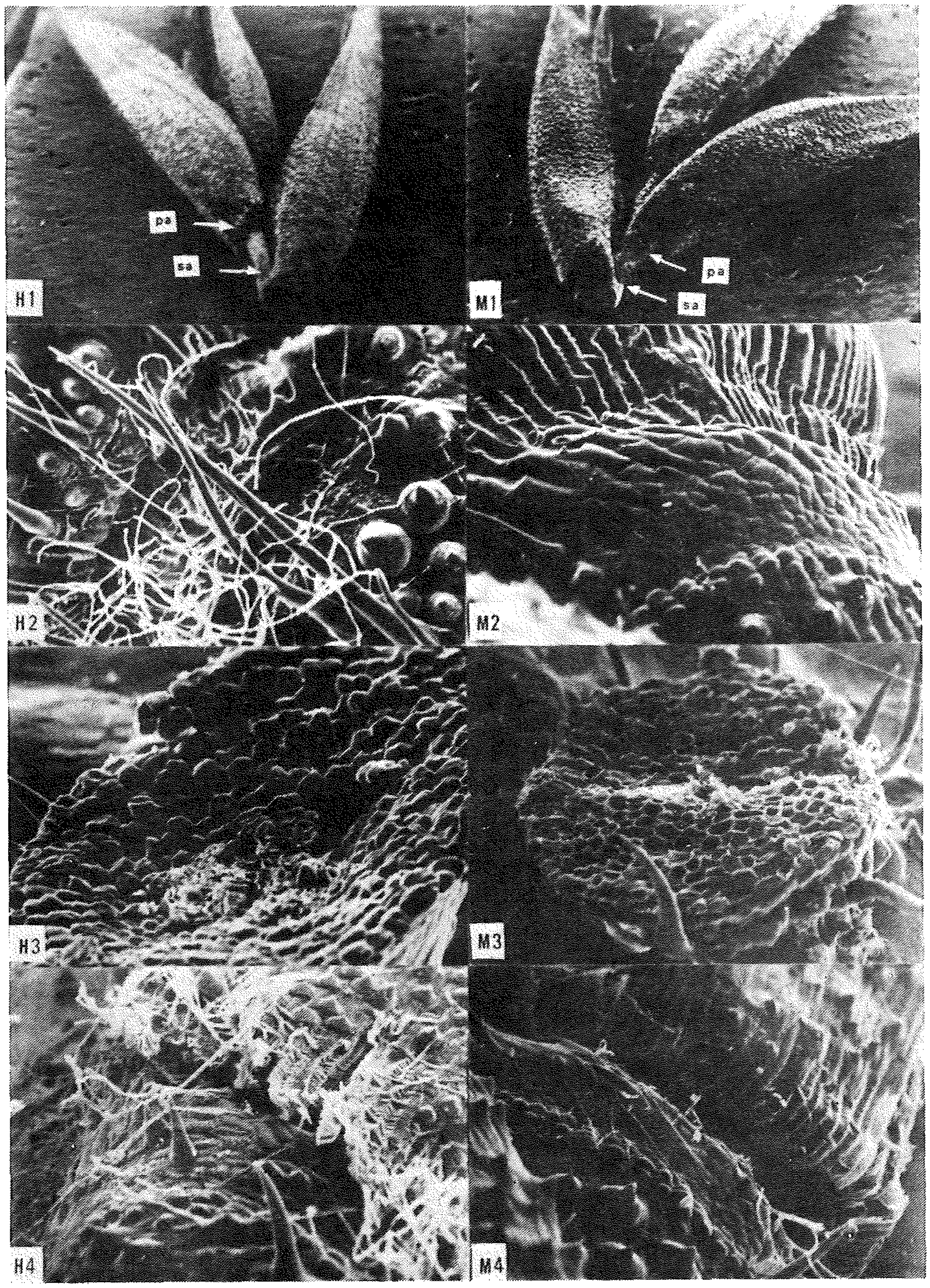

Figure 3. Development and subsequent disintegration of the abscission layer; H1 (Hallmark) and M1 (Marta), primary abscission zone (pa) and secondary abscission zone (sa) in the rachilla of the spikelet of Hallmark (H) and of Marta (M) (x 12, 6); H_2 and M_2, p.a. in H and in M four weeks after peak of anthesis (x 202, 5); H_3 and M_3, tip of rachilla when the caryopsis is torn (x 202, 5; H_4 and M_4, disarticulation of the caryopsis on the tip of the rachilla in H and M (x 202, 5).

Table 1. Panicle traits (mean ± standard error).

Populations	Panicle length (cm)	Internode length (cm)			Branch length (cm)		
		1st	2nd	3rd	1st	2nd	3rd
Hallmark	28.7 ± 1.29	9.0 ± 0.47	5.9 ± 0.40	3.9 ± 0.26	14.1 ± 0.61	9.8 ± 0.56	6.9 ± 0.48
Marta	22.7 ± 1.03	7.5 ± 0.41	4.7 ± 0.27	2.7 ± 0.16	12.1 ± 0.62	7.6 ± 0.46	4.7 ± 0.27
Hallmark x Marta	24.3 ± 0.81	7.8 ± 0.30	4.9 ± 0.18	3.0 ± 0.12	12.2 ± 0.50	7.7 ± 0.41	4.9 ± 0.34
Marta x Hallmark	27.3 ± 0.88	8.5 ± 0.41	5.5 ± 0.22	3.3 ± 0.17	13.1 ± 0.58	9.1 ± 0.36	5.9 ± 0.25
Hallmark Selfed	26.0 ± 0.98	7.6 ± 0.31	5.7 ± 0.28	3.4 ± 0.17	12.9 ± 0.54	8.3 ± 0.38	5.3 ± 0.30
Marta Selfed	20.8 ± 0.92	6.9 ± 0.41	4.6 ± 0.27	2.5 ± 0.14	10.7 ± 0.48	6.5 ± 0.41	4.0 ± 0.24

Table 2. Spikelet and caryopsis traits (mean ± standard error).

