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Crossing possibility for breeding promising orange-fleshed sweetpotato genotypes in Benin

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Abstract: Orange-fleshed sweetpotato (OFSP) is a sustainable and inexpensive source of vitamin A that contributes to food and nutritional security in developing countries. Its adoption is low due to unconformity of the variety with community food culture, limited cultivar selection and breeding studies. The current study aimed at breeding of promising OFSP genotypes in Benin using three parental lines. Two hundred and seventy-four seeds and one hundred and six genotypes were obtained through biparental crosses of Tio-joe (imported orange-fleshed variety), Vobodouaho (local white-fleshed variety) and ACAB220 (local orange-fleshed variety). The phenotypic diversity of genotypes was assessed using 10 leaf characters and storage root flesh colour through multiple correspondence analysis and hierarchical cluster analysis. The results indicated cross-compatibility between Tio-joe and ACAB220 when ACAB220 was used as female. Reciprocal cross-compatibility was found between ACAB220 and Vobodouaho. The genotypes could be separated into two main populations and classified into five cluster groups. Promising intermediate and pale orange genotypes were obtained indicating possibilities to incorporate beta-carotene into the white background of the Vobodouaho variety through further backcrossing.

Keywords: beta-carotene; hand pollination; local varieties; open pollination; promising genotypes; white-fleshed sweetpotato

Sweetpotato (*Ipomoea batatas* (L.) Lam) is a food and nutrition security crop, and an important source of energy for human diet in West Africa (Adubasim et al. 2017). Sweetpotato provides some nutritional security in developing countries, including starch from white-fleshed varieties, anthocyanin from purple-fleshed varieties, and pro-vitamin A from yellow/orange-fleshed (OFSP) varieties (Wang et al. 2016). OFSP variety provides a good source of β-carotene with a high potential to overcome calorific and vitamin A deficiency (VAD) in children, pregnant and breast-feeding women (Neela & Fanta 2019). Nevertheless, VAD is still considered as a major public health problem leading to severe night blindness. More than 250 million of preschool-aged children and approximately 19 million pregnant women suffer from VAD (WHO 2018; Bastos Maia et al. 2019). Nowadays, the production and consumption of OFSP varieties are increasing in Eastern and Southern Africa (ESA) regions unlike some West African countries (Low et al. 2007, 2017a, b). Most farmers in West Africa still grow white or cream-fleshed landraces that are typically less nutritious (Sanoussi et al. 2016, 2017). White and cream-fleshed varieties are more preferred due to their high dry matter and low sugar content (Baafi et al. 2015). Furthermore, Sweetpotato project (AUG II-2-247-2018) in Benin and Niger reported more than 80% producer households that have never been in contact with OFSP landraces or improved varieties (Sohindji 2022). According to Sohindji et al. (2022), the non-exposition of the whole population to OFSP varieties, the limited number of improved OFSP varieties available to farmers, and the inadequacy of improved OFSP varieties to smallholder farmers led to the low production and consumption of OFSP in West Africa. This unconformity of OFSP varieties is basically due to the negative correlation between beta-carotene and dry matter leading to low dry matter OFSP varieties (< 25%) (Afuape et al. 2015). Nevertheless, the identification and selection of good parental materials for hybridization may favour total progress towards the development of high dry matter OFSP varieties (Mwanga et al. 2007; Afuape et al. 2019). In Japan, the identification of compatible/incompatible parents is important for specific trait breeding programs (Katayama et al. 2017) and may increase the number of promising genotypes if right parents are selected (Simion 2018).

Inadequate knowledge on sweetpotato cultivars selection and development was reported as a key constraint limiting farmers production capacity in most major sweetpotato producing areas in developing countries (Fuglie 2007). Thirteen local breeding programs were reported as the most important OFSP technical scaling efforts achieved in sub-Saharan-Africa (mainly ESA) (Low & Thiele 2020). This also complicated the development and adoption of OFSP by the whole population in most West African countries. A number of factors driving OFSP adoption are country-specific leading to the development of country-specific OFSP varieties that are aligned with the food culture of local populations (Adekambi et al. 2020). Benin is a tropical country in Western Africa, highly dependent on agriculture. Sweetpotato ranked as the sixth most important crop and is predominant in southern and northern part (Dansi et al. 2012; Sanoussi et al. 2017; Adjatin et al. 2018; Ezin et al. 2018). Despite its importance as a food and source of income, sweetpotato production is constrained by a low degree of breeding and improvement. In Benin, sweetpotato improvement has been limited to the promotion of local white-fleshed genotypes and the identification of farmer's preference traits including some agronomic factors (high productivity, pest and disease resistance, large tuberous root, early maturing cultivars), culinary factors (high dry matter content, high sugar content), and economic factors (good market value).

