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ORIGINAL PAPER

Hybrid performance in taro (*Colocasia esculenta*) in relation to genetic dissimilarity of parents

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Abstract Taro (*Colocasia esculenta*) breeding, as other root crop breeding, is based on the production and evaluation of large numbers of hybrids. The selection of parents is based on their phenotypic value in the absence of information concerning general combining ability (GCA), specific combining ability (SCA), or genetic distances between varieties. By combining data from heritability trials and from genetic diversity studies conducted with AFLP and SSR markers, we aimed at studying the relationship between hybrid vigour and genetic dissimilarity between parents. The traits studied included number of suckers, corm weight, corm dimensions, and dry matter content. Correlation coefficients between hybrid gain and dissimilarity values were calculated. The prediction of hybrid performance based on the mid-parent value was compared to the prediction based on a modified expression that takes into account the genetic relationships between parents. Correlations were all but one positive but not statistically significant for all traits, with the exception of the number of suckers, when using SSR markers for dissimilarity calculations. Accordingly, the genetic dissimilarities in the prediction of hybrid performances did not increase the correlation between predicted and observed hybrid vigour values. However, large differences were observed among the residual means from the regression between predicted and observed values when using AFLP or SSR markers, mainly due to the much higher polymorphism revealed by the latter. Models need to be further adapted to the type of molecular marker used, since their ability to reveal different rates of polymorphism will have a direct incidence on the calculation of genetic dissimilarities between genotypes. Nevertheless, since SSR markers are more polymorphic and more informative than AFLP markers, they should be preferentially used for these studies. Low genetic dissimilarity of parents yielded weak heterosis effects and future studies need to be conducted by using a broader genetic base. This is the first study assessing the relationship of hybrid vigour with the genetic distances between parents, conducted on a tropical root crop.

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Introduction

Taro (*Colocasia esculenta* (L.) Schott, Araceae) is an important root crop in the wet tropics such as the Caribbean, West Africa, Southeast Asia, and the Pacific. It ranks fifth among root crops, after potato (*Solanum tuberosum*), cassava (*Manihot esculenta*), sweet potato (*Ipomoea batatas*), and yams (*Dioscorea* spp), with an estimated annual production of 12 million tons of corms from an area of 2 million ha (FAO 2007, http://www.fao.org). In some tropical regions such as several Pacific islands (e.g., Vanuatu) taro is however, the main staple food (Weightman 1989). Taro is a highly polymorphic, vegetatively propagated, and

predominantly allogamous species, characterised by protogyny (Purseglove 1979). These features are consistent with a relatively high heterozygosity among cultivars, observed in biochemical and molecular studies, conducted either with isozymes (Lebot and Aradhya 1991) or with microsatellites (Mace and Godwin 2002; Noyer et al. 2006).

The first taro breeding programmes were initiated in the early 70s in Hawaii, Fiji, and Samoa. They were based on biparental crosses of local cultivars, and aimed at the improvement of yield and quality (Sivan and Tavalqia 1984; Wilson et al. 1991). The genetic base used in hybridisation was relatively narrow but high phenotypic variation was observed within progenies and breeders managed to select good hybrids by crossing the best varieties. Two successful varieties, 'Samoa Hybrid' and 'Alafua Sunrise', were widely distributed throughout numerous Pacific countries. However, after the outbreak of taro leaf blight (TLB) in Samoa in 1993, high breeding priority was given to the resistance breeding against *Phytophthora colocasiae* Racib. The first programmes based on recurrent selection were initiated in the late 1980s in the Solomon Islands and Papua New Guinea and involved germplasm from diverse origins, including wild materials (Ivancic and Okpul 1995). The method employed was based on the introgression of horizontal or durable resistances through numerous cycles of recurrent selection. The main drawback of these programmes was the difficulty of eliminating wild, undesirable traits such as irregular corm shapes, high numbers of stolons, and high levels of acridity (Okpul 2002). In the last decades, breeders have tried to search for TLB resistances within a much wider range of cultivars and a regional network facilitating the collection and exchange of elite cultivars, with varying degrees of resistance to TLB, was established (TANSAO 2002).

