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Genetic diversity of taro, *Colocasia esculenta* (L.) Schott, in Southeast Asia and the Pacific

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Abstract The genetic diversity of 255 taro (*Colocasia esculenta*) accessions from Vietnam, Thailand, Malaysia, Indonesia, the Philippines, Papua New Guinea and Vanuatu was studied using AFLPs. Three AFLP primer combinations generated a total of 465 scorable amplification products. The 255 accessions were grouped according to their country of origin, to their ploidy level (diploid or triploid) and to their habitat—cultivated or wild. Gene diversity within these groups and the genetic distance between these groups were computed. Dendrograms were constructed using UPGMA cluster analysis. In each country, the gene diversity within the groups of wild genotypes was the highest compared to the diploid and triploid cultivars groups. The highest gene diversity was observed for the wild group from Thailand (0.19), the lowest for the diploid cultivars group from Thailand (0.007). In Malaysia there was hardly any difference between the gene diversity of the cultivars and wild groups, 0.07 and 0.08, respectively. The genetic distances between the diploid cultivars groups ranges from 0.02 to 0.10, with the distance between the diploid accessions from Thailand and Malaysia being the highest. The genetic distances between the wild groups range from 0.05 to 0.07. First, a dendrogram was constructed with only the diploids cultivars from all countries. The accessions formed clusters largely according to the country from which they originated. Two major groups of clusters were revealed, one group assembling accessions from Asian countries and the other assembling accessions from the Pacific. Surprisingly, the group of diploid cultivars from

Thailand clustered among the Pacific countries. Secondly, a dendrogram was constructed with diploid cultivated, triploid cultivated and wild accessions. Again the division of the accessions into an Asian and a Pacific gene pool is obvious. The presence of two gene pools for cultivated diploid taro has major implications for the breeding and conservation of germplasm.

Introduction

Taro, *Colocasia esculenta* (L.) Schott, is a vegetatively propagated root crop that belongs to the monocotyledonous family Araceae. Although it is propagated vegetatively, it can also flower and set seed. Taro is grown in almost all tropical regions of the world and is a crop of considerable socio-economic importance in Southeast Asia and the Pacific. A wealth of genetic resources exists, but attempts to conserve the germplasm and use it to solve production problems have not been successful. The centre of origin of taro is generally believed to be between Myanmar and Bangladesh (Plucknett 1976). There are two botanical varieties characterised by their corm shape and described as var. *esculenta* (dasheen type) and var. *antiquorum* (eddoe type). It has been suggested that of the two varieties, *C. esculenta* var. *esculenta* is diploid and var. *antiquorum* is triploid (Kuruvilla and Singh 1981; Irwin et al. 1998). It is generally accepted that the majority of triploids are of Asian origin (Matthews 1990).

Lebot and Aradhya (1991) studied the genetic relationships between taro cultivars from Asia and the Pacific using isozymes. Their results showed a higher level of genetic variation in Asia than in the Pacific, with Indonesia being the area with the greatest diversity. Irwin et al. (1998) screened taro germplasm with RAPD markers and also found that Asian cultivars were genetically distant from the Pacific genotypes. We wanted to study the Asian and Pacific germplasm in more detail and with more refined molecular techniques such as AFLP.

The AFLP technique, a polymerase chain reaction (PCR)-based DNA fingerprinting technique, was devel-

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oped by Vos et al. (1995). This technique is very useful for the assessment of genetic diversity because the markers are highly reproducible, have a high multiplex ratio, are genome-wide and have low developmental costs. The AFLP technique has been used for mapping studies (Van Eck et al. 1995), phylogeny reconstructions (Kardolus et al. 1998), to elucidate the genetic relationships between wild and domesticated taxa (Hill et al. 1996), to study locus specificity (Roupe van der Voort et al. 1997) and to study the relation between the genetic structure and the geographical distribution of a species (Singh et al. 1999; Sharma et al. 2000; Shim and Jorgensen 2000).

In order to study the genetic diversity of Asian and Pacific taros, we included in our analysis diploid and triploid cultivars as well as wild germplasm. Overall, we used 255 accessions which were sampled in different geographical regions from Thailand, Malaysia, Vietnam, Indonesia, the Philippines, Papua New Guinea and Vanuatu. An improved understanding of the genetic

diversity of taro will contribute to the ongoing efforts for the genetic improvement of the crop and to the conservation of its germplasm.

