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Genetic Diversity in Horticultural Plants

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Genetic Diversity in Horticultural Plants

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Chapter 7
Genetic Diversity in Taro (*Colocasia esculenta*)

Susan C. Miyasaka, M. Renee Bellinger, Michael B. Kantar, Martin Helmkampf, Thomas Wolfgruber, Roshan Paudel and Michael Shintaku

Abstract Taro [*Colocasia esculenta* (L.) Schott] is an ancient, tropical root crop that is morphologically diverse with over 10,000 landraces. It is the fifth most produced root crop in the world and is mainly grown in tropical Africa, China, New Guinea, and many Pacific islands. Taro typically is grown for its starchy corm (i.e., underground stem), although leaves and flowers also are eaten as vegetables. There is controversy over its geographic center of origin, but this is likely to be in the Indo-Malayan area. Evidence indicates that it was domesticated, possibly independently, across an area that ranges from northeast India to Yunnan province in China to New Guinea. Within Micronesia and Polynesia, where taro is a staple crop, the genetic base is very narrow. Genetic diversity within the taro germplasm is significantly greater in Asia and New Guinea. The exploitation of this diversity could lead to the development of cultivars with greater disease resistance, and improved yields and corm quality. Taro is a neglected crop in terms of recent advances in molecular biology, with only a limited number of studies utilizing next-generation transcriptome and genome sequencing. At present, a high-quality reference genome is lacking; however, recent genotyping-by-sequencing (GBS) approaches promise to improve our understanding of taro genetics.

Keywords *Colocasia esculenta* · Tropical root crop · Genetic diversity · Genetic markers

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7.1 Introduction

Taro [*Colocasia esculenta* (L.) Schott] belongs to the family Araceae (i.e., Arum family), a large, ancient, monocot plant family with mainly tropical distribution across the world. This family is characterized by its morphological diversity, the presence of many forms of calcium oxalate crystals, and flowers with a spadix of small, bisexual, or unisexual flowers, covered by a spathe (Henriquez et al. 2014; Matthews 1995).

The number of species in the genus *Colocasia* is disputed, but ranges from 5 to 10, with approximately 60 synonyms (Catalogue of Life 2017; The Plant List 2017; Matthews 1991, 1995). Three species are only known from single specimens in herbarium collections: *C. gracilis* from Sumatra, *C. manii* from upper Assam, and *C. virosa* from Bengal. Of the more common species, *C. affinis* and *C. fallax* occur in Northeast India and Southeast Asia, while *C. gigantea* is found wild in Indonesia and cultivated throughout Southeast Asia. Taro (*Colocasia esculenta*) is the most widely cultivated species with over 10,000 landraces worldwide (Ivancic and Lebot 2000).

Taro, as a species, is characterized by rare and erratic flowering (Ivancic et al. 2004a; Ivancic and Lebot 2000). The female, pistillate flowers are located at the base of the spadix, and male, staminate flowers are located near the top. Typically, cross-pollination is required, because the female flowers become receptive before the pollen is shed. Following successful pollination, the highest number of seeds recorded per fruit cluster was over 22,000 seeds (Ivancic and Lebot 2000).

Taro is one of the oldest cultivated crops, with evidence of its use by at least 6950–6440 cal yr B.P. in New Guinea (Denham et al. 2003). It is the fifth most produced root crop in the world, with global production of 10.1 million metric tons in 2014 (FAOSTAT 2014). Taro is consumed primarily for its starchy corm or underground stem. In Hawaii, the corm is cooked and mashed into a paste (i.e., poi) that could be served fresh or fermented after several days. Taro leaves serve as a vegetable, providing good sources of dietary fiber and vitamin C (Ferguson et al. 1992). Interestingly, in Yunnan province in China, one morphotype of taro produces abundant flowers that are eaten as a high-value vegetable (Jianchu et al. 2001).

In Hawaii, poi has been reported to be easily digested, with potential uses as a probiotic due to high levels of *Lactococcus lactis* bacteria found during fermentation (Brown and Valiere 2004). Its ease of digestibility may be due to the small size of its starch granules (1–7 μm) compared to those of arrowroot (*Zamia floridana*), canna (*Canna edulis*), or potato (Langworthy and Deuel 1922). Also, poi has been reported to be hypoallergenic due to its low protein content, and it has been fed to infants with failure to thrive or those with allergies to cow's milk (Brown and Valiere 2004). In China, taro was used to treat some gastrointestinal disorders in traditional Chinese medicine (Yu et al. 2015).

Taro is the root crop that has the greatest diversity of flavonols when compared to sweet potatoes, cassava, five species of yams, and giant taro, with 20 compounds identified (Champagne et al. 2011). Phenolic compounds (including flavonols) have

been reported to protect against a variety of human diseases, such as cancers, cardiovascular disease, diabetes, and Alzheimer's (Soto-Vaca et al. 2012).

Taro also contains anti-nutritive compounds, such as oxalates, trypsin inhibitors, uracil, and lectins. Oxalates could lead to hypocalcemia and kidney stones in humans, while trypsin inhibitors could cause growth depression, pancreatic hypertrophy, and hyperplasia (Guchhait et al. 2008). Uracil and glycol–protein lectin have been identified as compounds that could explain the acridity (i.e., irritation) of taro mucilage (Yu et al. 2015).

In the wet tropics and subtropics, taro is a vital component of many subsistence farming communities. In 2014, Nigeria was the world's largest taro producer (3.27 million metric tons), followed by China, Cameroon, Ghana, and Papua New Guinea (PNG) (FAOSTAT 2014). In the Pacific Islands, it is one of the most important staple food crops, and it is also widely cultivated throughout the Caribbean and South America (Kreike et al. 2004; Plucknett 1970; Plucknett et al. 1970).

Taro is typically grown in subsistence farming societies, so production issues that affect supply are serious food security concerns. In Vanua Lava (in Vanuatu) where it is grown as the staple crop, taro is consumed at 0.43 kg of dry matter per person per day (Caillon et al. 2006). Regional taro collections have been made through Taro Genetic Resources: Conservation and Utilization (TaroGen) and Taro Network for Southeast Asia and Oceania (TANSAO) (Singh et al. 2010). However, despite its emerging importance as a crop in many areas of the world, and its cultural significance in Pacific Island societies, no International Agricultural Research Center (i.e., CGIAR) has a mandate to conserve and carry out research on taro. Similarly, in the USA, there is no USDA Germplasm Repository with responsibility for conserving and distributing taro germplasm.

