



DNA fingerprinting: an overview on genetic diversity studies in the botanical taxa of Indian Bamboo

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Abstract Bamboo is an economically important member of the grass family Poaceae with over 1500 documented uses. India has the 2nd largest reserve of bamboo in Asia after China. It is also called “Poor man’s timber”, “Green Gold” and “twenty-first century steel”. They are extensively used as raw material for various industries besides serving the rural population through several uses. Their immense versatility and utility have resulted in the genetic erosion and over-exploitation of bamboos leading to a constant decline in their natural populations. This has made it indispensable to conserve and propagate bamboo species. For utilization and conservation of genetic resources, germplasm characterization and screening are noteworthy. For the characterization of bamboo species, multiple attempts have been taken with the support of molecular markers and with the emergence of molecular biology, different molecular markers are now being used to study genetic variability, genetic diversity and genotype identification. These markers include RAPDs, ISSRs, SSRs, RFLPs and AFLPs. Other marker types which have been employed for molecular characterization in bamboo but not

particularly in Indian bamboo can also be used as a potential marker choice such are SCoT, IRAP, SRAP, SNP. The present review majorly deals with the role of different molecular markers in the genetic diversity study of natural populations of Indian bamboo species. It will provide information on the availability of different molecular markers to identify diversity in Indian bamboo species. It will give an ease of access for different researchers working in the field of bamboo to design primer for different markers accordingly. Further, this fingerprinting-based diversity study will also help in proper breeding of bamboos for its improvement program.

Keywords Molecular markers · DNA fingerprinting · Bamboo species · Bamboo germplasm · India

Abbreviations

RAPD	Randomly amplified polymorphic DNA
RFLP	Restriction fragment length polymorphism
AFLP	Amplified fragment length polymorphism
ISSR	Inter simple sequence repeat
SSR	Simple sequence repeat
SCAR	Sequence characterized amplified region
ScoT	Start codon targeted
IRAP	Inter-retrotransposon amplified polymorphism
SRAP	Sequence related amplified polymorphism
SNP	Single nucleotide polymorphism

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Introduction

Bamboo is a member of the Grass Family Poaceae and sub-family Bambusoideae which grows in many parts of the world. With more than 1575 species from 111 genus, it is quite distinct from regular grass because of its size, width, height, and branches at internodes (Singh et al. 2013; Xiu-hua et al. 2017). Bamboos does not seem to be the only non-timber forest trees having about 1500 documented uses but also one in every of the important cultivated crops (Azeez and Orege 2018). They are one of the foremost economically important plants with diverse applications in many industries and households (Nongdam and Tikendra 2014). With reference to the whole bamboo community, India with 160 species is second largest bamboo producing country after China with 800 species having the highest number (Bystriakova 2003).

Bamboo distribution: India

In India, bamboo forest area in 2019 increased by 3229 km² compared to 2017 because of its environmental and commercial importance. Bamboo covers almost 22.5% (160,037 km²) of area of the entire Indian forest. The North-eastern states of India which comprises of seven sister states i.e., Assam, Arunachal Pradesh, Manipur, Mizoram, Meghalaya, Tripura and Nagaland contribute 25% to bamboo forest and have almost 100 plus species of bamboo which is equivalent to 50% of Indian bamboo species (Amom et al. 2020; Nongkynrih et al. 2019; Singh et al. 2017; Tamang et al. 2013). Other states of India cover approximately 40% of total bamboo area of India i.e., Madhya Pradesh with 14%, Maharashtra with 10%, Arunachal Pradesh with 10% and Odisha with 8%. Uttar Pradesh, West Bengal and Bihar have large area but in terms of bamboo area cover it is only 3226 km² (Fig. 1).

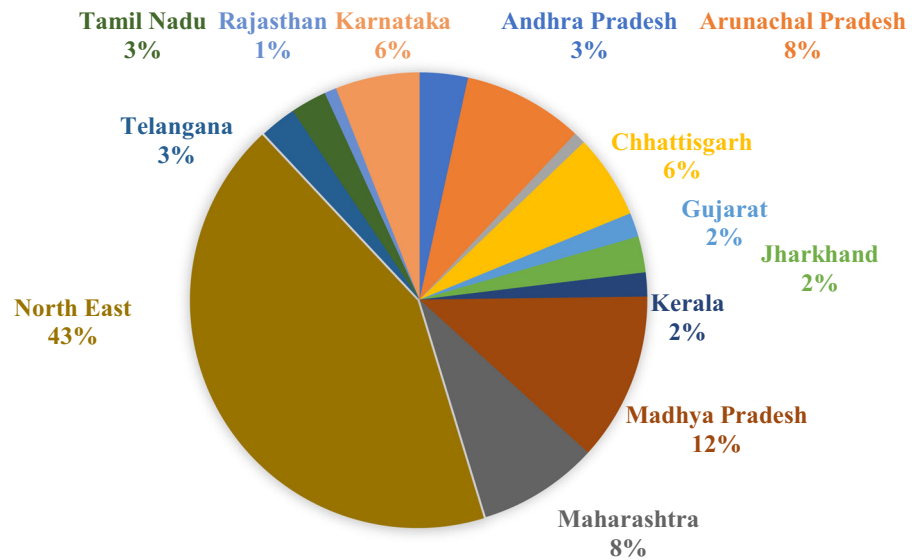
Of the 160 species of bamboo in India, essential and commercial species of various genera are identified as *Bambusa bambos* (L.) Voss, *B. balcooa* Roxb., *B. nutans* Wall. Ex Munro, *B. cacharensis* R.B. Majumdar, *B. tulda* Roxb., *B. polymorpha* Munro, (Synonym of *B. multiplex*), *B. multiplex* (Lour.) Raeush. Ex. Schult., *B. vulgaris* Schrad., *Bambusa pallida* Munro, *Bambusa polymorpha* Munro, *Dendrocalamus giganteus* Munro, *D. asper* (Schult.) Backer, *D. hamiltonii* Nees & Arn. Ex Munro, *Pseudoxytenanthera stocksii* (Munro) T.Q. Nguyen, *D. brandisii* (Munro) Kurz, *D.*

strictus (Roxb.) Nees, *Pseudoxytenanthera ritcheyi* (Munro) H.B. Naithani, *Ochlandra scriptoria* (Dennst.) C.E.C. Fisch, *O. travancorica* (Bedd.) Gamble, *O. ebracteata* Raizada & Chatterji, *Thyrsostachys oliveri* Gamble, *Schizostachyum dullooa* (Gamble) R.B. Majumdar, *Drepanostachyum falcatum* (Nees) keng f., *Melocanna baccifera* (Roxb.) Kurz, *Thamnocalamus spathiflorus* (Trin.) Munro, *Gigantochloa rostrata* K.M. Wong, *G. atroviolacea* Widjaja (Sharma and Nirmala 2015; Kaur et al. 2016; Singh and Kumari 2018). For commercial purpose, the ten prominent bamboo species used in India are *Bambusa bambos*, *B. balcooa*, *B. nutans*, *B. tulda*, *Dendrocalamus hamiltonii*, *D. strictus*, *Ochlandra scriptoria*, *O. ebracteata*, *O. travancorica*, *Melocanna baccifera* (Seethalakshmi et al. 1998). Figure 2 represents some of the commercially important bamboo species grown in India.

Bamboo usage

Because of its excellent mechanical, chemical and physical properties along with enormous diversity of application in around 10,000 products, it is called “Poor man’s timber”, “Green Gold” and “twenty-first century steel” (Ahmad and Kamke 2003, 2005; Archila et al. 2018; Azeem et al. 2020). A major number of bamboo products is used not only by traditional artists but also by big industries such as fibre boards, charcoal, paper making, house scaffolding etc., (Awoyera and Ede 2017; Bajpai 2018; Nguyen et al. 2018; Tanpichai et al. 2019). Almost 35% of the bamboo produced is used in the paper industry (Tripathi et al. 2018). Bamboo is also an excellent and healthy source of food (Choudhury et al. 2012; Silva et al. 2020). Around 200 bamboo species are considered edible worldwide (Basumatary et al. 2017; Bhatt et al. 2003, 2004). It also has many nutrients majorly nitrogen (N), Phosphorous (P) and Potassium (K). Due to its mechanical property bamboo is considered suitable for the construction industry. Mainly *Bambusa tulda*, *B. balcooa*, *B. nutans*, *B. polymorpha*, *B. pallida*, *D. hamiltonii* and *Melocanna baccifera* which are available in India are used for construction purposes (Borah et al. 2008). Bamboo also have certain desirable characteristics which make them excellent candidates to be used as a source of fuel for example low ash and alkali index content.

Fig. 1 Bamboo distribution in protected forest in states of India Commercially important species: India (Source: Forest survey of India 2019, Cajee 2018)



(A) *Bambusa nutans*



(B) *Bambusa vulgaris*



(C) *Bambusa multiplex*



(D) *Dendrocalamus hamiltonii*



(E) *Dendrocalamus giganteus*



(F) *Bambusa tulda*

Fig. 2 Commercial important bamboo species grown in India (Source: www.chhajedgarden.com/blogs)

Need for characterization of bamboo species

Due to genetic erosion and overexploitation of bamboo species, it becomes important to collect germplasm for the purpose of conservation (Goyal et al.

2012). In compliance with collection of germplasm, more awareness is needed in the identification and classification of bamboos species (Goyal et al. 2012). Characterization is an important link between utilization and conservation of germplasms (Nayak et al.

2003). Recently much significance has been placed on ex situ and in situ conservation of bamboo to set up bamboo collections with genotypes of interest. To avoid collection duplication, molecular markers can serve as an effective tool to avoid one from getting drowned in the genepool and to supplement the bamboo knowledge of local people. One of the research strategies needed for in situ conservation is to assess genetic variation present in specific areas to document its relationship to overall patterns of geographic differences among and within populations (Stapleton and Rao 1995). Bamboo species that have constricted distribution and are naturally rare may be extremely vulnerable to overharvesting or habitat changes. With an aim to conserve bamboo crop in the country Government of India initiated National Bamboo Mission (NBM) in 2006, under ministry of Agriculture, Government of India with an effort to increase the area under bamboo plantation in non-forest Government, private lands and further for the growth of bamboo industry many state governments (Kerala, Maharashtra, all North-East) have their states-run programs. Also, many state governments are providing subsidies for bamboo farming (Sharma and Nirmala 2015).

Identification and classification of bamboo through morphological characterization

At the earliest in the year 1896, J.S. Gamble based on various reproductive and vegetative characters identified old world bamboos. Later, Chatterjee and Raizada (1963) prepared different culm-sheath and other potential vegetative descriptors for the identification of 22 bamboo taxa. According to them, “size, texture, general appearance, blades, shape and texture of the sheath” proved to be efficient traits for distinguishing different species. Triplett and Clark (2003) assessed the diversity and relationship within the members of *Chusquea culeou* species complex due to geographical and ecological variations. They studied 14 floral or reproductive characters and 7 vegetative characters. The analysis based on reproductive and vegetative traits showed that the differences in the characters is continuous and cannot be considered or used to separate the species into a group that are morphologically distinct. Lately, Bhattacharya et al. (2006) characterized *B. tulda* from 17 eco-geographical locations in various districts of West Bengal. They

reported 17 culm-sheath and 15 culm characters and the study was in accordance with the previous taxonomic classifications given by Gamble (1896). Using these 32 key characters (15 culm and 17 culm-sheath), phylogenetic relationship among 15 species of bamboo were studied by Das et al. (2008). The clustering pattern generated from the morphological descriptors were not in accordance with the taxonomic classification of Gamble (1896).

Need for molecular markers

Despite the fact that characterization of bamboo species has long been done based on morphological traits, yet the classification is not dependable since these characters are often influenced by environmental elements. Das et al. (2008) reported that only vegetative characters are inadequate to differentiate closely related species. The clustering pattern of the 15 species of bamboo studied were not in conformity with the taxonomic patterns of Gamble (1896). *Bambusa atra* (synonym of *Neololeba atra* (Lindl.) Widjaja), *B. wamin* E.G. Camus, *B. striata* (synonym of *Bambusa vulgaris* Schrad.) as these names were reported by Das et al. 2008. As per editor I have added the latin name of species. Similarly, *D. strictus* was clustered with *B. atra*, *B. wamin* and *B. striata*. The cycle of reproduction for bamboo is extensively long i.e. 3–120 years and hence the identification and classification with floral characteristics is difficult (Bhattacharya et al. 2009; Yesmin et al. 2015). The taxonomic classification in case of bamboo is mostly based on vegetative characteristics and are greatly influenced by environment (Ohrnberger 2002). Therefore, not considered reliable for taxonomic classification. Das et al. (2008) reported in his study that differentiation among and within bamboo species based on only morphological characterization are inefficient. *B. wamin* and *B. striata* of *Bambusa* genus were separated from the some of the other *Bambusa* species. Similarly, *D. strictus* was grouped with *B. atra*, *B. wamin* and *B. striata* (Yesmin 2015). Also, there are only limited numbers of genes which are involved in expression of morphological characteristics which does not give the exact scenario of the entire genome (Brown-Guedira et al. 2000). Ample and effectual molecular data are needed to separate and regroup many bamboo species for better evolutionary understanding, molecular phylogeny and

determination of genetic diversity (Stapleton et al. 2009; Nilkanta et al. 2017).

