ACCELERATION METHODS FOR GENERATION ADVANCEMENT IN HYBRID POPULATIONS OF RICE

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Introduction

The rapid generation advancement of breeding materials is of major importance in a plant breeding program and such idea has been proposed by many researchers (Goulden, 1939, Amatatsu and Nagata, 1941, Akemine, 1954, Wiggans and Frey, 1955, Wellensiek, 1962, Grafius, 1965, Okabe, 1966).

Shortening the breeding cycle is particularly helpful to rice breeders in the temperate zone where low temperature prevents rice from growing during the winter season. In Japan, this procedure was carried out at Aichi Agricultural Experimental Station in 1932, but at that time F_1 generation only was accelerated in the greenhouse in winter (Okabe, 1967).

It is since the 1950's that acceleration method for generation advancement has been developed and adopted widely in a practical rice breeding program. Such an extensive utilization of this procedure was initiated and stimulated by two factors (Akemine, 1966, Okabe, 1967). The first was concerned with keeping new varieties sufficiently constant in the face of the ever-changing situations in agricultural production. Since it usually takes more than ten years to develop new varieties with the customary pedigree or bulk breeding methods, an accelerated-generation increase program was an urgent need to meet the demand of the time. The second was concerned with the wide adoption of the bulk method of breeding in self-pollinated species such as rice, wheat, barley, etc. in Japan. Although this method has been used extensively since 1950, its disadvantages were pointed out as, compared with the pedigree method, a somewhat longer time and wider field area are required. With the bulk breeding method, however, controlled environment conditions or off-season nurseries can be used to accelerate the generation cycle, and moreover dense spacings of materials can save the field area (Akemine, 1954).

Several experiments demonstrated the possibility of advancing three generations in rice hybrids (Kikuchi, 1958, Asakuma, 1959). Using the greenhouse for shortening the breeding-cycle, Aichi Prefectural Agricultural Experimental Station for the first time succeeded in developing a new variety "Nippon Bare" in a short time (seven years) (Nishio *et al.*, 1963). Since its release in 1963, this variety has been widely grown in central and western Japan, owing to various superior characteristics. In 1976, this variety was planted on 359,000 hectares or 14.3 percent of the total rice area, ranking first among rice varieties.

The facilities used for rapid generation advancement have been installed at the rice breeding stations, and shortening the breeding-cycle has now been established as the most useful procedure used in rice breeding programs in Japan.

The scope of the present paper is to review briefly the practical methods of rapid generation advancement in rice breeding in Japan as well as some related subjects.

Practical methods of rapid generation advancement

Practical methods of rapid generation advancement are now being carried out by rice breeders in the following two ways, namely the nursery box method and the nursery bed method (Akemine, 1966, Okabe, 1967).

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1. Nursery box method

With this method, hybrid populations are grown without transplantation in a small nursery box in the greenhouse. Seeds are planted at close spacing of about 3 x 3 cm, that is 1,100 seeds/m^2. A small amount of fertilizer is applied at planting time: N, P_2O_5 and K_2O, about 5 g./m^2 respectively. Top dressing is also given as needed.

A combination of short-day and high temperature treatment is necessary for shortening the life-cycle of rice plants. Short-day treatment of 8 to 10 hours photoperiod will usually start 15 days after planting, when the plants are at the fourth-leaf stage, and be continued for about one month. Two kinds of methods are being used for short-day treatment in the greenhouse. The first one consists of covering the nursery boxes with a black curtain or the like. The second consists of carrying truck loading nursery boxes into the dark room in the greenhouse (Fig. 1).