7.2 Morphological Diversity of Taro

As a species, taro is highly polymorphic (Purseglove 1972), with phenotypic descriptors related to size of corms and abundance of cormels. Jianchu et al. (2001) studied taro diversity in the Yunnan Province of China and determined that there were five uses based on morphotypes of taro categorized by farmers: (1) inflorescence, that produces abundant flowers eaten as a vegetable; (2) single corm, of up to 2 kg fresh weight with few cormels; (3) multicormel, having many cormels with better quality and yield than the corm; (4) multicorm, that has similar sized corms and cormels; and (5) petiole, where that structure is eaten as a vegetable but corms are poorly developed and long stolons are produced. In addition, there is the stolon or wild-type morphotype (*Colocasia esculenta* var. *aquatilis*) that has a poorly developed corm, no cormels and many, long stolons that are eaten as a pickled vegetable.

Two variants of taro are widely cultivated: (1) *C. esculenta* var. *esculenta* and (2) *C. esculenta* var. *antiquorium* (Deo et al. 2009). *Colocasia esculenta* var. *esculenta*, called the 'dasheen' type of taro, has a large, cylindrical corm with only a few cormels and is similar to the single-corm morphotype described by Jianchu et al. (2001).

Colocasia esculenta var. *antiquorium* called the 'eddoe' type has a small, globular corm with relatively large cormels and is similar to the multicormel morphotype described earlier (Jianchu et al. 2001). Most taros cultivated in Asia and the Pacific are the dasheen type. Analysis of 32 accessions of these two variants from India using randomly amplified polymorphic DNA (RAPD) was not able to distinguish between these two phenotypes based on these genetic markers (Lakhanpaul et al. 2003).

Cheema et al. (2007) analyzed 24 accessions of taro grown in India for 14 characters: number of leaves per plant, plant height, petiole length, days to maturity, number of corms per plant, corm weight, corm length, corm girth, number of cormels per plant, total yield per plant, dry matter, protein, starch, and oxalate content. Highly significant differences were found among accessions for all 14 characters. Singh et al. (2008) evaluated 859 accessions from PNG using 10 quantitative characters: number of cormels, weight of cormels, corm length, corm breadth, corm weight, leaf length, leaf width, plant height, number of stolons, and number of suckers. In addition, they measured 20 qualitative traits, including color of corm flesh and fiber, color of various parts of the leaf blade and petiole, and Taro Leaf Blight (TLB) resistance. They found high variability among taro accessions for these phenotypic traits.

Typically, taro is grown from vegetative propagules and not from seed. Species-specific insect pollinators of taro are endemic to New Guinea and Indonesia, with one insect species found also in northern Queensland (Hunt et al. 2013; Matthews 1995; Carson and Okada 1980). In countries without these insect pollinators, there is a little natural hybridization which results in the development of morphotypes that are quite distinct, even though they share the same genotype (Kuruvilla and Singh 1981).

7.3 Genetic Diversity of Taro

Cytological studies show that taro has diploid forms ($2x = 2n = 28$) as well as triploid forms ($3x = 3n = 42$) (Kokubugata and Konishi 1999; Coates et al. 1988; Yen and Wheeler 1968). Analysis of triploid clones indicates autotriploidy, which occurs when unreduced gametes are produced by a diploid parent during meiosis (Ochiai et al. 2001; Matthews 1995; Coates et al. 1988). Triploids are inherently sterile, because of their uneven number of chromosome sets. However, while they are characterized by increased hardiness at high altitudes or latitudes and are found in cooler climates, they must have developed in tropical areas where sexual reproduction of diploids was possible. Triploids are common in Asia (including China, India, Indonesia, Japan, Thailand, and Vietnam), Africa, and South America (e.g., Costa Rica) (Chaïr et al. 2016, 2016; Lebot et al. 2004; Matsuda and Nawata 2002; Ochiai et al. 2001; see Table 7.1). Diploids are common throughout Asia, Oceania, and South America. Interestingly, in Polynesia, only diploid forms are found (Kreike et al. 2004; Coates et al. 1988).

Several types of genetic markers have been applied to study the genetic diversity of taro (Table 7.1). In general, these markers fall into two categories: (1) band-based,

Table 7.1 Summary of taro studies that have incorporated genetic markers

Authors	Marker type	Purpose	Collections sampled	Sample details
Caillon et al. (2006)	AFLP/ethnobotanical data	Morphological and genetic variation	Vanuatu	118 accessions (collected for Vanuatu Agricultural Research and Technical Centre); 74 accessions genotyped
Chaïr et al. (2016)	SSR	Origin, diversification, and dispersal/genetic diversity/ploidy	19 countries in Asia, the Pacific, Africa, and America	357 cultivars
Cheema et al. (2007)	Heritability	Phenotypic and genotypic coefficients of variation	North India	24 clones
Coates et al. (1988)	Cytotype	Chromosome variation	Australia, New Zealand, PNG, the Philippines, Thailand, Japan, Nepal, Huahine in the Society Islands, and Easter Island	~112 cultivars
Das et al. (2015)	Chromosomal variation/RAPD	Chromosomal variation/phylogenetics/drought resistance	India	1 sample from each of 10 populations
Deo et al. (2009)	Genetic transformation	Disease and pests of taro	Not applicable (n/a)	n/a
Doungous et al. (2015)	Inter-retrotransposon amplified polymorphism (IRAP) fingerprints	Intraspecific variability	Cameroon (Africa)	7 accessions of *Colocasia esculenta* var *antiquorum* Schott compared to 20 accessions of *Xanthosoma sagittifolium*

(continued)

Table 7.1 (continued)

