FORAGE SORGHUM BREEDING BY USING MALE-STERILE LINES

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Introduction

In the southern part of Japan, approximately 2 million cattle are raised, 40 percent of these animals are for beef and 60 percent are for milk production. For forage production in this area, perennial temperate grasses such as tall fescue (*Festuca elatior* L.) and orchardgrass (*Dactylis glometata* L.) are grown in the mountains, and most dairy and beef cattle farmers in the plains grow silage corn (*Zea mays* L.) or forage sorghum (*Sorghum vulgare* Pers.) in the summer and Italian ryegrass (*Lolium multiflorum* Lam.) in the winter. Practically, no grain sorghum has been grown in Japan after World War II, owing to severe damage on seed production caused by birds and to rainfalls which affected the crops at maturity.

In 1976, a total of 1.3 million tons (in fresh weight) of forage sorghum were harvested from 20,000 hectares of the cultivated area (65 ton/ha). When we started forage sorghum breeding in 1963, its cultivation area was about 500 hectares and the production per hectare was less than 40 tons. Why has the cultivation area of forage sorghum increased so much and so rapidly? One reason was that farmers demanded much more forage production per unit of land and the other our data disclosing many kinds of favorable characteristics and the high yielding potential of forage sorghum. Among the favorable characteristics of forage sorghum, better re-growing habits, higher resistance and/or tolerance to lodging, drought, insects and diseases and adaptability to higher plant density in our environmental and cultural conditions compared with other tropical and sub-tropical grasses and crops, especially corn, led the farmers to think that they would be able to easily grow and manage forage sorghum. In addition to these promising characteristics, the high yielding potentiality which was mainly demonstrated by our new forage sorghum hybrids, I believe, fascinated the farmers. Several newly developed forage sorghum hybrids yielded more than 150 fresh ton/ha in our 1966-68 yield trials (Tarumoto et al., 1969).

In this report, I would like to describe how we bred high yielding forage sorghum hybrids and also propose an efficient breeding method for utilizing male sterility and hybrid vigor. Additionally, I would like to make suggestions aiming at the improvement of digestibility and animal acceptability, which are major drawbacks of forage sorghum as compared with silage corn.

Breeding Hybrids by Using Male-sterile Lines

Many investigators reported that heterosis is remarkably expressed in F_1 hybrids of grain sorghum, and everyone is familiar with the impact on production achieved by the commercial use of grain sorghum hybrids. In contrast, studies on heterosis in forage sorghum were few and forage sorghum hybrid was unknown in commercial production by 1963 when we initiated our forage sorghum breeding in Japan.

Early in our breeding for improving growth rate and forage yield in the case of 2-3 harvestings at heading stage, we found that among the F_1 hybrids, even those produced by using dwarf grain sorghum male-sterile lines as seed parents, gave high forage yield due to remarkable hybrid vigor. After breeding studies and works conducted for ten years, sorghum-sudangrass hybrid, "Sendachi" (Sorghum Norin 1), and sorghum-sorghum hybrid, "Hiromidori" (Sorghum Norin 2), were officially licensed in 1971 and 1975, respectively.

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Table 1. Classification of *sorghum* spp. (Tarumoto, 1971)

Type	Group	Scientific name	Chromosome number (2n)
Grain sorghum	Feterita	*S. vulgare* Pers.	20
	Kafir (including male-sterile lines)	*S. vulgare* Pers.	20
	Hegari	*S. vulgare* Pers.	20
	Milo	*S. vulgare* Pers.	20
	Special purpose	*S. vulgare* Pers.	20
Sorgo	Exotic sorgo *	*S. vulgare* Pers.	20
	Domestic sorgo *	*S. vulgare* Pers.	20
Grass sorghum	Sudangrass	*S. vulgare* Pers. (var.) sudanenses	20
	Colombus grass	*S. almum* Parodi	40
	Johnsongrass	*S. halepense* (L.) Pers.	40
Broomcorn	Broomcorn	*S. vulgare* Pers.	20

* Adapted from Furudoi et al. (1973) and Doi et al. (1974)

The progress of forage sorghum breeding by utilizing male sterility in Japan is outlined in this part together with suggestions for improving the breeding method.