Bamboo and DNA based molecular markers

DNA based molecular markers are way better than morphological markers as the former are cost-effective, highly informative, not tissue or age specific, neutral and are not influenced by environmental factors (Uchoi et al. 2017; Kumar et al. 2011). The use of DNA based molecular markers has given rise to significant improvement in understanding phylogenetic relationships within the bamboo species with the help of genetic diversity studies, which was previously constricted with limited phenotypic based characteristics (Das et al. 2008; Bhandari et al. 2021). The most practical and most important application of the use of molecular markers in bamboo is doubtlessly the precise identification of bamboo species and genetic variation assessment within species within a short period of time. Taxonomists and others working with bamboo are very much aware with the difficulties associated with identification and genetic variation assessment of bamboo genotypes, which itself is important for effectively selecting superior genotypes. But with the rise of molecular marker tools, which allows one to objectively assess genetic variation within species and to determine genotype irrespective of the environmental locations and other aspects contributing to morphological variability (Stapleton and Rao 1995). Various marker systems have been used in explaining the genetic diversity of bamboo using molecular markers such as Random Amplified Polymorphic DNA (RAPD) (Giels et al. 1997a, 1997b; Hodgkinson et al. 2000), restriction fragment length polymorphism (RFLP) (Friar and Kochert 1991, 1994), amplified fragment length polymorphism (AFLP) (Isagi et al. 2016), Sharma et al. (2009), simple sequence repeats (SSRs) (Tang et al. 2010), expressed sequence tags-SSR (EST-SSR) (Zhang et al. 2011), inter-simple sequence repeats (ISSRs) (Lin et al. 2010) and single nucleotide polymorphism (SNP) (Zhou et al. 2011). Suitably, this approach is extensively used for studying phylogenetic relationship (Amom et al. 2020; Liu et al. 2016), genetic diversity (He et al. 2019; Tanzeem et al. 2019), DNA fingerprinting (Afshari et al. 2016) and varietal identification (Odunayo et al. 2019). These above mentioned markers are frequently used for molecular

characterization of Indian bamboos but there are some other DNA based molecular markers also which had been employed for the characterization of bamboos other than India like SCoT (Start codon Targeted) (Amom et al. 2020), IRAP (Inter- retrotransposon amplified polymorphism) (Li et al. 2020) and SRAP (Sequence related amplified polymorphism) (Feng et al. 2010; Zhu et al. 2013). Detail of the markers used to explore genetic diversity among different bamboo species of India by different groups of works was shown in Table 1. Many hybridization, PCR and sequence-based marker systems have acquired existence over a period of time.

Random amplified polymorphic DNA (RAPD)

The most widely employed DNA marker for identification of rapid plant genotype is RAPD which is the cheapest and most simple molecular marker using arbitrary primers (Arumugam et al. 2019). The RAPD reactions are carried out on genomic DNA with the help of an arbitrary primer which results in the amplification of many discrete DNA products and these products are usually separated by gel electrophoresis. Genetic variation within individuals results from the sequence differences in the primer binding sites. The efficacy of RAPD markers in detection of DNA polymorphism and phylogenetic study in bamboos species has been previously studied by various researchers (Das et al. 2008; Nayak et al. 2003; Bhattacharya et al. 2006; Agnihotri et al. 2009; Desai et al. 2015; Waghmare et al. 2013). Nayak et al. 2003 in his work distinguished bamboo species of genera *Dendrocalamus*, *Cephalostachyum*, *Dinochloa* and *Bambusa* with the help of RAPD markers. They investigated genetic relationships in 12 species of bamboo using RAPD technique which started by using 30 ten-mer primers that differentiated 12 species and hence selectively reduced the set of primers. In total, 137 different polymorphic DNA bands were amplified by 10 selected primers. Similarly, Bhattacharya et al. (2006) characterized populations of *B. tulda* from west Bengal using RAPD marker for species identification and reported that no polymorphism detected between various populations of *B. tulda* and also no polymorphism between the phenotypic variants. Agnihotri et al. (2009) performed genetic fidelity test of tissue culture generated plant from *D. hamiltonii* using RAPD marker. Shalini et al. (2013) investigated

Table 1 List of markers used for exploring genetic diversity among different bamboo species of India

Marker type	Species	Purpose	Primer ID/primer sequence	Findings	References
ISSR	<i>Melocanna baccifera</i>	Genetic variation among 7 populations of <i>Melocanna baccifera</i> from 5 districts of Manipur were studied using ISSR technique	UBC-813, UBC-822, UBC-828, UBC-868, and UBC-878	The 7 populations of <i>M. baccifera</i> revealed high genetic diversity within the population. Analysis of molecular variance showed 78% genetic variation within the population and 22% among populations. The 93 individuals of 7 population of <i>M. baccifera</i> were clustered into major three clusters	Nilkanta et al. (2017)
	<i>Bambusa vulgaris</i> 'Vittata' <i>B. multiplex</i> ; <i>B. bambos</i> <i>B. multiplex</i> ; <i>B. balcooa</i> <i>B. vulgaris</i> Schrad. 'Wamin' <i>B. longispiculata</i> ; <i>B. atra</i> <i>B. oliveriana</i> ; <i>B. sinospinosa</i> <i>B. tulda</i> ; <i>B. pallida</i> <i>Cephalostachyum latifolium</i> <i>Dendrocalamus hamiltonii</i> <i>D. sikkimensis</i> ; <i>D. asper</i> ; <i>D. strictus</i> <i>Drepanostachyum khasianum</i> <i>D. intermedium</i> ; <i>Gigantochloa Himalayacalamus hookerianus</i> <i>Melocanna baccifera</i> ; <i>Phyllostachys nigra</i> ; <i>P. argenteo striatus</i> <i>Pseudosasa japonica</i> ; <i>Sasaella ramosa</i> <i>Shibataea kumasaca</i> ; <i>Yushania maling Chinese bamboo (unidentified)</i>	Genetic diversity of 13 genera (29 accessions) found in North Bengal were studied	UBC-810, UBC-815, UBC-818, UBC-822, UBC-824, UBC-825, UBC41, UBC856, UBC87	ISSR analysis showed that majority of the <i>Bambusa</i> species and its varieties were found to be clustered together, except for <i>B. oliveriana</i> (B9) and <i>B. atra</i> . <i>B. pallida</i> was segregated from all the other varieties and genera of bamboos under study showing monophyly origin of <i>Bambusa</i> genus. <i>B. multiplex</i> 'Alphonse-Karr' and <i>B. multiplex</i> 'Rivierorum' shared 96% similarity. Similarly <i>B. vulgaris</i> 'Vittata' and <i>B. vulgaris</i> 'Wamin' were closely linked with 85.3% similarity. Of the 4 <i>Dendrocalamus</i> accessions, <i>D. strictus</i> and <i>D. hamiltonii</i> formed a cluster with 83.3% similarity, while <i>D. sikkimensis</i> was clustered with <i>B. sinospinosa</i> and <i>D. asper</i> formed a separate cluster which was totally segregated. The 2 <i>Drepanostachyum</i> , i.e., <i>D. intermedium</i> and <i>D. khasianum</i> were placed distinctly with similarity coefficient of 66.7%	Goyal and Sen (2014)
	<i>Bambusa arundinacea</i> <i>Bambusa glaucescens</i> <i>Bambusa</i> sp. (Nangal) <i>Bambusa nutans</i> <i>Bambusa</i> sp. (Tapi); <i>Bambusa tulda</i> <i>Bambusa ventricosa</i>	Study of Genetic relationship among 20 species (22 accession) grown in Regional Plant Resource	ISSR1; ISSR5; ISSR6; ISSR8; ISSR9; ISSR10; ISSR14; ISSR17; ISSR18; ISSR19; 12PT20C4; RM240F; RM254F; RM254R	Most of the <i>Bambusa</i> species except <i>B. glaucescens</i> and <i>B. arundinacea</i> were clustered together. <i>Dendrocalamus strictus</i> was separated from all the other	Mukherjee et al. (2010)

Table 1 continued

Marker type	Species	Purpose	Primer ID/primer sequence	Findings	References
	<i>Bambusa vulgaris</i> ; <i>Bambusa vulgaris</i> var. <i>vittata</i>	centre, Bhubaneswar and various states of India		species and genera of bamboo. <i>Bambusa</i> sp.(Tapi) and <i>Bambusa</i> sp. (Nangal) shared 81% similarity, were the two unidentified species of North-eastern India. Similarly, <i>B. vulgaris</i> var <i>vittata</i> (striated culm) and <i>B. vulgaris</i> (green culm) were closely grouped, as were <i>B. nutans</i> and <i>B. tulda</i> . The 2 <i>Dendrocalamus giganteus</i> accessions (1 and 2) formed a cluster with a similarity level of 49%. All the 4 species of <i>Dendrocalamus</i> were separated widely from each other with <i>Dendrocalamus strictus</i> singled out from other species of bamboo	
	<i>Dendrocalamus giganteus</i>				
	<i>Dendrocalamus hamiltonii</i>				
	<i>Dendrocalamus membranaceus</i>				
	<i>Dendrocalamus strictus</i>				
	<i>Oxytenanthera nigrociliata</i>				
	<i>Phyllostachys nigra</i> ;				
	<i>Thyrsostachys oliveri</i> ;				
	<i>Pleioblastus fortunei</i> ; <i>Pleioblastus pumilus</i> ; <i>Schizostachyum pergracile</i> ; <i>Sasa auricoma</i>				
	<i>Bambusa bambos</i> ; <i>Bambusa tulda</i> ;	Genetic diversity study between elite species of bamboos	UBC 824; UBC 834; UBC 840; UBC 855; ISD4; ISD9 ISD13; ISD16; ISD20; ISD28; ISD32; ISD40	Based on ISSR analysis, three major clusters were formed. Clusters 1 consisted of GAU-1 (<i>Bambusa bambos</i> from Anand, Gujarat), GFC- 2 (<i>Bambusa tulda</i> from Anand, Gujarat) and GSF-5 (<i>Bambusa multiplex</i> from Anand, Gujarat), cluster II consisted of GKU-3 (<i>Bambusa balcooa</i> from Kutch Gujarat), GVP- 6 (<i>Bambusa balcooa</i> Anand, Gujarat) and GKU-4 (<i>Bambusa balcooa</i> from Kutch, Gujarat) and cluster III consisted of GNU-7 (<i>Bambusa vulgaris</i> from Anand, Gujarat), OVP-8 (<i>Bambusa vulgaris</i> from Anand, Gujarat), YKE-11(<i>Phyllostachys vivax</i> from Thiruvananthapuram, Kerala), YVI- 2(<i>Phyllostachys vivax</i> from Anand, Gujarat), YNU-10(<i>Phyllostachys vivax</i> from Anand, Gujarat) and YVP-13(<i>Phyllostachys vivax</i> from Anand, Gujarat). Meanwhile, OCT-	Desai et al. (2015)
	<i>Bambusa balcooa</i> ; <i>Bambusa multiplex</i> ; <i>Bambusa vulgaris</i> ;				
	<i>Bambusa multiplex</i> ; <i>Phyllostachys vivax</i>				