Authors	Marker type	Purpose	Collections sampled	Sample details
Henriquez et al. (2014)	Illumina sequencing/plastid and mitochondrial	Phylogenetics/family Araceae	No data	32 genera of Araceae; 5 other samples including *Colocasia esculenta*
Hunt et al. (2013)	SSR	Field evidence for natural breeding	Northern Queensland Australia; PNG	Australia Hopevale site, 45 wild; PNG 2 wild, 1 feral, 1 cultivar
Irwin et al. (1998)	RAPD	Phylogeographics/genetic diversity	Thailand, Hawaii, Indonesia, Micronesia, Western Samoa, PNG	44 taro accessions, 2 *Xanthosoma* spp. and 1 *C. gigantes*
Ivancic et al. (2004b)	Agro-morphological characters/crosses	Genetic control of traits	Vanuatu national taro germplasm collection	453 accessions
Ivancic and Lebot (2000)	Origin, domestication, and spread	Review	n/a	n/a
Ivancic and Lebot (1999)	Isozyme/morphological traits/reproduction systems	Evaluate endemism	SW Pacific, New Caledonian Wild Taro	3 morphotypes, up to 160 samples for morphological characterization
Kokubugata and Konishi (1999)	Ploidy	Chromosomal variation	India, Thailand, Costa Rica, Japan, Pakistan	7 cultivars
Kreike et al. (2004)	AFLP/ploidy	Genetic diversity; association between botanical variety and ploidy level	Southeast Asia and Oceania: Vietnam, Thailand,, Indonesia, Malaysia, the Philippines, PNG, Vanuatu	170 accessions from TANSAO
Lakhanpaul et al. (2003)	RAPD	Phylogeographics/intraspecific variability	India	32 taro accessions belonging to 28 morphotypes

(continued)

Table 7.1 (continued)

Authors	Marker type	Purpose	Collections sampled	Sample details
Lebot et al. (2004)	AFLP/isozymes/ploidy/morpho-agronomic descriptors	National germplasm collections as part of TANSAO	Indonesia, Malaysia, Thailand, Vietnam, the Philippines, PNG, and Vanuatu	2298 accessions
Lebot and Aradhya (1991)	Isozyme (compared to morphological/ploidy other studies)	Genetic variation/diversity	Asia and Oceania	1417 cultivars and wild forms
Liu et al. (2015)	Illumina sequencing/transcriptome	Whole transcriptome profiling; gene annotation	China	Leaf tissue
Mace et al. (2006)	SSR	Identify duplicates/assess allelic diversity within national collection	Oceania: PNG, Solomon Islands, Vanuatu, New Caledonia, Fiji, Palau, Niue, Tonga, Cook Islands, and Samoa	515 accessions
Mace and Godwin (2002)	SSR	Geographical structure/identify duplicates in collections	Vanuatu, Hawaii, Samoa, Fiji, Niue, Tonga, Cook Isle, New Caledonia, Palau, PNG, Japan, China, Vietnam	17 accessions: 13 *C. esculenta* var. esculenta (dasheen type); from Fiji, 1 *C. esculenta* var. *antiquorum* (eddoe type), and one *Xanthosoma* species
Matsuda and Nawata (2002)	RFLP at ribosomal DNA/isozymes	Geographical structure/routes of human transfer	China (mostly Yunnan province), Japan, Taiwan, and Vietnam	227 accessions

(continued)

Table 7.1 (continued)

Authors	Marker type	Purpose	Collections sampled	Sample details
Matthews et al. (1992)	Restriction digest with rRNA ITS/mtDNA genes/ploidy	Genetic diversity and routes of dispersal	Japan compared to Australia	Taro collection at National Research Institute of Vegetables, Ornamental Plants and Tea: 80 Japanese accessions and 1 Queensland, Australia sample
Ochiai et al. (2001)	RAPD/isozyme	Geographical differentiation/phylogenetic relationships	China	121 accessions
Okpul et al. (2004)	Agro-morphological characters	Formation of TANSAO regional core collection	PNG	276 accessions
Parvin et al. (2008)	Karyotype	Karyotype	Bangladesh	7 cultivars
Paul et al. (2014)	Morphological characters/genotypic trait correlations	Genotypic–phenotypic correlations	Bangladesh	457 samples from 13 districts
Quero-Garcia et al. (2006)	AFLP/SSR	Quantitative trail loci for trait mapping	Vanuatu	2 crosses; 223 progeny
Quero-Garcia et al. (2004)	AFLP/agro-morphological descriptors	Vanuatu taro national germplasm collection	Vanuatu	452 accessions
Sardos et al. (2012)	SSR	Eco-geographical survey of landraces in Vanuatu/genetic diversity/relatedness	Vanuatu, Indonesia, Philippines, Thailand	344 landraces
Sharma et al. (2009)	Subtractive hybridization/expressed sequence tags	Differentially expressed genes/host–pathogen interactions	India	63 cultivars and 5 wild wetland taros

(continued)

Table 7.1 (continued)

Authors	Marker type	Purpose	Collections sampled	Sample details
Sharma et al. (2008a)	AFLP	Geographical differentiation/phylogenetics/disease resistance	India	14 accessions
Sharma et al. (2008b)	RAPD/isozyme	Geographical differentiation/phylogenetics/disease resistance	India	14 accessions
Shintaku et al. (2016)	Illumina GBS to identify SNPs	Linkage map/disease resistance	Hawaii	2 parents and 96 progeny
Singh et al. (2012)	RAPD/ISSR/agro-morphological characters	Genetic diversity/phylogenetics/association with agro-morphological characters	Andaman islands, India	21 accessions
Singh et al. (2008)	SSR/agro-morphological traits	Core collection development	15 provinces of PNG	859 accessions for creation of a core collection of 81 accessions; 151 genotypes characterized
Sreekumari and Mathew (1991)	Karyomorphology	Karyomorphology	India	5 morphotypes
Trujillo et al. (2002)	Disease resistance	Cultivate cultivars resistant to taro leaf blight	Palau, Polynesia	Developed three new TLB-resistant cultivars
Xu et al. (2001)	Morphotypes/cytotypes	Ethnobotany/folk taxonomy	China	53 samples
You et al. (2015)	SSR	Marker development; 5278 SSRs developed, identified 62 polymorphic SSRs	China	Two lines of taro, TLB resistant and susceptible

