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Polyploidy in the Ginger Family from Thailand

Kesara Anamthawat-Jónsson and Puangpaka Umpunjun

Abstract

Polyploidy is common in the ginger family Zingiberaceae. The aims of the present paper are (1) to provide a general introduction on species diversity with emphasis on conservation; (2) to highlight the human-use significance of this family, focusing on the two major genera, *Zingiber* (ginger) and *Curcuma* (turmeric); (3) to present chromosome number data from 45 natural and cultivated *Curcuma* taxa from Thailand, of which polyploids are predominant; and (4) to describe our own work on cytotaxonomy of selected Thai *Curcuma* species. We obtained somatic chromosome numbers from root tips and analysed meiotic chromosome behaviour from flowers. We also used the molecular cytogenetic method of ribosomal gene mapping on chromosomes to infer mechanism of polyploidization and reveal genomic relationships among closely related species. The main results of our cytogenetic studies include the following. The most sought-after medicinal *Curcuma* cultivars growing on a large-scale basis are secondary triploids, so as taxa in natural habitats that are harvested for local utilisation. These triploids are sexually deficient, due to meiotic pairing abnormalities, but they are propagated asexually via rhizomes. The ribosomal mapping results indicate natural triploidization process via hybridisation, either within populations or across the species boundaries.

Keywords: *Curcuma*, cytogenetics, cytotaxonomy, ethnobotany, ginger, medicinal plants, polyploidy, triploidy, turmeric, *Zingiber*

1. Introduction

Taxonomic classification of the ginger family (Zingiberaceae) is still under revision for many floras, as more than 3000 species names have been used worldwide, but only half of these are accepted. These aromatic herbs grow in moist areas of the tropics and subtropics, including some regions that are seasonably dry. The ginger family comprises about 50 genera and more than 1300 species worldwide, and in Thailand 21 genera with about 200 species have been described. Numerous species are endemic to Thailand, but the majority has a wider distribution, especially over Southeast and South Asia. A few species of this family are commercially cultivated, such as ginger (*Zingiber officinale* Rosc.), turmeric (*Curcuma longa* L.) and aromatic ginger (*Kaempferia galanga* L.). Interestingly, these widely cultivated species are sexually deficient triploid or pentaploid plants—the elite cultivars are therefore propagated by rhizomes. These polyploid species are superior to their diploid relatives in terms of growth and yield, while the sought-after quality characters remain unchanged.

2. The ginger family (Zingiberaceae), with emphasis on *Curcuma*

The ginger family or Zingiberaceae comprises about 50 genera and more than 1300 species worldwide [1, 2]. The family distribution is pantropical, with centre of species diversity in South and Southeast Asia. Some species are found in America and subtropical and warm-temperate Asia. In China, 20 genera and 216 species (141 endemic, four introduced) have been recorded [1]. Geographically, Thailand is part of the Indochinese region that harbours the highest ginger genetic resources [3, 4]. Several of these species are rare and endemic to Thailand [5]. A large number of Thai taxa of Zingiberaceae are known as edible, ornamental or medicinal plants, from which commercial products beneficial to human can be developed.

Two best known genera in the context of cultivation and human uses worldwide are *Zingiber* Miller (ginger) and *Curcuma* Linnaeus (turmeric). The largest genus *Zingiber*, which comprises 100–200 species, is native to Southeast Asia especially in Thailand [6], China [7], the Indian subcontinent and New Guinea [8]. It contains the true gingers, plants grown for their medicinal and culinary value. The best known is *Z. officinale*, the garden ginger.

Curcuma is a genus of about 120 accepted species in the family Zingiberaceae that contains such species as turmeric (*C. longa*) and Siam tulip (*C. alismatifolia* Gagnep.). They are native to Southeast Asia, southern China, the Indian subcontinent, New Guinea and northern Australia [6, 8–11]. Tropical Asia and South Asia are the diversity hotspots of the genus. Although the species diversity is very high and new species are being discovered regularly, other species are disappearing. Habitat loss, due to global warming, deforestation, agricultural expansion and anthropogenic activities, is one of the main causes of biodiversity loss worldwide [12–14]. In addition, overharvesting for use in traditional medicine has raised a serious concern that wild plants will be disappearing from nature.