Plant introduction, evaluation and classification (Step 1 and 2): We introduced more than 300 cultivars from domestic and foreign research organizations in 1961-64. Based on 1962-64 field evaluation tests and cytogenetical studies, we developed a classification shown in Table 1, in which eleven sorghum cultivar groups were classified into four major types. Moreover, the cultivars were classified into subgroups within each group based on major characters like plant height, heading response, growth rate and brix degree. The classification proved helpful in advancing our forage sorghum breeding. Thus, evaluation tests depending upon the breeding aim and a classification which emphasizes the specific characters according to the breeding aim are considered to be effective for proceeding with breeding.

Determination of a profitable breeding method (Step 3): After the classification in Step 2, diallel crosses among the cultivars representing each of three types except broomcorn were conducted for obtaining genetic information of forage yield and its components. In these

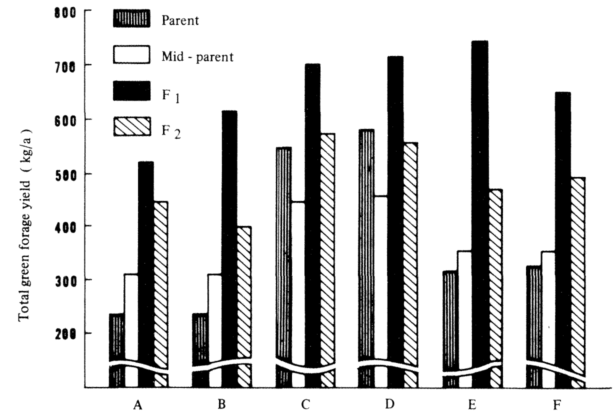

Fig. 1. Average performances of parents, mid-parents, F_1's and F_2's of diallel crosses in total green forage yield. (Tarumoto, 1971) (A&B, C&D, and E&F were representative cultivars of grain sorghum, sorgo and grass sorghum types, respectively.)

studies it should be possible to determine: (1) if heterosis in F_1 hybrids is large enough to recover the seed production cost, (2) if available male-sterile lines are suitable for developing excellent F_1 hybrids, and (3) which procedure is the most effective for advancing the breeding.

In our forage sorghum breeding, the results of F_1 and F_2 diallel sets brought the following conclusions: (1) F_1 hybrid forage sorghum proved as advantageous for producing forage as F_1 grain sorghums are for producing grain (Fig. 1), (2) it should be possible to develop F_1 hybrids with high forage yield even when using the dwarf male sterile lines of grain sorghum as seed parents, and (3) general combining ability as well as specific combining ability should be emphasized in selecting superior F_1 crosses. Especially, F_1 hybrids between cultivars of distant relatives, for example, F_1's of grain sorghum x sudangrass were most promising (Tarumoto and Oizumi, 1967a; Tarumoto, 1971). Therefore, it was considered that the development of F_1 hybrids using grain sorghum male-sterile lines as seed parents will be an efficient way for forage sorghum breeding.

Selection of promising combination types (Step 4): After proving in Step 3 that male-sterile lines obtained from other organizations are suitable for developing excellent F_1 hybrids, it is easier and more beneficial to make top crosses between male-sterile (A) lines and pollen fertility restoring (R) lines, by taking advantage of the cytoplasmic male-sterility mechanism as proposed by Stephen and Holland (1954). A set of top crosses had been considered for a long time to give only the information of general combining ability. However, as shown in

Table 2. Analysis of variance adapted from Design II (Comstock and Robinson, 1948) for analyzing quantitative genetic traits in forage sorghum populations. The appropriate F-test should be performed by repeated use of Error mean square for both G.C.A.'s and S.C.A.'s (Tarumoto, 1971)

1) Trials in a single year and location

Source of variations	D.F.	Expectation of mean squares
Replications	$r-1$	
Hybrids	$f-1$	
Gi's (G.C.A. of R-lines) [1]	$m-1$	$\sigma^2 + rf\sigma^2_{gi}$
Gj's (G.C.A. of A-lines)	$f-1$	$\sigma^2 + rm\sigma^2_{gj}$
Sij's (S.C.A.)[2]	$(m-1)(f-1)$	$\sigma^2 + r\sigma^2_{sij}$
Error	$(r-1)(mf-1)$	σ^2