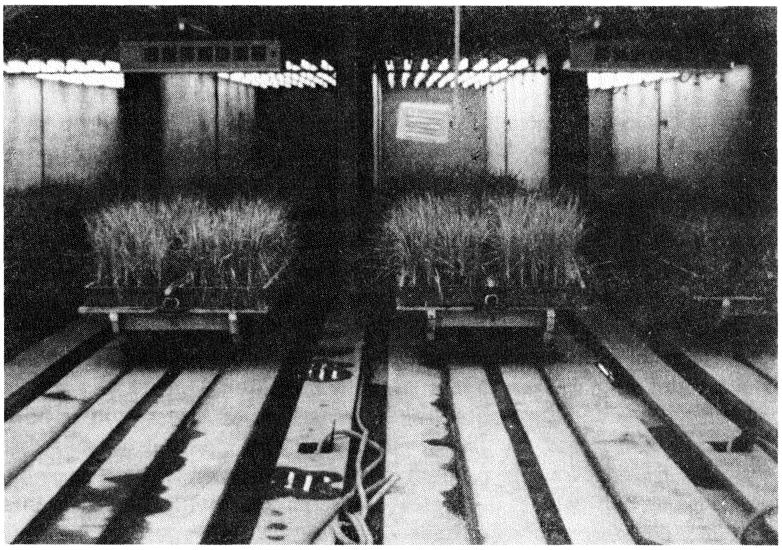

Fig. 1. "Short-day" treatment facility for shortening the breeding-cycle at Toyama Prefectural Agricultural Experimental Station.

During the winter season, the temperature in the greenhouse must be kept above 20°C in order to prevent cold weather from damaging the plants.

Under these artificially controlled environments, plants take 50 to 70 days from germination to heading, in crosses between Japanese varieties. Taking the ripening period of 30 days into consideration, we can accelerate the time required for one generation within 100 days, and thereby advance at least three generations of breeding materials in one year.

Harvesting of seeds is handled in two ways, namely by the bulk method and the single seed descent method. For the bulk method, all plants are harvested in the mass to produce the bulk population of the next generation. Single seed descent method consists of taking a single seed from each plant and compositing the seeds to maintain the next generation.

Table 1 shows an example of the nursery box method which is being adopted in the rice breeding program of Chugoku Agricultural Experimental Station (Yamamoto, 1972, 1975). With this procedure, shortening the breeding-cycle is continued until F_4 generation, after which, line and individual selections for agronomic characters are carried out in the successive generations in field environments. In such a breeding program, the time required to develop new varieties will be accelerated by three years compared to traditional breeding systems.

Table 1. **Rice breeding scheme with an accelerated-generation at Chugoku National Agricultural Experimental Station.**

(Yamamoto, 1972)

Year and season	Generation		Cultivation conditions and some tests
1) Summer	Crossing	G.	About 30 combinations
Winter	F_1	G.	Pot culture, 15 pots per combination
2) Spring	F_2	G.	Box culture, Density 3.0cm x 2.5cm 1,000 plants per cross combination Harvested one seed from one plant
Summer	F_3	G.	Ditto
Winter	F_4	G.	Ditto. Harvested one panicle from one plant
3) Summer	F_5	F.	Transplanting, Density 30cm x 20cm 1,000 panicles per cross combination, 5 plants per panicle Line and individual selection
4) Summer	F_6	F.	Direct seeding Yield trial by micro plot design Test of disease resistance and grain quality Line selection, 10 panicles from each line
5) Summer	F_7	F.	Direct seeding and transplanting Yield trial by large plot Test of disease resistance, lodging and grain quality Ecological adaptability test Line and individual selection
6) Summer	F_8	F.	Direct seeding and transplanting Yield trial by large plot Test of disease resistance, lodging and grain quality Line and individual selection "Local Number" is assigned
7) Summer	F_9		Forwarded to the respective Pref. Agric. Expt. Stations

G. : Greenhouse, F. : Field

2. Nursery bed method

With this method, seeds of hybrid populations are broadcast at dense spacings on the nursery bed and the plants are left on it until harvest time. Seeding rate is 1,000 to 2,000 seeds/m^2. This procedure enables rice breeders to advance two generations in one year, that is, from March through June and from July through November. The practical application of this method is limited to two rice breeding stations, Miyazaki and Kagoshima, located in the southernmost regions where off-season rice growing seldom meets with serious difficulties because of comparatively high mean temperatures. However, in order to protect plants from low temperatures in both early growth stage of the first culture and late growth stage of the second culture, nursery beds are covered with vinyl cloth temporarily or prepared in the glass house.

Merits of this method are that neither special facilities nor much labor are needed and that a larger number of plants can be treated compared to the nursery box method.

At present, breeding materials from several rice breeding stations are sent to the above-mentioned two stations and usually four generations, from F_1 or F_2 through F_5 generation, are advanced over two years.

Achievements of rice breeding with an accelerated-generation program

In 1976, 30 promising lines of lowland rice have been developed at the 15 national and designated prefectural rice breeding stations, among which 29 lines, that is, 97% of the total, have been bred by employing the above-mentioned method of rapid generation advancement (Table 2). It is apparent from this table that shortening the breeding-cycle has been established in the rice breeding program in Japan.