In addition, sweetpotato breeding was confronted with the problem of the absence of flowers, or scanty flower formation of landraces mostly grown by farmers such as cv. Mètché and Vobodouaho. Lack of flowering or poor flowering, and self- and cross-incompatibilities were major constraints to sweetpotato improvement (Onwueme 1978; Baafi et al. 2016). Flowering in sweetpotato can be promoted by grafting non-flowering sweetpotato onto flowering stocks of other landraces or wild relatives of the *Ipomoea* species; by using growth regulators such as 2.4-dichlorophenoxyacetic acid (2.4D), gibberellins acid (GA), phosphoric acid (ethephon); and by exposing sweetpotato to various environmental stresses including short photoperiod, moderate temperature, limited water supply, trellising vines, overwintering, vine girdling, and nutrition manipulation (Van Rheenen 1965; Lardizabal & Thompson 1990; Mutasa et al. 2013; Mubayiwa et al. 2016). A genetic diversity analysis among Benin local sweetpotato varieties indicated phenotypically and genetically distinct genotypes indicating possibilities of overcoming cross-incompatibility issue (Sohindji 2022). Therefore, it is important to assess how the existing genetic potential can be used to develop improved and adapted OFSP varieties.

Most of the improved OFSP varieties added to the sweetpotato catalogue have been developed from poly-cross nursery. Poly-cross nursery offers less labour and more cross combination but is theoretically less efficient than controlled cross where superior combinations can be found and recreated (Barb 2016). Partial diallel (controlled crosse) was used for best progeny development and more genetic advancement per cycle than an open-pollinated or poly-cross nursery (Shumbusha et al. 2010; Balcha 2015; Andrade et al. 2017). Ssali et al. (2019) recommended controlled crosses with recurrent selection for population improvement, and poly-crosses for variety development. Afuape et al. (2019) reported the possibility to combined elevated content of antagonist quality traits such as dry matter and beta-carotene using biparental crossing. Grüneberg et al. (2022) reported large genetic gains for tuber yield and other quality traits (iron and zinc micronutrients) in OFSP hybrids developed from reciprocal recurrent selection. The current research aimed at developing OFSP genotypes that meet the food culture of local communities in Benin and other West African countries. The objectives were to (*i*) identify cross compatible parents for the development of promising OFSP genotypes, and (*ii*) characterize the F_1 progenies for useful genetic variation for the development of promising OFSP genotypes.

MATERIAL AND METHODS

Experimental sites. The study was conducted at the University of Abomey-Calavi (6°25'00.8''N, 2°20'24.5''E) (Figure S1 in Electronic Supplementary Material (ESM)). The soil type was ferralitic and annual rainfall was 1 000 mm with a mean temperature of 27 °C and relative humidity up to 80%. The experiment covered the period of March 2021 to November 2021 for seed and genotype development, and December 2021 to February 2022 (dry season) for genotypes' evaluation.

Parental varieties. The parental cultivars used were ACAB220, Tio-joe, and Vobodouaho. The key traits of the parental genotypes are presented in Table 1.

Sweetpotato genotypes' development. Three crossing blocks were established. Each crossing block consisted of three sub-blocks, and a sub-block contained 21 plants. Each variety was established on one crossing block. Sub-blocks were used for pollination and to ensure the availability of flowers as long as possible. The transplanting date was varied within each block. Vobodouaho and Tio-joe did not flower simultaneously when the crossing blocks were first established resulting in first environment dominated by ACAB220 and Tio-joe, and second one dominated by Vobodouaho and ACAB220. Thus, training of tendrils to racks and biparental crossing (hand and open pollination) were used for all experiments. Pollination was carried out within 50 days according to Afuape et al. (2019) and labelled regularly (Figure S2 in ESM). Seeds were collected per crossing type, dried if applicable and stored under cold condition. Stored seeds were firstly soaked in moistened filter paper with tap water for 12 hours. Soaked seeds were afterwards kept in Petri dishes overnight and then sown individually in germination bag for a period of four weeks. Seedlings obtained were transferred to polythene bags filled with compost for a period of six weeks. Genotypes were multiplied separately in large multiplication beds for observational trial within 10 weeks after transplanting (Barb 2016).