Along with resistance to TLB, breeders seek to improve plant architecture (e.g., optimal number of suckers, absence of stolons, optimal number of leaves, and vertical petioles), corm yield, and quality traits such as high dry matter content, corm shape, and low level of irritant substances (*i.e.*, calcium oxalate crystals). Vanuatu, one of the participants in the regional project, has recently initiated a modified recurrent selection programme aiming at the genetic investigation and improvement of these key agronomic traits. In the absence of an accurate assessment of GCA (general combining ability), and SCA (specific combining ability), and of the genetic distances between local varieties, breeders select parents on their phenotypic value. Recent molecular studies based on AFLP and SSR markers (Quero-García et al. 2004; Quero-García et al. 2006a) opened new possibilities for studying relationships between hybrid performance and parent genetic distances.

Different types of information concerning the parents can be used for the prediction of hybrid performance: their phenotypic value, the results of progeny tests or their genetic relationships. Unfortunately, GCA values are sometimes complex to determine with great precision (White and Hodge 1988). Concerning the genetic relationships between parents, these can be estimated using the coefficient of co-ancestry (Malécot 1948) or polymorphisms generated by molecular markers (Charcosset and Gallais 2003). Methods for predicting hybrid performance based on the genetic relationships among parents and their mid-parent values typically assume three conditions (Panter and Allen 1995): (1) the progeny of a biparental cross receives half of its (nuclear) genes from each parent, (2) the parents are inbred and unrelated, and (3) the studied traits are strictly determined by additive variance.

In Vanuatu, the genetic base is relatively narrow (Lebot and Aradhya 1991; Kreike et al. 2004; Noyer et al. 2006) and cultivars from the National germplasm collection are most probably related. Moreover, recent heritability studies have shown moderate values of narrow-sense heritability for several important agronomic traits, such as corm yield, suggesting a non negligible role of dominance variance (Quero-García et al. 2006b).

The recently initiated Vanuatu breeding programme is based on crosses between local taro cultivars for which no pedigree data exist. Moreover, a moderate number of combinations (disconnected full-sib progenies) are available. Thus, the relationship between parents' genetic distances and hybrid performance was assessed by: (a) computing correlation coefficients between hybrid gain and dissimilarity values of parents and (b) comparing the prediction of hybrid performance based on mid-parent values and on a modified expression taking into account the genetic relationships between parents.

The aim of the present article is to evaluate a practical approach for assessing the relationship of genetic dissimilarity of parents with hybrid performance in taro.

Materials and methods

Genetic materials and field experiments

Artificial hybridization in taro was carried out from November 1999 to February 2000. The parents were the flowering accessions of the national taro collection at VARTC (Vanuatu Agricultural Research and Technical Centre), on the Island of Espiritu Santo, Vanuatu. The hybridization methodology employed has been described elsewhere (Ivancic et al. 2003). The total number of successful combinations was 92 but only the largest 42

families (from 16 to 80 individuals) were selected for heritability trials (Quero-García et al. 2006b).

The experimental site at VARTC (80 m a.s.l., latitude 15°26.7'S and longitude 167°11.5'E) has a deep and fertile soil, covering a limestone plateau, 2.8 km from the seashore. The climate of Espiritu Santo is tropical oceanic, averaging 2,745 mm rainfall per year (1989–2000). During the hot and rainy season (from December to April), average rainfall is 335 mm per month whereas during the drier season (from July to September) it averages 117 mm per month. The annual mean temperature is 24.7°C with the highest in January (26.1°C) and the lowest in August (21.9°C).

Two incomplete block designs (hereafter called α1 and α2), including parents and offsprings, were used during the second clonal generation (C2), as described by Quero-García et al. (2006b). Out of the 42 initial progenies, genetic dissimilarities between parents, estimated with AFLP and SSR markers, were available for 30 and 24 progenies, respectively. However, complete data on phenotypic characterization of parents and offsprings were available only for 20 progenies (Table 1). AFLP data were available for the parents of these 20 progenies but SSR data were available only for the parents of 16 progenies (Table 1). Six quantitative traits were measured on individual plants, viz., number of stolons, number of suckers, corm weight, corm length, corm width, and dry matter content. The trait, number of stolons, was too heterogeneous to be included in the analysis. For the trait, number of suckers, a root-square transformation allowed the stabilisation of variance and its inclusion in the analysis.