Materials and methods

Plant material

The plant material was obtained from the Taro Network for Southeast Asia and Oceania (TANSO). For this EU-financed project, approximately 1,700 taro accessions were characterised and their genetic diversity was analysed using morpho-agronomic traits (30 international standardised descriptors) and isozymes. A core sample of 170 cultivars was selected based on their geographic origin, their agronomic performances and their zymotypes. Great care was taken not to select cultivars with identical zymotypes based on eight enzyme systems.

The core sample of 170 taro accessions were obtained from eight countries in Southeast Asia and Oceania: Vietnam (VN), Thailand (TH), Indonesia (ID), Malaysia (MY), the Philippines (PH), Papua New Guinea (PG), Vanuatu (VU). Wild accessions included in this

Table 1 Taro accessions collected for AFLP analysis. Each accession was grouped according to its country of origin, ploidy level (2x or 3x) and to its wild or cultivated status

Country	Group	Number of plants	Accession number
Vietnam	2x Culti- vars	3	VN044, VN045, VN047
	3x Culti- vars	24	VN003, VN010, VN016, VN029, VN034, VN050, VN053, VN080, VN089, VN094, VN095, VN098, VN113, VN115, VN117, VN121, VN125, VN126, VN134, VN137, VN143, VN182, VN183, VN276
	Wild	3	T3, T4, T5
Thailand	2x Culti- vars	33	TH001, TH003, TH004, TH005, TH007, TH008, TH010, TH022, TH025, TH030, TH031, TH032, TH036, TH039, TH041, TH047, TH048, TH055, TH056, TH071, TH091, TH092, TH098, TH101, TH108, TH138, TH144, TH147, TH148, TH156, TH158, TH160, TH206
	3x Culti- vars	2	TH015, TH016
	Wild	16	TH061, TH096, TH242, TH243, TH244, TH245, TH246, TH247, TH253, TH264, TH287, TH288, TH290, TH292, TH293, TH295
Indonesia	2x Culti- vars	50	ID010, ID033, ID058, ID061, ID081, ID083, ID101, ID136, ID150, ID155, ID167, ID178, ID217, ID218, ID239, ID245, ID265, ID270, ID311, ID328, ID331, ID338, ID350, ID366, ID377, ID383, ID392, ID399, ID400, ID407, ID409, ID411, ID450, ID453, ID472, ID507, ID509, ID511, ID512, ID519, ID521, ID525, ID526, ID548, ID552, ID555, ID561, ID562, ID2 M, ID3 M
	3x Culti- vars	10	ID191, ID231, ID235, ID257, ID316, ID452, ID497, ID517, ID518, ID524
	Wild	8	ID009, ID054, ID233, ID237, ID283, ID315, ID320, ID478
Malaysia	2x Culti- vars	13	MY028, MY030, MY045, MY050, MY118, MY121, MY127, MY131, MY136, MY142, MY148, MY149, MY164
	Wild	11	MY035, MY056, MY085, MY087, MY092, MY108, MY110, MY140, MY144, MY146, MY147
The Philip- pines	2x Culti- vars	31	GC396, GO049, GO104, GS336, GS362, GS377, GS382, GS406, PRG005, PRG042, PRG686, PRG690, PH014, PH023, PH038, PH039, PH049, PH054, PH055, PH056, PH057, PH058, PH067, PH074, PH086, PH103, PH121, PH123, PH129, PH157, PH164
Papua New Guinea	2x Culti- vars	35	PG654, PG669, PG753, PG770, PG772, PG773, PG776, PG781, PG786, PG790, PG791, PG792, PG793, PG794, PG802, PG803, PG813, PG814, PG825, PG826, PG827, PG828, PG833, PG843, PG847, PG851, PG853, PG859, PG862, PG864, PG869, PG880, PG883, PG908, Golba
Vanuatu	2x Culti- vars	16	VU010, VU017, VU025, VU056, VU065, VU066, VU117, VU165, VU191, VU217, VU224, VU257, VU302, VU314, Mateo Rose, Paita
Total		255	

study were of both eddoe and dasheen types. Although these wild accessions were collected at a distance from agricultural fields, it cannot be excluded that they are not feral and from cultivated origin.