including isozymes (enzymes), RAPDs, amplified fragment length polymorphisms (AFLPs) and simple sequence repeats (SSRs, microsatellites), and (2) sequence-based, including single-nucleotide polymorphisms (SNPs), expressed sequence tags, and transcriptome profiling with next-generation sequencing (RNA-seq). The disadvantage of RAPD and AFLP markers is that the bands are 'anonymous,' with genomic locations unknown, so they provide no corresponding gene-specific data. The RAPD technique was somewhat supplanted by AFLPs, due to the latter marker's ability to generate more reproducible fingerprints. The SSR markers are better than RAPDs and AFLPs in terms of simplicity, amplification reliability, and co-dominance. In taro, SSRs are bi-allelic or tri-allelic depending on ploidy: due to the ploidy issue, partial heterozygosity makes it impossible to score genotypes exactly (Chaïr et al. 2016). The scoring of SSRs is generally considered more reliable and consistent than for RAPDs and AFLPs, and SSR scoring can be standardized across laboratories (Seeb et al. 2007). The advantages of sequence-based SNP markers in comparison to SSR markers will be discussed further in Sect. 7.5.

Diversity in morphological traits is not a good indicator of genetic diversity (Singh et al. 2008; Lebot et al. 2004; Okpul et al. 2004). In a study of 814 taro accessions from PNG, taro with contrasting morphological traits would cluster together in a dendrogram produced from 7 SSR markers, whereas accessions with the same morphological traits could be widely separated (Singh et al. 2008). In spite of morphological variability identified from 2298 accessions collected in Indonesia, Malaysia, Thailand, Vietnam, the Philippines, Papua New Guinea and Vanuatu, the genetic base of these accessions was narrow, based on isozymes and AFLP fingerprinting (Lebot et al. 2004).

Taro has a large genome, which is estimated to be 4.08 Gbp (C-value mean, Kew Royal Botanic Gardens 2016). This large size coupled with high heterozygosity due to its outcrossing nature has thus far prevented the creation of a reference genome of the species. However, a reference transcriptome was developed from messenger RNA isolated from leaf tissue and sequenced using next-generation sequencing strategies (Liu et al. 2015; Table 7.1), providing a first look at gene family characterizations within the species. Genomic efforts are further complicated due to the limited amount of information available on genetic maps. There is a single linkage map of the taro genome based on 169 AFLP markers and 8 SSR markers available (Quero-Garcia et al. 2006; Table 7.1); however, this map does not provide chromosome-level resolution, with the study identifying 18 linkage groups rather than the expected 14 (diploid taro having $2n = 2x = 28$ chromosomes).

Advances in high-throughput sequencing have resulted in the identification of 5278 SSR markers, of which 62% were identified as polymorphic based on a test set of 100 primers (You et al. 2015). Prior to this study, only 52 SSR taro-specific markers had been characterized (Lu et al. 2011; Hu et al. 2009; Mace and Godwin 2002; Table 7.1). Less attention has been focused on the development of SNP markers; however, Shintaku et al. (2016) published the first report on the use of SNPs in a population of taro that segregated for resistance to TLB. Unfortunately, they were not able to identify SNPs associated with resistance to TLB. More recently, Helmkampf et al. (2018) developed >1700 SNP markers for taro. In the future, the increasing

number of genetic and genomic tools associated with taro will provide breeders with many new types of resources.

While genetic resources are limited to recent times, taro is well studied with respect to its domestication history (Chaïr et al. 2016; Coates et al. 1988; Yen and Wheeler 1968). Human dispersal of taro across the globe has been studied using chromosome number, morphology, and genetics, as well as through references in ancient texts. Taro has a long history of use, having been consumed for ~9000 years (Rao et al. 2010). It is mentioned in texts as early as 2000 years ago (Whitney et al. 1939).

The center of origin for taro is uncertain (Chaïr et al. 2016). The fact that three species (now possibly extinct) of *Colocasia* were found in Sumatra (Indonesia), upper Assam (India), and Bengal (Bangladesh and India) is an indication that the Indo-Malayan region is the geographic center of origin for *C. esculenta* (Matthews 1991, 1995). However, an argument for a secondary center of origin in New Guinea for *Colocasia* is the co-evolution of several *Colocasiomyia* spp. (Diptera, Drosophilidae) as specific pollinators for species in the genus *Colocasia* (Sultana et al. 2006). Fruit flies *Colocasiomyia stamenicola* and *C. pistilicola* (Carson and Okada 1980) are endemic to New Guinea, and their entire life cycle depends on inflorescences of *Colocasia*. However, it is possible that these fruit flies evolved earlier elsewhere, but became extinct in those locations later. Another possible center of origin for taro is Hainan Island China, based on the co-evolution of *Phytophthora colocasiae*, the oomycete pathogen that causes taro leaf blight. *Phytophthora colocasiae* is host-specific to taro and Zhang et al. (1994) suggested that its center of origin was Hainan Island, based on the presence of three different mating types. Shrestha et al. (2014) confirmed the presence of three mating types in Hainan, but questioned whether this was sufficient evidence to show that the center of origin of *P. colocasiae* was on Hainan Island.

The center of origin for taro is expected to harbor the greatest genetic diversity (Fig. 7.1). Accordingly, genetic diversity is the focal subject of numerous studies that have utilized an array of molecular biological methods (Table 7.1). Irwin et al. (1998) evaluated 44 taro, two tanier (*Xanthosoma* spp.), and one C. *gigantea* accession using RAPD markers, and found the highest genetic diversity in taro accessions from Indonesia. Kreike et al. (2004) used AFLP markers to evaluate gene diversity in 255 taro accessions from Indonesia, Malaysia, New Guinea, the Philippines, Thailand, Vanuatu, and Vietnam and found that Thailand had the greatest gene diversity. Within the Pacific Island region, seven SSR markers indicated that the geographic areas with the greatest sources of genetic diversity were New Guinea and the Solomon Islands (Mace et al. 2006). Chaïr et al. (2016) used 11 SSR markers to compare taro accessions from 19 countries in Asia, the Pacific, Africa, and America, and found the greatest genetic diversity in Asian accessions (mainly from India).