Table 1 continued

Marker type	Species	Purpose	Primer ID/primer sequence	Findings	References
	<i>Bambusa balcooa</i> ; <i>Bambusa vulgaris</i> ; <i>Phyllostachys nigra</i> ; <i>Melocanna baccifera</i> ; <i>Sasa fortunei</i> ; <i>Dendrocalamus strictus</i> <i>Bambusa wamin</i> ; <i>Bambusa multiplex</i> ; <i>Sasa palmata</i> ; <i>Bambusa ventricos</i>	Genetic variation between different bamboo accession with respect to geographical origin were studied	814; 844A; 844B; HB14; ISSR 5; 17898B	9 (<i>Bambusa multiplex</i> from Anand, Gujarat) was totally separated from other bamboo species ISSR analysis grouped 20 species of bamboos in 2 major groups. First group comprised of <i>Bambusa ventricosa</i> , 5 <i>Bambusa balcooa</i> samples and 6 of <i>Bambusa vulgaris</i> samples collected from various locations. The second group included <i>Phyllostachys nigra</i> , <i>B. wamin</i> , <i>D. strictus</i> from 2 different locations	Gami et al. (2015)
AFLP	<i>Ochlandra travancorica</i>	Genetic variation in randomly collected <i>O. travancorica</i> species from regions of Kerala were studied	E-AAG/M-CTC; E-AAG/M-CTG E-ACG/M-CAA; E-ACG/M-CAC E-ACG/M-CTA; E-ACG/M-CTT E-ACG/M-CAG; E-ACG/M-CA	<i>O. travancorica</i> accessions were grouped into 3 different groups and were considered as distinct populations. Group-1 with accession numbers 1–11, Group-2 consisted of accession numbers from 21 to 28 and group-3 included accession numbers from 12 to 20. Analysis of molecular variance revealed that variation among the population was 46% and variation within population was 54%	Nag et al. (2013)
	<i>Bambusa nutans</i>	Genetic variation in Tissue culture generated and field established <i>Bambusa nutans</i> assessment	E-AGG/M-CAA; E-AGG/M-CTA E-AGG/M-CTG; E-AGC/M-CAA E-AGC/M-CAC; E-AGC/M-CTG	AFLP results showed that no such major genetic variation occurred in the in-vitro shoot regenerated <i>B. nutans</i> through somatic embryogenesis	Mehta et al. (2011)
	<i>Dendrocalamus hamiltonii</i>	Study of genetic variation of <i>D. hamiltonii</i> in Imphal-east and Chandel (commercial production districts)	EcoRI-AAG(Joe)/MseI-CTC EcoRI-ACG(Joe)/MseI-CAG EcoRI-AAC(Ned)/MseI-CTG EcoRI-ACC(Ned)/MseI-CTG	The cluster analysis based on AFLP analysis revealed that the ten accessions of <i>D. hamiltonii</i> were grouped into 2 clusters. Group-1 mainly consisted of populations from Imphal-East district with 59.2% similarity while group-2 included populations from Chandel district with 56.3% similarity. The	Waikhom et al. (2012)

Table 1 continued

Marker type	Species	Purpose	Primer ID/primer sequence	Findings	References
	<i>Bambusa balcooa</i>	Genetic relationships among 10 species of <i>Dendrocalamus</i> and 5 outgroup species from subtribe Bambusinae were studied	E33_M47; E35_M47; E32_M47; E33_M59; E33_M60	selected primers gave a good number of amplification products for the study of genetic diversity of <i>D. hamiltonii</i>	Pattanaik and Hall (2011)
	<i>Dendrocalamus brandisii</i>			The studied bamboo species were grouped in 3 major clusters. Cluster 1 comprised of <i>Dendrocalamus memberanaceus</i> and <i>D. somdev</i> with 93% similarity; cluster 2 comprised of <i>Dendrocalamus hamiltonii</i> <i>Bambusa balcooa</i> and <i>D. sikkimensis</i> with 89% similarity and cluster 3 comprised of <i>D. asper</i> and <i>D. giganteus</i> with 50% similarity <i>D. strictus</i> was outgrouped from the other species of <i>Dendrocalamus</i>	
	<i>Dendrocalamus callostachyus</i>				
	<i>Dendrocalamus giganteus</i>				
	<i>Dendrocalamus hamiltonii</i>				
	<i>Dendrocalamus membranaceus</i>				
	<i>Dendrocalamus sahai</i>				
	<i>Dendrocalamus sikkimensis</i>				
	<i>Dendrocalamus somdevai</i>				
	<i>Dendrocalamus strictus</i>				
	<i>Dinochloa maclellandii</i>				
	<i>Melocalamus compactiflorus</i>				
	<i>Oxytenanthera abyssinica</i>				
	<i>Thyrsostachys siamensis</i>				
	<i>Chimonobambusa callosa</i>	Taxonomic grouping of some edible species of bamboo for better understanding	EcoRI-ACA* + MseI-CAT EcoRI- ACT* + MseI-CTG EcoRI- ACT* + MseI-CTA EcoRI- ACA* + MseI-CTA EcoRI- AAG* + MseI-CTC EcoRI- AAC* + MseI-CTG	Two major clusters were formed with cluster 1 consisting of 5 species of <i>Bambusa</i> genus and cluster 2 consisting of 4 species of genus <i>Dendrocalamus</i> . <i>Bambusa cacharensis</i> , <i>Bambusa tulda</i> and <i>Bambusa manipureana</i> showed a similarity of 89.5%. Meanwhile, <i>B. nutans</i> and <i>B. oliveriana</i> showed similarity of 86%. The <i>D. hamiltonii</i> and <i>D. hookeri</i> in cluster2 are genetically close to each other with similarity of greater than 96%. The other two species included in cluster2 viz., <i>D. manipureanus</i> and <i>D. latiflorus</i> showed 83% similarity. <i>Chimonobambusa callosa</i> showed 83% similarity with <i>Dendrocalamus</i> and <i>Bambusa</i> genus where as <i>Schizostachyum dullooa</i> showed 79% similarity	Ghosh et al. (2011)
	<i>cacharensis</i>				
	<i>Bambusa manipureana</i>				
	<i>Bambusa tulda</i>				
	<i>oliveriana</i>				
	<i>latiflorus</i>				
	<i>hamiltonii</i>				
	<i>hookeri</i>				
	<i>manipureanus</i>				
	<i>Melocanna baccifera</i>				
	<i>Schizostachyum dullooa</i>				

Table 1 continued

Marker type	Species	Purpose	Primer ID/primer sequence	Findings	References
RFLP	<i>Bambusa vulgaris</i> 'Vittata'; <i>B. multiplex</i> ; <i>B. bambos</i> <i>B. multiplex</i> ; <i>B. balcooa</i> <i>B. vulgaris</i> Schrad. 'Wamin'; <i>B. longispiculata</i> ; <i>B. ara</i> <i>B. oliveriana</i> ; <i>B. sinospinosa</i> <i>B. tulda</i> ; <i>B. pallida</i> <i>Cephalostachyum latifolium</i> <i>Dendrocalamus hamiltonii</i> <i>D. sikkimensis</i> ; <i>D. asper</i> <i>D. strictus</i> ; <i>Drepanostachyum khasianum</i> ; <i>D. intermedium</i> <i>Gigantochloa</i> ; <i>Himalayacalamus hookerianus</i> ; <i>Melocanna baccifera</i> <i>Phyllostachys nigra</i> ; <i>P. argenteostriatus</i> ; <i>Pseudosasa japonica</i> ; <i>Sasaella ramosa</i> <i>Shibataea kumasaca</i> ; <i>Yushania maling</i> ; Chinese bamboo (unidentified)	Based on the amplification of tmL-trnF region molecular diversity of 29 bamboo species found in North Bengal through RFLP technique were studied	Tab e-5'- CGAAATCGGTAGACGCTACG-3' Tab f-5'- ATTGAACTGGTGACACGAG-3'	with <i>Dendrocalamus</i> genus and <i>Melocanna baccifera</i> showed 82% similarity with <i>Bambusa</i> The studied bamboo species were grouped into 2 clusters. <i>Shibataea kumasaca</i> and <i>Melocanna baccifera</i> were separated from all other bamboo species. Similarly, <i>Phyllostachys nigra</i> was totally separated. The first cluster comprised of total of 21 bamboo accession which was divided into 2 groups. The first group comprised of 18 species, which included ten species from <i>Bambusa</i> , all the 4 species of <i>Dendrocalamus</i> along with <i>Pleioblastus argenteostriatus</i> , <i>Drepanostachyum intermedium</i> , <i>Sasaella ramosa</i> and <i>Gigantochloa</i> spp. The second group comprised of <i>Pseudosasa japonica</i> and <i>Himalayacalamus hookerianus</i>	Sen et al. (2014)
SSR	<i>Bambusa arundinacea</i>	Microsatellites isolation and characterization in <i>B. arundinacea</i> and cross amplification in other bamboos	Ba10; Ba14; Ba18a; Ba18b; Ba20; Ba25 Ba58; Ba202	6 microsatellites of which three monomorphic (Locus: Ba18b, Ba14, Ba58) and three polymorphic (Locus: Ba10, Ba20, Ba18a) were characterized in <i>B. arundinacea</i> . and its cross-species amplification examined in 18 other species. Monomorphic SSRs cross amplified in most of the examined species while polymorphic in only 3–4 species	Nayak and Rout (2005)
	<i>Dendrocalamus hamiltonii</i>	Genetic diversity study of 19 naturally occurring <i>D. hamiltonii</i> distributed over northeast Himalayas	DLUGMS03; DLUGMS13; DLUGMS15 DLUGMS16; DLUGMS17; DLUGMS23 DLUGMS45; DLUGMS47; DLUGMS50 DLUGMS51; DLUGMS52; DLUGMS54; DLUGMS62	SSR analysis of <i>D. hamiltonii</i> (DH)grouped 19 accessions into 4 groups. Group 1 comprised DH only from the population of Mizoram with the exception of one population form Mizoram which was placed solely in group 3.	Meena et al. (2019)

Table 1 continued

Marker type	Species	Purpose	Primer ID/primer sequence	Findings	References
	<i>Bambusa oldhamii</i>	Identification of expressed sequence tags (EST)SSR from <i>Bambusa oldhamii</i> public database and check it's transferability in other species of bamboo	Boes-3; Boes-4; Boes-5; Boes-6; Boes-7; Boes-8; Boes-10; Boes-11; Boes-12; Boes-13	Exceptionally, one population of Assam was segregated from other Assamese populations and grouped with the population of Meghalaya in group 2 which indicates their common origin despite spatial separation while group 4 consisted of the majority of populations from Assam, Nagaland and Arunachal Pradesh. The analysis of molecular variance revealed 83.47% of genetic variation within populations and 16.53% among populations	Sharma et al. (2008)
SCAR	<i>Bambusa balcooa</i> and <i>Bambusa tulda</i>	Development of species-specific molecular markers of <i>Bambusa tulda</i> and <i>B. balcooa</i> for proper identification	F-TCGTCGGCGGTAGACGGAGAG R-TCGTCGGCGGTTCGAGCTTAT (<i>Bambusa balcooa</i>) F-GTGACGTAGGGGAACATGGC R GTGACGTAGGGCATACTTG (<i>Bambusa tulda</i>)	10 EST-SSR markers were identified and transferability rate in 25 bamboo species ranged from 30% (in <i>P. pubescens</i>) to 100% in 4 species (<i>D. membranaceus</i> , <i>B. pallida</i> , <i>D. hamiltonii</i> and <i>P. aurea</i>)	Das et al. (2008)
RAPD	<i>Bambusa vulgaris</i> ; <i>Bambusa vulgaris</i> var. <i>striata</i> ; <i>Bambusa ventricosa</i> ; <i>Dendrocalamus giganteus</i> ; <i>Dinocloa m'Clellandi</i> ; <i>Bambusa arundinacea</i> <i>Cephalostachyum pergracil</i> <i>Bambusa balcooa</i> ; <i>Bambusa multiplex</i> var. <i>Silver stripe</i> <i>Bambusa multiplex</i> ; <i>Sasa species</i> <i>Dendrocalamus strictus</i>	Investigation of genetic relationship in 12 bamboo species and its identification	OPA 04; OPA 11; OPA 19; OPA 17; OPA 20; OPN 11; OPN 13; OPN 19; OPN 20; OPN 04	Based on RAPD analysis, 12 taxa were grouped into two major clusters. The two major clusters were further subdivided into 3 minor clusters. First minor cluster consisted of <i>B. vulgaris</i> var. <i>striata</i> , <i>B. vulgaris</i> , <i>B. ventricosa</i> , <i>Dinocloa m'Clellandi</i> and <i>Dendrocalamus giganteus</i> . <i>Bambusa vulgaris</i> and <i>B. vulgaris</i> var. <i>striata</i> showed 80% similarity.	Nayak and Rout (2003)

Table 1 continued

Marker type	Species	Purpose	Primer ID/primer sequence	Findings	References
				Second minor cluster was composed of <i>B. balcooa</i> , <i>B. arundinacea</i> and <i>Cephalostachyum pergracile</i> . <i>Bambusa arundinacea</i> showed 30% similarity with <i>B. ventricosa</i> and about 20% similarity with <i>B. vulgaris</i> . The third minor cluster was formed by 4 taxa i.e. <i>B. multiplex</i> var. <i>Silver stripe</i> , <i>B. multiplex</i> , <i>Dendrocalamus strictus</i> and <i>Sasa sps</i>	
	<i>Bambusa tulda</i>	Characterization of <i>B. tulda</i> for RAPD profiles for species identification at different stages of life cycle	OPA-02; OPA-03; OPA-05; OPA-06; OPA-07; OPA-10; OPOB-02; OPOB-03; OPOB-04; OPOB-05; OPOJ-01; OPOJ-04; OPOJ-12; OPOJ-18; PW-01	No polymorphism detected between various populations of <i>B. tulda</i> studied and also no polymorphism between the phenotypic variants	Bhattacharya et al. (2006)
	<i>Bambusa tulda</i> ; <i>Bambusa nutans</i> ; <i>Bambusa balcooa</i> ; <i>Dendrocalamus strictus</i> ; <i>Dendrocalamus giganteus</i> ; <i>Dendrocalamus hamiltonii</i> ; <i>Bambusa vulgaris</i> ; <i>Bambusa bambos</i> ; <i>Dendrocalamus asper</i> ; <i>Guadua angustifolia</i>	Genetic relationship identification in 10 bamboo species and their morphological characters association	OPG4; OPE1; OPD1; OPB4; OPA12; OPY11; A17898; B17898; B17899	The 10 different species of bamboo under study were divided into two major clusters (A and B) with 22% similarity. Cluster A comprised of 9 species which was further sub-divided into 3 sub-groups (A1, A2 and A3). <i>Bambusa balcooa</i> and <i>Bambusa tulda</i> showed maximum level of similarity at the genetic level. Both subgroups A1 and A2 had 3 species which showed 34% and 35% similarity respectively. <i>Guadua angustifolia</i> was out grouped from all the other species which was also shown at morphological level	Shalini et al. (2013)
	<i>Dendrocalamus hamiltonii</i>	Checking genetic fidelity of <i>Dendrocalamus hamiltonii</i> generated by tissue culture	OPA 3; OPA 4; OPA; OPA 11; OPC 15; OPA 19	The amplification products generated by the primers were monomorphic across the mother plant and the corresponding in-vitro propagated plants which indicated the presence of genetic fidelity among	Agnihotri et al. (2009)