According to the IUCN Red List of Threatened Species, seven *Curcuma* species have been declared endangered to extinction (EN) and six additionally critically endangered (CR). The endemic EN species are *C. caulina* J. Graham, India [15]; *C. colorata* Valetton, Indonesia [16]; *C. coriacea* Mangaly & M. Sabu, India [17]; *C. corniculata* Skornick., Lao [18]; *C. prasina* Skornick., Thailand [19]; *C. sahyinhensis* Skornick. & N.S. Lý, Vietnam [20]; and *C. vitellina* Skornick. & H.D. Tran, Vietnam [21]. The endemic CR species are *C. bhatii* (R.M.Sm.) Skornick. & M. Sabu, India [22]; *C. leonidii* Skornick. & Luu, Vietnam [23]; *C. newmanii* Skornick., Vietnam [24]; *C. pygmaea* Skornick. & Sida f., Vietnam [25]; *C. supraneeana* (W.J. Kress & K. Larsen) Skornick., Thailand [26]; and *C. vamana* M. Sabu and Mangaly, India [27]. There clearly is an urgent need to protect these *Curcuma* species in their natural habitats while at the same time encouraging ex situ conservation and supporting researches aiming to find viable methods for sustainable cultivation of species of economic potential.

3. Recent publications on the ginger family

The survey of recent (2019) publications on Zingiberaceae in the Web-of-Science database, using “ginger” as keyword in titles (**Figure 1**), shows that the genus *Zingiber* (ginger) is by far the most investigated worldwide. The most researched topics concern medicinal properties and health benefits of ginger (1); pharmaceutical, biochemical and molecular characterisation (2); applications in food science and chemistry (3); other technologies and industrial applications (4); as well as some effort in improving cultivation (5). On the other hand, research on *Zingiber* diversity, taxonomy, ecology and genetics (6) is limited.