It is possible that wild taro was widespread over a geographic area ranging from northeast India to Southeast Asia to Melanesia (including New Guinea), and that domestication happened at several independent locations (Chaïr et al. 2016; Matthews 1991, 1995). Domestication of taro is hypothesized to have occurred in two separate geographic locations based on archaeobotanical evidence (Denham

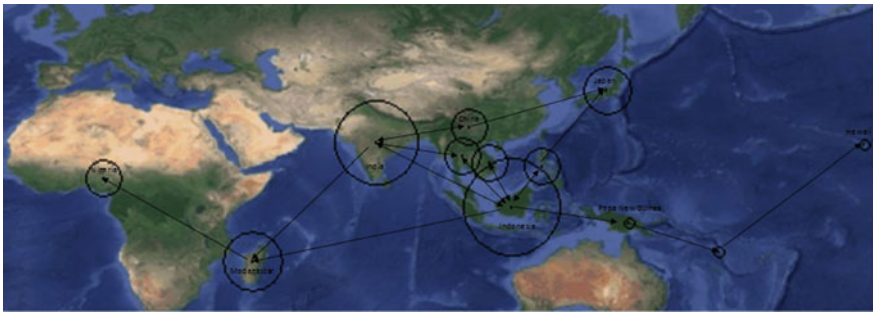

Fig. 7.1 Potential movement of taro from the putative center of origin of the species to areas of production and diversity today. The literature is not consistent as to the center of origin and center of domestication (Coates et al. 1988; Matthews 1991, 1995), but concurs that centers of diversity are found in Indonesia and India. Here, size of the circle represents the reported genetic diversity (Lebot and Aradhya 1991; Lebot et al. 2004; Chaïr et al. 2016) within the region and arrows indicate potential movement patterns (Ivancic and Lebot 2000; Xu et al. 2001; Matsuda and Nawata 2002)

et al. 2003), cytological studies (Coates et al. 1988), and SSR markers (Sardos et al. 2012): (1) India–Southeast Asia and (2) New Guinea. Two distinct, separate gene pools (one in Asia and one in the Pacific) have been confirmed by isozyme analysis (Lebot and Aradhya 1991), AFLP markers (Kreike et al. 2004; Lebot et al. 2004; Quero-Garcia et al. 2004), and SSR markers (Chaïr et al. 2016). Ochiai et al. (2001) used isozyme analysis and RAPD analyses to support their contention that Yunnan province in China was another center of taro diversification and dispersal into temperate Far East Asia, particularly for triploid taros.

Identifying the center of origin for taro and subsequent domestication patterns has important ramifications for understanding human migrations. The distribution of some taro cultivars is understood, with Western African cultivars believed to have come from India (Ivancic and Lebot 2000). When taro started moving across the Pacific, only a few domesticated genotypes were carried by Austronesians as they spread from PNG to Polynesian and Micronesian islands, with Hawaii being settled in A.D. 1190–1290 (Wilmshurst et al. 2010).

7.4 Conventional Breeding of Taro

Modern taro breeding programs started during the 1970s after the discovery that treatment of plants with gibberellic acid (GA, 300–1000 mg GA L^{-1}) induced flowering and allowed synchrony of flowering of parents, making hand-pollination possible (Ivancic and Lebot 2000; Wilson 1979). Hand-pollination is required because specialized insect pollinators are either rare or non-existent outside of the Solomon Islands, Australia, and New Guinea (Hunt et al. 2013; Sultana et al. 2006; Plucknett 1970).

Sustainability of existing taro landraces or cultivars is limited by low yields (see Sect. 7.4.1), diseases (see Sect. 7.4.2), or quality issues (see Sect. 7.4.3). Taro breeders seek to improve plant architecture (e.g. optimal number of suckers, absence of stolons, optimal number of leaves, vertical petioles), corm yield, and quality traits (e.g., high dry matter content, low levels of irritant substances) (Quero-Garcia et al. 2009). In addition, in Hawaii two other desirable qualities are purple corm color and 'stickiness' of the mashed corm to produce poi.

Plant vigor is often associated with heterozygosity (Quero-Garcia et al. 2009; Lebot et al. 2005). Breeding of taro with parents that come from diverse genetic pools could result in improved vigor and yield of progeny. However, breeding of taro is problematic, because inbred lines are not possible due to predominant self-incompatibility and severe inbreeding depression (Quero-Garcia et al. 2009; Ivancic and Lebot 2000). The use of wild-type parents in conventional breeding requires seven generations of modified backcrosses to introgress the desired gene into traditional landraces/cultivars, while removing such undesirable traits as irregular corm shapes, high numbers of stolons, and high levels of acridity (Okpul 2002 as cited in Quero-Garcia et al. 2009). Breeders also must take care to avoid the introduction of viruses when trying to broaden the genetic base in breeding programs (Sukal et al., 2015). For taro, the chances of breeding and selecting a high-yielding clone with excellent eating qualities are generally very low and become much lower when additional traits are sought (e.g., disease resistance). In PNG, a recurrent selection program for taro only produced eight clones from over 100,000 progeny (less than 0.008%) that had high yield, good eating quality, and resistance to TLB (Okpul 1997 as reported by Lebot et al. 2005).

The success of breeding programs depends on the availability of diverse genetic resources (Okpul et al. 2004). However, conservation of taro collections is difficult with many national collections having been made and lost over the years, due to natural disasters and loss of funding (Lebot et al. 2005). A method of selecting a limited core collection has been proposed to represent a useful diversity of taro landraces/cultivars, based on diverse geographic origins, wide genetic distances, quality, agronomic performances, and functional sexuality (Lebot et al. 2005).

Taro breeding has been initiated in many countries within the South Pacific including Samoa, PNG, and Vanuatu under two main programs, TaroGen and TANSAO (Singh et al. 2010). The main thrust of these breeding programs was developing through sexual hybridization, new cultivars that would maintain taste and yield, while incorporating disease resistance. Modern taro breeding at the University of Hawaii started in the late 1980s. This program focused on bringing in novel diversity from different geographic regions to increase yield and disease resistance (Cho et al. 2007).