Table 1 continued

Marker type	Species	Purpose	Primer ID/primer sequence	Findings	References
	<i>Bambusa bambos</i> ; <i>Bambusa tulda</i> <i>Bambusa balcooa</i> ; <i>Bambusa multiplex</i> ; <i>Bambusa vulgaris</i> ; <i>Bambusa multiplex Phyllostachys vivax</i>	Genetic variation present in elite species of bamboo for exploiting paper industry	OPA-02; OPA-03; OPA-04; OPA-07; OPA-09; OPA-10; OPA-18; OPA-20; OPC-02; OPC-04; OPC-05; OPC-08; OPD-13; OPD-18; OPM-02; OPM-04; OPM-05; OPM-11 OPM-12; OPN-01; OPN-02; OPN-04; OPN-09; OPN-10; OPN-11; OPN-13; OPN-15; OPN-20; OPO-15; OPO-20	regenerants of <i>Dendrocalamus hamiltonii</i> observed in the study The cluster analysis based on RAPD analysis grouped 13 bamboo genotypes in 3 main clusters (Fig. 3). Clusters I consisted of GAU-1(<i>Bambusa bambos</i> from Anand,Gujarat),GFC-2(<i>Bambusa tulda</i> from Anand,Gujarat) and GSF-5(<i>Bambusa multiplex</i> from Anand, Gujarat), cluster II consisted of GKU-3(<i>Bambusa balcooa</i> from Kutch Gujarat),GVP-6(<i>Bambusa balcooa</i> from Anand,Gujarat),GKU-4(<i>Bambusa balcooa</i> from Kutch,Gujarat) and OCT-9(<i>Bambusa multiplex</i> from Anand,Gujarat) and cluster III consisted of GNU-7(<i>Bambusa vulgaris</i> from Anand,Gujarat),OVP-8(<i>Bambusa vulgaris</i> from Anand,Gujarat), YKE-11(<i>Phyllostachys vivax</i> from Thiruvananthapuram,Kerala),YVI-2(<i>Phyllostachys vivax</i> from Anand,Gujarat),YNU-10(<i>Phyllostachys vivax</i> from Anand,Gujarat) and YVP-13(<i>Phyllostachys vivax</i> from Anand, Gujarat)	Desai et al. (2015)
	<i>B. bambus</i> ; <i>P. ritcheyi</i> ; <i>P. stocksii</i> and <i>D. strictus</i>	Comparative genetic examination of four species of bamboo from different areas of Raigad, Maharashtra	OPA-01; OPA-13; OPD-08; OPD-20; OPN-05	Of the 4 species <i>D. strictus</i> and <i>B. bambos</i> , shares maximum number of similarity which are convincing with their similar vegetative characteristics. Pseudo <i>Renanthera ritcheyi</i> and <i>P. stocksii</i> shared similar characteristics on genetic level due their less genetic distance. The comparative RAPD	Waghmare and Bagde (2013)

Table 1 continued

Marker type	Species	Purpose	Primer ID/primer sequence	Findings	References
	<i>Bambusa vulgaris</i> 'Vittata' <i>B. multiplex</i> ; <i>B. bambos</i> <i>B. multiplex</i> ; <i>B. balcooa</i> <i>B. vulgaris</i> Schrad. 'Wamin' <i>B. longispicata</i> <i>B. atra</i> ; <i>B. oliveriana</i> <i>B. sinospinosa</i> ; <i>B. tulda</i> <i>B. pallida</i> ; <i>Cephalostachyum Latifolium</i> , <i>Dendrocalamus hamiltonii</i> <i>D. sikkimensis</i> ; <i>D. asper</i> <i>D. strictus Drepanostachyum khasianum</i> <i>D. intermedium</i> ; <i>Gigantochloa Himalayacalamus hookerianus</i> <i>Melocanna baccifera</i> <i>Phyllostachys nigra</i> <i>P. argenteostriatus</i> <i>Pseudosasa japonica</i> <i>Sasaella ramosa</i> <i>Shibataea kumasaca</i> <i>Yushania maling</i> Chinese bamboo (unidentified)	Genetic diversity of 13 genera (29 accessions) found in North Bengal were studied	OPA01; OPA03; OPA04; OPA05; OPA07; OPA08; OPA11; OPA 17; OPA20; OPB01; OP F09; OPG 19; OPH04; OPN04; OPN13; OPN 19	examination of the 4 species under study showed 65.79% polymorphic loci The cluster analysis based on RAPD analysis showed that majority of <i>Bambusa</i> were close to each other, except for <i>B. oliveriana</i> and <i>B. balcooa</i> , which clustered differently, and <i>B. tulda</i> and <i>B. atra</i> which were grouped in a minor clade with 82.2% similarity. <i>B. pallida</i> was found to be totally segregated in a different clade from the other <i>Bambusa</i> under study. The 2 species of <i>Drepanostachyum khasianum</i> and <i>D. intermedium</i> were distantly placed with 72.8% similarity. The genetic similarity between <i>Melocanna baccifera</i> and <i>Shibataea kumasaca</i> was 83.3%. Similarly, the genetic similarity between <i>D. strictus</i> and <i>Gigantochloa</i> sp. and <i>Yushania maling</i> and <i>Sasaella ramosa</i> was 79.4% and 80% respectively	Goyal and Sen (2014)

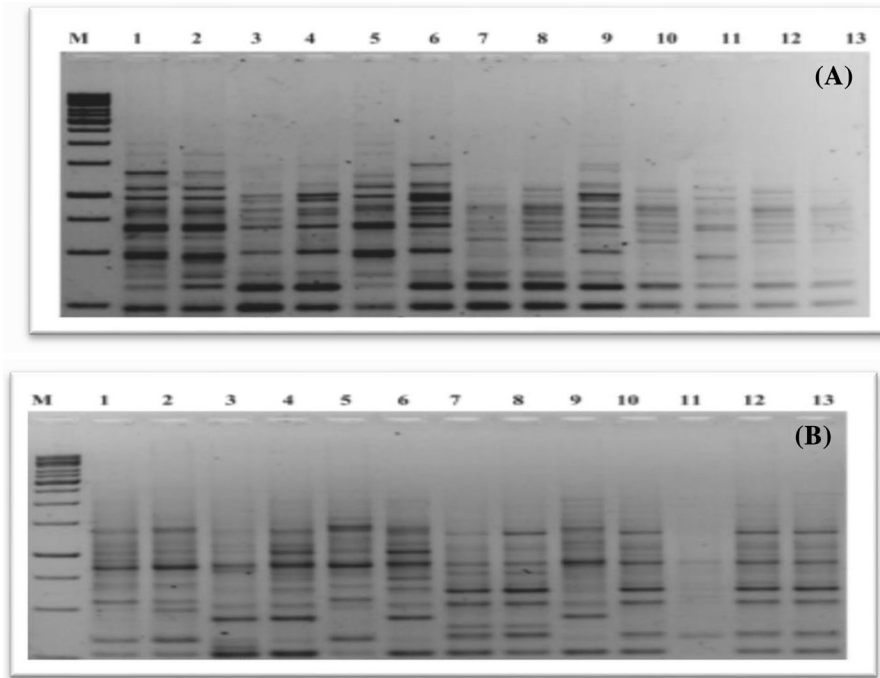


Fig. 3 RAPD amplification pattern of 13 Indian bamboo species generated by RAPD primer Legends: **a** 5'CCGCATCTAC 3' **b** 5'ACAACGCCTC3'; lane M-1 kb ladder; lanes 1–13 thirteen bamboo species (*Source*: Desai et al. 2015)

genetic relationships in 10 bamboo species using 21 RAPD markers and reported 100% polymorphism between the studied species. Similarly, Desai et al. (2015) assessed the genetic diversity of 13 bamboo species using 120 RAPD markers in which 30 RAPD generated 645 fragments out of which 623 were polymorphic. The RAPD banding patterns and the dendrogram generated by RAPD analysis is represented in Figs. 2 and 3 respectively. The number of amplified fragments generated by primers varied from 6 (OPC-02, OPA-02, OPN-01, OPD-M4, OPO-15,

OPD-18) to 29 (OPM-11), with size range 285–2168 bp (Fig. 3). The average polymorphic bands generated per primer is 20.76 (Desai et al. 2015). The UPGMA analysis based dendrogram grouped 13 bamboo genotypes in 3 main clusters (Fig. 4). Clusters 1 consisted of GAU-1 (*Bambusa bambos* from Anand, Gujarat), GFC-2 (*Bambusa tulda* from Anand, Gujarat) and GSF-5 (*Bambusa multiplex* from Anand, Gujarat), cluster II consisted GKU-3 (*Bambusa balcooa* from Kutch Gujarat), GVP-6 (*Bambusa balcooa* Anand, Gujarat), GKU-4

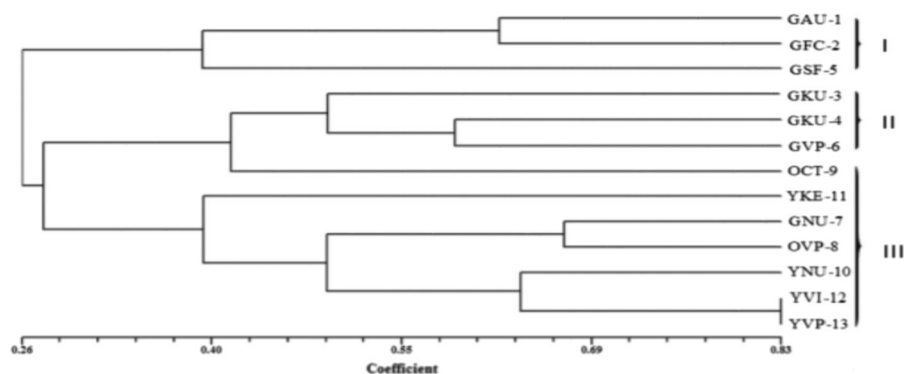


Fig. 4 Dendrogram of 13 Indian bamboo species based on RAPD analysis (*Source*: Desai et al. 2015)

(*Bambusa balcooa* from Kutch, Gujarat) and OCT-9 (*Bambusa multiplex* from Anand, Gujarat) and cluster III consisted of GNU-7 (*Bambusa vulgaris* from Anand, Gujarat), OVP-8 (*Bambusa vulgaris* from Anand, Gujarat), YKE-11 (*Phyllostachys vivax* from Thiruvananthapuram, Kerala), YVI-2 (*Phyllostachys vivax* from Anand, Gujarat), YNU-10 (*Phyllostachys vivax* from Anand, Gujarat) and YVP-13 (*Phyllostachys vivax* from Anand, Gujarat) (Desai et al. 2015).

Genetic relationship of four bamboo species (*P. stocksii*, *P. ritchey*, *D. strictus* and *B. bambusa*) collected from Maharashtra's Raigad district was analysed by Waghmare et al. (2013) using PCR-RAPD technique. Makmur et al. (2020) evaluated 8 bamboo types using RAPD markers to investigate the differences in the generated DNA sequence. A total of 20 primers were selected and from that 12 primers with clear and prominent amplification were selected.