The plant material derived from Thailand, Vietnam and Indonesia consisted of di- and triploid cultivated and wild forms. Originally, five wild accessions from Vietnam were analysed with AFLPs, but fingerprints of two of these wild accessions (T1 and T2) were very distinct from the *C. esculenta* fingerprints. Because of their deviating AFLP patterns, it is assumed that they belong to another *Colocasia* species, and were therefore omitted from the subsequent data analysis. Also the AFLP pattern of accession ID451 from Indonesia did not resemble *C. esculenta* AFLP patterns, but was more similar to the AFLP patterns of accessions T1 and T2 from Vietnam and was therefore also omitted from the subsequent data analysis.

Accessions from Malaysia consisted of diploid cultivated and wild forms. Accessions from the Philippines, Papua New Guinea and Vanuatu were represented by diploid cultivars. Golba, Paita and Mateo Rose are cultivars that were analysed using their commercial names instead of a given number. The PH-numbered accessions from the Philippines are common cultivars, while the other accessions, numbered GC, GO, GS and PRG, are described as promising new breeding lines. A comprehensive list of all the accessions used in this study is given in Table 1.

Accessions were planted after shipment in a greenhouse in 10-in pots under a 12/12 dark/light regime, 25°C and high relative humidity (95%). Young leaves were harvested and kept frozen (−80°C) until DNA extraction.

Ploidy analysis

Ploidy levels of cultivars were determined using flow cytometry to study the relationship between ploidy level and corm type. Ploidy levels of in vitro material of the cultivars were analysed by Plant Cytometrix Services (Schijndel, The Netherlands)

AFLP analysis

DNA was extracted from frozen material according to Roger and Bendich (1988). The AFLP protocol has been described by Vos et al. (1995). The DNA was digested with the restriction enzymes *Pst*I and *Mse*I. The first amplification was carried out using *Pst*+0 and *Mse*+A primers. The second amplification was carried out using different primer combinations:

- P+/M+: 5'-GAC TGC GTA CAT GCA GAA-3'/5'-GAT GAG TCC TGA GTA AAA C-3'
- P+/M+: 5'-GAC TGA GTA CAT GCA GGG-3'/5'-GAT GAG TCC TGA GTA AAC C-3'
- P+/M+: 5'-GAC TGC GTA CAT GCA GGG-3'/5'-GAT GAG TCC TGA GTA AAG G-3'.

We used AFLP template generated using a *Pst*/*Mse* enzyme combination instead of the more commonly used *Eco*/*Mse* combination because *Pst*/*Mse* generated markers are thought to be more evenly distributed along the chromosomes. In addition *Pst*+2/*Mse*+3 primers yielded more complex AFLP fingerprints than *Eco*+3/*Mse*+3 primers and were therefore also more efficient in generating AFLP markers (C.M. Kreike, unpublished results).

Data analysis

Presence or absence of an AFLP fragment was scored as 1 or 0. In case of doubt, a missing value was noted. The gene diversity was computed within groups (country, ploidy, habitat—cultivated or wild), using POPGENE. Subsequently the genetic distance between the diploid groups and the wild groups were calculated using Nei's (Nei 1978) unbiased measures of genetic identity, and genetic

distance also available in POPGENE. Finally dendrograms were constructed using Nei and Li (1979), bootstrapping (100×) and UPGMA cluster analysis, all available in the package TREECON. One dendrogram was constructed that contained only the diploid cultivars and one that contained di- and triploid cultivated and wild accessions as well.

Results

Ploidy analysis

Ploidy levels of the cultivars determined by flow cytometry allowed verification of the alleged association between botanical variety and ploidy level. The botanical variety *C. esculenta* var. *esculenta* has a dasheen-type corm and is said to be diploid, while the *C. esculenta* var. *antiquorum* has an eddoe-type corm and is said to be triploid (Kuruville and Singh 1981; Irwin et al. 1998). The results of the flow cytometric analysis, which could discriminate very clearly between diploid and triploid accessions, are shown in Table 1. The majority of the cultivated accessions were diploid. The few triploid accessions were mainly from Vietnam (24), Indonesia (ten) and Thailand (two) (Table 1). Their corm shape was determined and compared with their ploidy level.

To start with the triploid accessions from Vietnam, most accessions of Vietnam had a dasheen- or intermediate-type corm. Only five were clearly eddoe (VN055, VN134, VN143 and VN276). The triploid accessions from Thailand had a dasheen-type corm as well. Only one of the triploid accessions from Indonesia was noted as eddoe. We could not find any relation between triploidy and an eddoe-type corm shape. For the diploid accessions, we did not observe any correlation with dasheen-type corm shape, either. Although most of the diploid accessions from Indonesia, Thailand, Papua New Guinea and Vanuatu had a dasheen-type corm as expected; the diploid cultivars from the Philippines and Malaysia were almost all eddoe type.