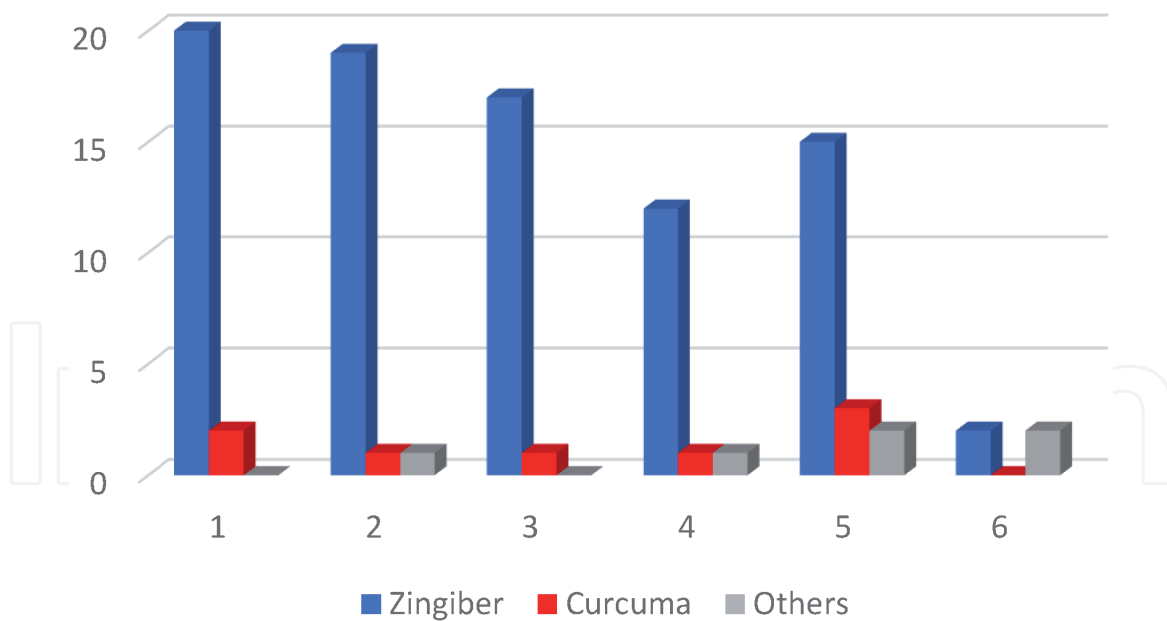


Figure 1.
Distribution of recent publications by research topics in 2019, obtained from web-of-science database (webofknowledge.com/WOS_), using the single keyword “ginger” in title. Research topics (x-axis): 1, medicinal properties and health benefits; 2, pharmaceutical, biochemical and molecular research; 3, food science and chemistry; 4, other technologies and industrial applications; 5, cultivation and agriculture; and 6, biodiversity, taxonomy, ecology and genetics. Y-axis: Percentages of the number of publications in 166 totals. Blue columns include papers on Zingiber, ginger, gingerols and ginger-related topics. Red columns include papers on Curcuma, turmeric, curcumins and related topics. Grey columns include other species in the ginger family Zingiberaceae.

Ginger (*Z. officinale*) is a very popular spice used worldwide, whether it be used to spice up meals, or as a medicine [28]. Ginger can be used for a variety of food or medicine items, as vegetables, candy, soda, pickles and alcoholic beverages. It is one of the most versatile, ancient, significant, medicinal, nutritional herbs with several ethnomedical values. This plant is recognised due to its therapeutic properties, including antibiotic, antimicrobial, antioxidant and anti-inflammatory effects [29]. Phenolic acids, diarylheptanoids, terpenoids and flavonoids are reported to exist in ginger rhizomes [30]. A list of 72 gingerols and diarylheptanoids derivatives from ginger rhizomes is presented in Asamenew et al. [31], and among these compounds, gingerol- and shogaol-related derivatives are the principal medicinally active components contributing to the characteristic pungent flavour of ginger together with essential oil major component, zingerone. These bioactive compounds have been shown in experiments to be effective for inflammatory diseases [32] and osteoarthritis [29], to help induce apoptosis in cancer cells [33] and to show anti-leukaemic effect [34]. Ginger has a great pharmaceutical potential.

Our survey of recent (2019) publications on Zingiberaceae in the Web-of-Science database, using “*Curcuma*” as keyword in titles (**Figure 2**), shows that *C. longa* (turmeric, saffron turmeric) is the single most researched *Curcuma* species. The results show that this species has received much attention in the area of pharmaceutical research and medicinal applications. Turmeric is commonly used as spice, dye, drug and cosmetics [35], but recent research efforts have further characterised its medicinal properties and have identified its biochemical components in high resolution and specificity. The genus *Curcuma* is rich in flavonoids, tannins, anthocyanin, phenolic compounds, oil, organic acids and inorganic compounds [36]. The biological activities of *Curcuma* have been attributed to the non-volatile ingredients of the rhizome, cucurminoids (e.g. curcumin), as well as to the volatile terpenoids [37]. Curcumin has been shown in experiments to have strong anti-inflammatory and antioxidant effects [29, 36]. The European Union has