Observational trial of genotypes. Approximately a minimum of 30 cm long (displaying five nodes of non-rooted genotype) apical vine cuttings were harvested. Three vine cuttings of each genotype were planted on mounds and laid out in a randomized complete block design with three replications. Individual plots consisted of one cutting of each genotype planted on a mound and were watered twice per day in the morning and evening. Predominant and secondary vine colour, vine tip pubescence, leaf traits (area, general appearance, lobe type, central lobe shape, mature and immature leaf colour, petiole pigmentation), predominant skin and flesh tuber colour were collected (Huaman 1991) (Table S1 in ESM).

Data analysis. The number of successfully developed and propagated genotypes were recorded and frequencies were calculated according to the parental varieties included in the crossings. All genotypes were evaluated at the same location of the observation trial at the University of Abomey-Calavi. All data were subjected to descriptive statistics. Data were analysed through Pearson's correlation analysis, Fisher exact test, multiple correspondence analysis (MCA) and hierarchical cluster analysis (HCA). Open-source

Table 1. Characteristics of parental lines used in the study

Cultivar	Source	Flesh colour	Other key traits
ACAB220	landrace (Benin)	orange	high natural flowering rate; storage root yield > 25 t/ha; 3.5–4.5 months
Vobodouaho	landrace (Benin)	white	mostly used by communities; moderate natural flowering rate and storage root yields < 10 t/ha, 4.5–6 months; big tubers, high dry matter, poor storage ability
Tio-joe	introduced variety (Mozambique)	orange	high natural flowering rate; medium maturity period with storage root yield of 20.2 t/ha, 4.5–6 months; high resistance to sweetpotato virus diseases; low dry matter

R software packages "Hmisc", "corrplot", "FactoMineR" and "factoextra" were used respectively for correlation analysis, correlogram obtention, MCA and related graphics (R-Core-Team 2018).

RESULTS AND DISCUSSION

Number of seeds and genotypes used to generate F_1 populations. Two hundred and seventy-four seeds were harvested and sown in germination bags out of which only 127 germinated. One hundred and nineteen genotypes were successfully transferred to multiplication beds under field conditions (Table 2). The population developed composed of 8.49% derived from hand pollination and 91.51% from open pollination. Also 6.6% were harvested from white-fleshed mother plant (Vobodouaho) and 93.4% from the orange-fleshed mother plant (ACAB220). In all, 106 genotypes were effectively multiplied and classified within five groups based on crossing conditions as:

- 83 genotypes coded with the name FER and derived from mother plants ACAB220 through open pollination in an environment dominated by ACAB220 and Tio-joe,
- 7 genotypes coded with the name VOBO and derived from mother plants Vobodouaho through open pollination in an environment dominated by Vobodouaho and ACAB220,
- 7 genotypes coded with the name ADE and derived from mother plants ACAB220 through open pollination in an environment dominated by Vobodouaho and ACAB220,
- 3 genotypes coded with the name TAN and derived from mother plants ACAB220 through hand pollination between Vobodouaho and ACAB220,
- 6 genotypes coded with the name SOH and derived from mother plants ACAB220 through hand pollination between ACAB220 and Tio-joe.

The number of successful seeds produced depend on the flowering ability of varieties and the type of pollination used. Vobodouaho produced few flowers limiting crossing possibilities of the variety when used as female. Flowers that are hand-pollinated usually produce less seeds than capsules that are open-pollinated (Barb 2016).

