COMPARISON OF BIPARENTAL AND MELTING POT METHODS OF CROSSING SUGARCANE IN HAWAII

By

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Abstract

SUGARCANE (*Saccharum* spp.) breeders at the Hawaiian Sugar Planters' Association used biparental and melting pot (modified polycross) crossing methods concurrently from 1935 to 1985. While the annual effort expended to make biparental crosses exceeded the effort to make melting pot crosses over this 50-year period, annual viable seed yield from biparental crosses was usually less than 15% of that from melting pot crosses and, hence, the numbers of seedlings planted to the field from those crosses usually accounted for less than 20% of the total seedling population. In 1985, nine of the 10 sugarcane cultivars listed in Hawaii's variety census originated from melting pot crosses; only one originated from a biparental cross. In the face of a shrinking sugar industry in Hawaii and a smaller work force in the breeding program, the decision was made in 1985 to rely primarily on melting pot crosses for the production of commercial cultivars. From 1985 to 2005, twelve additional clones that were bred prior to 1985 eventually attained 'commercial cultivar' status by exceeding 1% of the total cane growing area. All twelve originated from melting pot crosses. Over the 50-year period that the two crossing methods were used, the melting pot method proved to be more labour efficient and ultimately contributed more than the biparental crossing procedure toward the development of new commercial cultivars for the Hawaiian sugar industry. From 1985 forward, the biparental crossing method was used more for introgressing desired traits from exotic germplasm than for the development of commercial cultivars.

Introduction

Since 1935, sugarcane breeders at the Hawaiian Sugar Planters' Association (HSPA) Experiment Station have employed the melting pot (MP) crossing method. This method was used sparingly until World War II. From 1942 to 1946, the MP method was used almost exclusively because of employee shortages at the Experiment Station; only 32 biparental (BP) crosses were made during this period.

After World War II, MP crossing remained an important method for developing new commercial cultivars in Hawaii. MP crossing was adopted at a few other sugarcane breeding stations around the world. However, it has not become the mainstay breeding procedure at most other breeding stations, including those in the USA.

The term ‘melting pot crossing,’ first coined by Dr. A. J. Mangelsdorf (1953), is a modified polycross. While the MP crossing method was being used in Hawaii, breeders working on other crops in the United States and Europe developed the polycross method for obtaining combining ability information in forage species. Tysdal *et al*. (1942) proposed the term ‘polycross’ to describe the progeny from a line that was subject to out crossing with selected lines growing in the same nursery. A true polycross would consist of a collection of selected parents replicated in an isolated nursery in such a manner as to assure random inter-mating through open pollination. Ideally, every clone has an equal chance of being pollinated by every other clone in the polycross (Allard, 1960).

Thus, MP crossing, as conducted in Hawaii, does not constitute a true polycross because tassels from each clone may not be interspersed randomly, unequal numbers of flowers may be used from each clone, and tassels vary greatly in pollen production. Throughout this paper, the term ‘female’ refers to parents that shed little to no viable pollen at anthesis, and ‘male’ refers to parents that shed moderate to abundant viable pollen at anthesis at 20–30°C.

Warner (1953) stated that the MP crossing method was first explored in Hawaii with the object of evaluating the breeding value of a large number of parents at minimum expense. After several years of experience, a number of advantages to the use of the MP method were observed.

Cost efficiency: Considering labour, time, physical facilities, and space, the MP method produced a large number of seedlings at minimal cost. In Hawaii, establishing MP crosses is a one-day operation per crossing date. Stalks with tassels at early anthesis are cut and tagged in the field, then brought to the MP crossing shelters where they are interspersed. In contrast, erecting BP crosses is more labour-intensive and requires two days of activity per crossing date. The first day is spent recording numbers of tassels available by clone, determining the level of pollen production of individual parents by examining florets, then determining desired combinations based on individual pollen production and tassel availability. Relatively male-sterile parents (low- to non-pollen producers) are used as females, while moderate to abundant pollen producers are used as males. On the second day, tassels are collected and crosses are erected. In MP crossing, hundreds of tassels are compactly arranged in large shelters to achieve wide distribution of pollen shed from each tassel. In BP crossing, each cross must be kept isolated in order to prevent pollen contamination. Large cloth lanterns, first described by Skinner (1959) in Australia, were adopted on a large scale in Hawaii following the building of new crossing facilities at the HSPA Sugarcane Breeding Station in Maunawili Valley on Oahu 1975 in order to minimise cross contamination (Heinz and Osgood, 2009).