Table 1 Genetic dissimilarity and mean parental heterozygosity of 20 hybrid combinations

Progeny No.	AFLP dissimilarity	SSR dissimilarity	Mean parental heterozygosity
VU373 × VU314 (1)	0.227	0.545	0.614
VU185 × VU197 (2)	0.277	0.545	0.591
VU185 × VU112 (3)	0.323	0.568	0.591
VU002 × VU112 (4)	0.227	0.636	0.659
VU373 × VU285 (5)	0.273	0.659	0.659
VU219 × VU036 (6)	0.209	0.386	0.614
VU097 × VU379 (7)	0.332	n.d.	n.d.
VU379 × VU086 (8)	0.327	n.d.	n.d.
VU285 × VU314 (9)	0.268	0.682	0.591
VU325 × VU285 (10)	0.309	0.545	0.614
VU118 × VU366 (11)	0.227	0.568	0.659
VU350 × VU302 (12)	0.300	0.614	0.591
VU350 × VU373 (13)	0.291	0.636	0.636
VU054 × VU379 (14)	0.318	n.d.	n.d.
VU373 × VU057 (15)	0.250	n.d.	n.d.
VU373 × VU137 (16)	0.291	0.568	0.659
VU036 × VU281 (17)	0.327	0.568	0.682
VU222 × VU372 (18)	0.232	0.500	0.591
VU159 × VU340 (19)	0.304	0.614	0.705
VU246 × VU222 (20)	0.177	0.500	0.568
Mean	0.27	0.571	0.626
SEM	0.045	0.072	0.040
CV (%)	16.56	12.68	6.35

n.d. Not determined

Estimation of progeny performance

Assuming that parents are inbred, unrelated, and with equal contribution to their progeny's genotype, the simplest approach to estimate bi-parental hybrid performance is to calculate mid-parent values. But the taro cultivars intercrossed in our study are at least partly heterozygous and presumably not unrelated. For this reason, a modified approach was adopted, by considering the genetic relationships (estimated with AFLP and SSR markers) between parents (Eq. 1):

$$H_{ij} = \frac{(P_i + P_j)}{2} \times \left[1 + \ln\left(2 - f_{ij}\right)\right] \quad (1)$$

where H_{ij} indicates the expected value of the hybrid produced from the i and j parents; P_i and P_j are the observed values of the i and j parent, respectively; f_{ij} is the coefficient of similarity among parents i and j, and $1-f_{ij}$ is the coefficient of dissimilarity between parents.

Equation 1 has two components: an additive component which is the average of parental phenotypes and a multiplicative component which reflects heterotic or inbreeding effects. This type of logarithmic expression was initially adopted in Nei's formula (1972) for the calculation of genetic distances and has already been used for the same purpose as ours by Tenkouano et al. (1999). Accordingly, the expected progeny performance should vary as a function of the genetic distance among parents. Thus, if parents are genetically very similar, the logarithmic expression will approach zero and the progeny expected value will consequently approach the mid-parent value (the extreme case being the selfing of an inbred line). On the opposite, crossing two distant parents should entail hybrid vigour effects.

For AFLP analysis, the coefficient of similarity was calculated by using the Simple Matching index (Sokal and Michener 1958), after the detection of 197 polymorphic fragments (out of 895 fragments produced by 14 enzyme combinations), as described by Quero-García et al. (2004). These authors considered all electromorphs, both monomorphic and polymorphic bands, which resulted in rather low values of genetic dissimilarity, reflecting the narrow genetic base of Vanuatu cultivars. However, in order to

have comparable ranges of dissimilarity values between both AFLP and SSR markers, only polymorphic AFLP bands were taken into account in this study. Out of these 14 enzyme combinations, 11 have been used for the construction of the first taro genetic maps (Quero-García et al. 2006c) and thus, the derived markers are expected to have relatively good genome coverage. For SSR markers, a direct allelic coding system was used and the genetic similarity was calculated as the mean of the number of shared alleles at all loci, after the identification of 134 alleles at 22 loci (Quero-García et al. 2006a). Parental heterozygosity was calculated as the mean of heterozygous loci among the 22 studied loci. Mean parental heterozygosity, for each progeny studied, was calculated as the mean of individual parental heterozygosities.

Statistical analysis

Data from α1 and α2 were pooled in order to include the maximum number of progenies in the calculation, as well as all the available information. A fixed effects model, as described in Quero-García et al. (2006b), was considered, and the LSMEANS procedure of the statistical package SAS 8.02 (SAS Institute Inc. 1999–2001) was used to estimate the adjusted means for all treatments.