7.4.1 Phenotypic Trait: Yield

Taro has the lowest average yield (5.83 t ha^{-1}) of the major root crops (Quero-Garcia et al. 2006). In Oceania and elsewhere, there are only two options for meeting the food needs of a rapidly growing human population: (1) increase agricultural production or (2) increase food imports (Lebot 2013). Increasing agricultural production of taro could involve improved cultivation methods, such as increased irrigation. In Vanuatu, taro productivity was reported to vary from 7.1 t ha^{-1} of dry matter when grown under non-permanent irrigation to 20.1 t ha^{-1} when inundated between river stones.

Morphological characters such as number of cormels per plant, protein, corm weight, and corm length were highly and positively correlated with total yield (Cheema et al. 2007). Quero-Garcia et al. (2006) studied F_1 progenies of 123 and 100 individuals obtained from crosses between local cultivars from Vanuatu and found the strongest correlation between corm length, corm width, and corm yield. They found several quantitative trait loci (QTLs) associated with corm yield and corm dimensions, as well as a dominant gene responsible for the yellow color of corm flesh.

7.4.2 Phenotypic Trait: Disease Resistance

There are several oomycete and fungal pathogens that infect taro, suppressing yield (Ivancic and Lebot 2000; Ooka 1994). The oomycete *Phytophthora colocasiae* causes TLB, resulting in water-soaked lesions on leaf blades that spread rapidly under warm, wet, humid conditions (Miyasaka et al. 2013). This pathogen can also cause a rot of the petiole and corm. *Pythium aphanidermatum*, as well as several other *Pythium* species, is another oomycete that causes corm rot. Fungal pathogens that cause leaf spots, decreasing functional photosynthetic tissue, are *Cladosporium colocasiae* and *Phyllosticta colocasiophila*. Other fungal pathogens that cause corm rots are *Sclerotium rolfsii* and *Ceratocystis fimbriatum*. Under specific conditions, these various oomycete and fungal pathogens could cause significant losses. However, the greatest losses in yield are caused by *P. colocasiae*.

Several viruses infect taro and reduce its yield (Sukal et al. 2015). The most widespread is dasheen mosaic virus, and it is believed to infect the majority of vegetative planting material in Hawaii (Ooka 1994). Taro vein chlorosis virus (TaVCV) has been recently established in the Hawaiian Islands, providing another challenge, but its effects on yield are still unknown (Long et al. 2016). Colocasia bobone disease virus (CBDV) and taro bacilliform virus (TaBV) occur in New Guinea and the Solomon Islands (Ivancic and Lebot 2000). Importantly, co-infection of taro plants with CBDV and TaBV results in the lethal alomae–bobone disease. An effort to breed taro plants with resistance to the alomae–bobone disease resulted in a few hybrids that recovered after initial infection, gaining some tolerance (Ivancic et al. 1993).

Some nematodes also cause taro diseases, including *Hirschmaniella miticausa*, *Pratylenchus* sp., *Helicotylenchus* sp., and *Meloidogyne* sp. (Ooka 1994). Mitimiti disease caused by *H. miticausa* could result in dramatic losses, but is limited to the Solomon Islands (Bridge et al. 1983). Ortiz et al. (2008) screened taro germplasm from Thailand, Vietnam, and Nepal, as well as 11 taro cultivars (derived from Hawaiian, Thai, Samoan, Guamanian, New Guinean, Palauan, and Indonesian parents) for resistance to root-knot nematode *Meloidogyne javanica*. They found one accession from Thailand, and one cultivar (#19) had consistently lower reproduction factors (Rf) and higher growth ranking, suggesting possible resistance.

In Hawaii and in many other areas of the world, the most important taro disease is TLB. *Phytophthora colocasiae* was present in Hawaii during the 1920s and probably contributed toward the extinction of more than 270 traditional Hawaiian cultivars (CTAHR 2009). Current research on the genetic diversity of *P. colocasiae* using SNPs and mating types confirmed that this pathogen was introduced into Hawaii (Shrestha et al. 2014). Evaluation of existing, traditional Hawaiian taro genotypes showed that only a few had moderate resistance to this disease and almost all were very susceptible (Miyasaka et al. 2012). In Hawaii, it was estimated that 25–50% of taro corms were lost due to oomycete and fungal diseases (Miyasaka et al. 2001; Trujillo 1967).

When TLB spread to the Samoan Islands during the 1990s, it resulted in 95% losses in traditional, TLB-susceptible taro genotypes (Fig. 7.2). The introduction of TLB-resistant taro cultivars helped to increase the production of taro in Samoa after 1998 (Trujillo and Menezes 1995). When TLB reached the Dominican Republic in 2004, 70–95% of commercial taro plantings were lost and dramatic losses in production of the TLB-susceptible, commercial taro genotype occurred (R. P. Duverge, personal communications).

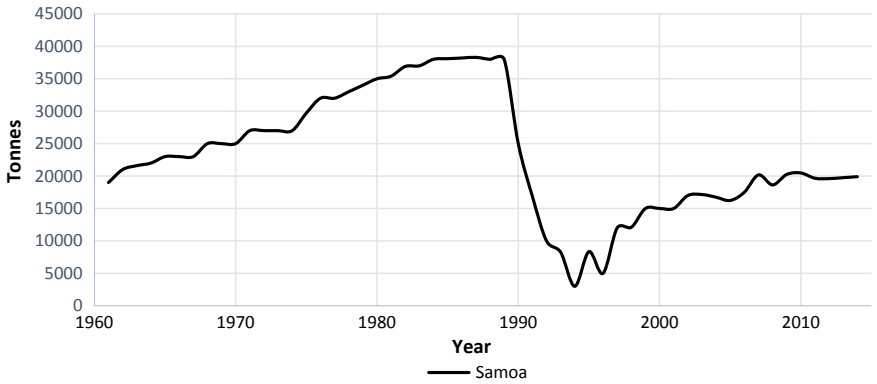

Fig. 7.2 Production of taro in Samoa between 1961 and 2014 (FAOSTAT, 1961 to 2014). The dramatic decrease in taro production during the early 1990s was due to the introduction of taro leaf blight (TLB), followed by some recovery of production due to the development of TLB-resistant taro cultivars