Seed set: Substantially more viable seeds per tassel are produced from the MP crosses than from the BP crosses. Low pollen viability of certain parents used as males and mating incompatibilities probably contribute to poor seed set in certain BP crosses. By contrast, a large amount of pollen is dispersed from a wide range of tassels in the MP crosses. Consequently, resulting recombinations obtained in MP crossing must be viewed as biased, rather than random.

Genetic combinations: With the same number of parents available, the potential number of possible parental combinations in MP crosses is exponentially greater than in BP crosses. To illustrate, assuming ten male-fertile tassels representing ten different parents were available, as many as 90 crosses [n*(n-1)] or 45 unique genetic combinations [n*(n-1)/2], discounting reciprocal crosses, are possible in a polycross arrangement. With the same number of male-fertile tassels and parents, only five BP crosses could be arranged in a manner that would assure cross fidelity.

The primary disadvantage of the MP crossing method is loss of pedigree information (inability to repeat crosses giving high selection rates, track inbreeding coefficients, determine specific combining abilities, etc.; Stevenson, 1965) and hence, a theoretically lower level of parent selection efficiency (Empig *et al*., 1972), since half-sib rather than full-sib progeny are being assessed. Since the HSPA used both the BP and MP crossing methods concurrently for 50 years (discounting the World War II era), sufficient data have accumulated to assess the relative performance of the two procedures in Hawaii in relation to the production of commercial cultivars.

Breeding methodology

Melting pot crosses

The MP crosses, as arranged in Hawaii, consist of tassels from highly selected male-fertile cultivars, with more diverse, less highly selected male-sterile (female) cultivars (Warner, 1953). The number of tassels of individual parents in MP crosses is dependent on breeding interest, availability of tassels, and estimated pollen fertility. Seed is harvested from both male-fertile and male-sterile parents. In Hawaii, four principal MPs have evolved:

General MP: This was the largest and genetically most diverse MP. In addition to proven parents, recently tested clones with only limited yield information, as well as vigorous wild-derivative male-sterile (or sterilised) clones were included as parents.

Leeward MP: Clones adapted to irrigated leeward environments were included.

Windward MP: Clones adapted to rain-fed windward environments were included.

Quality MP: Relatively small numbers of elite clones and proven parents were included on the basis of exceptional individual and/or progeny performance in yield tests. Emphasis was placed on those clones with above-average sucrose content.

Special MP crosses were arranged for brief periods, often not greater than five consecutive years, to improve characteristics such as smut (*Ustilago scitaminea* H. & P. Sydow) resistance, drought tolerance, salt tolerance, and biomass potential. From 1974, wild-derivative MPs began to be made as an efficient method of incorporating into elite germplasm, genes from wild germplasm sources (Meyer and Heinz, 1975). Initially, both male (elite as female, wild derivative as male) and female (wild derivative as female, elite as male) wild-derivate MPs were made. Because very few wild-derivative clones were male sterile, the female wild-derivative MP was discontinued. The male wild-derivative MP was refined by forming three *S. spontaneum* L.-derivative MPs, namely Spont. 1, Spont. 2, and Spont. 3 (Meyer *et al*., 1982). These *S. spontaneum*-derivative MPs received tassels from first-generation (F_1), first backcross (BC_1), and second backcross (BC_2) male-derivative clones. Each derivative MP received tassels from at least 40 male sterile (or emasculated) commercial-type parents.