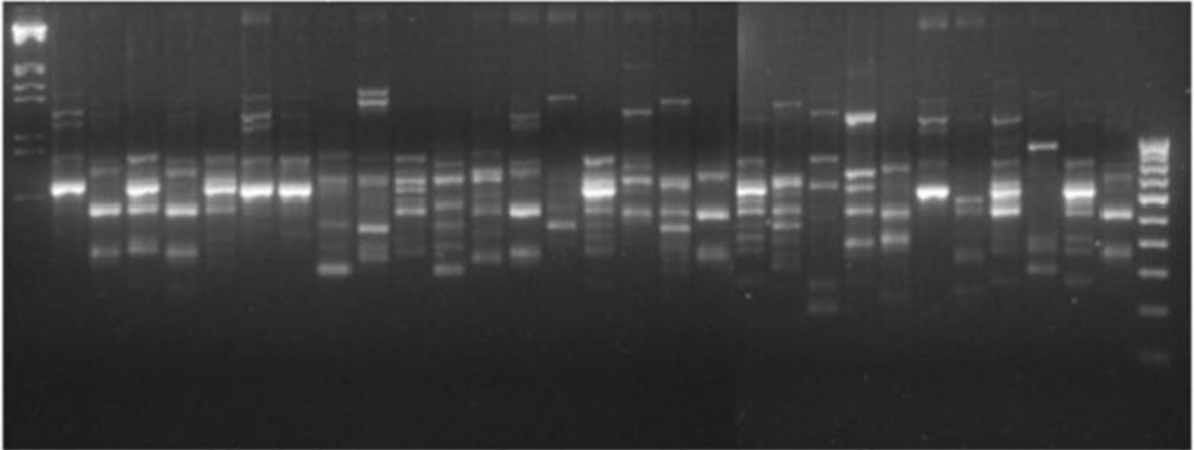
This wide range use of RAPD technique is due to its low-cost, speed and efficiency which generate large marker numbers in a short period as compared to other techniques. RAPD technique has also attracted several criticisms pointing towards its reproducibility, despite numerous advantages. RAPD has many limitations which includes uncertain locus homology, dominance and sensitivity to reaction conditions. RAPD being neutrally selective has advantage over RFLP as the former does not use radioisotopes and is able to use low quality DNA and also the primers are more accessible. However, due to low annealing temperatures RAPDs are less reproducible. The disadvantages of RAPD also include polymorphism detection at a limited level, low resolution profile and it detects dominant allelomorphs. It is also unable to distinguish homozygotes and heterozygotes. Co-migration problems may raise questions like "Do same sized bands in the gel correspond to DNA fragments?" The presence of identical bands with the same molecular weight in different samples does not provide evidence that the samples share homologous fragments of DNA.

Inter simple sequence repeat (ISSR)

To overcome the limitations of RAPD markers, ISSR markers came into effect. ISSRs are regions that are present within the microsatellite repeats (Joshi et al. 2000; Poczai et al. 2000) and provide considerable potential to determine inter-genomic and intra-

genomic diversity in comparison to other arbitrary primers, since they bring out dissimilarity within unique regions of DNA at various locus simultaneously. Microsatellites have several properties such as high copy number, high variability among taxa and ubiquitous occurrence in the eukaryotic genome, make ISSRs immensely useful markers. For many scientists working on bamboo, ISSR has become a popular technique for the study of genetic relationships (Lin et al. 2010; Mukherjee et al. 2010; Sarwat 2012). Till date Genetic diversity study using ISSR based markers has been done by Mukherjee et al. 2010; Goyal and Sen 2014; Desai et al. 2015; Gami et al. 2015; Nilkanta et al. 2017). Mukherjee et al. (2010) reported genetic diversity and phylogenetic relationship in 22 bamboo taxa through EST and ISSR-based random markers. Similarly, Gami et al. (2015) assessed genetic variation within 20 bamboo accessions which were collected from different parts of India. The molecular marker approach used by them was ISSR which used 8 primers to distinguish twenty bamboo accessions. Genetic diversity of 13 bamboo genotypes were analysed by Desai et al. (2015) using RAPD and ISSR. Total 63 ISSR primers were used of which 12 ISSR primers gave a good amplification profile. 246 fragments were generated by the 12 ISSR primers in which 241 were polymorphic. Genetic diversity study of 29 accessions of bamboos encountered in North Bengal were done through ISSR technique (Goyal and Sen 2014) with the help of 9 ISSR primers which recorded 100% polymorphism between the studied species. Among the 9 ISSR primers used (Table 1), the highest number of bands (33) was produced by (TC)8G, while (TC)8A produced only 22 bands with each band averaging 27.11 distinct scorable bands. ISSR banding patterns of 29 accessions of bamboo generated by primer UBC824 and UBC815 are represented in Fig. 5. The range of Genetic similarity between the species was 0.613–0.960 with lowest value found between *B. pallida* (B12) and *B. vulgaris* 'Vittata' (B1), while the highest value was found between *B. multiplex* 'Alphonse-Karr' (B2) and *B. multiplex* 'Riviereorum' (B4) (Goyal and Sen 2014). The dendrogram assembled based on ISSR analysis showed that majority of the *Bambusa* species and its varieties were found to be clustered together, except for *B. oliverianna* (B9) and *B. atra* (B8) (Fig. 6). Nilkanta et al. (2017) investigated the population genetic structure and genetic

(A)



(B)

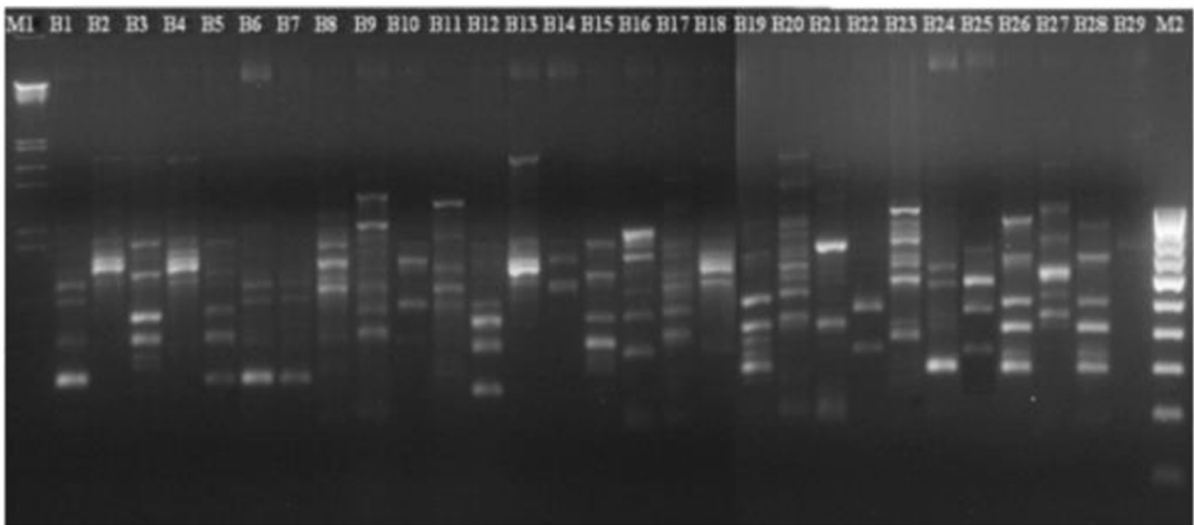


Fig. 5 Banding patterns of 29 accession of bamboo species generated by ISSR primers UBC-824 (a) and UBC-815 (b); M1-lambda DNA/EcoR1/Hind111 double digest ladder, M2-

10 bp mol marker, Lanes B1 to B29 studied bamboo species (Source: Sen and Goyal 2014)

diversity of *M. baccifera* using ISSR markers in 5 districts of Manipur.

Since then, several authors have attempted RAPD technique for the study of genetic relationships among species of bamboo but there have been only a limited number of studies on bamboo using ISSR markers. Thus, keeping this in mind Goyal and Sen (2014) employed both RAPD and ISSR markers to study the phylogenetic relationship of 29 accessions found in North Bengal. The ISSR technique has been frequently applied for genetic diversity analysis in bamboo species as these are effective multi-locus

markers and no prior knowledge of sequence is required. ISSR markers are used more than SSR and are also more reliable than RAPD markers mainly due to the method of detection and also longer primers are used, and hence more stringent PCR conditions.

It has several advantages as various loci can be assessed simultaneously which make ISSR a fast technique, also the obtained PCR products are specific to microsatellite sequence and are more reliable than the random primer sequence-based techniques. ISSR technique is economical and less time consuming than other microsatellite-based techniques as there is no

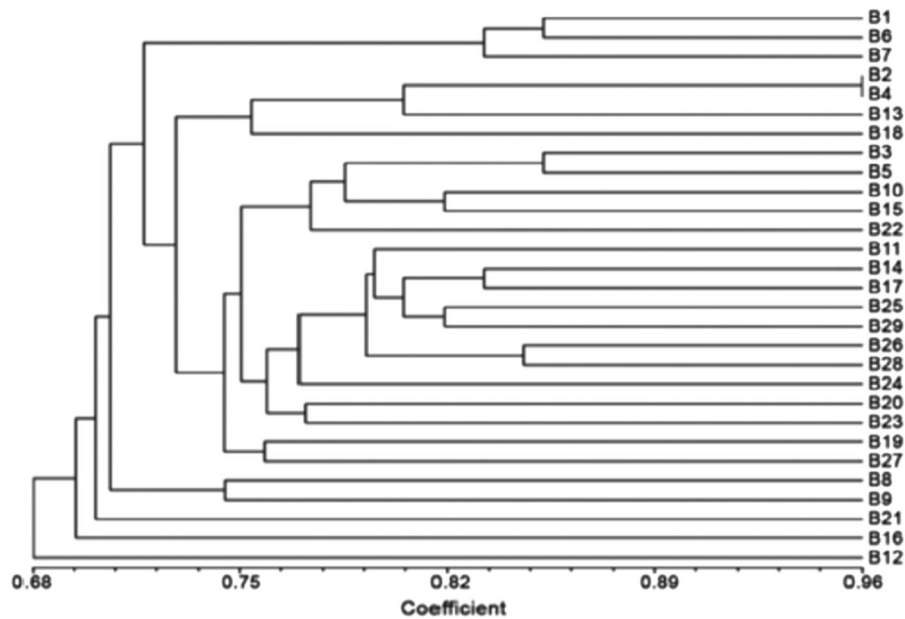


Fig. 6 Dendrogram of 29 accession of bamboo generated by ISSR profiling (Source: Goyal and Sen 2014)

requirement of characterization and cloning is required. However, there are certain disadvantages like sometimes the primers have less specificity to the scanned genome which could lead to questionable fingerprints and they are dominant hence unable to discriminate between heterozygotes and homozygotes.

Simple sequence repeat (SSR)

The accessibility of SSR markers in bamboo is very limited and only few simple sequence repeats (SSR) markers have been constructed for bamboo (Nayak and Rout 2005; Kaneko et al. 2008). However, the progress of SSR markers has traditionally been bounded by labor intensive and time-consuming methods of SSRs development. Hence, identification of simple sequence repeats (SSRs) from the expressed genome provides a substantial source of valuable markers. EST-SSRs linked with known function genes tend to be more extensively transferred at species and generic level (Bouck and Vision 2007; Bhandawat et al. 2019). In Bamboo, the first set of ten EST-SSRs were reported by Sharma et al. (2008) which would be valuable for phylogenetic studies and genetic diversity in bamboo and similarly Nayak and Rout (2005) isolated and characterized microsatellites in *B.*

arundinacea and in other bamboos for cross species amplification. They characterized 6 microsatellites in a bamboo species, *B. arundinacea*, 3 polymorphic and 3 monomorphic. Another molecular characterization in bamboo species was done by Meena et al. (2019) of 19 populations of *D. hamiltonii* distributed over northeast Himalayas with the help of nuclear simple sequence repeats (nSSR). Nuclear microsatellite markers are distributed ubiquitously in the genome which are highly polymorphic, show co-dominant inheritance and are often transferable over related species (Fan et al. 2013). For this, total sixty-eight (68) nSSR primer pairs of *B. arundinacea* and *D. latiflorus* was tested in *D. hamiltonii* for their transferability, out of the 68 primers 17 showing polymorphic amplification was used for genotyping. The SSR gel pattern generated by 3 different primer sets is shown in Fig. 7 and the respective dendrogram analysis is shown in Fig. 8. For genetic mapping, genetic diversity and genotype fingerprinting studies, SSR markers have become the marker class of choice as SSR markers are highly reproducible, co-dominant and abundant in genome (Saha et al. 2004). Utilising SSR markers in polyploid species remained uncertain, because of their allelic and co-dominant nature. In such cases, SSR markers are analyzed by considering them as dominant markers. It has been examined that SSR markers

are still an effective tool for genotyping polyploid species because reproducible alleles per locus are available in large numbers (Meena et al. 2020). The advantages of SSRs are that they are abundantly present and dispersed in all genomes with high levels of polymorphism in comparison to other markers. As a disadvantage, analysis of SSR is a time consuming and an expensive process especially when it comes to library creation.