Table 2. Classification based on breeding methods of 30 promising lines which were developed in 1976.

Breeding station	Acceleration procedure			Pedigree method
	Nursery box	Nursery bed	F_1 only	
Kamikawa *	1		3	
Hokkaido			1	
Fujisaka *	1		2	
Tohoku		2		
Furukawa *	1			
Hokuriku	4			1
Fukui *	1		1	
Central Agric. (Konosu)		2		
Aichi * (Inahashi)	2			
Chugoku	2			
Kyushu	2			
Miyazaki *	2			
Kagoshima *		2		
Total	16	6	7	1

* Designated Prefectural Station

Subjects connected with methods of rapid generation advancement

As greenhouse or nursery environments under which the acceleration procedures are carried out differ in many respects from field environments, rice breeders have been confronted with new problems. Much research has been undertaken in order to solve these problems.

1. Seed dormancy

For shortening the breeding-cycle, it is necessary to reduce the period from seed to seed as much as possible. The length of a life-cycle is determined by the duration of the germination period, the time from germination to flower initiation, the time from flower initiation to heading, and the ripening period. Seed dormancy is one of the disadvantages of the rapid generation advance, when it is necessary to plant seeds of successive generations immediately after harvest (Roberts, 1961).

As the duration from harvesting to sowing is generally short, germination of freshly harvested seeds often proceeds very irregularly and extends over a long period of time due to dormancy and immaturity. Such an irregular germination may cause inter-plant competition and consequently genetic shift of hybrid population. Therefore, it is necessary to break dormancy immediately after harvesting.

Many investigations aimed at breaking dormancy have been carried out and these results have been consistent in proving that heat treatment is very effective (Oka and Tsai, 1955, Robert, 1962, Jennings and Jesus, 1964, Iwashita, 1970, Ishizaka and Samoto, 1975, Hayashi, 1977).

Freshly harvested seeds gave rapid and high germination percentages when the seeds were kept at 40° to 43° C for 10 days or at 50° to 55° C for 5 days in a dryer and also at 45° to 50° C for 3 to 5 days in a humid atmosphere (Iwashita, 1970).

There were clear differences in duration and intensity of dormancy among the Japanese varieties. Low viviparous and photoperiod-sensitive varieties showed poor germination when sown immediately after harvest. The slow germination, however, was overcome when freshly harvested seeds were kept at 43° C for 10 days or the ripening period was more than 40 days. Duration of heat treatment for breaking dormancy depended on the ripening period of seeds (Table 3), that is, the shorter the period of ripening is, the longer the heat treatment is required (Ishizaka and Samoto, 1975).

Table 3. Effects of heat treatment length on percentage of germination of seeds with different ripening periods.

Days after flowering	Length of heat treatment (days)		
	5	10	15
	%	%	%
20	0	10	35
25	32	66	81
30	52	94	100
35	80	99	99
40	88	100	100

After Ishizaka and Samoto (1975)

Variety : Koshihikari (a low viviparous and high dormant variety)

Heat treatment : at 43° C in a dryer

Percentage germination was measured 4 days after treatment.

Using 27 *indica* varieties varying in grain size and origin, Jennings and Jesus (1964) investigated the effectiveness of heat treatment for breaking dormancy and found that treatment at 50° C for 4 to 5 days broke dormancy in nearly all the varieties. A more dormant variety, Seraup 27, required treatment for 9 to 10 days. The authors also noted that seeds must be treated in open or paper containers to enable a rapid loss of moisture content and to prevent damage from the heat treatment.

2. Changes in genetic composition of hybrid population during accelerated-generation cycle

The major concern in the method of rapid generation advancement is to know whether any changes in the genetic composition of hybrid populations actually occurred through successive cultivation of rice plants under specific environments.

Nishio *et al.* (1966) advanced four generations, F_1 to F_4, of three hybrid populations in the greenhouse over two years. Harvest of seeds in each generation was done according to the bulk method. Some of the seeds were stored for field comparison. The populations of the four successive generations, from F_2 to F_5, were planted in the field in the same year and were compared for several characters. Fig. 2 shows histograms of these generations for characters investigated in a cross between Yamabiko and Sachikaze from which the previously described "Nippon Bare" variety was developed. Significant differences were not found among generations with respect to means and variances of four characters, indicating that any significant directional selection did not occur for those characters in the process of shortening the breeding-cycle.