Pearson's coefficients of correlation were calculated between genetic dissimilarities (both based on AFLPs and SSRs) and hybrid performance (or hybrid gain, that is, the difference between progeny means and mid-parent values). Regression analysis was performed to assess the predictive value of the parental phenotype on hybrid performance, using the mid-parent values and the mid-parent models described in Eq. 1. However, only correlation coefficients between the observed hybrid mean and the expected hybrid mean, as estimated with the different models, were presented. Differences between observed and predicted values of the hybrid mean performance were calculated. By deriving standard errors for these differences, two-tailed *t*-tests were performed to examine the hypothesis that these differences were equal to zero. The following formulas were used for the calculation of variances for the differences between predicted and observed values (for each cross) for the mid-parent (Eq. 2) and the modified (Eq. 3) models, respectively:

$$Var(D) = Var(Y_{ij}) + \frac{(Var(P_i) + Var(P_j))}{4} \quad (2)$$

$$Var(D) = Var(Y_{ij}) + \frac{(Var(P_i) + Var(P_j)) \times (1 + D_{ij})^2}{4} \quad (3)$$

where Var(D) is the variance of the difference between observed and predicted values; var(Y_{ij}) is the variance of observed values for the ij hybrid combination; Var(P_i) and Var(P_j) are the variances of the i and j parental means and D_{ij} is the genetic dissimilarity between i and j parents. For Eq. 3 the approximation $\ln(1 + D_{ij}) = D_{ij}$ was used. A mean variance was then calculated over the whole set of hybrid combinations studied.

By using these variance calculations, two models using AFLP (referred hereafter as AFLP model) and SSR (referred hereafter as SSR model) dissimilarities were compared through paired *t*-tests to determine whether they were significantly different from each other. When using AFLP data, all analyses were performed both on the 20 available progenies and the 16 progenies for which SSR data were available, in order to accurately compare the results produced with these two types of markers.

Results

Correlations between hybrid performance and genetic relationships among parents

Progeny means were superior to mid-parent values for all studied traits with the exception of dry matter content (Table 2). For corm dimensions and corm weight, two progenies had particularly low mid-parent-values: no. 18 (VU222 × VU372) and no. 20 (VU246 × VU222). Indeed, due to mortality problems, parents VU222 and VU246 presented adjusted means that were not significantly different from zero for these traits. Consequently, these two progenies were not further included in the analyses for traits such as corm weight, corm length, and corm width, for which 18 and 14 progenies were used for AFLP and SSR models, respectively.

When computing correlations between hybrid performance (or hybrid gain) and genetic dissimilarity among parents, only the correlation for the number of suckers estimated by using SSR dissimilarity was statistically significant (Table 3). When dealing with AFLP data, higher correlation coefficients were obtained for corm weight and corm width when working with 20 progenies, whereas the opposite was observed for number of suckers. Correlations between hybrid gain and SSR dissimilarity seemed to be slightly higher than those calculated with AFLPs for all traits with the exception of dry matter content.

Comparison of the models for the prediction of hybrid performance

Mid-parent values (MPV1 or MPV2, Table 4) were good predictions for progeny means for number of suckers, corm width, and dry matter content, both with 16 or 20 progenies. Nevertheless, the predictions were weaker when

Table 2 Mid-parent and mean offspring values calculated for the 20 analysed progenies