Biparental crosses

Until 1985, most BP crosses were commercial-type (*Saccharum* spp. hybrids) x commercial-type combinations. The traditional approach in making such combinations was to match elite parents with complementary traits (windward x leeward environment adaptation, high tonnage x high sucrose, etc.), until tassels were no longer available to make further crosses. A fully computer-driven procedure for determining usage of available tassels in BP combinations, such as the proven cross method used in Australia (Hogarth and Skinner, 1986), was never implemented in Hawaii, although data were electronically organised to assist breeders in arranging optimum crosses among available tassels.

Since 1985, BP crossing was principally used for population improvement, rather than the direct development of commercial cultivars. First-generation hybridisation between wild or foreign commercial clones × commercial-type clones, and early-generation backcrossing toward the commercial type was accomplished using the BP crossing method.

Results and discussion

The mean distribution of crosses made and seedlings produced at generational intervals from 1935 to 1985 is shown (Table 1).

Table 1—Proportion of crosses, seedlings, and number and proportion of clones that achieved commercial status, from biparental and melting pot crosses in Hawaii by decades from 1935–1985.

Decade	Biparental crosses			Melting pot crosses		
	Crosses (%)	Seedlings (%)	No. cultivars (%)	Crosses (%)	Seedlings (%)	No. cultivars (%)
1935–1944	35	44	3 (37%)	65	56	5 (63%)
1945–1954	14	21	3 (25%)	86	79	9 (75%)
1955–1964	13	18	1 (10%)	87	82	9 (90%)
1965–1974	11	16	0 (0%)	89	84	11 (100%)
1975–1984	14	19	0 (0%)	86	81	5 (100%)
Total			7 (15%)			39 (85%)

Since 1950, approximately 13% (520) BP and 87% (3480) MP crosses were made per year in spite of the greater effort that was required to erect BP crosses. The highest number of BP crosses achieved in Hawaii in a single year was 1200. The MP crosses could be placed directly from the field into the crossing house where they remained until seed harvest. By contrast, tassels in BP crosses had to be handled two additional times prior to placement in crossing lanterns in the BP crossing facility.

First, they were set in a staging area where the male and female parents were paired, and then they were moved to a temporary location where the desired male and female were secured together with the male tassels positioned approximately 20 cm higher than the female tassels, and the exposed anthers on the female tassels trimmed off.

Numbers of crosses per MP are determined by counting the number of parents used per crossing date, then summing over crossing dates. The General MP usually accounted for about 50–55% of the total MP crosses. Windward and Leeward MPs each accounted for approximately 15%, and the Quality MP for 5%.

Specialty MPs accounted for the remainder of crosses. Since 1972, following the formation of the first specialty MP (Smut Resistance MP), specialty MPs generally accounted for <5% of the total number of MP crosses arranged each year, thereafter.

The number of seedlings planted from BP and MP crosses does not necessarily correspond with the number of crosses arranged for or seed produced from each type of cross. Nearly all seed from BP and Quality MP crosses was planted, as was most seed from the Leeward and Windward MP crosses. By contrast, most seed from the General MP was not planted, unless there was a shortage of seed from other crosses.

During the 1977–1978 crossing season, BP and General MP crosses accounted for 12% and 51% of total crosses, respectively (Table 2). However, BP crosses accounted for nearly 18% of the seedling population, compared with only 32% for the General MP. Selection intensity from Stage 1 (seedling stage) to Stage 4 (preliminary yield testing) appeared to be nearly constant among MP and BP crosses.

From 1950 to 1980, approximately 15 to 20% of sugarcane seedlings planted each year originated from BP crosses. About 33% of all seedlings were from General MP crosses while roughly 50% of seedlings were from Leeward, Windward, Quality MP crosses, and special MP crosses.

Table 2—Number of clones selected from various MP and BP crosses in the 1977–1978 crossing season, a year representative of the 1965–1985 period.