Cross compatible parents' identification. The successful production of seeds depends on the cross compatibility between varieties. One hundred and three seeds obtained for reciprocal crossing between ACAB220 and Tio-joe were harvested only on ACAB220 indicating cross compatibility between the two varieties when ACAB220 was used as female. Eighty-one seeds were produced from the reciprocal crosses between ACAB220 (71 seeds) and Vobodouaho (10 seeds) indicating reciprocal cross-compatibility. According to Gurmu et al. (2013), the identification of candidate parents belonging to the same compatibility group in sweetpotato helps combine desirable traits. Previous studies reported that ACAB220 and Vobodouaho were genetically distant from one another limiting possible inbreeding depression and cross-incompatibility (Sohindji 2022). Self and cross incompatibility, limited flowering ability, and limited number of seeds (< 2) per successful crossing are main challenges for sweetpotato breeding (Onwueme 1978; Baafi et al. 2016). According to Simion (2018), cross-pollination barriers between suitable parental lines hindered progress toward the development of drought-tolerant genotypes. Here, results highlighted some conventional breeding possibilities to improve the genetic background of the local predominant white-fleshed variety (Vobodouaho) for quality traits such as beta-carotene content (Yan et al. 2022). Katayama et al. (2017) reported the use of landrace in the development of OFSP genotypes for processed foods and juice in Japan. However, sweetpotato breeders referred to modern

Table 2. Seeds and genotypes generated per specific crossing types

Parents	Crossing types											
	open pollination						hand pollination					
	Tio-joe*		ACAB220*		Vobodouaho*		Tio-joe*		ACAB220*		Vobodouaho*	
	S	G	S	G	S	G	S	G	S	G	S	G
Tio-joe⁺	–		–		–		–		–		–	
ACAB220⁺	163	83	–		66	7	30	6	–		5	3
Vobodouaho⁺	–		10	7	–		–		–		–	

*Male parents; ⁺female parents; S – number of seeds sown; G – number of genotypes multiplied

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breeding and biotechnology methods to overcome the complexity of sweetpotato genome sterility and cross-incompatibility (Khan et al. 2022; Shankar & Kaushik 2022).

Relationship between variables. The Pearson correlation coefficients between measured variables within the sweetpotato genotypes ranged from −0.4 to 0.8 and some correlations are low (Figure 1). Significant and positive correlations (Table S2 in ESM) were observed between the number of lobes and petiole pigmentation ($P < 0.001$), vine pubescence and lobe type ($P < 0.01$), number of lobes and leaf appearance ($P < 0.01$), vine tip pubescence and predominant vine colour, mature leaf colour, lobe number, petiole pigmentation, general leaf appearance ($P < 0.05$). Variables were reported as discriminant variables for genetic diversity study among sweetpotato germplasm (Reddy et al. 2018; Monteros-Altamirano et al. 2021). Positive correlations between flesh colour and sweetpotato virus disease resistance (Aliou et al. 2020) and between flesh colour and beta-carotene concentrations (Burgos et al. 2009) were used for best genotype identification and selection.

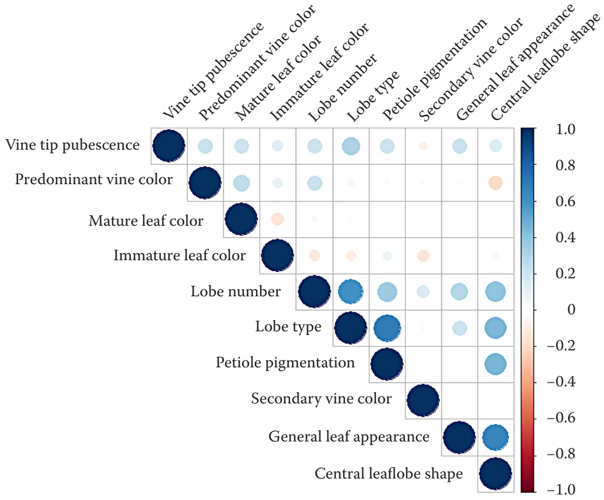

Figure 1. Correlation among phenotypic variables collected within 106 sweetpotato genotypes