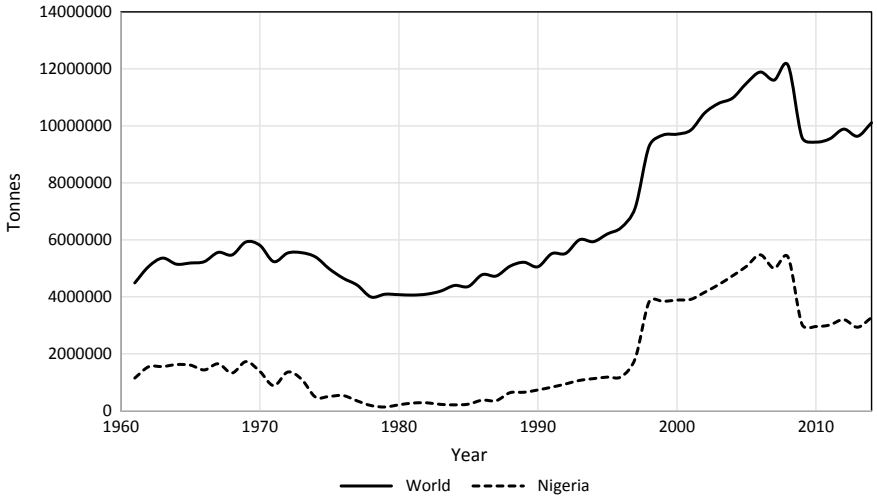

Fig. 7.3 Global taro production compared with Nigeria's production from 1961 to 2014 (FAOSTAT, 1961 to 2014). The downward deflection observed in 2009 resulted from the arrival of TLB in Western Africa

Nigeria has tripled its production of taro since 1996 and is now responsible for over a third of the world's taro output (Fig. 7.3). In 2009, many farmers there reported complete destruction of their crop due to TLB (Bandyopadhyay et al. 2011). Cameroon and Ghana also started to experience losses due to TLB around that time (Omane et al. 2012). The significance of Western Africa as source of taro production and the impact of TLB there on global taro production are illustrated in Fig. 7.3. Similar to Samoa, Western Africa is unlikely to regain former production levels without TLB-resistant cultivars.

Natural resistance to TLB has been found within the taro germplasm from Palau and Pohnpei (Miyasaka et al. 2012), and there have been efforts in Hawaii from the mid-1980s to increase yields and TLB resistance of traditional taro genotypes in Hawaii using conventional breeding (Miyasaka et al. 2013; Cho et al. 2007; Trujillo et al. 2002; Trujillo and Menezes 1995). After the efforts of three separate Hawaiian taro breeding programs that were conducted over the past 30 years, three new taro cultivars (BC99-6, BC99-7, and BC99-9) have been accepted by farmers (Miyasaka et al. 2013; Cho et al. 2007). However, there are still problems due to the breakdown of TLB resistance, loss of vigor, and/or susceptibility to other pests (R. Yamakawa, personal communications).

In Hawaii, current research efforts are focused toward transferring TLB resistance from TLB-resistant taro cultivars into traditional Hawaiian taro genotypes by hand-pollination. A cross between '230' × '255' is promising, based on a larger proportion (22%) of progeny with TLB resistance as measured by a detached leaf assay (Shintaku et al. 2016; Brooks 2008). The identification of molecular markers for disease resistance or other desirable traits may help to reduce the number of gen-

erations needed to produce taro cultivars with desirable traits, high yield, and disease resistance.

7.4.3 Phenotypic Trait: Quality

Lebot et al. (2004) characterized over 2000 accessions preserved in seven national germplasm collections in TANSAO for quality traits. They found that several corm quality characteristics were highly variable and likely to be genetically controlled. These quality traits were dry matter, minerals, and amounts of lipids, proteins, amylose, glucose, fructose, saccharose, and maltose. In addition, they found that good taste was correlated with high contents of dry matter, starch, and amylose. Dry matter ranged from 1.5 to 55.9%, while starch content ranged from 36.6 to 55.9%.

Ferreres et al. (2012) measured 41 phenolic compounds in leaves of two taro cultivars from the Azores and found quantitative differences among individual compounds. In particular, 'red' taro was richer in hydroxycinnamic acid derivatives than 'giant white' taro, and these compounds could be important for improved nutritional value.

Taro corms are rich in carotenoids and flavonoids that could have healthful properties that protect against cancers, cardiovascular diseases, and cell dysfunction. Lebot and Legendre (2015) used high-performance thin-layer chromatography (HPTLC) to screen corms of more than 1800 taro hybrids for flavonoids (e.g., anthocyanins, flavonols, and flavanols). Variation in contents of screened compounds was found, and the characteristics were heritable. Similarly, Guchhait et al. (2008) found significant differences among genotypes for dry matter content, mineral concentrations (potassium, calcium, magnesium, and phosphorus), anti-nutrient compounds (trypsin inhibitor, soluble oxalate, calcium oxalate, and total oxalate), and antioxidant enzymes (peroxidase, polyphenol oxidase, and catalase) in cormels from 31 taro cultivars from West Bengal, India. Based on these results, it is evident that breeding of taro for improved nutritional quality is possible.

7.5 Our Current Research Efforts on SNPs as Genetic Markers

Next-generation sequencing methods (GBS and RNA-seq) have advantages of providing thousands if not millions of markers that could be used for phylogenomics, trait mapping, and genome-wide association study, and to understand tissue-specific response to pathogens. Similar to microsatellite markers, SNP markers have bi-allelic or possibly tri-allelic states (triploid only); tri-allelic genotypes are otherwise predicted to be rare because of the low likelihood of a point mutation occurring three times at the same chromosomal location. Unlike SSRs, SNP markers do not require

standardization across laboratories, making them ideal for joint research efforts conducted across multiple laboratories. For trait mapping, many loci are necessary to cover genome intervals that capture linkage groups. While SSRs and SNPs are both options, recent advances in sequencing permit scoring great numbers of SNPs (thousands to millions) at much lower costs and greater ease (Schielzeth and Husby 2014).