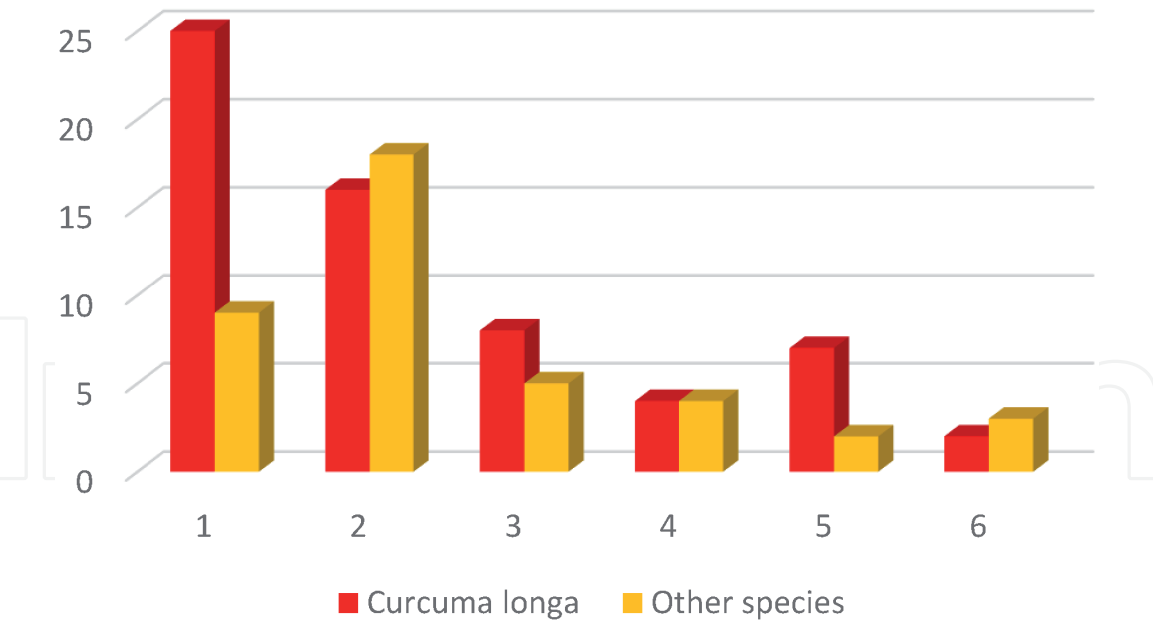


Figure 2. Distribution of recent publications by research topics in 2019, obtained from web-of-science database (webofknowledge.com/WOS_), using the single keyword “Curcuma” in title. Research topics (x-axis): 1, medicinal properties and health benefits; 2, pharmaceutical, biochemical and molecular research; 3, food science and chemistry; 4, other technologies and industrial applications; 5, cultivation and agriculture; and 6, biodiversity, taxonomy, ecology and genetics. Y-axis: Percentages of the number of publications in 200 totals. Red columns include papers on *Curcuma longa* (turmeric). Yellow columns include papers about all other *Curcuma* species, e.g. *C. zedoaria* (white turmeric, 7%), *C. caesia* (black turmeric, 5%), *C. xanthorrhiza* (Javanese ginger/turmeric, 5%), *C. amada* (mango ginger, 5%), *C. aromatica* (fragrant turmeric, 3%) and 17 other *Curcuma* species with less than 3% each.

recommended the use of numerous medicinal plants for the treatment of gastrointestinal disorders, and among them are ginger root (*Z. officinale*) and turmeric root (*C. longa*) [38].

Some 23 other *Curcuma* species have recently been explored in search for new medicinal applications (**Figure 2**). The top five *Curcuma* species investigated are *C. zedoaria* (Christm.) Rosc. (white turmeric, native to South and Southeast Asia, cultivated in Thailand), *C. caesia* Roxb. (black turmeric, native to Northeast India, natural species of Thailand), *C. xanthorrhiza* Roxb. (Javanese ginger/turmeric, originated from Java island, cultivated in Thailand), *C. amada* Roxb. (mango ginger, originated from East India, natural species of Thailand) and *C. aromatica* Roxb. (fragrant turmeric, natural species of South Asia, cultivated in Thailand). Bioactive ingredients, including terpenes (more than 40 monoterpenes and sesquiterpenes), antioxidants flavonoids and phenolic compounds are present in all these species [39, 40]. Curcumin from *C. zedoaria*, as from *C. longa*, shows good anti-inflammatory effects [36]. Zederone and zedoarondiol, from rhizomes of En-Lueang (*Curcuma* cf. *amada*), show strong cytotoxicity in a leukaemic cell line and in peripheral blood mononuclear cells, as well as having antioxidant and haemolysis properties [41]. Dry extracts from rhizomes of *C. xanthorrhiza* and *C. zedoaria* have been shown to have anticancer and antiviral properties [42–44]. Furthermore, volatile oils extracted from leaves of *C. caesia* have broad antioxidant, anti-inflammatory and antimicrobial effects in vitro [45, 46]. In contrast to *C. longa*, many of the medicinal *Curcuma* species are not in large-scale cultivation, and this increases the risk of overharvesting of rhizomes from wild plants. The good news is that researchers are beginning to improve local cultivars and finding suitable methods of micropropagation of these *Curcuma* species, for example, *C. angustifolia* Roxb. [47].