Progeny	NSU		CWE (in kg)		CL (in cm)		CWI (in cm)		DMC (in %)	
	P	O	P	O	P	O	P	O	P	O
VU373 × VU314 (1)	1.02	2.22	0.79	0.75	9.09	10.87	8.82	8.57	31.47	29.60
VU185 × VU197 (2)	0.63	1.14	0.68	0.70	9.56	9.83	8.13	8.43	25.56	26.75
VU185 × VU112 (3)	0.67	1.13	0.71	1.04	9.71	10.60	9.03	9.31	27.91	27.19
VU002 × VU112 (4)	0.98	1.28	0.65	0.77	9.05	10.33	8.38	8.80	27.77	27.18
VU373 × VU285 (5)	1.61	2.22	0.69	0.68	8.64	8.30	9.20	7.84	27.34	28.83
VU219 × VU036 (6)	1.21	1.09	0.67	0.78	8.58	10.09	8.66	8.67	26.44	26.37
VU097 × VU379 (7)	0.49	0.82	0.64	0.82	7.28	8.78	10.06	11.06	26.97	27.02
VU379 × VU086 (8)	1.26	1.20	0.60	0.99	8.05	10.04	9.43	10.71	27.43	24.95
VU285 × VU314 (9)	1.41	2.23	0.59	0.91	7.89	11.31	7.89	9.66	27.44	26.82
VU325 × VU285 (10)	1.94	2.44	0.63	0.80	8.40	10.42	8.53	9.67	25.41	26.89
VU118 × VU366 (11)	0.84	1.80	0.65	0.84	7.78	8.97	8.69	10.38	35.27	28.95
VU350 × VU302 (12)	1.40	1.77	0.62	0.72	7.80	9.75	7.57	7.85	29.73	32.99
VU350 × VU373 (13)	1.27	2.15	0.77	0.98	9.17	10.24	9.13	9.76	30.76	30.65
VU054 × VU379 (14)	0.31	0.28	0.73	0.93	7.92	7.45	9.45	12.01	26.68	24.77
VU373 × VU057 (15)	1.06	1.65	1.12	0.69	8.50	8.93	8.66	9.41	30.73	30.82
VU373 × VU137 (16)	0.56	1.54	0.78	0.56	8.25	8.33	7.86	7.19	28.67	25.55
VU036 × VU281 (17)	1.04	1.78	0.61	0.64	7.59	10.33	7.95	8.95	33.97	30.91
VU222 × VU372 (18)	1.46	1.16	0.50	0.93	5.70	10.42	7.23	9.19	27.89	27.80
VU159 × VU340 (19)	0.24	1.44	0.59	0.86	8.51	9.27	8.76	8.61	25.80	27.44
VU246 × VU222 (20)	1.47	1.33	0.34	0.77	3.61	10.85	5.62	9.14	28.20	30.30
Mean	1.04	1.53	0.67	0.81	8.05	9.76	8.45	9.26	28.57	28.09
SEM	0.46	0.60	0.10	0.13	1.40	1.01	0.96	1.16	2.68	2.21
CV (%)	43.64	36.00	22.00	15.70	17.00	10.40	11.40	12.50	9.38	7.87

NSU Number of suckers, *CWE* Corm weight, *CL* Corm length, *CWI* Corm width, *DM* Dry matter content, *P* Mid-parent values, *O* Offspring mean, *SEM* Standard error of mean, *CV* Coefficient of variation

Table 3 Correlation coefficients between hybrid gain and genetic dissimilarity between parents

	AFLP (20 fam.)	AFLP (16 fam.)	SSR (16 fam.)
NSU	0.173	0.456	0.554*
CWE[a]	0.352	0.155	0.219
CL[a]	0.024	0.028	0.035
CWI[a]	0.229	0.015	0.073
DMC	−0.028	0.073	0.045

NSU Number of suckers, *CWE* Corm weight, *CL* Corm length, *CWI* Corm width, *DMC* Dry matter content

* $P < 0.05$; ** $P < 0.01$ (P values from the t-test)

[a] 18 and 14 families for AFLP and SSR analyses were respectively used for traits corm weight, corm length and corm width

analysing 16 instead of 20 progenies, especially for corm width. For corm weight, correlations were not significant and remarkably lower than for corm dimensions. None of the two modified models considered for the prediction of progeny means yielded significantly higher correlation coefficients, as compared with the simplest mid-parent model (Table 4). This result might reflect the homogeneity of the Vanuatu germplasm and is in accordance with the generally low values of correlation observed between hybrid gain and genetic relationships among parents (Table 3). Even for the trait, number of suckers, for which this correlation was statistically significant and above 0.5 when using the SSR model, the inclusion of the genetic relationships among parents in the prediction model did not dramatically improve the accuracy of progeny performance prediction (Table 4).