2) Trials over several years or locations

Source of variations	D.F.	Expectation of mean squares
Replicates	$\kappa(r-1)$	
Experimental Field	$\kappa-1$	$\sigma^2 + rmf\sigma_l^2$
Hybrids	$mf-1$	
Gi's (G.C.A. of R-lines) [1]	$m-1$	$\sigma^2 + rfk\sigma^2_{gi}$
Gj's (G.C.A. of A-lines)	$f-1$	$\sigma^2 + rmk\sigma^2_{gj}$
Sij's (S.C.A.) [2]	$(m-1)(f-1)$	$\sigma^2 + rk\sigma^2_s$
Hybrid x Field	$(mf-1)(\kappa-1)$	
Gi's x Field	$(m-1)(\kappa-1)$	$\sigma^2 + rf\sigma^2_{gil}$
Gj's x Field	$(f-1)(\kappa-1)$	$\sigma^2 + rm\sigma^2_{gjl}$
Sij's x Field	$(m-1)(f-1)(\kappa-1)$	$\sigma^2 + r\sigma^2_{sl}$
Error	$\kappa(mf-1)(r-1)$	σ^2

1) General combining ability
2) Specific combining ability

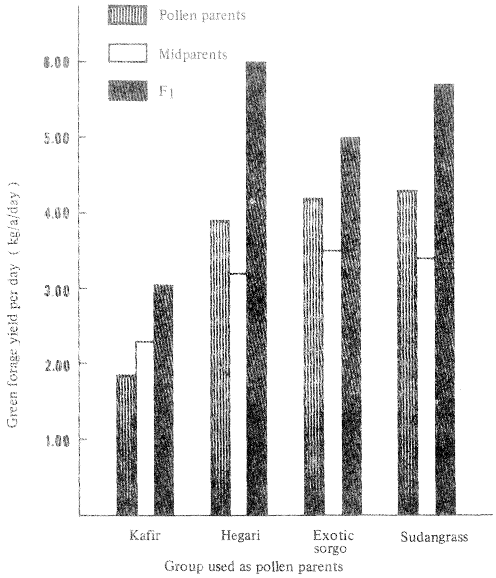

Fig. 2. Average green forage yield per day for pollen parents, mid-parents and F_1's (Tarumoto and Oizumi, 1968a)

Table 2 (Tarumoto, 1971), we got enough information about gene actions even from a set of top crosses.

Several sets of top crosses were made between grain sorghum male-sterile lines (A-lines), representing 2-, 3-, and 4-dwarf gene types, and representative cultivars of promising four groups which were selected in Steps 2 and 3 as distant relatives to grain sorghum A-lines and sweet-juicy stalk genotypes. Cultivars of hegari and sudangrass groups were found to be good general combiners with grain sorghum A-lines as shown in Fig. 2 (Tarumoto and Oizumi, 1968a; Tarumoto, 1968b and 1969a). Lately at Hiroshima Prefectural Agricultural Experiment Station, cultivars of domestic sorgo group also proved to be good general combiners with grain sorghum A-lines (Doi, Mogami and Furudoi, 1974).

From the results of the top crosses, it was suggested that general combining ability should be emphasized for selecting both seed and pollen parents.

Selection of excellent F_1 hybrids in each of the promising combination types (Step 5 and 6): More top crosses were made in Step 5 for clarifying genetical and physiological basis of heterosis and obtaining information on combining ability in each of the promising combination types which were selected in Step 4. From the results, the following selection method for excellent hybrids was suggested:

The high forage yield of F_1 hybrids resulting from crosses between grain sorghum A-lines and hegari cultivars (designated as MS-HE hybrid thereafter) was associated with tall growth, as a result of multiple gene action affecting height, and later maturity controlled by complementary gene action on maturity. Another aspect of MS-HE hybrids was that progeny tests could be more effectively done in a droughty field, where differences in combining ability are better expressed (Table 3). General combining ability was found to be an important selection criterion for forage yield and its components. From these results, the following scheme was considered as the most effective way to develop the MS-HE hybrids with high forage yield. The first step is to test many top crosses in relatively small-sized plots using the "Successive Cutting Method" (each plot is cut when 50% headed) to identify genotypes of

Table 3. Different expression of genetic variations in dry and moist fields in hybrids of MS-HE combination type. (Tarumoto, 1971)