4. The genus *Curcuma* in Thailand

Forty-five species are found in Thailand or almost 50% of the total species diversity of *Curcuma* worldwide (**Table 1**). At least 12 of these species are endemic to Thailand. New species have recently been described. For example, *C. saraburiensis* Boonma & Saensouk from Saraburi province, Central Thailand [48] and *C. putii* Maknoi & Jenjitt [49]. Several species of *Curcuma* are cultivated throughout Thailand for commercial purposes. The whole plant has economic values: the above-ground part of the plant bears attractive flowers that have been exported worldwide as cut flowers, such as Siam tulip (*C. alismatifolia*) and *C. parviflora* Wall. [50], whereas the below-ground rhizomes are harvested and sold in local markets for use as crude extracts in the traditional medicine or for the production of certified pharmaceutical products. Medicinal species, such as *C. comosa* Roxb., has received much attention in recent years for being a phytoestrogen-producing plant (e.g. [51, 52]). Products from rhizomes of *C. comosa* have been developed for use as an anti-inflammation remedy and for treatment of uterine abnormalities and ovarian hormone deficit [53, 54].

Species of <i>Curcuma</i> L.	2n chromosome number	Ploidy	Natural	Cultivated	References
<i>C. aeruginosa</i> Roxb.	63	Triploid		x	4, 6, 9
<i>C. alismatifolia</i> Gagnep.	32		x	x	9
<i>C. amada</i> Roxb.	42	Diploid	x		1, 2, 4, 9, 10
<i>C. angustifolia</i> Roxb.	42 (64)	Diploid	x		4, 6, 9, 10
<i>C. aromatica</i> Roxb.	42, 63, 86	Di-, tri-, tetraploid		x	1, 2, 3, 4, 6, 7, 9, 10
<i>C. aurantiaca</i> van Zijp	42	Diploid	x	x	4, 6, 9, 10
<i>C. bella</i> Maknoi*, K. Larsen & Sirirugsaa					
<i>C. bicolor</i> J.Mood & K. Larsen			x	x	
<i>C. caesia</i> Roxb.*b	63	Triploid	x		9, 10
<i>C. candida</i> (Wall.) Techapr.*c	42	Diploid	x		12
<i>C. cochinchinensis</i> Gagnep.			x		
<i>C. comosa</i> Roxb.	42, 63	Di-, triploid	x	x	5, 9, 11
<i>C. ecomata</i> Craib			x		
<i>C. elata</i> Roxb.*d	63	Triploid		x	4, 5, 7, 9, 11
<i>C. flaviflora</i> S.Q.Tong	42	Diploid	x		7
<i>C. glans</i> K. Larsen & J. Mood			x		
<i>C. glacillima</i> Gagnep.	ca. 32		x		
<i>C. hermandii</i> Gagnep.	20		x	x	9
<i>C. latifolia</i> Roxb.	63, 84	Tri-, tetraploid	x	x	4, 5, 9, 11
<i>C. leucorhiza</i> Roxb.		Triploid		x	6,

Species of <i>Curcuma</i> L.	2n chromosome number	Ploidy	Natural	Cultivated	References
<i>C. longa</i> L.	63 (32, 48, 62-64)	Triploid		x	1, 2, 4, 6, 9, 10
<i>C. maehongson</i> <i>C. Maknoi</i>			x		
<i>C. mangga</i> Val.	42 (63)	Diploid		x	4, 9
<i>C. nakornsawan</i> <i>C. Maknoi</i>			x		
<i>C. parviflora</i> Wall.	28, 30, 32, 36, 42		x		9
<i>C. petiolata</i> Roxb.	42, 64	Di-, triploid	x	x	9, 10
<i>C. pierreana</i> Gagnep.			x		
<i>C. putii</i> Maknoi & Jenjitt.*e					
<i>C. ranong</i> C.Maknoi			x		
<i>C. rhabdota</i> Sirirugsa & M. Newman	24		x	x	9
<i>C. roscoceana</i> Wall.	42	Diploid	x	x	4, 9
<i>C. rubescens</i> Roxb.	63	Triploid		x	9
<i>C. rubrobracteata</i> Skornickova, Sabu & Prasanth k.	63	Triploid	x		7
<i>C. saraburi</i> C.Maknoi			x		
<i>C. saraburiensis</i> Boonma & Saensouk*f			x		
<i>C. singularis</i> Gagnep.	42		x		9
<i>C. sparganiifolia</i> Gagnep.			x	x	
<i>C. stenochila</i> Gagnep.			x		
<i>C. tak</i> C.Maknoi			x		
<i>C. ubonratchani</i> C.Maknoi			x		
<i>C. viridiflora</i> Roxb.			x		
<i>C. woodii</i> N.H.Xia & J. Chen*g	42	Diploid			8
<i>C. xanthorrhiza</i> Roxb.	63	Triploid		x	3, 6, 7, 9, 10
<i>C. zedoaria</i> (Christm.) Rosc.	63, 64, 84, 105	Tri-, tetra-pentaploid		x	2, 4, 6, 9, 10, 11
<i>C. cf. Zedoaroides</i> Chaveer. & Tanee*h	63	Triploid	x		11
Total number of taxa = 45			33	19	