AFLP analysis

The three primer combinations yielded 465 scorable AFLP markers. About 7% of these markers were completely monomorphic in all accessions. Twenty-four percent of the scored AFLP markers had very high allele frequencies (0.9–1.0). These bands showed a very distinctive AFLP fingerprint pattern that was typical for *C. esculenta*. The closely related species like *C. gigantea*, *Alocasia* sp., *Xanthosomasagittifolium*, *X. violacaum*, *X. brasiliense*, *X. robustum* and *Amorphophalluscampulanatus* did not show any resemblance to the *C. esculenta* AFLP banding patterns and therefore they could not be included in this genetic diversity analysis.

The 255 accessions analysed in this study were selected out of a larger collection in order to capture as much diversity as possible. However, the selection process could not prevent that we did observe some identical or nearly

identical AFLP patterns. This was most clearly observed in a large number of diploid cultivars from Thailand. Also, some triploid accessions from Vietnam had nearly identical AFLP patterns as well as two accessions from Malaysia. The AFLP markers could not discriminate between di- and triploid accessions.

Gene diversity

For this diversity study, we used accessions from different countries, with different ploidy levels and from different habitats, i.e. cultivated or wild. In order to study the possible relationships between cultivars from different countries or between cultivars and wild accessions from one country, we decided to group the accessions according to the following classifications: country, ploidy level and habitat. The resulting groups are shown in Table 1.

We calculated the gene diversity of these groups and the results are shown in Table 2. The gene diversities of the wild groups are the highest with the wild group from Thailand having the highest value of all (0.19). Further, it is clear that Indonesia holds the highest gene diversities among the cultivars. The group from Thailand comprising the triploid cultivars consisted of only two genotypes that had almost identical AFLP patterns. This is reflected in the low estimate of their gene diversity (0.007). Similarly, in the group of diploid cultivars from Thailand, many genotypes with nearly identical AFLP patterns were observed (0.03). The gene diversities of the cultivated (2x) and wild groups from Malaysia are similar, 0.07 and 0.08, respectively. The gene diversity for the Indonesian cultivated (2x) and wild groups, which are 0.11 and 0.15, respectively, are among the highest values. For the three countries in the Pacific, Papua New Guinea, the Philippines and Vanuatu, only diploid cultivars were available and it is obvious from Table 2 that gene diversity in this region is decreasing from east (Indonesia) to west (Vanuatu).

Genetic distance

To improve our understanding of the associations and possible connections between the diploid and the wild groups of the different countries, we calculated the genetic distances between these groups. These results are shown in Tables 3 and 4, respectively. The diploid group from Vietnam was omitted from this analysis because the number of accessions in that group was too low (only three) for a reliable comparison.

Genetic distances between the diploid groups are given in Table 3. The high genetic distance, 0.10, between the diploid cultivated groups of the Asian countries Thailand and Malaysia is clearly visible. The genetic distances between the cultivar groups from the Pacific countries, Papua New Guinea, the Philippines and Vanuatu, are much lower, and they range from 0.02 to 0.05. Genetic distances between the Asian and Pacific diploid groups range from 0.05 to 0.08. The classification of Indonesia into the Pacific or Asian gene pool is somewhat ambiguous since it seems to be related to both gene pools.

Genetic distances between the wild groups are shown in Table 4. The genetic distances between these group range from 0.05 to 0.07, with the wild group from Thailand being the most distant of all. We also looked at the genetic distances between the cultivated and wild groups that were derived from the same country and observed that the genetic distances of the groups from both Indonesia and Malaysia was very low (0.02, data not shown).

Dendrograms

In order to determine the genetic structures between the Asian and Pacific genotypes in more detail dendrograms were constructed using UPGMA cluster analysis, first, of all the diploid accessions (Fig. 1) and second, of the diploid, triploid and wild accessions (Fig. 2).