Source of variation	D F	40 days old plant		First harvesting time			
		Plant height	Tiller number	Plant height	Tiller number	Stalk diameter	Green forage yield
Dry field							
Hybrids:	15						
G. C. A. of R-line	3	NS	NS	**	**	**	*
G. C. A. of A-line	3	**	NS	**	**	**	**
S. C. A.	9	**	NS	**	NS	**	NS
C. V. (%)		5.2	5.0	2.3	12.2	2.6	10.3
Moist field							
Hybrids:	15						
G. C. A. of R-line	3	**	**	**	**	NS	NS
G. C. A. of A-line	3	**	NS	*	**	**	NS
S. C. A.	9	**	NS	*	NS	*	NS
C. V. (%)		4.3	5.6	3.5	13.8	3.8	9.4

Source of variation	Early regrowth		Second harvesting time				Total green forage yield
	Plant height	Tiller number	Plant height	Tiller number	Stalk diameter	Green forage yield	
Dry field							
Hybrids:							
G. C. A. of R-line	**	**	**	**	**	**	**
G. C. A. of A-line	**	**	**	NS	**	**	**
S. C. A.	NS	NS	**	NS	NS	NS	NS
C. V. (%)	5.8	9.9	5.1	11.8	3.0	13.7	10.0
Moist field							
Hybrids:							
G. C. A. of R-line	**	**	**	NS	**	**	**
G. C. A. of A-line	**	NS	**	**	**	NS	NS
S. C. A.	NS	NS	**	**	**	NS	NS
C. V. (%)	2.8	10.7	3.2	9.0	3.0	11.9	9.4

* Significant at the 5% level of probability.
** Significant at the 1% level of probability. NS: Not significant.

suitable plant height and maturity and to roughly select parents for high general combining ability. This should be followed by a large-sized plot test using the "Simultaneous Cutting Method" (all plots in a test are cut simultaneously at each harvesting date) in a relatively droughty field for selecting the best crosses (Tarumoto, 1969b and 1971).

In F_1 hybrids between grain sorghum A-lines and sudangrass cultivars (designated as MS-SU hybrid hereafter), the high yielding ability was presumably attributed to: (1) the rapid elongation of leaves and stems at the initial and regrowing stages, and (2) the higher percentage of effective tillers. All the MS-SU hybrids resembled each other in both morphological and ecological types, because the sudangrass cultivars used were not much different from each other especially in tillering, maturity, and height compared with hegari cultivars. Several progeny tests conducted in different years and locations suggested that quantitative gene action in the MS SU hybrids was easily affected by the artificial and natural external conditions

Table 4. **Differences in total forage yield (kg/a) of MS-SU hybrids in dry and moist fields.** (Tarumoto, 1971)

Grain sorghum[1)] A lines	Field condition	Sudangrass[2)]				Mean of A-lines crossed to sudangrass
		A	B	C	D	
1	Dry	686.9 abc	636.4 c	687.2 abc	790.5 a	700.3 a[3)]
	Moist	1030.2 abc	1008.0 bc	938.0 c	1015.5 bc	998.0 b
2	Dry	748.3 ab	706.4 abc	727.5 abc	715.8 abc	724.5 a
	Moist	1000.8 bc	985.2 c	985.5 c	971.3 c	985.7 b
3	Dry	788.0 a	657.5 bc	704.7 abc	736.9 abc	721.8 a
	Moist	1140.0 ab	1033.6 abc	1166.3 a	1021.9 bc	1090.5 a
4	Dry	746.3 ab	650.3 bc	676.3 bc	708.3 abc	695.3 a
	Moist	1136.7 ab	1010.0 bc	1030.3 abc	1130.3 ab	1076.8 a
Mean of sudangrass crossed to A-lines	Dry	742.4 a	662.7 b	699.0 ab	737.9 a	710.5[4)]
	Moist	1076.9 a	1009.2 b	1030.1 ab	1034.8 ab	1037.7[4)]

1) Grain sorghum A lines: (1) 3128, (2) Wheatland, (3) Redbine 58, (4) Texas Blackhull Kafir
2) Sudangrass varieties: (A) Lahoma, (B) Greenleaf, (C) Sweet 372, (D) Sweet Sudan
3) Measured by Duncan's multiple range test (5% level).
4) Mean of all F_1 hybrids.