Restriction fragment length polymorphism (RFLP)

Konzen et al. (2017) recommended RAPD-RFLP for the analysis of divergence among bamboo species and their genetic diversity. They recommended RAPD-RFLP as an informative and reproducible technique for screening differences among species of bamboo. Providing an accurate and cost-effective method for identification of species and their characterization which would result in breeding, management and

conservation of bamboo. PCR-RFLP is an alternative and simple technique for genotyping bamboos. In RFLP the PCR products are digested with different restriction enzyme combinations. The digested products are then separated with the help of gel electrophoresis. PCR-RFLP has been regularly conducted by digesting PCR products of Internal Transcribed Spacer (ITS) regions in plant (Biswas et al. 2016) and genomes and organelle gene. Based on the TrnL-trnF region, some studies have been performed on bamboo species *schizostachyum* and *arundinaria* to determine phylogeny respectively (Yang et al. 2007; Qiang et al. 2005). Multigene phylogenetic studies including TrnL-trnF have been performed to sort out significant phylogenetic groupings within *Bambusoideae* (Sungkaew et al., 2009). Similar study was conducted by Sen et al. (2014) to study the phylogeny of bamboos encountered in North Bengal (29 accessions) by amplification of TrnL-trnF region of chloroplast genome followed by restriction enzyme digestion

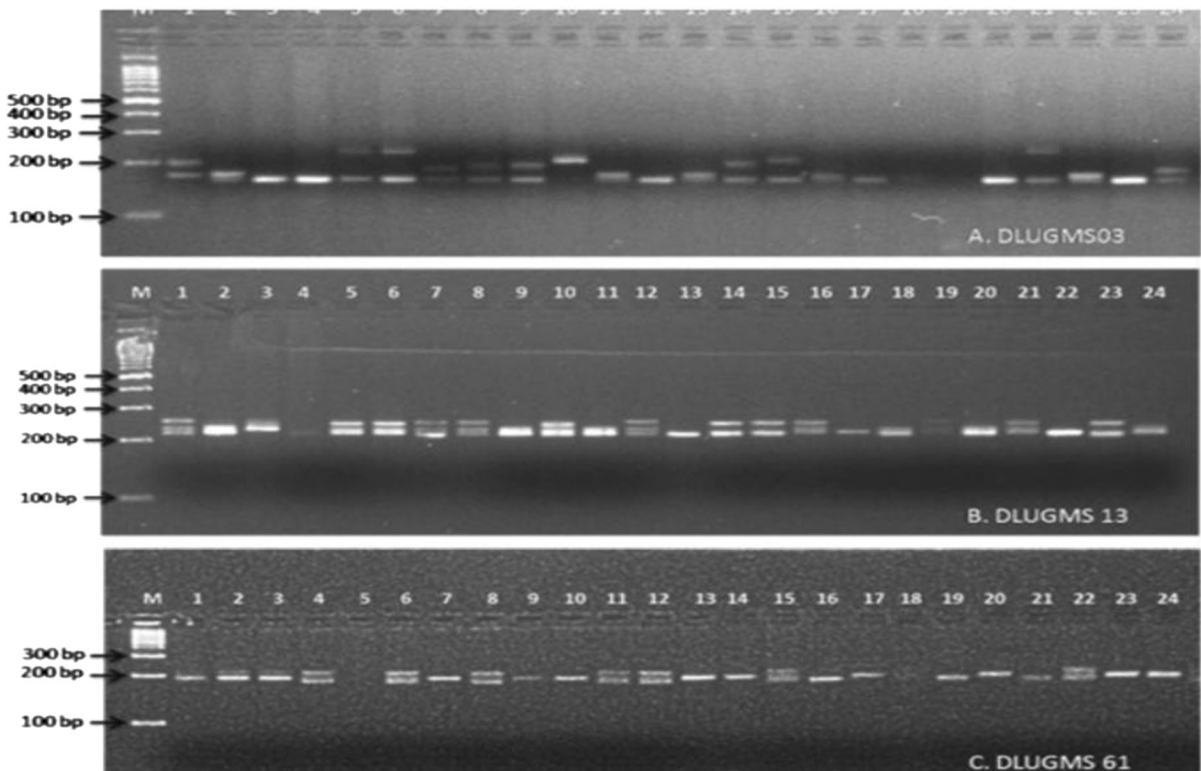


Fig. 7 SSR banding patterns generated by 3 different primer sets using 24 random *Dendrocalamus hamiltonii* samples (Source: Meena et al. 2019). Lane M-100 bp DNA ladder; Lane 1 to 24 represents 24 random samples

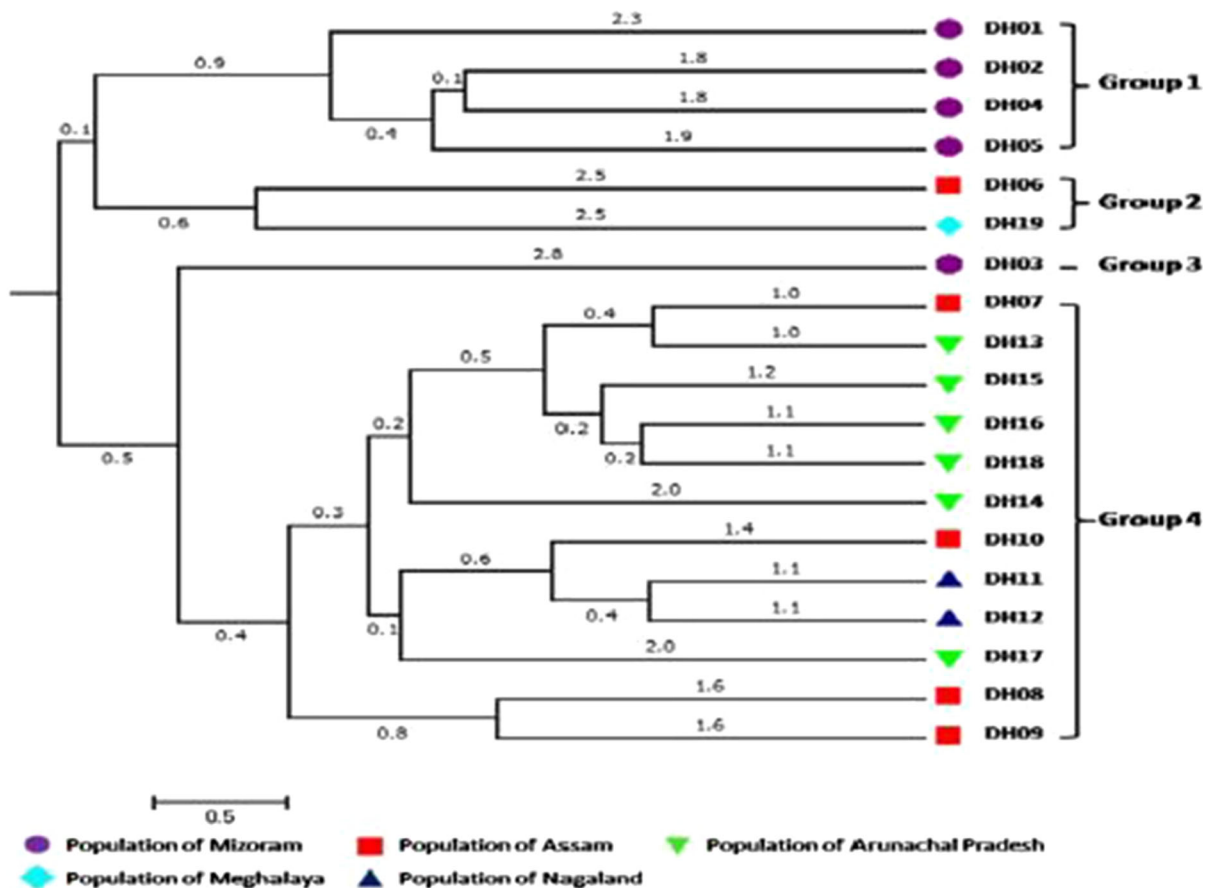


Fig. 8 Dendrogram showing genetic distance among nineteen populations of *Dendrocalamus hamiltonii* (Source: Meena et al. 2019)

using TaqI, AluI and HinfI Restriction enzymes and showed considerable polymorphism among the bamboo species in non-coding regions of the genomic DNA (chloroplast). The different restriction digestion enzymes produced in total of Nineteen Scorable bands which ranged from 200 to 1986 bp. Out of the 19 bands, 9 bands were polymorphic and the band number varied from 1 in HinfI and TaqI to 7 in AluI (Figs. 9, 10). Two clusters were made in the dendrogram formed. The first cluster consisted of 21 bamboo accessions and this cluster is further divided into 2 groups. The first group with 18 species, included 10 species of *Bambusa* from the 12 species of *Bambusa* studied. Two species *Pseudosasa japonica* (B25) and *Himalayacalamus hookerianus* (B21) were included in the second group of the first cluster. *Phyllostachys nigra* (B23) is completely isolated and in the similar way *Shibataea kumasaca* (B27) and *Melocanna baccifera* (B22) is separated from other bamboo

species. The second cluster comprised of 5 species of which *B. multiplex* ‘Rivierorum’ (B4), *Bambusa multiplex* ‘Alphanso Karr’ (B2) and *Cephalostachyum latifolium* (B13) clustered under the same sub-group (Fig. 11).

Since RFLPs are co-dominant, they are able to distinguish between heterozygotes and homozygotes. They are highly reproducible, stable, locus specific and are transferable across the population hence prove to be a reliable method. The requirement of high quality and quantity of DNA put RFLPs on the back side and they are not neutrally selective as radiolabeled probes are required. These are time consuming, expensive and labor-intensive procedures which are many of its limitations.

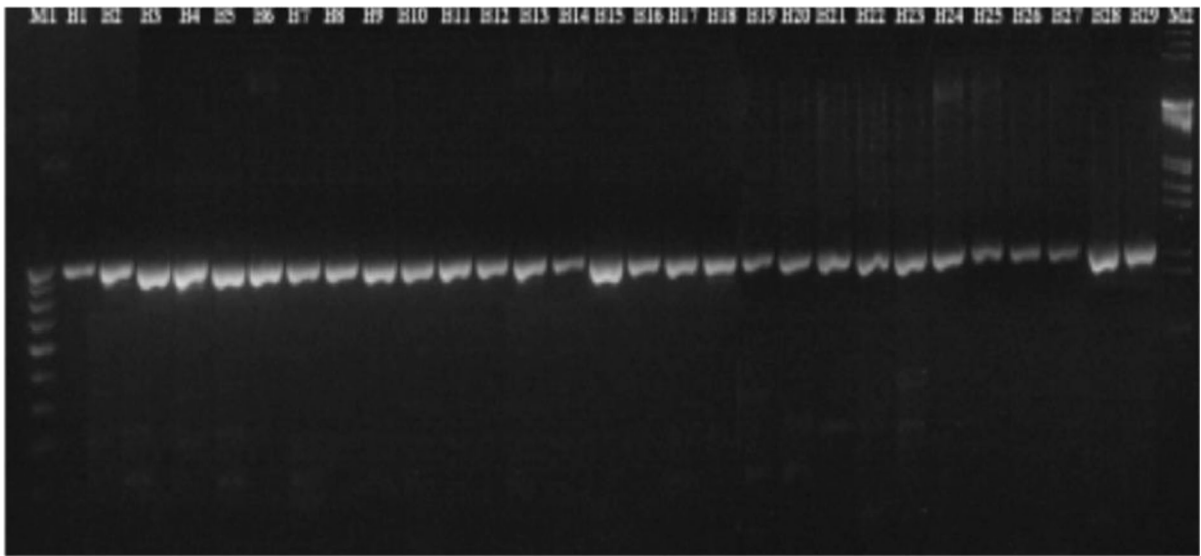


Fig. 9 Gel showing amplified bamboo accessions with primer Tabc-f(TrnL-trnF) (Source: Sen et al. 2014)

Amplified fragment length polymorphism (AFLP)

AFLP is another class of markers which were screened for defining phylogenetic relationships and detecting genetic variability among bamboo species in India (Waikhom et al. 2012) and Singapore (Loh et al. 2000). The DNA fingerprinting technique Amplified fragment length polymorphism (AFLP) is a novel technique that allows precise characterization of DNA under tough experimental conditions. AFLP helps to explore the entire genome within a short period of time. Thus, this method is useful for identification of genotype within a short duration of time with precision. AFLP integrated with automated fluorescence dye-labelling is a recent technique and in comparison, with conventional AFLP technique has advantage of precision, enhanced resolution and analytical power for higher reproducibility and large-scale DNA fingerprinting (Ghosh et al. 2011). Mehta et al. (2011) for the first-time reported analysis of tissue culture raised plants and somatic embryogenesis using AFLP fingerprinting technique in *B. nutans*. Similarly, Ghosh et al. (2011) conducted AFLP analysis on 12 distinct edible species of bamboo from Manipur belonging to 5 genus of tribe *Bambuseae* (including *Bambusa* and *Dendrocalamus*) to study the genetic diversity in different bamboo species in this hotspot region. Pattanaik and Hall (2011) investigated relationships among ten *Dendrocalamus* and five outgroup species