The dendrogram in Fig. 1 depicts the genetic distances between all diploid cultivars (181). It can be clearly observed in the dendrogram that the accessions form clusters that reflect their geographic origin. Further, the dendrogram can be divided into two major clusters—one cluster showing the Pacific germplasm from countries like Papua New Guinea, the Philippines and Vanuatu and one cluster comprising the Asian germplasm including Indonesia and Malaysia. The large cluster of nearly identical diploid cultivars from Thailand show remarkable similarity with the accessions that belong to the Pacific gene pool. Also the diploid Vietnamese accession VN045 shows similarity with the Pacific gene pool. Only a few cultivated accessions from Thailand (TH022 and TH148) are related to the Asian gene pool, just as the other diploid Vietnamese accessions (VN044 and VN047). The large group of diploid cultivars from Indonesia has been divided into two clusters, ID-I and ID-II. The genetic distances in cluster ID-II are relatively high. The diploid accessions from the Philippines are also divided in two clusters. The first cluster harbours traditional breeding lines, while the second cluster contains new breeding lines.

To determine the possible origin of the triploid cultivars and to assess the relationships between wild and cultivated

Table 2 Gene diversity within the groups of cultivars according to each cultivar's respective country of origin

Country	Thailand	Malaysia	Vietnam	Indonesia	The Philippines	Papua New Guinea	Vanuatu
2x Cultivars	0.03	0.07	0.05	0.11	0.08	0.06	0.05
3x Cultivars	0.007		0.13	0.14			
Wild accessions	0.19	0.08	0.10	0.15			

Table 3 Genetic distances between diploid cultivars grouped per country. [The group consisting of 2x Vietnamese cultivars was omitted from this analysis because the number of accessions (three) was too low]

Country	Thailand (2x)	Malaysia (2x)	Indonesia (2x)	The Philippines (2x)	Papua New Guinea (2x)	Vanuatu (2x)
Thailand (2x)	–					
Malaysia (2x)	0.10	–				
Indonesia (2x)	0.07	0.04	–			
The Philippines (2x)	0.05	0.05	0.02	–		
Papua New Guinea (2x)	0.06	0.07	0.04	0.02	–	
Vanuatu (2x)	0.06	0.07	0.04	0.03	0.03	–

Table 4 Genetic distances between the wild accessions per country

Country	Thailand	Malaysia	Vietnam	Indonesia
Thailand	–			
Malaysia	0.07	–		
Vietnam	0.07	0.05	–	
Indonesia	0.05	0.05	0.05	–

accessions within countries, we constructed a dendrogram using all 255 accessions (Fig. 2). Again, it can be clearly observed in the dendrogram that the accessions form clusters according to their origin, i.e. country, ploidy level and habitat—cultivated or wild.

A large part of the dendrogram shown in Fig. 2, from the top cluster of accessions from Papua New Guinea (PG) to the cluster containing the new breeding lines from the Philippines (PH, new lines), is the same as in Fig. 1. The lower part of the dendrogram is more dissimilar. Some groups have been divided into several clusters. The Indonesian cluster ID-II has been divided into smaller clusters ID-IIa and ID-IIb. In cluster ID-IIb, the cultivated and wild accessions from Indonesia are clustered together. The wild accessions from Malaysia merged with the cluster of cultivated accessions, now forming one large cluster containing all accessions from Malaysia. The wild accessions from Thailand also form two clusters (TH) with high genetic diversity. These clusters containing the wild germplasm from Thailand are genetically very distinct from the Thai cultivars. The overall high genetic diversity of the triploid and wild accessions from the different countries is clearly visible in the dendrogram. The triploids originating from different countries are clustered together in cluster TRI-I and TRI-II. We did not observe a close resemblance in AFLP pattern between a diploid or triploid accession and therefore we could not shed any light on the possible ancestry of the triploid accessions.

Discussion

Association between botanical variety and ploidy level

We did not observe any positive correlation between the corm shape and the ploidy level of the accessions. Based on these results we conclude that there is no association

between the number of chromosomes in a taro plant and its botanical variety: *esculenta* or *antiquorum*. Lebot and Aradhya (1991) could not differentiate between the two ploidy levels with isozymes. We could not discriminate between diploid and triploid accessions with AFLP markers. This in contrast to the observations of Irwin et al. (1998), who observed unique RAPD bands in the two triploids which were absent in 42 diploids. We did observe alleles with higher gene frequencies in the triploid compared to the diploid accessions, but these markers were not convincing enough to clearly separate the diploid and triploid accessions from each other.