(Table 4). It was concluded that the following scheme would be one of the most convenient means to develop high yeilding MS-SU hybrids. A top-cross test with at least two locations or years should be conducted by using the "Simultaneous Cutting Method", for selecting parents with high general combining ability. Performance tests should follow the test to screen the best hybrids for various environmental conditions, because of their sensitivity to natural conditions (Tarumoto, 1970 and 1971)

The F_1 hybrids between grain sorghum A-lines and domestic sorgo cultivars showed the intermediate plant types between MS-HE and MS-SU hybrids, expressed a high degree of heterosis and gave high forage yield which was not at all inferior to that of MS-HE hybrids (Doi et al., 1974). Although general conclusions were not drawn, the results seemed to be explained by distant relationships between grain sorghum A-lines and domestic sorgo cultivars. However, at the present time, the hybrids experience serious trouble in stalk-breaking probably owing to the genetic background of domestic sorgo cultivars and seed multiplication (Furudoi, et al., 1973 and 1975).

In the sixth step, the promising F_1 hybrids in each of the selected combination types were selected by using the efficient selection method obtained in Step 5. In the selection procedure quality and resistance to diseases, insects and drought as well as yield performance were assessed. As far as I am concerned, I selected four MS-HE hybrids and three MS-SU hybrids.

Performance test of developed F_1 hybrids and release of new cultivar (Step 7 to New cultivar): From Step 7 to the development of the new variety, the ordinary procedures were applied. In Japan, it is requested that at least two years' yield tests at the breeding station and three years' evaluation tests in many prefectures on adaptability and major agronomic characteristics including yield be conducted in the framework of the forage grass breeding scheme. The bred lines have their particular strain names when released for the evaluation test (Step 8). When strains show the outstanding performance in Step 8, they are assessed at an annual meeting organized by the Ministry of Agriculture and Forestry of Japan and if judged to be satisfactory they are licenced and get a number and a name

MS SU-1 and MS-HE-1 were designated as "Chugoku-ko 1" and "Chugoku-ko 2" in 1968 (Tarumoto et al., 1969) MS-HE-II was designated as "Chugoku-ko 3" in 1971. Chugoku-ko 1 was licensed as "Sorghum Norin-ko 1" with the cultivar name "Sendachi" in 1971 (Arata et al., 1972) and Chugoku-ko 3 was licensed as "Sorghum Norin-ko 2" with the cultivar name "Hiromidori" in 1975 (Mogami et al., 1975).

Sendachi is taller, and has more effective tillers, greater stalk diameter and longer and wider leaf blades and more rapid growth rate in comparison with sudangrass cultivars. Sendachi yielded 8% and 12% more forage compared with Sweet Sorgo and Sudax-11 (leading commercial hybrids in 1967-69), respectively (Table 5). Hiromidori is taller and has relatively more tillers, greater stalk diameter and longer and wider leaf blades in comparison with sorgo cultivars. Hiromidori yielded 16% more forage compared with Hybrid Sorgo (leading commercial hybrid in 1967-74), (Table 6).

Remark: The above mentioned breeding work with 8 steps is schematically presented in Fig 3. The breeding scheme shown is expected to be applied to other crops, in which male sterile lines will be available for developing F_1 hybrid varieties.

Proposal for Breeding Better Quality Forage Sorghum Hybrids

In the past, the most important objective of forage sorghum breeding was high yield performance. Animal utilization and performance were less often considered in varietal improvement. However, increasing costs and alternate high income use of land make both high yield potential and improved quality important objectives for the forage breeder.

Table 5. Forage yield and its components of Sendachi compared with commercial sorghum-sudangrass hybrids. (Tarumoto, 1971)

	Plant height (cm)			Stem number/m			Stalk	Forage yield (kg/a)			
	1st cut	2nd cut	3rd cut	1st cut	2nd cut	3rd cut	diameter	1st cut	2nd cut	3rd cut	Total
Sendachi	219	196	214	40	50	79	1.4cm	460	382	479	1321
	(96)	(93)	(100)	(100)	(96)	(95)	(108)	(100)	(111)	(113)	(108)
Sudax-11	228	198	216	31	46	76	1.5	427	328	419	1174
	(100)	(94)	(101)	(78)	(89)	(92)	(115)	(93)	(95)	(100)	(96)
Sweet Sorgo	229	210	213	40	52	83	1.3	461	344	421	1226

Average performance for 3 fields in 1967–68 at Chugoku Natn'l Agr. Exp. Sta. (Fukuyama, Hiroshima).
Relative values in % to Sweet Sorgo were shown in ( ).