*Species references: a, Maknoi et al. [55]; b, Puangpairote [56]; c, Jenjittikul and Larsen [57]; d, Larsen [6]; e, Maknoi et al. [49]; f, Boonma and Saensouk [48]; g, Chen et al. [58]; and h, Puangpairote et al. [59]. Chromosome/ploidy references: 1. Ramachandran [60]; 2. Ramachandran [61]; 3. eFlora [9]; 4. Leong-Skornikova et al. [10]; 5. Soontornchainaksaeng and Jenjitikul [51]; 6. Zaveska et al. [62]; 7. Chen et al. [63]; 8. Chen et al. [58]; 9. Puangpairote [56]; 10. Rice et al. [64]; 11. Puangpairote et al. [59]; 12. Nopporncharoenkul et al. [65].

Table 1.
List of *Curcuma* species found in Thailand, based on Maknoi [11] (except *), with 2n somatic chromosome number, ploidy level and distribution.

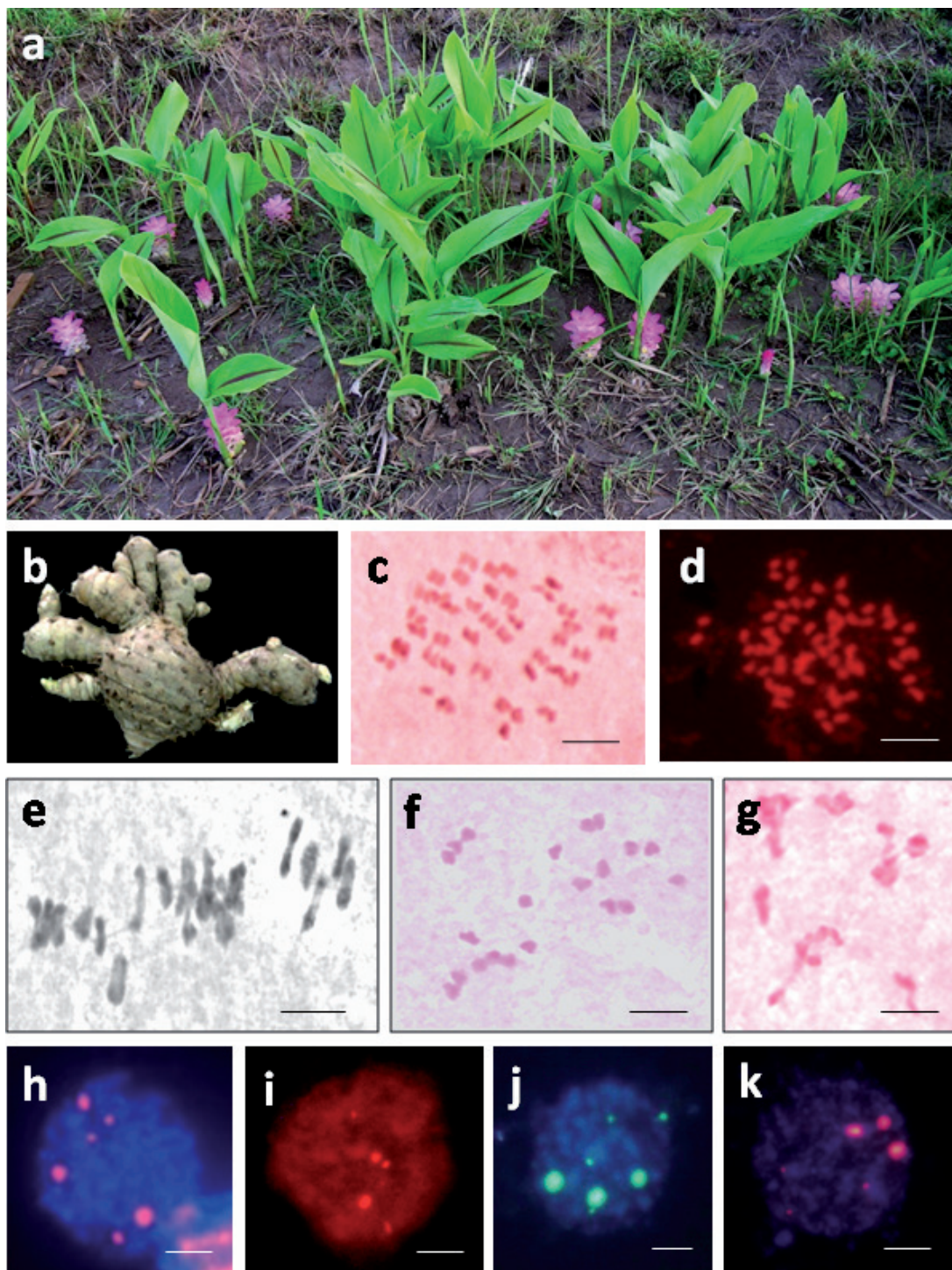


Figure 3.

Our own research work on selected *Curcuma* species from Thailand. (a) Triploid *Curcuma comosa* plants, showing the above-ground part of the plant with 60–150-cm-tall leafy shoots and 15–32-cm-long inflorescences with short peduncle and dark pink flowers. (b) Rhizome of the triploid *Curcuma* sp. “*elata-latifolia*”. Typical rhizome of this species is ovoid-ellipsoid in shape and about (7–15) × (6–10) cm in size, with 2–7 lateral rhizomes, 2–12 cm long and up to 5 secondary lateral rhizomes. (c) Mitotic metaphase cell of *C. candida* showing diploid chromosome number $2n = 42$. (d) Mitotic metaphase cell of *C. comosa* showing diploid chromosome number $2n = 42$. (e) Male meiotic cell of the diploid *C. candida* showing normal chromosome pairing with 21 bivalents at metaphase-I. (f) Male meiotic cell of the triploid cytotype of *C. comosa* showing chromosome pairing at metaphase-I with 21 trivalents, indicating