Asian and Pacific gene pools for cultivated diploid taro

The molecular data obtained from AFLP analysis are extensive and conclusive as indicated from Tables 2, 3 and 4 and Figs. 1 and 2, which are in good agreement with each other. From this study, we are able to understand the genetic diversity of taro accessions derived from Asian and Pacific countries. Both Lebot and Aradhya (1991) and Irwin et al. (1998) observed two different gene pools for cultivated taro, one in Asia and one in the Pacific. We confirmed these results in our study with AFLP markers.

The origin of domestication of Pacific taro cultivars is most likely located in Papua New Guinea and the Solomons (Lebot 1999). From there on it must have been spread by humans to the Philippines and eastwards to Vanuatu, since natural spread of taro through vegetative reproduction is slow.

The unexpected high gene diversity within Indonesian diploid cultivars (0.11) might be explained by the fact that Indonesia has cultivars originating from the Pacific gene pool as well as cultivars that are derived from the Asian gene pool. This becomes apparent in Fig. 1, where the Indonesian group of diploid cultivars is separated into two clusters, ID-I and ID-II. Cluster ID-I clearly has relationship to the Pacific gene pool while cluster ID-II has relationship to the Asian gene pool. Irian Jaya is part of the island of New Guinea but is an Indonesian province. In fact, Indonesian provinces are located on both sides of the Wallace line. The high genetic diversity of the Indonesian germplasm was also observed by Lebot and Aradhya (1991).

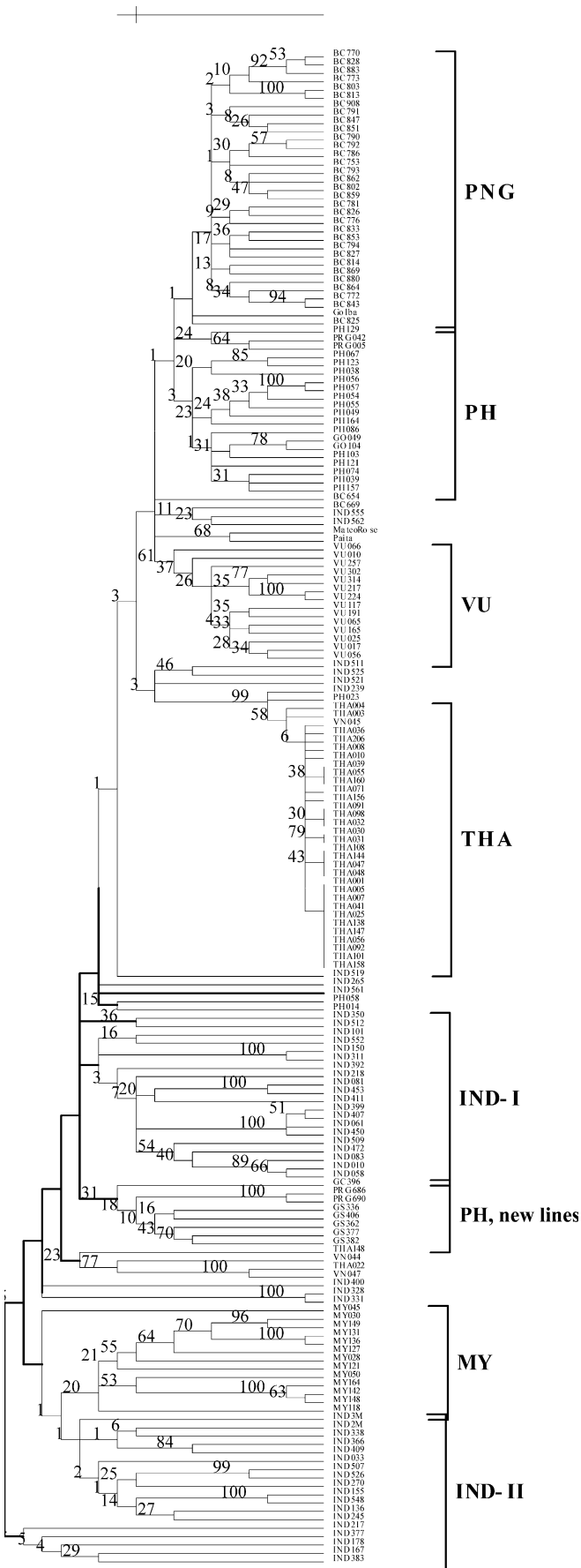


Fig. 1 Dendrogram, drawn from the UPGMA cluster analysis, depicting the genetic distance based on AFLP polymorphisms between the diploid cultivated accessions. Above the dendrogram the genetic distance is shown. Branching points in the dendrogram with a bootstrap value higher than 40 are shown. *PG* Papua New Guinea, *PH* the Philippines, *VU* Vanuatu, *TH* Thailand, *ID* Indonesia, *MY* Malaysia

The origin of the majority of the diploid cultivars from Thailand is certainly also Pacific. This unexpected origin has not been observed before, but has major implications for the subsequent breeding of improved cultivars in Thailand.