Cross	No. (%) of crosses	No. (%) of seedlings	No. (%) of Stage 4	Stage 4 seedling selection rate
BP	295 (11.7%)	196 448 (17.5%)	335 (16.8%)	0.17%
MP	2226 (88.3%)	925 416 (82.5%)	1655 (83.2%)	0.18%
General	*1291 (51.2%)*	*360 168 (32.1%)*	*668 (33.5%)*	*0.19%*
Quality	*69 (2.7%)*	*116 480 (10.4%)*	*178 (8.9%)*	*0.15%*
Lee	*465 (18.4%)*	*258 848 (23.1%)*	*442 (22.2%)*	*0.17%*
Wind	*363 (14.4%)*	*153 280 (13.7%)*	*333 (16.7%)*	*0.22%*
Other	*38 (1.5%)*	*36 640 (3.3%)*	*34 (1.7%)*	*0.09%*
Total	2521 (100%)	1 221 864 (100%)	1990 (100%)	

Both BP and MP crosses played a significant role in the early production of commercial cultivars. Heinz and Osgood (2009) published a list of major cultivars in Hawaii (along with their parentages) in their review of the history of HSPA from 1946 through 1996. Three of the 22 cultivars they listed (H 37-1933, H 49-5, and H 59-3775) originated from BP crosses. All three pre-dated 1960. By 1985, nine of the 10 cultivars then being commercially grown in Hawaii (representing 97% of the area in sugarcane) were progeny of MP crosses. While there was a trend toward a decreased percentage of seedlings being planted from BP crosses, the proportion never dropped below 15%, between 1947 and 1975, and actually increased during the 1975 to 1985 decade. None of 21 cultivars that became commercial after H 59-3775 came from BP crosses. The under-representation of commercial cultivars originating from BP crosses, relative to the proportion of seedlings planted from 1955 to 1985, would suggest that the MP crosses were more effective in producing clones that would eventually gain commercial status.

In 1985, to investigate whether the lack of cultivars from BP crosses was likely to persist, the origin of clones having the greatest potential of attaining commercial status was investigated. Potential commercial clones were defined as those with a sugar yield per unit area matching or exceeding that of the major cultivar planted at the time in at least two advanced yield tests. Of the 51 clones that had commercial potential, only 4 (8%) were derived from BP crosses. Only eleven (22%) of the potential commercial clones were derived from General MP, suggesting that the more conservative and specialty (MPs) were the most efficient in producing commercial cultivars (70% of total).

Generating a large amount of viable seed from BP crosses is widely acknowledged as being more difficult than from MP crosses. However, the lower productivity of BP crosses, in proportion to their relative representation in the seedling population, is more difficult to explain. Although most parents used in BP crosses were selected primarily on the basis of their own performance, rather than proven parental performance, considerable effort went into making the most desirable combinations possible.

Unless the formation of BP crosses is based on the known specific combining abilities of the parents, the advantages associated with BP crosses are more than offset by their lower relative fertility. While BP crosses involving parents with known high specific combining ability will in theory produce more elite progeny and hence, have a higher probability of producing commercial cultivars, the challenge to the breeder is the time and effort needed to obtain and make use of specific combining ability data.

Results from a combining ability study in which families (rather than individual clones) were planted in yield test plots, indicated that non-additive genetic variation for sugar yield is important in cane harvested at 24 months (Wu and Tew, 1990). The performance of elite x elite crosses is difficult to predict without specific combining ability data. Perhaps the far greater number of combinations represented in MP crosses may be more advantageous than previously acknowledged, especially where selection and yield testing programs are designed to evaluate large numbers of seedlings. In spite of the shortfalls of MP crossing, results of this retrospective study suggest that MP crossing has been the more effective crossing method for exploiting specific combining ability in sugarcane.