Storage root flesh colour diversity within genotypes. Flesh colour is one of the most important phenotypic traits indicating the richness of sweetpotato varieties in carbohydrates, beta-carotene and anthocyanins (Amoanimaa-Dede et al. 2020). The storage root flesh diversity has been successfully assessed for 64 genotypes (Table S3 in ESM, Figure 2). The Fisher exact test results showed a significant relationship between crossing type and storage roots flesh colour (P-value = 0.01 < 0.05; X-squared = 35.245). The use of a colour chart indicated that genotypes from the cross ACAB220 × Vobodouaho (ACAB220 as female) were intermediate orange whereas genotypes from Vobodouaho × ACAB220 (Vobodouaho as female) had pale orange in flesh colour with different intensity. Genotypes from open or hand-pollinated ACAB220 with Tio-joe were mostly intermediate orange, followed by pale orange, yellow, cream and white (Table 3). The uniform flesh colour of F_1 progenies from a cross between Vobodouaho and ACAB220 can be explained by the hypothesis that varieties are homozygous for storage root flesh colour. Furthermore, the beta-carotene responsible for orange-flesh colour may be controlled by major or few genes even though sweetpotato is highly heterozygous. The change of F_1 progenies flesh colour induced by the reciprocal crossing can be due to the maternal effect reported in the control of beta-carotene content (Rukundo et al. 2017). The intermediate orange F_1 and pale orange F_1 obtained can be explained by dominant and additive effects

Table 3. Diversity of storage root flesh colour of progeny per each crossing type

Female parent	Predominant male parent	No. of genotypes evaluated for flesh colour	Progeny flesh colour diversity
ACAB220	Tio-joe	53	white (1.89%) yellow (1.89%) cream (5.66%) pale orange (11.32%) intermediate orange (79.24%)
ACAB220 (intermediate orange)	Vobodouaho (white)	7	intermediate orange (100%)
Vobodouaho (white)	ACAB220 (intermediate orange)	4	pale orange (100%)

reported in the control of beta-carotene content (Mbusa et al. 2018; Ngailo et al. 2019). Similar results were reported for traits in sweetpotato such as root number per plant, storage root yield, biomass, harvest index, dry matter content and resistance to SPVD (Mwanga et al. 2002; Gurmu et al. 2018; Mbusa et al. 2018; Kagimbo et al. 2019). The different proportions of storage root flesh colour obtained

FER36 FER40 FER60 FER67

FER68 FER69 FER91 FER76

FER77 FER81 FER83 FER87

FER89 FER90 FER92 ADE7

VOBO1 VOBO2 VOBO5 VOBO6

SOH1 SOH2 SOH6

Figure 2. Picture showing flesh and skin colour of some genotype's storage roots

from crossing between ACAB220 and Tio-joe are because Tio-joe is a hybrid developed from NC99573 × polycross (Tumwegamire et al. 2014). This support that storage root flesh colour in sweetpotato is under many linked gene actions with crossing-over effect (Jones 1967). Results are not aligned with the point of view of Lebot (2010) who reported that white flesh seems to be dominant over orange flesh colour. With regards to these results, orange flesh variety should be used as female parent for the best capture of beta-carotene in the progeny, whereas for combination of dry matter and beta-carotene, white fleshed variety must be used as female parent. This enabled positive genetic gains of high dry matter and beta-carotene content in a high root yield background (Afuape et al. 2019).

Clustering of sweetpotato genotypes and parental lines. The objective of the multiple correspondence analysis was to identify genotypes with a similar phenotypic profile, and associations between categories of phenotypic variables (Table S4 in ESM). Five clusters were formed and figured out from the dendrogram generated by the hierarchical clustering analysis (Figure 3). Cluster 1 is represented by the parental line Tio-joe. Cluster 2 contains about 93% of the breeding population including the parental line ACAB220. Clusters 3 and 5 consisted of FER11 and VOBO5 respectively. Cluster 4 composed of parental line Vobodouaho and genotypes as VOBO6, FER33, and FER36. The cluster 1 individual has edentate central leaf lobe and cordiform leaf. The cluster 2 individuals have triangular leaf with semi-elliptic central leaf lobe and no lateral lobes. The cluster 3 individual has semi-circular central leaf lobe. The cluster 4 individuals have moderately lobed leaf where the central leaf lobe is elliptic. The cluster 5 is characterized by deep leaf lobe type, and lanceolate central leaf lobe. These different cluster groups can stand for distinct germplasm pools or populations that can be used to develop heterotic groups and explore heterosis effect in combining specific traits (David et al. 2018). For instance, population derived from Tio-joe and ACAB220, and population derived from Vobodouaho and ACAB220. Positive heterosis effects were reported for resistance to sweetpotato virus diseases, storage root yield, beta-carotene and dry matter content (Ngailo et al. 2019), and explored using poly-cross and diallel mating design (Musembi et al. 2015; Naidoo et al. 2016; Baafi et al. 2017; Mbusa et al. 2018), bi-parental crossing (Afuape et al. 2019) and reciprocal recurrent selection (Grüneberg et al. 2022). So far, VOBO genotypes can be used for further backcrossing to stabilise beta-carotene content in the background of Vobodouaho.