Wild taro

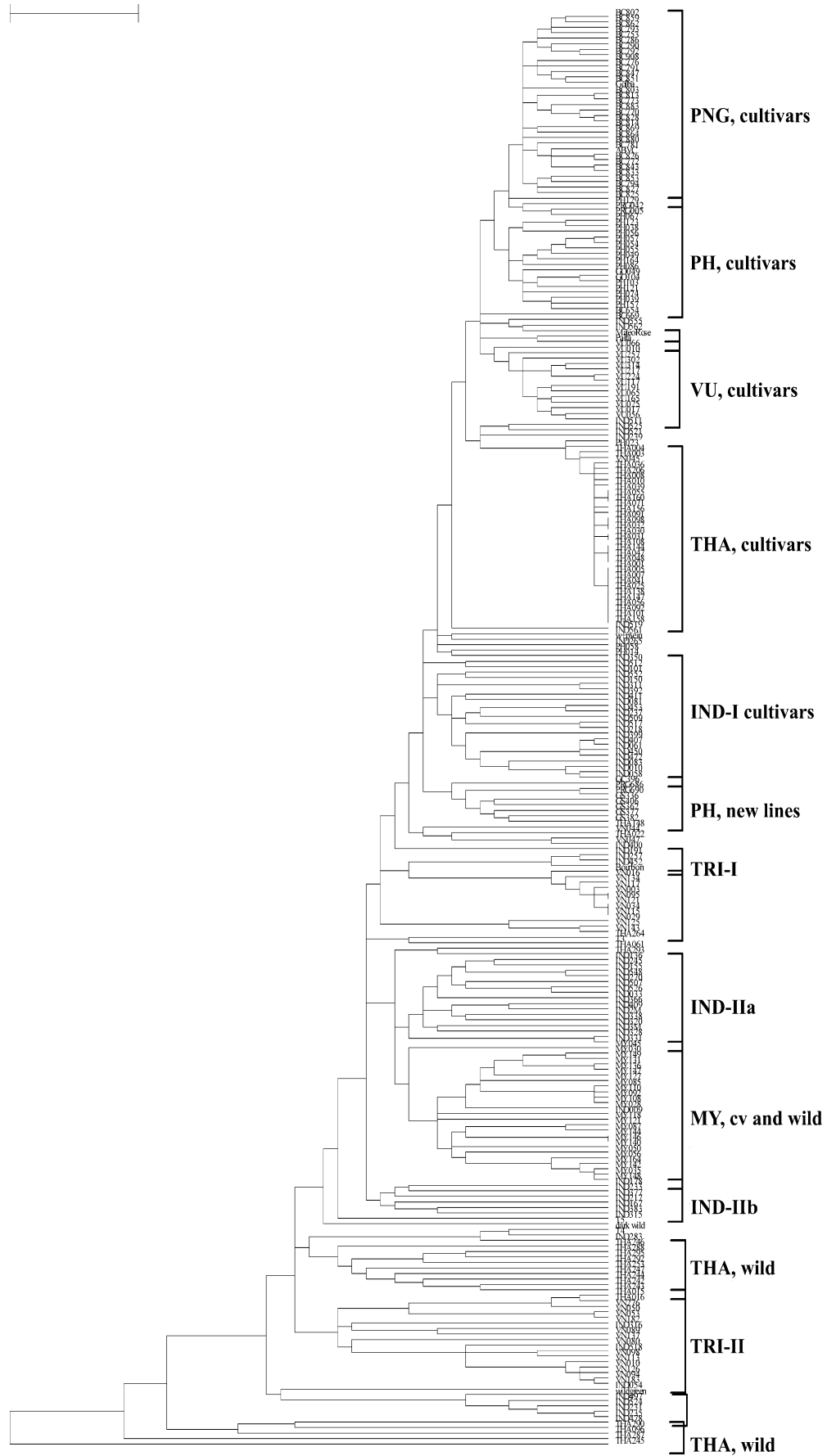
As mentioned in the introduction, the centre of origin of wild taro is generally believed to be between Myanmar and Bangladesh (Plucknett 1976). We analysed only a modest set of wild accessions from Thailand, Vietnam, Malaysia and Indonesia. Unfortunately, we did not obtain wild accessions from Papua New Guinea. In the Philippines and Vanuatu no naturally occurring wild taros exist. Thailand has the highest gene diversity within its wild accessions (0.19, Table 2), which is not surprising, considering its close location to the centre of origin.