Populations	Spikelet length (mm)	Glume length (mm)	Glume width (mm)	Caryopsis length (mm)	Caryopsis spikelet
Hallmark	8.13 ± 0.250	6.12 ± 0.177	1.37 ± 0.045	7.13 ± 0.161	3.55 ± 0.154
Marta	6.94 ± 0.127	5.42 ± 0.126	1.47 ± 0.057	5.96 ± 0.155	2.55 ± 0.114
Hallmark x Marta	7.53 ± 0.159	5.84 ± 0.201	1.38 ± 0.064	6.60 ± 0.126	2.95 ± 0.154
Marta x Hallmark	7.49 ± 0.145	5.99 ± 0.113	1.51 ± 0.058	6.52 ± 0.147	2.45 ± 0.114
Hallmark	7.05 ± 0.136	5.19 ± 0.142	1.36 ± 0.046	6.56 ± 0.134	2.65 ± 0.131
Marta	6.75 ± 0.169	5.35 ± 0.174	1.38 ± 0.056	6.06 ± 0.163	2.50 ± 0.136

cm) and for 3rd branch length 6.9 cm vs 4.7 cm). The progenies from Marta x Hallmark showed higher values than Hallmark x Marta but were between the Hallmark and Marta values. The progenies of Hallmark selfed and Marta selfed gave lower values than their parents (Table 1).

The spikelets and glumes are longer in Hallmark than in Marta (8.13 mm vs 6.94 mm and 6.12 mm vs 5.42 mm, respectively) while the glumes are wider in Marta than in Hallmark (1.47 mm vs 1.37 mm) (Table 2). Hallmark has longer caryopsis than Marta (7.13 mm vs 5.96 mm) and more caryopsis per spikelet (3.55 vs 2.45). The crossed progenies (Hallmark x Marta and Marta x Hallmark) showed intermediate behavior between Hallmark and Marta. The selfed progenies of Hallmark and Marta showed values lower than their parents, respectively (Table 2).