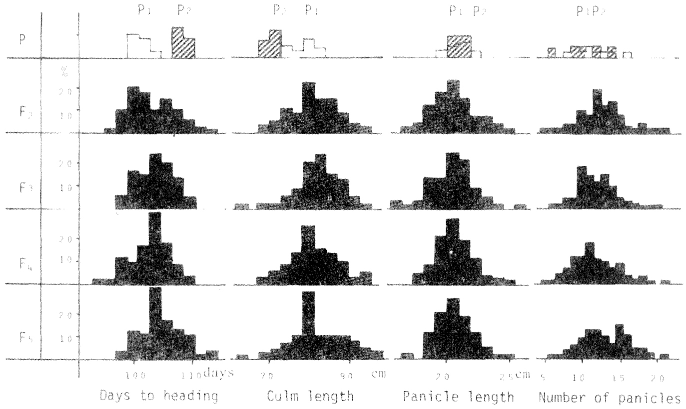

Fig. 2. Histograms of four characters in a rice hybrid population, Yamabiko x Sachikaze, grown for successive generations in the greenhouse by shortening the breeding-cycle (Nishio et al. 1966).

Okochi et al (1958) advanced in bulk three generations of rice hybrid populations, from F_3 to F_5, in the nursery bed without transplantation under three kinds of seeding rate, namely 500 seeds, 1,100 seeds, and 2,200 seeds per square meter. These three populations were compared in the field environment after reaching F_6 generation. No significant differences on means and variances were found for several characters among the populations of the different spacings and also between control populations grown under normal field environment.

The results of the above-mentioned two experiments are consistent in that genetic compositions of hybrid populations were not influenced by unusual environments and maintained a large amount of variation. Under accelerated growth conditions, each plant produces a small plant and a few seeds, and consequently differences in fitness among genotypes are minimized (Fig. 3) This might be one of the reasons why the bulk populations grown under such extreme environments did not show any striking genetic shift.

On the other hand, we cannot deny that genetic shift might actually occur for particular characters under particular environments. Therefore, it is desirable to handle breeding materials in using careful culture methods and appropriate techniques of seed sampling (Okabe, 1967). Although the bulk method saves labor, it is only advantageous if competition effects are not important. If physiological and morphological factors that affect competitive ability are not fully known the single seed descent method is more useful (Tee and Qualset, 1975).

Using two rice crosses between the earliest varieties and the latest variety in Japan, Kikuchi (1958) advanced five generations, from F_2 to F_6, over two years in the greenhouse according to the SSD method. On the other hand, the same hybrids were grown successively in the field, one generation in one year, according to the bulk method. F_7 populations, which were developed in using both the SSD and bulk procedures, were compared for several characters in the field. The results related to heading time and apiculus color are shown in Fig. 4 and Fig. 5. Despite unavoidable seedling deaths and environmentally induced sterility, the SSD

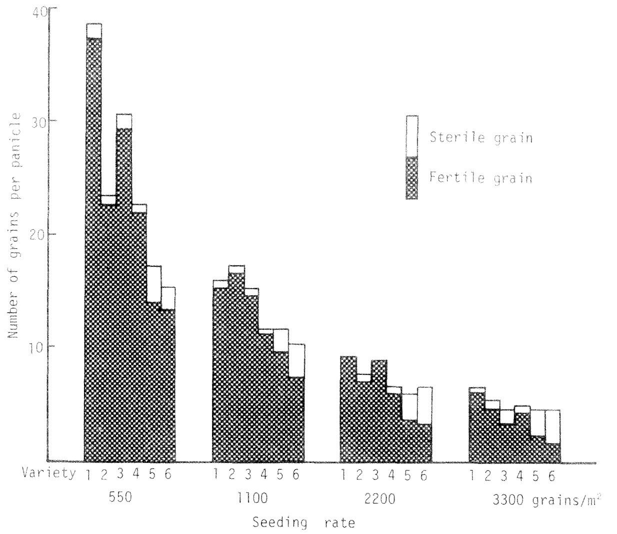

Fig. 3. **Variation and varietal differences in number of grains per panicle at different seeding rate.** Variety name : 1 = Towada, 2 = Honen Wase, 3 = Ginmasari, 4 = Koshi-sakae, 5 = San-in 17, 6 = Kinmaze (Ishizaka and Samoto 1975).