The mean differences between predicted and observed progeny means were more similar between the mid-parent models (MPV1 and MPV2) and the AFLP model than between the mid-parent models and the SSR model (Figs. 1, 2, 3, 4 and 5). This result was consistent with the much higher dissimilarity values between accessions observed with SSR as compared with ALFP markers (Table 1). For the trait number of suckers, the mean difference between predicted and observed progeny means was not statistically different from zero when using the SSR model (Fig. 1). Predictions based on mid-parent value or the AFLP model produced residuals which were significantly different from zero, reflecting a general parental inferiority for sucker

Table 4 Correlation coefficients between the observed hybrid mean and the expected hybrid mean, estimated with different models

	MPV1	AFLP1	MPV2	AFLP2	SSR
NSU	0.615**	0.627**	0.495	0.529*	0.544*
CWE[a]	0.242	0.210	0.080	0.057	0.027
CL[a]	0.328	0.286	0.183	0.167	0.152
CWI[a]	0.652**	0.670**	0.315	0.279	0.298
DMC	0.607**	0.545*	0.572*	0.570*	0.589*

NSU Number of suckers, *CWE* Corm weight, *CL* Corm length, *CWI* Corm width, *DMC* Dry matter content

* $P < 0.05$; ** $P < 0.01$ (P values from the t-test)

[a] 18 and 14 families for AFLP and SSR analyses were respectively used for traits corm weight, corm length and corm width. *MPV1-MPV2* Mid-parent values were used for 20 and 16 progenies respectively, *AFLP1-AFLP2* Mid-parent values and AFLP similarities were used for 20 and 16 progenies respectively (Eq. 1), *SSR* Mid-parent values and *SSR* similarities were used for 16 progenies (Eq. 1)

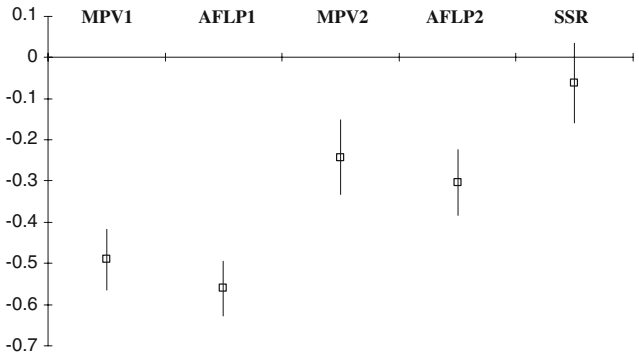

Fig. 1 Mean differences associated with different methods of predicting the number of suckers of progeny based on parental performance (MPV1, 20 crosses; MPV2, 16 crosses), AFLP similarity (AFLP1, 20 crosses; AFLP2, 16 crosses) and SSR similarity (SSR, 16 crosses)

production. For traits such as corm weight, corm length, and corm width, the sign of the difference between predicted and observed progeny means changed when dealing with 20 or 16 progenies for the mid-parent and the AFLP models (Figs. 2–4). For these traits as well as for dry matter content, the differences observed with the SSR model were all positive and much higher than those observed with the mid-parent or the AFLP models. For these traits, for which hybrid superiority was not as high as for the number of suckers, the use of SSR dissimilarities on Eq. 2 clearly over-estimated the predicted values.

Discussion

Taro breeders consider heterosis to be one of the key factors for the development of hybrid varieties (Ivancic and

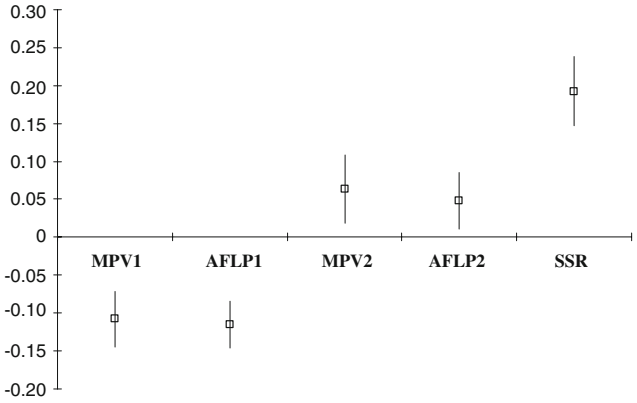

Fig. 2 Mean differences associated with different methods of predicting the corm weight of progeny based on parental performance (MPV1, 18 crosses; MPV2, 14 crosses), AFLP similarity (AFLP1, 18 crosses; AFLP2, 14 crosses) and SSR similarity (SSR, 14 crosses)