Seed shattering scores were very low in Marta and in Marta selfed (2.53 and 2.04, respectively) but very high in Hallmark and Hallmark selfed (8.02 and 8.52, respectively) (Fig. 4). The two F_1 populations from reciprocal crosses had approximately the same score and for this reason were grouped in Fig. 4. Seventy-five percent of Marta plants had a score of three or less while no Hallmark plants had these scores. Contrastingly, 65% percent of the Hallmark plants scored between 8 and 9. Sixty-eight percent of Marta selfed plants had a score of 1 while 72% of Hallmark selfed had a score of 9.

Seventy-one percent of Hallmark x Marta plants were scored from 6 to 9.

DISCUSSION

In orchardgrass shattering results from the disarticulation of caryopsis from the rachilla or of rachilla from the rachis followed by subsequent release of seed from the glumes. Although Marta has a more compact panicle and larger glumes than Hallmark, in our observations it seems that glume or panicle characteristics are secondary factors and are not very important in seed retention since a strong rachilla is the principal determinant of seed retention. The ontogeny of the two abscission layers in Hallmark and Marta is very similar. The major difference in abscission layer development is that in Hallmark, these layers are identifiable and more evident at an earlier stage of seed maturity. Conclusive evidence of the above can be obtained from anatomical studies at frequent intervals.