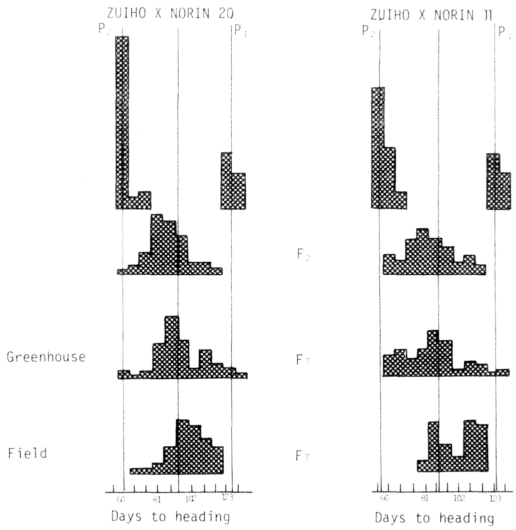

Fig. 4. **Histograms of heading time in the two rice hybrid populations grown for successive generations in the greenhouse and the field** (Kikuchi, 1967).

populations maintained a larger genetic variation in heading time compared to the bulk populations which shifted their means toward lateness. As for the apiculus color, the phenotypic frequencies of the SSD populations changed over a period of six generations in the same way as the theoretical curve, while the remarkable elimination of colored plants occurred in the bulk populations with advancing generations (Kikuchi, 1967). These results indicate clearly that the SSD method is the procedure which is the least influenced by natural selection (Brim, 1966, Casali and Tigchelaar, 1974).

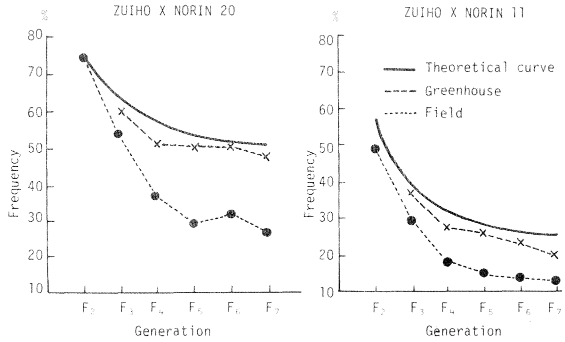

Fig. 5. **Changes in frequency of plants with apiculus color in successive generations when two rice hybrid populations were grown in the greenhouse and the field** (Kikuchi, 1967).

Because the method of rapid generation advancement is carried out under limited space in the greenhouse, population size of one cross is practically restricted to a few thousand plants. Therefore, breeders might be faced with the additional problem of random genetic drift. Ikehashi (in preparation) showed in the simulation experiment that multiplication of population size from F_3 to F_4 may be effective for preserving desirable genotypes, even if the initial population size is relatively small.

3. Artificial selection during shortening of the breeding-cycle

There is a possibility of mass selection for agronomic characters, such as heading time, disease and insect resistance, cold tolerance, etc., during shortening of the breeding-cycle, if the proper conditions for the expression of characters are applied.

At Kyushu Agricultural Experimental Station, rice breeders are now carrying out mass selection for bacterial leaf blight by artificial spraying at the seedling stage during the accelerated-generation cycle.

Koumura et al. (1976) investigated the effectiveness of mass selection for grain size and grain quality on hybrid populations over three generations during shortening of the breeding-cycle. Response to selection was slightly significant for grain quality but was not definite for grain size.

It must be noted that genotypes may react differently under accelerated growth conditions and field environment, because the former differ considerably in many respects from the latter. Matsushita et al. (1975) applied two-way selection for heading time during the accelerated-generation cycle, using five rice hybrid populations. In the F_5 generation, early and late heading plants were selected from these populations respectively. Then, the early and the late populations were grown in the field with the unselected populations for evaluation of response to selection. Fig. 6 shows histograms for heading time of the three populations of a cross between Nippon Bare and Koshijiwase. These distributions illustrate that selection for heading time was effective in changing population means. However, it should be noted here that responses to selection occurred in the opposite direction, that is, the late plants in the greenhouse headed earlier in the field than the early ones. This result may be explained by the fact that two parents are genetically different in the internal components controlling heading time, namely one parent has a relatively shorter basic vegetative growth and a higher photoperiod sensitivity than another parent. This is an indication of genotype x environment interaction.

It must also be taken into consideration that selection for one character may result in undesirable changes in other characters because of genetic correlation. Therefore, breeders must consider carefully the complications that may arise in making selection during the rapid generation advance.