Several efforts have been made to refine MP crossing. The most important recent improvement has been the effective hot water (50^{o}C, 5 min) emasculation treatment prior to anthesis (Nagai, 1985). This treatment should permit increased flexibility in the selection of parents entering MPs. For example, lesser-tested new parents could be rendered male sterile before they are entered into an MP, in order to assure a high proportion of pollen from elite clones. With the ability to emasculate, it has become possible to use wild-derivative clones as female parents rather than as male parents, in the derivative polycross scheme. Physical separation of backcross generations during crossing also is no longer necessary. Results from the 1984–1985 crossing season indicate that, even though the emasculation procedure reduces female fertility, nearly half of all wild-derivative clones produced adequate seedlings for effective selection. This demonstrated that a large increase in the number of female parents could be achieved through the use of the emasculation procedure.

Presently, it is difficult to retrace the specific MP origins from which Hawaii's commercially important sugarcane cultivars were derived. However, the MP origins of those cultivars deemed important enough to have been registered as commercial cultivars are known. Based on the MP origins of registered cultivars, it is apparent that the more elite MPs have been especially productive, particularly since 1960. Cultivars H 62-4671 (Heinz *et al*., 1979) and H 70-144 (Heinz *et al*., 1983) originated from the Quality MP. Cultivars H 65-7052 (Heinz *et al*., 1981a), the current leading cultivar in Hawaii, H 68-1158 (Heinz *et al*., 1981b), and H 73-7324 (Tew *et al*., 1992a), came from the Windward MP. Cultivar H 73-6110 (Heinz *et al*., 1984) came from the Leeward MP. Somewhat surprisingly, three cultivars, H 74-1715 (Tew *et al*., 1988), H 74-4527 (Tew *et al*., 1992b), and H 78-4153 (Wu, 2003) originated from a special MP set up shortly after the discovery of smut in Hawaii that involved smut-resistant parents. This MP was referred to as the Smut MP (1972–1978). Cultivar H 78-292 (Tew *et al*., 1992c) is the only registered cultivar of recent vintage that originated from the General MP.

Conclusions and recommendations

The MP crossing method has been more productive than the BP crossing procedure in the development of new commercial cultivars for the Hawaiian sugar industry. From 1955 to 1985, only one commercially important cultivar was produced from BP crossing compared with 26 cultivars from MP crossing. Without the availability of specific combining ability data, the only demonstrated advantage BP crossing has over MP crossing is the preservation of ancestral information. Obtaining specific combining ability data in Hawaii is difficult because the crop is grown to an average of 24 months of age. After eight months' age, the crop forms an entangled mat of cane, precluding effective visual evaluation in small plots. The correlation between cane volume at eight months and cane weight at 24 months is negligible (Wu, 1983). Entry of full-sib families, rather than individuals, into yield tests may allow a reliable measure of specific combining ability at harvest (Wu and Tew, 1990), but this procedure is so costly and time consuming as to be impractical. Limited BP crossing for specific purposes, such as conducting genetic studies, or evaluation of specific combining ability among commercially important cultivars, for example, may be justified.

After 2010, there will only be one plantation remaining in Hawaii, namely Hawaii Commercial and Sugar Company (HC&S) on the Island of Maui. It is therefore unlikely that the remaining breeding program, tailored to one plantation's needs, will accommodate more than one MP in the future. In most breeding programs around the world, including Hawaii's, the turnover rate of parents tends to be conservative; the majority of parents used in one year will be used the following year.

We recommend the continued inclusion of recently yield-tested clones as experimental parents in this MP. Parents with only preliminary yield data could be emasculated and older proven parents be used as the primary pollen source. This modification should result in an increase in the mean performance of progeny from this MP and allow a more meaningful comparison of the relative performance of the newer clones as parents, since the pollen source is controlled.

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COMPARAISON DES MÉTHODES DE CROISEMENT BI-PARENTAL ET DU CREUSET POUR LA CANNE À SUCRE À HAWAÏ

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MOTS CLÉS: Croisements Bi-Parentaux, Polycroisements, Aptitude Spécifique à la Combinaison.