Table 6. Forage yield and its components of Hiromidori compared with commercial sorghum hybrid. (Calculated from the data in Tarumoto, 1971)

	Plant height, cm		Stem number/plant		Stalk diameter, cm		Forage yield (kg/a)		
	1st cut	2nd cut	1st cut	2nd cut	1st cut	2nd cut	1st cut	2nd cut	Total
Hiromidori	265	221	2.2	1.8	1.8	1.6	520	593	1113
	(108)	(100)	(110)	(113)	(113)	(100)	(123)	(110)	(116)
Hybrid Sorgo	244	220	2.0	1.6	1.6	1.6	423	537	960

Average performance for 2 fields in 1967-69 at Chugoku Natn'l Agr. Exp. Sta. (Fukuyama, Hiroshima).
Relative values in % to Hybrid Sorgo were shown in ( ).

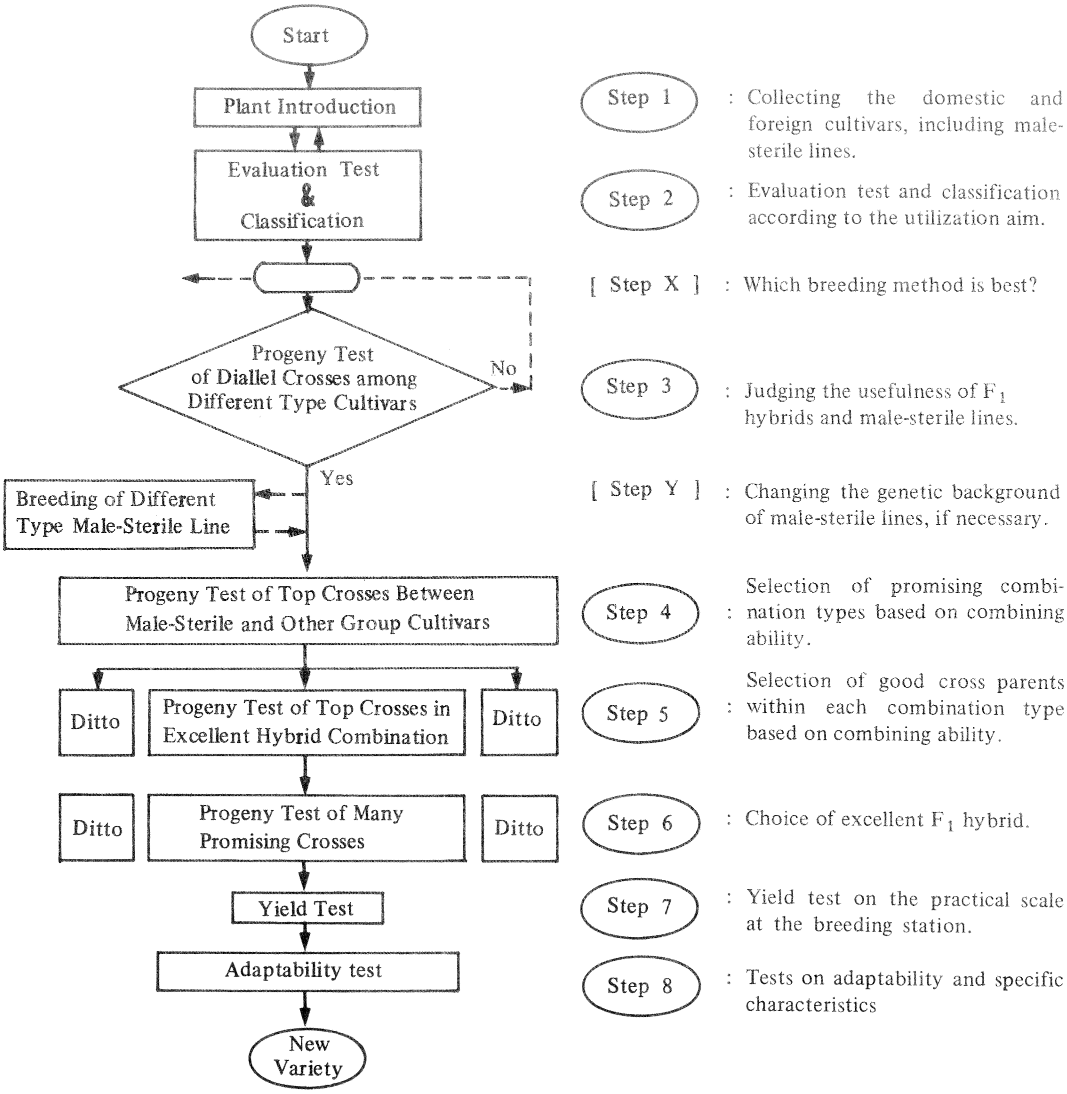

Fig. 3. Breeding procedure for using male sterility (Tarumoto, 1975)

A number of dairymen in Japan as well as in the United States of America producing both corn and sorghum silages have experienced serious drop in milk production when switching from corn to sorghum silage in the feeding program. The decreased milk from the cows fed sorghum silages appears to be due to both low intake and digestibility (Gourley, 1975).

The ultimate means of determining digestibility and animal intake is feeding trial. However, digestibility correlates well in most cases with animal intake and production (milk or meat). Therefore, digestibility should be first taken into consideration. According to Gourley, 1975; Cummins, 1972; and others, forage sorghum hybrids carrying the following genes and/or characters will improve their quality: (1) bloomless gene (recessive monogenic inheritance), which speeds up the rate of fermentation of sorghum silage in the rumen, (2) brown midrib gene (recessive monogenic inheritance), which reduces lignin contents of stems and leaves, (3) tanninless or low-tannin content (multigenic inheritance), which will remove or reduce tannin interference in digestion, (4) tan plant (recessive monogenic inheritance), which may improve digestibility (personal communication), (5) dry and insipid stalk (dominant monogenic inheritance, independently), which will reduce seepage from sorghum silage during fermentation, (6) limber stalk (unknown inheritance), which may increase animal intake when feeding as green chop and grazing, (7) high grain to stover ratio which will make high quality silage, suggesting the development of dual type hybrids which ideally have about the same maturity irrespective of seeding time, and (8) others (low hydrocyanic acid, disease and insect resistance, etc.).