(*Dinochloa maclellandii*, *Oxytenanthera abyssinica*, *Thyrsostachys siamensis*, *Melocalamus compactiflorus* and *B. balcooa*) from subtribe *Bambusinae*. Waikhom et al. (2012) used AFLP technique with automated DNA sequencing to study the genetic relationship between *D. hamiltonii* and they also determined the specific association between biochemical traits (antioxidant and total cyanide content) and AFLP markers. Nag et al. (2013) studied 28 accessions of *O. travancorica* viz., OT1-OT28 collected randomly from dense forest of Kerala (southern region). Eight set of primers with good amplifications were utilized for the analysis of AFLP, which produced scorable band with an average of 75.3 bands per primer. The AFLP banding pattern of 28 accessions of *O. travancorica* generated by primer combination EACG-MCAC is depicted in Fig. 12. Dendrogram constructed based on AFLP analysis separated 28 accessions of *O. travancorica* into 3 major groups. Twenty accessions of OT collected from district Pathanamthitta were grouped into two different groups (I and II), while eight accessions of OT collected from Thrissur, Idukki and Ernakulam districts were grouped together in group II (Fig. 13). AFLP markers give fingerprints which are highly informative as a large number of bands are generated in this technique. Other advantages of AFLPs include quick scanning of the whole genome for polymorphism detection, high reproducibility and no need of prior information of

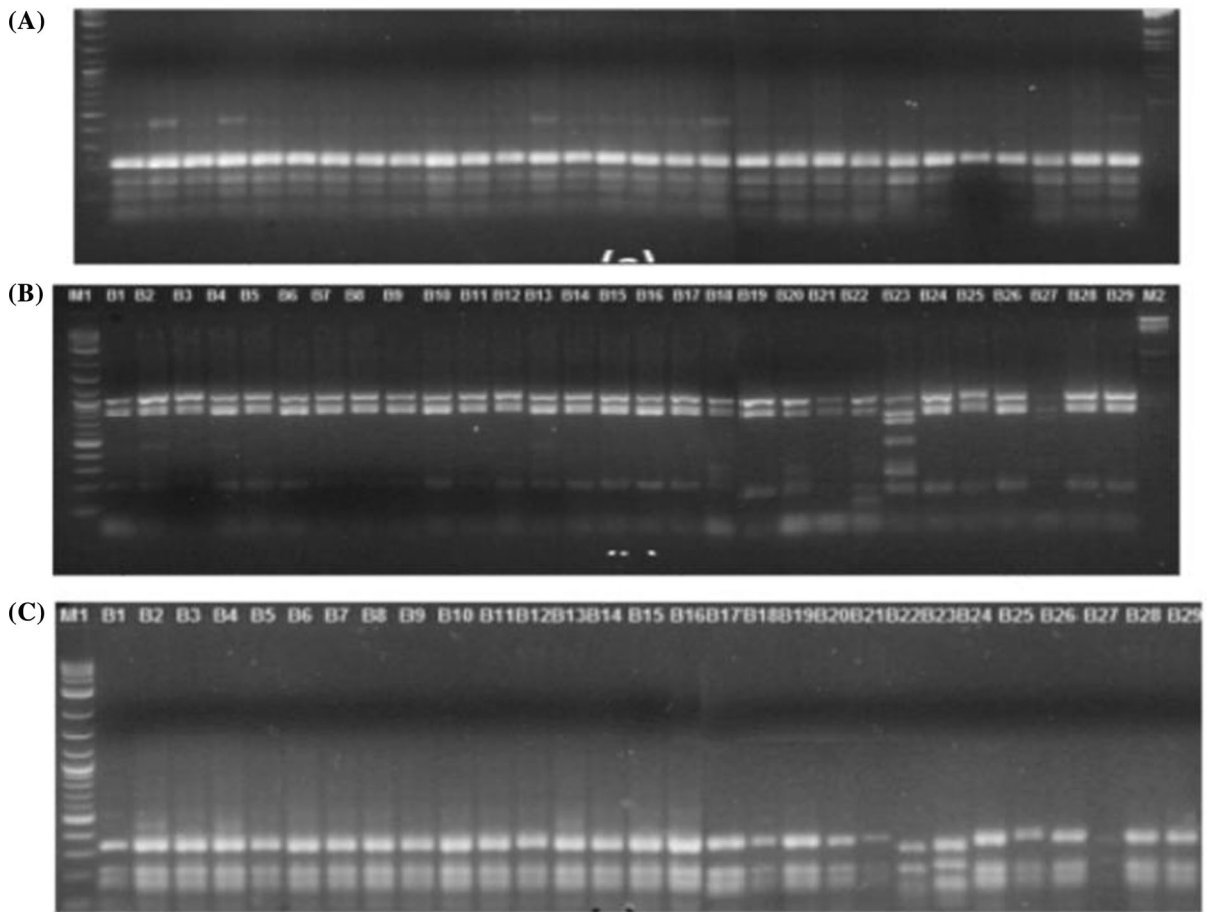


Fig. 10 Products of TrnL-trnF region of genome(chloroplast) digested with different restriction enzymes **a** TaqI; **b** AluI; **c** HinI. Lane-B1 to B29 with different species studied; Lane

M1-0.1-10 kb DNA ladder; Lane M2-lambda DNA/EcoRI/HindIII double digest DNA ladder (Source: Sen et al. 2014)

sequence. On the other hand, there are some disadvantages of AFLP. Since there are huge quantities of information generated, the data obtained may need automated analysis which is a daunting task and also, they are dominant in nature. AFLPs have a time cluster at telomeres and centromeres in genetic mapping which may interfere with the data collection.

Sequence characterized amplified regions (SCARs)

Sequence characterized amplified regions (SCARs) are PCR-based markers that are extension or modification of RAPD with better reproducibility because of higher annealing temperature (Rangsiruji et al. 2018). SCARs have been useful in genotypic

identification (Rangsiruji 2018). Especially, at the seedling stage when the vital morphological characters are unable to differentiate. Das et al. (2008) designed 2 species-specific SCAR markers, ‘Tuldo609’ for *B. tulda* and ‘Balco836’ for *B. balcooa* from sequenced, putative species-specific, RAPD bands for accurate species identification. Figures 14 and 15 show the amplified band generated by designed SCAR primers ‘Balco836’ in *B. balcooa* and ‘Tuldo609’ in *B. tulda* respectively.

Other molecular markers employed to study bamboo species around the world

The availability of bamboo genome (<http://www.bamboogdb.org>, BambooGDB) have enabled

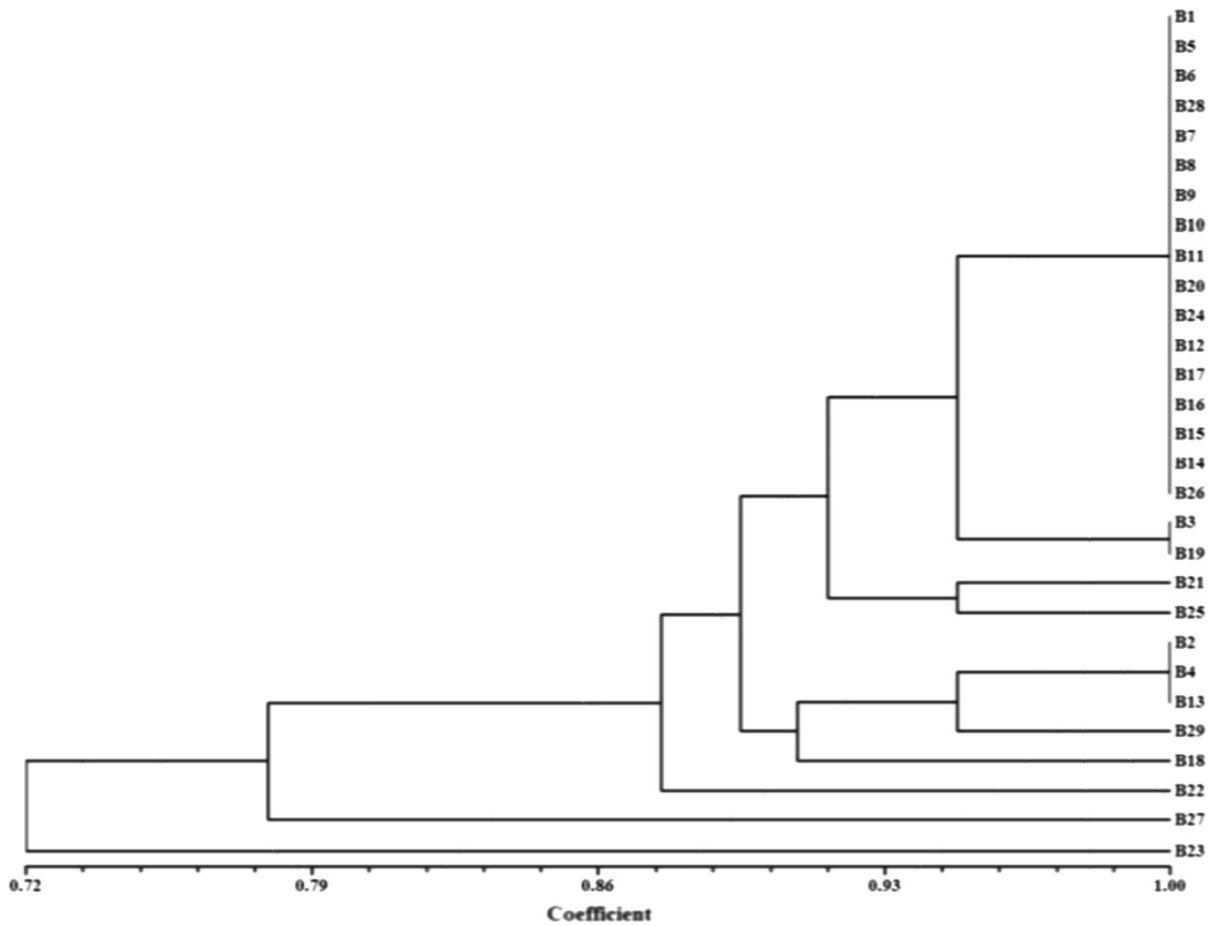


Fig. 11 Dendrogram based on digested products of TrnL-trnF genome with different restriction enzymes (Source: Sen et al. 2014)

different researchers to use other molecular marker techniques also and these markers have not been used frequently as compared in the molecular characterization of bamboo and that too specifically Indian bamboo (Poczai et al. 2013; Zhao et al. 2014). Some of these techniques which have been employed are SCoT (Start codon Targeted); IRAP (Inter-Retrotransposon amplified polymorphism); SRAP (Sequence related amplified polymorphism); SNP (Single nucleotide polymorphism); SRAP (Sequence related amplified polymorphism).

Start codon targeted (SCoT) polymorphism

Start Codon Targeted (SCoT) polymorphism is a novel molecular marker technique that targets ATG start codon regions in plant genes (Collar and Mackill 2009). It has various advantages over ISSR, AFLP and

RAPD, as it produces more reliable and reproducible bands. This marker is also an effective technique for assessing genetic variation, population studies and DNA fingerprinting (Collar and Mackill 2009; Etmnan et al. 2016; Hao et al. 2018). SCoT markers have been used to study the genetic fingerprinting and genetic diversity in rose (Agarwal et al. 2019), kalmegh (Tiwari et al. 2016), orchard grass (Zeng et al. 2014), *Jatropha L.* (Mulpuri et al. 2013) and mango (Luo et al. 2010). Amom et al. 2020 studied the efficiency of marker techniques such as RAPD, ISSR, iPBS and SCoT in determining the genetic relationship between four economically important and native bamboo species of North-east India (*B. cacharensis*, *B. mizorameana*, *D. manipureanus*, *D. sikkimensis* and *D. hamiltonii*). They reported that of all the above markers, SCoT markers produced the highest number

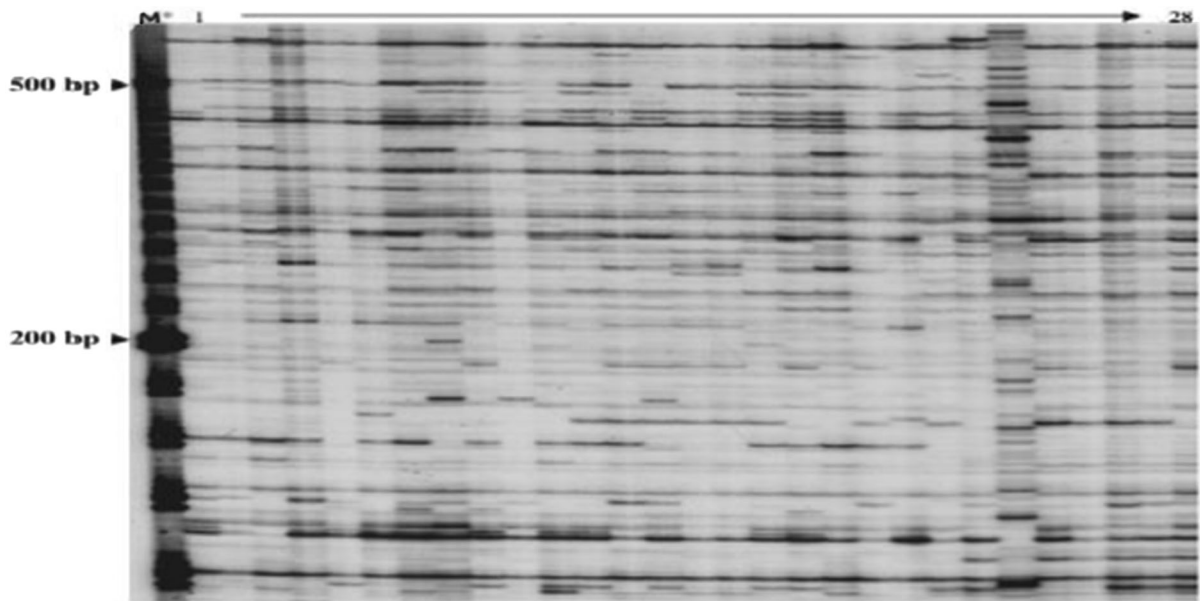


Fig. 12 Gel showing amplified products generated by primer combination EACG-MCAC; lane M-20 bp DNA ladder, lane 1–28 amplified bands of different *O. travancorica* (Source: Nag et al. 2013)

of bands per primer depicting high efficiency compared to other markers.