autotriploidy. (g) Male meiotic cell of the triploid *C. latifolia* showing irregular synapsis at metaphase-I chromosome pairing with 21 trivalents, indicating allotriploidy. (h) A mitotic interphase cell of the triploid cytotype of *C. comosa* showing three major sites of the 45S ribosomal genes, confirming triploidy in this species. (i) A mitotic interphase cell of the triploid cytotype of *C. comosa* showing three major sites of the 45S ribosomal genes, one large *C. comosa* marker site Cc1 and two smaller sites. (j) A mitotic interphase cell of the triploid cytotype of *C. elata* showing three major sites of the 45S ribosomal genes and three minor sites, confirming triploidy in this species. (k) A mitotic interphase cell of the triploid cytotype of *C. elata* showing three major sites of the 45S ribosomal genes, again confirming triploidy in this species. Scale bars represent 5 μ m. References: (a–b) [51]; (c, e) [65]; (d, f–g) [59]; (h, j–k) [66]; and (i) [56].

We have studied *C. comosa* and its related species, collectively called wan-chak-motluk in Thai language for its phytoestrogen properties. The plant produces bright colourful flowers in the form of inflorescences (**Figure 3a**). Its rhizomes are ovoid to ovate spheroidal in shape and about 8–15 cm in diameter (**Figure 3b**). Wan-chak-motluk belongs to three *Curcuma* species: *C. comosa*, *C. elata* Roxb. and *C. latifolia* Rosc. [51]. *Curcuma comosa* is recognised by its inflorescences with short peduncles (**Figure 3a**), whereas the other two species have long peduncles more suitable for flower arrangements. *Curcuma elata* and *C. latifolia* produce large and branchy rhizomes (**Figure 3b**).