Genetic distance of cultivated and wild groups from the same country (Table 3; Fig. 2) were compared and revealed that in Malaysia and Indonesia, these two groups were genetically very similar. Previous studies with wild and cultivated accessions from Papua New Guinea showed that these groups also do not differ much genetically (Lebot and Aradhya 1991). The low genetic distances between the cultivated and wild accessions countries can have two reasons. First, it is well possible that the wild group consists of escaped cultivars. But the fact that the Indonesian and Papua New Guinean wild accessions flower frequently and set seeds easily indicate that they are probably true wild types and not ferals, as cultivars hardly flower. Secondly, it is more likely that the low genetic distance between the cultivated and wild accessions indicates that there has been little progress in breeding of taro.

Triploid taro

The origin of the triploid taro accession has not been studied before. It was noted that triploids were mainly present in Asia and absent in the Pacific (Matthews 1990). We also found that most of the triploid accessions were present in Asia—predominantly Vietnam—but they were also found in Thailand and Indonesia. Polyploidisation could have happened through cross-hybridisation with unreduced gametes. The presence of unique alleles in the triploid accessions and the observation that the triploids had a slightly higher number of AFLP markers per PXE suggests that $2n$ gametes could have played a role in the

Fig. 2 Dendrogram, drawn from the UPGMA cluster analysis, depicting the genetic distance based on AFLP polymorphisms between the diploid and triploid cultivated accessions and the wild accessions. Above the dendrogram the genetic distance is shown. Branching points in the dendrogram with a bootstrap value higher than 40 are shown. *PG* Papua New Guinea, *PH* the Philippines, *VU* Vanuatu, *TH* Thailand, *ID* Indonesia, *MY* Malaysia, *TRI* triploids, *w* wild



origin of triploid taro. We did observe $2n$ gametes in taro pollen (C.M. Kreike, personal observation).

The relationships between diploid and triploid accessions are shown in the dendrogram in Fig. 2. However, no close relationships between di- and triploid cultivars were observed, leaving the origin of the triploid cultivars, from certain diploid parents unresolved. The presence of two clusters of triploid accessions in the dendrogram might indicate that polyploidisation has occurred several (at least two) times. Both clusters contain triploids from different countries, which reveals that there has been exchange of cultivars between these countries. The high gene diversity of triploid accessions suggests that the polyploidisation events must have happened a long time ago.

Breeding

The results of this study have major implications for future breeding programmes. For the successful breeding of novel taro varieties with new combinations of desired characters, a high genetic diversity between the parents is desirable. This study shows that the genetic diversity of the diploid cultivars within most countries is rather low, and that crosses between accessions derived from only one country are not desirable. However, the genetic variability within Indonesia is that high that combinations within this country alone would be a practical approach. Also, crosses between material from neighbouring countries will not create a very diverse offspring if the countries have material that is derived from the same gene pool, i.e. Asian or Pacific. The genetic diversity between these gene pools is rather large, and by using cultivars as starting material the chance for unwanted 'wild' characters like acidity or stolon formation will be minimised in the offspring. By following this approach, to capture as much heterosis as possible, it is well possible that already in the F_1 , potential new cultivars can be discovered and that improvement can be accomplished in a very short time.

Conservation

This study provided new insights into the genetic composition of the taro crop in Asia and the Pacific. The existence of two gene pools—an Asian and a Pacific—for cultivated taro has been confirmed, with Indonesia hosting the greatest diversity. These results will be of major concern for future conservation strategies. But this study also showed that caution has to be taken if sampling only occurs based on morphological characters. A high morphological variation between cultivars is not a guarantee for a high genetic variation. Wild taro is highly diverse and comprises important material for long-term breeding purposes.

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