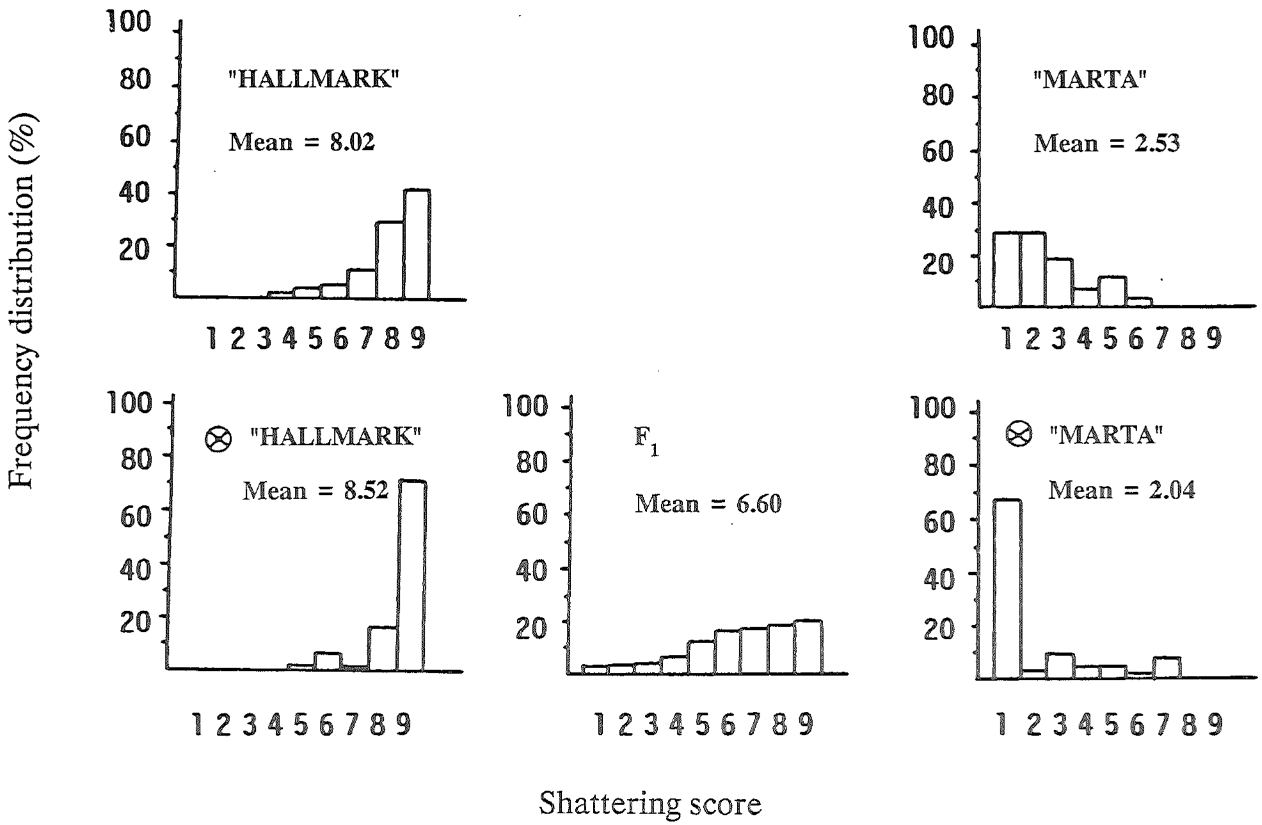

Figure 4. **Frequency distribution of seed shattering values (1 min - 9 max) for Hallmark, Marta, Hallmark Selfed ⊗, F_1 and Marta selfed. ⊗**

The results showed a large difference in seed retention between Hallmark and Marta; furthermore the character seems well-fixed in the two populations. From the results of this and previous studies (Falcinelli et al., 1983; 1984) on a wide range of ecotypes, it appears that seed shattering is less pronounced in genotypes from the drier southern regions of Italy. Highest seed retention has been found for plants with short rigid inflorescences containing a large number of densely packed spikelets. Nevertheless, the decision to base selection for seed retention on the cross Hallmark x Marta (Fig. 5) would appear to be justified on the evidence of Marta as a cultivar with a high level of seed retention and Hallmark as a productive American cultivar. Although techniques for harvesting *D. glomerata* have been developed to reduce the loss of seed from shattering, these invariably add substantially to the cost of the operation and ultimately to seed cost. A cultivar that retained virtually all of its seed at maturity could be harvested in one operation, and the quality and yield of the seed would be greatly improved.

Italian genotypes such as Marta have genetic resistance to shattering. Combining this resistance to seed shattering has great potential to improve seed yield characteristic of new forage cultivars. Thus, the development of a high seed-retaining cultivar of *D. glomerata*, would make an important contribution to the economics of seed production in this species.

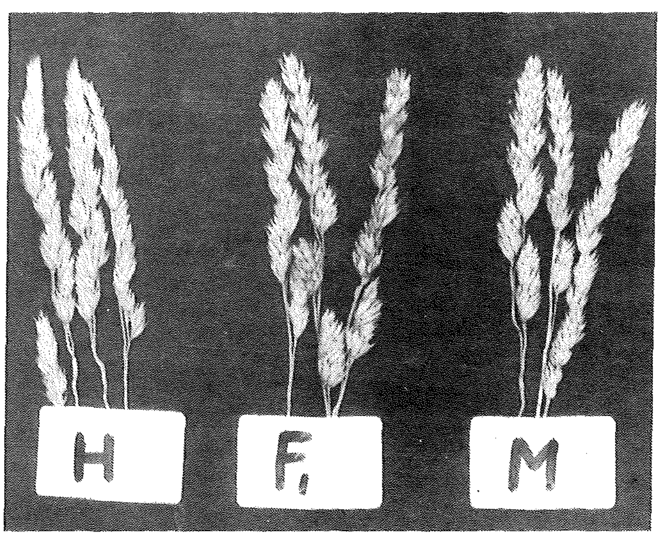

Figure 5. Hallmark (H), Hallmark x Marta (F_1) and Marta (M) panicles.

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