Taking advantage of a taro breeding program established at the University of Hawaii (Cho et al. 2007), progress has been made recently to acquire a genome-wide set of genetic markers representing a range of taro genotypes from Hawaii, the South Pacific, and mainland Asia (primarily from China). The objectives of these efforts are to study the genetic basis of phenotypic traits relevant to taro breeding (e.g., TLB resistance), obtain a linkage map of the taro genome, and shed light on the phylogeography and cultivation history of taro in the Pacific.

Approximately 60 samples representing the majority of extant genotypes from Hawaii, several genotypes from Palau, as well as several genotypes each of South Pacific and mainland Asian origin (introduced to Hawaii post-European contact) were SNP typed using reduced representation methods based on restriction enzyme digest (GBS) and Illumina next-generation sequencing. After pooling and assembling the resulting libraries to serve as a reference, >1700 SNPs, were identified after quality filtering (Helmkampf et al. 2018).

Principal component analysis of this dataset (Fig. 7.4) revealed several distinct groups among the represented Hawaiian, South Pacific, and mainland Asian genotypes. The largest differences were found between a large but tightly clustered Hawaiian group containing many genotypes selected for their purple corm color (e.g., 'Lehua') and all remaining cultivars. Hawaiian cultivars characterized by striped petioles ('Manini') and large, undulating leaves ('Lauloa') also clustered separately. Phylogenetic analysis provided further resolution within the remaining cultivars: alongside the above-mentioned groups 'Lehua,' 'Manini' and 'Lauloa,' 'Ula'ula' (Hawaiian, red petioles), 'Mana' (Hawaiian, branched petioles), 'Kāī'(Hawaiian), Palauan, and Asian cultivars were also recovered as monophyletic groups with high to moderate support.

While the phylogenetic relationships between groups could not be resolved reliably, these results demonstrate that the traditional Hawaiian classification scheme based on morphological traits (elaborated upon by Whitney et al. 1939) is largely congruent with phylogenetic kinship. The fact that traits used to define groups (e.g., corm color, petiole color, leaf shape) are consistently and usually only found within monophyletic groups further suggests that these traits are under strong genetic control and were carefully maintained during centuries of selection. Hybridization between established Hawaiian groups consequently seems to have occurred rarely.

Interestingly, five cultivars introduced to Hawaii from the South Pacific after European contact were found contained within groups consisting of old Hawaiian genotypes (e.g., 'Tahitian,' within Mana group), instead of being paraphyletic with respect to Hawaiian genotypes. This finding caused us to hypothesize that the split between the Hawaiian taro groups occurred before Hawaii (and possibly other East Polynesian islands) was colonized by the first Austronesian settlers. It is congruent with recent evidence that Austronesians colonized East Polynesia in one major pulse

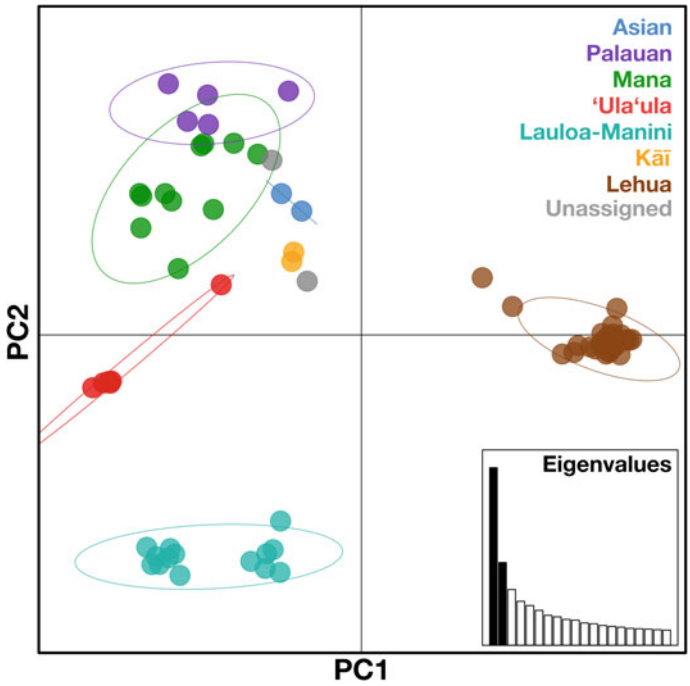

Fig. 7.4 Principal component analysis (PCA) of >1700 SNPs obtained from Hawaiian, Palauan, and Asian (e.g., China) taro landraces/cultivars (Helmkampf et al. 2018). Samples fall into several distinct clusters that are consistent with results from phylogenetic analyses (indicated by symbols or colors) and traditional, morphology-based nomenclature (Whitney et al. 1939). The first two principal components explain 16.3% (PC1) and 7.6% (PC2) of the variance. Reproduced with permission of Oxford University Press

between A.D. ~1190 and 1290 (Wilmshurst et al. 2010). In conclusion, the taro groups probably originated further back in the colonization history of the Pacific, and were brought to Hawaii as established groups where they further diversified by selection of desirable mutations or occasionally occurring cross-pollinations.

7.6 Summary

Taro is one of the oldest cultivated crops. As a species, it has great morphological diversity, with over 10,000 landraces. Various genetic markers have been used to study the genetic diversity of taro, and although the center of origin is uncertain, there is general agreement that there are two separate gene pools: (1) India to Southeast Asia and (2) New Guinea. When breeding taro for improved yield, disease resistance, and quality, it is important to include taro genotypes with wide genetic diversity. Although it is the fifth most produced root crop in the world, taro has been neglected in terms

of genetic resources. While there are regional collections of taro cultivars, there is no international center (i.e., CGIAR) with a mandate to conserve and carry out research on taro. Taro has been neglected also in regard to recent advances in molecular biology, with only a limited number of studies utilizing next-generation sequencing to generate genetic markers for trait mapping and one next-generation transcriptome. At present, a high-quality reference genome is lacking; however, recent genotyping-by-sequencing (GBS) approaches promise to improve our understanding of taro genetics.

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