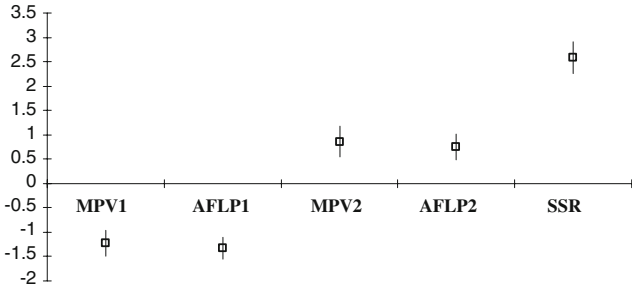

Fig. 3 Mean differences associated with different methods of predicting the corm length of progeny based on parental performance (MPV1, 18 crosses; MPV2, 14 crosses), AFLP similarity (AFLP1, 18 crosses; AFLP2, 14 crosses) and SSR similarity (SSR, 14 crosses)

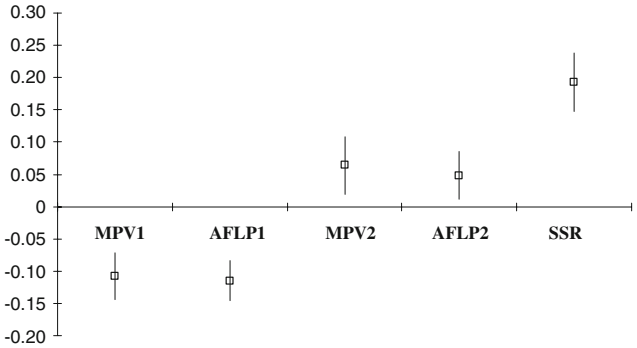

Fig. 4 Mean differences associated with different methods of predicting the corm width of progeny based on parental performance (MPV1, 18 crosses; MPV2, 14 crosses), AFLP similarity (AFLP1, 18 crosses; AFLP2, 14 crosses) and SSR similarity (SSR, 14 crosses)

Lebot 2000). However, the identification of high yielding hybrids is expensive and involves the evaluation of large numbers of hybrid combinations in multi-location trials. This constraint is more problematic for crops that have undergone relatively little breeding efforts, such as taro. On the other hand, stronger heterosis effects might be

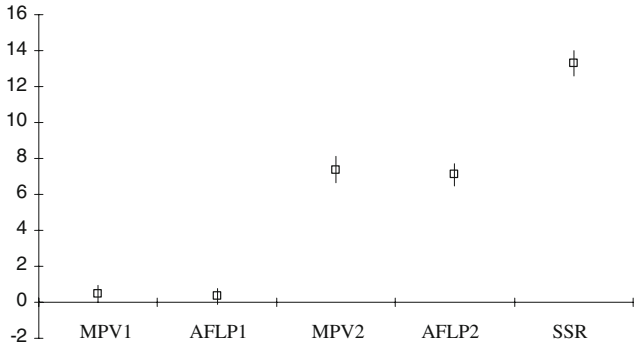

Fig. 5 Mean differences associated with different methods of predicting the dry matter content of progeny based on parental performance (MPV1, 20 crosses; MPV2, 16 crosses), AFLP similarity (AFLP1, 20 crosses; AFLP2, 16 crosses) and SSR similarity (SSR, 16 crosses)

expected as compared to crops that have undergone higher selection efforts.

The simplest way to study the relationship between parents and heterosis of hybrids is to compute correlation coefficients. Two factors complicated this analysis in our study: first, inbred lines are not used in taro breeding (due to predominant self-incompatibility and severe inbreeding depression) and second, a relatively low number of combinations were available. However, interesting differences were observed between traits and several correlations were statistically significant, although highly dependent on the number of analysed progenies (Table 3). Differences between correlations estimated with AFLP or SSR dissimilarities were also observed, particularly for corm weight and corm width. Quero-García et al. (2006a) confirmed this low agreement while comparing the structures (dendrograms) produced for the parents of the taro programme in Vanuatu, analysed both with AFLPs and SSRs. This result could be explained by the absence of a clear structure (*i.e.*, absence of clearly differentiated groups, very low values of bootstrap values for the main branches of the dendrograms) within the studied Vanuatu germplasm.