Inter-retrotransposon amplified polymorphism (IRAP)

Another molecular marker group which is widely used in assessing genetic relationships and variability are Inter Retrotransposon Amplified Polymorphism (IRAP). These markers can be generated with the help of one or two primers and amplify the regions in between two long terminal repeats (LTRs). IRAP markers are widely employed in the study of cladistic relationship and genetic diversity analysis (Mansour 2008; Ramakrishnan et al. 2019; Gozukirmizi et al. 2015; Ramakrishnan 2019). LTR retrotransposons are highly abundant in bamboo (46%) which contribute to the diversity of the genome. These LTR retrotransposons are the main class (Class I) of mobile genetic elements in the genome of plants. The interspaces of retrotransposons can significantly vary among bamboo species because of their random behavior of insertion. Taking advantage of this feature, IRAP is an efficient marker system to evaluate the genetic diversity of plant species (Kalendar et al. 1999). To date, there is only one transposon-based marker reported by

Li et al. (2020) from the genome of bamboo, particularly using IRAP markers to study the genetic diversity of 58 Asian bamboo species. The availability of bamboo genome (<http://www.bamboogdb.org>, BambooGDB) helped in a comprehensive investigation of LTR-retrotransposons and their copy numbers which enabled for development of 16 IRAP primers (CL3-F;CL4-R;CL15-R;CL22-F;CL22-R;CL34-F;CL34-R;CL37-F;CL37-R;CL42-R;CL54-R;CL58-F;CL59-F;CL61-F;CL62-F;CL63-R) with clear and distinguishable amplification which generated an average of 13.3 polymorphic alleles per primer. Based on IRAP analysis, 58 accessions of *Phyllostachys* were clustered into five groups. He concluded from the IRAP polymorphism pattern that LTR retrotransposons notably lack polymorphism among 58 bamboo accessions under study of their abundance in the genome of bamboo; only 29% IRAP markers showed polymorphism. This insufficiency of IRAP polymorphism suggested that the inter-LTR regions were conserved significantly in the studied bamboo species which implies that in the contribution of genome wide variation, LTRs are not much active and the genome of bamboo is still under evolution. Another type of retrotransposon-based marker technique is inter Primer Binding Site amplification (iPBS) which is not

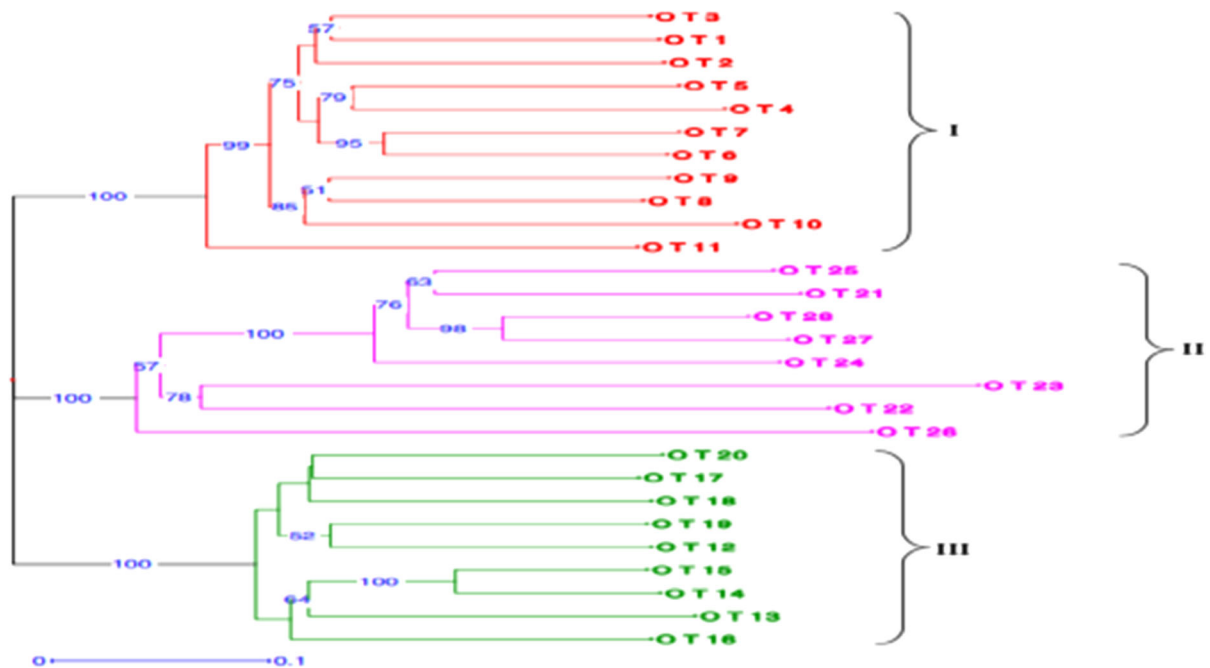


Fig. 13 Dendrogram showing relationship among *O. travancorica* based on 8 AFLP and 42 RAPD markers (Source: Nag et al. 2013)

much used to study the genetic diversity in bamboo especially in Indian bamboo. Amom et al. (2020) has mentioned the use of iPBS and other markers like RAPD, RFLP and SCoT to check their efficiency in genetic relationship studies in five native bamboo species of North-east India.

Single nucleotide polymorphism (SNPs)

Because of their high abundance of source polymorphism, single nucleotide polymorphism (SNPs) has become a good choice of marker type but producing variable genetic markers with single-nucleotide polymorphisms (SNPs) is many a time difficult (Blair et al. 2013). However, next generation sequencing (NSGs) offers great possibility to produce large scale sequence data at reasonable cost from non-model organisms (Galindo and Ekblom 2011). For instance, the evolutionary relationship among 6 woody species of bamboo was resolved by the application of complete chloroplast genome (Zhang et al. 2011). The relationship among closely related species is better resolved by the study of their nuclear data. However, temperate bamboo being tetraploid in nature introduces additional challenges for the development of SNP markers

(Gielis et al. 1997a, b; Peng et al. 2013). One of the methods to reduced-representation of genomics is restriction site associated DNA (RAD) sequencing. RAD helps in the sequencing of short fragments of DNA flanking the cut sites of restriction enzymes, which allows identification of orthologous sequences across multiple samples to be targeted and score various genetic markers (Baird et al. 2008; Emerson et al. 2010). Till date, this RAD sequencing method is successfully applied to discover SNP in eggplants (Barchi et al. 2011), sunflowers (Andrew et al. 2013) and other organisms. Thus, RAD sequencing can identify a huge number of SNPs for analysis, even without a genome of reference. Wang et al. (2013) identified SNP markers to study the phylogenetic relationship among temperate bamboo species (*Arundinaria faberi* and *Yushania brevipaniculata*) using RAD sequencing. After filtering and grouping, Wang et al. (2013) recovered 29,443 presumed orthologs shared among the four populations of *Arundinaria faberi* and *Yushania brevipaniculata*, for a length of 2,129,079 bp which included 28,023 variable sites, out of which 13,650 were fixed between species; the rest were polymorphic. The rate of SNPs occurring was 0.95 SNP/RAD tag. To date, there are not any

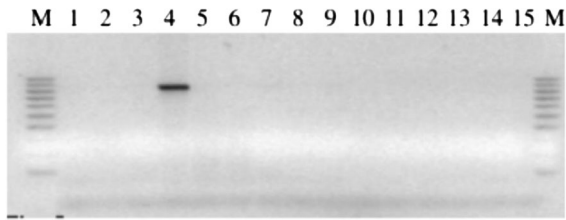


Fig. 14 Gel showing presence of amplified band from the genomic DNA of *Bambusa balcooa* using ‘Balco836F’ and ‘Balco836R’ SCAR primer pairs and there are no amplified bands in the other 14 species of bamboo (Source: Das et al. 2008)

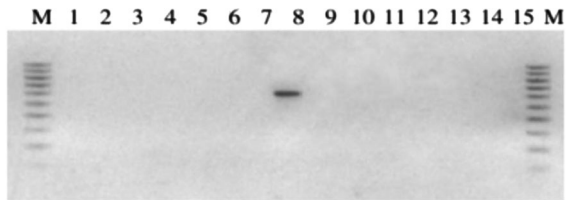


Fig. 15 Gel showing presence of amplified band from the genomic DNA of *Bambusa tulda* using ‘Tuldo609F’ and ‘Tuldo609R’ SCAR primer pairs and also there is no amplified bands in the other 14 species of bamboo (Source: Das et al. 2008)

genetic diversity studies done in Indian bamboo using SNP markers.

Sequence related amplified polymorphism (SRAP)

Genetic diversity among bamboo species using SRAP (sequence-related amplified polymorphism). Due to overexploitation and genetic erosion, there was a requirement for bamboo germplasm establishment and in this context Zhu et al. (2013) collected 13 species of bamboo from different regions of China. Examination of genetic relationships among species was done using different morphological and molecular markers. For molecular relationship, SRAP analysis was done. The SRAP analysis consisted of amplification of ORFs (open reading frames) using PCR. For this, 2 types of primer combinations were used. The forward primer was 17 bp in length containing GC rich 14 nucleotides and the reverse primer was 18 bp in length containing AT rich 15 nucleotides which amplifies promoter and intronic regions preferentially, which are generally AT rich. Feng et al. 2010 using SRAP and AFLP

molecular markers analyzed genetic relationships within 9 bamboo species. Total 359 bands were generated by 12 AFLP primer combinations and 258 bands by 24 SRAP primer combinations. But until now, there have been no such papers which have reported the use of SRAP technique to characterize Indian bamboo species.

Conclusion

Genetic erosion and over-exploitation of bamboo have made conservation and collection of bamboo germplasm indispensable. For this, accurate identification and evaluation of bamboo species is very important. Since, morphological markers are greatly influenced by environmental aspects and thus cannot be considered much reliable for identification and genetic relationship study. The knowledge of genetic diversity and relationship in bamboos is still constricted despite various studies due to irregular flowering pattern and improper phenotypic variations. With emerging molecular markers, the knowledge of diversity between different varieties is possible. For molecular characterization of bamboo, the different molecular markers used are RAPD, RFLP, AFLP, ISSR and SSR out of these the frequently used technique is RAPD because of its low-cost, speed and efficiency which generate large marker numbers in a short period as compared to other techniques. However due to several limitations associated with the use of RAPD, ISSRs are the marker of choice to study the genetic diversity in Indian bamboo species. RFLP, due to low polymorphism, is not used frequently. AFLP on the other hand, is technically tough to handle with multi step procedures, hence not chosen by many laboratories. Meanwhile, SCARs can be used efficiently for genotype identification with highest accuracy. While talking about other molecular marker types which are used around the world there are many which are employed to study plant diversity, out of which few are used in diversity studies of bamboo species. The availability of the bamboo genome database has given an insight into the development and use of SCoT, IRAP, SRAP and SNPs markers in bamboo species. This review will provide information on availability of different molecular markers to identify diversity in Indian bamboo species. It will give an ease of access to different researchers working in the field of bamboo to

design primer for different markers accordingly. It will provide information on availability of markers to identify diversity in Indian bamboo species. It will give an ease of access for different researchers working in the field of bamboo to design primer for different markers accordingly. For ex-situ and in-situ conservation of available species of Bamboo, it is very important to fingerprint this for proper utilization. Apart from conservation, fingerprinting based diversity study will also help in proper breeding of Bamboos for its improvement program. This highlights the likelihood and future trends in molecular markers and its application in bamboo. Undoubtedly, the most important application is the precise identification of genotypes of bamboo and the genetic variation assessment within species.

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Declarations

Conflict of interest The authors declare that they have no conflict of interests.

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