At the present time, the utilization of bloomless and brown midrib genes seems to be most promising for improving the quality of forage sorghum. Although these two genes are recessive, the genes can be transferred to the normal cultivars by back crossing and the genotypes carrying the genes are easily identified by the visual observation. Therefore, for improving the quality, another step should be added to the scheme between Step 4 and 5 (Fig. 1), for transferring the particular genes or characters to A-lines, their maintainers (B-lines) and R-lines.

Another aspect related to the improvement of the quality is represented by evaluation methods of digestibility. For this purpose, many kinds of *in vivo* and *in vitro* digestion techniques and proximate analyses were developed. The simple *in vitro* digestion techniques developed by Monson, et al. (1972) and Tarumoto and Masaoka (in press) will be helpful for evaluating digestibility of a large number of samples in breeding.

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Discussion

J. T. Rao, India: I would like to know more about the use of hybrid sorghum male sterile lines as a means of encouraging forage production. As we know, hybrid sorghum lines have been developed with the aim of increasing the seed component while reducing leaf and stem area. Would any other crop line hybrid be more useful in this direction?

Answer: In grain sorghum hybrids, stover yield is sacrificed to enable a better use of harvesting equipment (combine) and even now taller grain sorghum hybrids produce more grain and stover than dwarf ones. In the case of cotton, dwarf types are well adapted to the use of combine.

N. Murata, Japan: Lignification is often said to operate as a factor for resistance to some diseases. Aren't there any indications that reduced lignin content and other characteristics favorable for digestion show unfavorable side-effects in terms of disease resistance or tolerance to environmental stress?

Answer: Bloomless genotypes are not tolerant to drought. Unfavorable side-effects associated with improvement of digestibility have not been found in other genotypes.