Charcosset and Gallais (2003) reviewed numerous studies of correlation between heterosis and genetic distances, and concluded that divergence indexes generally showed a stronger relationship with the SCA, or specific heterosis, than with hybrid performance. SCA is generally considered as the component of hybrid value most difficult to predict. Nevertheless, even if regular flowering and synchronisation of flowering are problematical in taro breeding (Ivancic et al. 2004), efforts should be oriented to the implementation of relatively simple factorial or half-diallel designs, in order to estimate GCA and SCA parameters.

Several authors have also observed that results are largely dependant on the materials evaluated (Melchinger 1999; Charcosset and Gallais 2003). Generally, the highest correlations were observed when related hybrids were present in the analysis. This result was consistent with theoretical predictions (Bernardo 1992; Charcosset and Essioux 1994; Charcosset et al. 1991). Assuming that cultivars from Vanuatu could be at least partly related, higher correlations could have been expected. Nevertheless, it could be interesting to investigate the impact of parental heterozygosity on the conclusions of these theoretical models. Pedigree information should be considered in further generations of the Vanuatu taro breeding programme, in order to compare the prediction of hybrid vigour when estimating genetic relationships among parents through molecular or pedigree information.

Theoretical predictions outlined a set of conditions to usefully predict heterosis when using molecular marker diversity: (1) linkage of a majority of markers to QTLs controlling the studied traits, (2) gametic phase linkage disequilibrium between marker alleles and QTL alleles, (3) strong dominance effects and (4) relatively high trait heritability. Concerning conditions (1) and (2), QTL detection studies on taro have only recently been initiated and preliminary results allowed for the identification of only a small subset of QTLs for yield and related traits, such as corm dimensions (Quero-García et al. 2006c). Attempts to identify QTL-marker associations should be regarded cautiously, since several authors have reported that QTL regions affecting a given trait are not always consistent across different germplasm (Lübberstedt et al. 1998; Chardon et al. 2004).

Concerning the comparison between the different models used for the hybrid performance prediction, none of them yielded significantly superior correlation coefficients as compared with the simple mid-parent value equation (Table 4). Mid-parent values had a low predictive value for all traits except for dry matter content and number of suckers. The analysis of residual means from the regression between predicted and observed values of progeny means showed two factors of variation: the type of character considered and the type of molecular marker used (AFLP or SSR) for the estimation of genetic similarities among parents (Figs. 1–5). When using AFLP markers, similarities between parents were rather high and therefore residual means estimated with this model did not differ statistically from those estimated with the mid-parent model. In contrast, the high polymorphism observed with SSR markers entailed lower similarity estimates and inversely, significantly higher mean residuals. Since SSR markers are more polymorphic and more informative than AFLP markers, they should be preferentially used for these studies. Models should thus be better adapted to this type of marker.

This is the first study conducted on the relationships between genetic distance and hybrid vigour for taro. Moreover, we could not find similar studies conducted on

other tropical root crops, such as cassava, yams or sweet potato. Indeed, these crops share several traits that complicate these approaches, such as a predominant allogamy related to high heterozygosity levels, the difficulty of producing and evaluating from a phenotypical point of view large progenies and the difficulty of evaluating simultaneously parents and progenies.

Our results showed the possibilities that molecular markers can be used for the prediction of hybrid performance and the selection of parents, through the application of relatively simple empirical models. Although several correlations between hybrid vigour and genetic dissimilarity were statistically significant, the use of molecular markers information in predictive models did not increase their accuracy, as compared to classical mid-parent values. Along with the need of focusing on markers preferentially linked to stable QTLs responsible for hybrid vigour effects, future studies conducted on taro should include a broader genetic base and larger hybrid vigour effects could be expected. Moreover, the variation of genetic similarities among parents would be much higher and this could increase the correlation coefficients and improve the accuracy of prediction models. Finally, a higher number of parental combinations should be considered in future trials, despite the difficulty of dealing with and phenotyping very high numbers of plants.

It has been assumed that cassava improvement could benefit from the production of homozygous lines through tissue culture techniques for the purpose of capturing hybrid vigour. Selected inbred progenies have been crossed with high yielding released varieties and a few hybrids appear significantly better in yield than the released varieties (Ceballos et al. 2006). Double-haploid production would greatly facilitate the investigation of heterosis in cassava and this technique should be considered in future taro breeding programmes.

Nevertheless, further studies need to be pursued in order to improve the predictive value of empirical models applied to allogamous crops for which double-haploid production techniques are not easy to implement.

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