Résumé

LES GÉNÉTICIENS-SÉLECTIONNEURS de la canne à sucre (*Saccharum* spp.) au Hawaiian Sugar Planters' Association avaient recours aux méthodes de croisement bi-parental et du creuset (polycroisements modifiés) de 1935 à 1985. Alors que l'effort annuel déployé à entreprendre les croisements bi-parentaux excédait celui du creuset pendant cette période de 50 ans, la viabilité des graines issus des croisements bi-parentaux était de 15% inférieure à celle du creuset. Par conséquent, le nombre de plantules provenant de ce type de croisement était généralement inférieur de 20% à la population totale des plantules. En 1985, neuf des 10 cultivars de la canne à sucre du recensement variétal de Hawaï provenaient des polycroisements et un seul cultivar provenait des

croisements bi-parentaux. Face à une industrie hawaïenne en régression et une main d'œuvre réduite pour le programme d'amélioration variétale, la décision était prise d'avoir recours aux croisements du creuset pour le développement des cultivars industriels. De 1985 à 2005, douze clones additionnels, provenant des croisements effectués avant 1985, ont finalement atteint le statut de « cultivar industriel » et cultivés sur plus de 1% de la superficie cannière, les douze sont issus des polycroisements du creuset. Au cours des 50 ans que les deux méthodes ont été utilisées, la méthode du creuset s'est avérée être plus efficiente en main d'œuvre et a contribué davantage au développement des nouveaux cultivars pour l'industrie sucrière hawaïenne. Depuis 1985, la méthode de croisement bi-parental a été utilisée principalement pour l'introgression des caractères provenant du germoplasme exotique plutôt que pour le développement des cultivars industriels.

COMPARACIÓN DE LOS MÉTODOS DE CRUZAMIENTOS BIPARENTALES Y CRUZAS MULTIPLES (POLICRUZAMIENTO MODIFICADO) EN CAÑA DE AZÚCAR EN HAWAI

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PALABRAS CLAVE: Cruzas Biparentales, Policruzamientos, Habilidad Combinatoria Específica.

Resumen

Los mejoradores de caña de azúcar (*Saccharum* spp.) en la Asociación de Cultivadores de Caña Hawaianos, usaron los métodos de cruzamientos biparentales y la fusión de varios parentales o cruzas múltiples (policruzamiento modificado, 'melting pot') en forma concurrente desde 1935 hasta 1985. Mientras los esfuerzos usados para hacer cruzamientos biparentales excedieron a cruzas múltiples durante un periodo de 50 años, la producción de semillas viables anualmente de los biparentales usualmente fueron menores al 15% comparados al método de cruzas múltiples, por esta razón el número de plántulas sembradas en el campo de estos cruzamientos generalmente fueron 20% menos en el total de la población de plántulas. En 1985, nueve de 10 cultivares de la lista del censo de variedades Hawaianas se originaron de cruzas múltiples (melting pot); solamente una se originó de cruzas biparentales. Debido a la reducción de la industria azucarera de Hawái y al pequeño grupo de trabajo en el programa de mejoramiento genético, la decisión tomada en 1985 fue depender principalmente de los cruzamientos por cruzas múltiples para desarrollar cultivares comerciales. Desde 1985 al 2005, doce clones adicionales provenientes de cruzas previas a 1985, eventualmente fueron denominados 'cultivares comerciales' por exceder el 1% del total del área de cultivo de caña. Los doce materiales se originaron de cruzas múltiples ('melting pot'). Durante el período de 50 años en que los dos métodos de cruzamientos fueron usados, se probó que el sistema de cruzas múltiples es más eficiente en el uso de mano de obra comparado con el sistema biparental en el desarrollo de variedades de caña de azúcar en la industria azucarera Hawaiana. Desde 1985 en adelante, los cruzamientos biparentales se usaron mayormente para realizar introgresión de genes específicos, usando materiales foráneos que para el desarrollo de variedades comerciales.