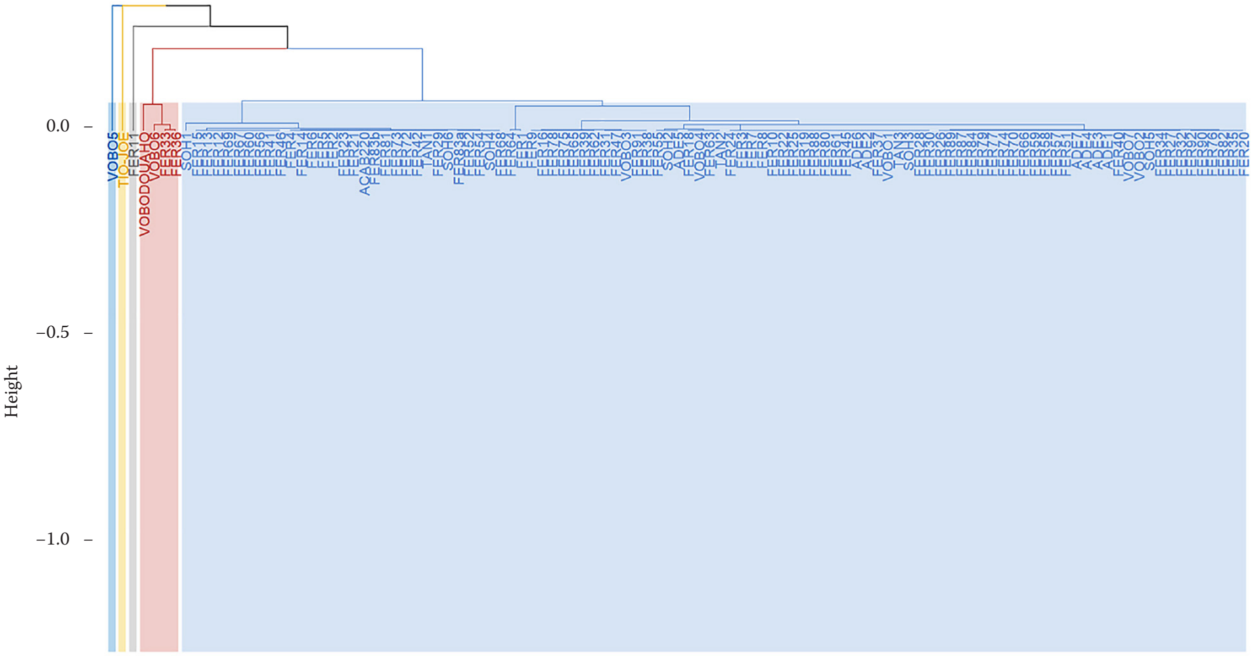

Figure 3. Clustering of 106 sweetpotato genotypes and three parental varieties (Vobodouaho, ACAB220, Tio-joe)

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CONCLUSION

This study successfully developed 106 sweetpotato genotypes from biparental crossings (hand and open pollination) within three parental lines. Results indicated reciprocal cross-compatibility between ACAB220 and Vobodouaho and reciprocal cross-incompatibility between ACAB220 and Tio-joe where only ACAB220 can be used as female. Phenotypic diversity of genotypes showed that ACAB220 and Vobodouaho are homozygous for flesh colour trait, reciprocal crosses induce changes in progeny flesh colour, and orange flesh colour is dominant over white flesh colour. Progenies were structured in two populations useful to develop heterotic groups. Progenies and parental lines have been clustered in five different phenotypic groups where genotypes obtained from mother plant Vobodouaho can be used for further backcrossing to stabilise beta-carotene content in the background of Vobodouaho. This study could serve as reference for further research towards the development of OFSP varieties, the floral induction in local varieties, and the determination of genotype combining ability.

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