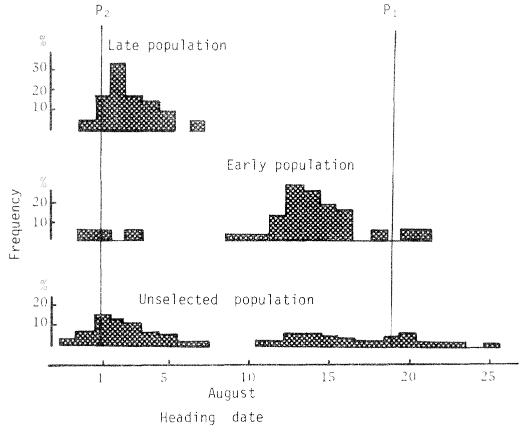

Fig. 6. **Responses to mass selection for earliness and lateness during the accelerated-generation cycle in a rice hybrid population, Nippon Bare x Koshiji Wase.** The selection was practiced in F_5 generation and the response to selection was evaluated in F_7 generation in the field (Modified from Matsushita *et al.*, 1975).

4. Application of shortening of the breeding-cycle to the backcross breeding method

In a wide cross such as *indica* x *japonica* rice cross, the backcross method has been used extensively to transfer a few characters, such as disease and insect resistance, from one parent to the recurrent parent. Shortening the breeding-cycle can be used advantageously in backcross breeding, particularly when the introduced characters are controlled by recessive genes where extra generations of self-pollination are necessary to recover the homozygous recessive genotype compared to dominant characters.

Using new techniques for the germination of immature seed and for seed-green vernalization, Mukade *et al.* (1973) could advance five or six generations in one year by successive backcrossing in the practical breeding of leaf rust resistant wheat varieties.

In rice improvement programs, such procedures have been recently developed at several breeding stations in Japan. In order to transfer dwarf disease resistance of an Indonesian variety Rantaj emas 2 to Japanese varieties, Shumiya et al. (1976) carried out successive backcrossings and backcrossing followed by selfing by means of rapid generation advancement. Clipping method was applied to artificial crossing, but seed-setting was poor varying with cropping seasons. The low seed-setting was thought to be due to low pollen fertility caused by abnormal growth conditions in the greenhouse and short-day treatment. Therefore, culture methods must be improved to avoid the occurrence of pollen sterility and thereby to carry out backcrossing effectively.

Conclusions

Research and experiments carried out over two decades have led to the wide and successful adoption of the rapid generation advancement procedure in rice breeding programs. Most of the recently released rice varieties in Japan have been developed through this method.

The acceleration procedure can be used advantageously in three- and four-way crosses as well as backcross breeding (De Pauw and Clarke, 1976). Moreover, the methods of progressive improvement by Palmer (1953) and cumulative selection by Richmond (1949) can be effectively carried out by means of the rapid generation advancement (Okabe, 1967).

Further investigations are required for the effective screening of desirable characteristics under controlled environments as well as for further acceleration of generation advancement.

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Discussion

S. Iyama, Japan (comment) : I should like to make a comment on the size of population maintained for the bulk method of breeding. Single seed descent method (SSD) is a well adapted modification of the bulk method for shortening the breeding period in view of the small area required. It enables to avoid undesirable natural selection or competition in utilizing the frequency of recombination, etc. The size of population to be maintained depends on the number of pairs of genes to be recombined and on the intensity of linkage. For instance, with four pairs of recombinants genes and a crossing-over frequency of 0.3, the population size would be 2423. In early generations, one can start with a smaller population size than that required for SSD. But as chances of getting recombinations are greater in the early generations and decreases rapidly in the later generations, the increase of population size in the later generations is ineffective. Instead, one has to increase the size of population in early generations. In this case, eventual size of population should exceed that of SSD. According to my calculations, provided that multiplication is done in early generations, i.e., F_3 and F_4 and that the population is maintained thereafter by SSD, it is possible to start with a population whose size is 1/4 to 1/10 of that of SSD in keeping the inflation size in the final population within 20% compared with that of SSD.

I. Tarumoto, Japan (comment) : If it were possible I would like to send my breeding materials to sub-tropical or to tropical areas in the winter to accelerate the generations and to select particular characters like disease resistance. If such a breeding scheme were available we could save energy and we would not need to worry about population size.