Our chromosome number investigations have shown that the three wan-chak-motluk species can be further separated into five cultivars or cytotypes ([51]; see also **Table 1**): *C. comosa* has two cytotypes, diploid with $2n = 2x = 42$ (**Figure 3d**) and triploid with $2n = 3x = 63$ (**Figure 3f**); *C. elata* (and *C. cf. "elata-latifolia"*) is triploid with $2n = 3x = 63$; but *C. latifolia* has two cytotypes, triploid with $2n = 3x = 63$ (**Figure 3g**) and tetraploid with $2n = 4x = 84$. The group of wan-chak-motluk has been extended to cover more Thai taxa [59], including triploid *C. caesia*, triploid *C. cf. zedoaroides* Chaveer. & Tanee and tetraploid *C. cf. zedoaria* (Christm.) Rosc.

We have also recently described cytotaxonomy of the white flowering *C. candida* (Wall.) Techapr., to be diploid with $2n = 2x = 42$ ([65]; **Figure 3c, e**). *C. candida* is a conservation-vulnerable species, rare and endemic to the Tenasserim Range bordering Thailand and Myanmar. As this species has the potential to be developed as an ornamental or medicinal plant [67], efforts are being made to promote cultivation rather than harvesting it from the wild.

5. Polyploidy in *Curcuma*

Our studies and those of others have shown that while most Thai *Curcuma* species are diploid ($2n = 42$), other species are polyploid (**Table 1**). This ploidy level determination is based on the meiotic chromosome pairing in pollen mother cells, i.e. a diploid plant shows 21 bivalents, resulting from a complete synapsis of homologous chromosomes at metaphase-I of the meiotic cell division (e.g. **Figure 3e**). Therefore, we have concluded that the base chromosome number for *Curcuma*, at least the Thai species investigated, to be 21 ($x = 21$), but we have also identified this as “secondary” base chromosome number, possibly deriving from three times primary base number $x = 7$ [59, 66]. Leong-Skornickova et al. [10] measured genome size of 51 Indian *Curcuma* taxa using flow cytometry and obtained chromosome counts from about one-third of the plants. They established that the base number was $x = 7$ for Indian *Curcuma* because all the $2n$ numbers in their study were multiples of seven, from hexaploids ($2n = 42$) up to 15-ploids. This $x = 7$ is most likely an ancestral base number of *Curcuma*. Most angiosperms, woody and herbaceous, are considered being ancient polyploids with the original base numbers $x = 6$ and $x = 7$ [68]. The major crop plants of the world are polyploid, for example, wheat, maize, potatoes, banana, cotton, oilseed rape and coffee beans, and most of these highly productive plants are ancient polyploids [69]. Therefore, in this context, all Thai *Curcuma* species (**Table 1**) are basically (ancient) polyploids, ranging from $2n = 42$ (primary hexaploid, secondary diploid) to $2n = 63$ (primary 9-ploid, secondary triploid) and $2n = 84$ (primary 12-ploid, secondary tetraploid). However, for the matter of consistency among our studies, we treat all Thai *Curcuma* taxa based on the secondary base number $x = 21$. This is in line with most other chromosome studies, whereby the meiotic

analysis is used to determine ploidy levels, for example, the most cultivated turmeric species *C. longa* is triploid with $2n = 63$ [60, 64].

The genus *Curcuma* contains chromosome numbers spanning the full range of the family Zingiberaceae, from $2n = 20$ to 105 [10, 51, 59, 61, 63, 64, 70], but is characterised by chromosomes of particularly small sizes, usually less than $2\ \mu\text{m}$. A large number of *Curcuma* species (at least 25 species) have the diploid chromosome number $2n = 42$ (base number $x = 21$), several (ca. 12) species have $2n = 63$, and other numbers such as 20, 24, 32, 34, 84 and 105 have also been reported. Polyploidy is indeed very common in the ginger family Zingiberaceae.

Fluorescent in situ hybridization (FISH) mapping of the tandemly repeated 45S (18S–25S) ribosomal DNA on chromosomes of wan-chak-motluk supports the occurrence of triploidy among the species and cytotypes with $2n = 63$ [66]. Sets of three ribosomal FISH signals (loci) are apparent in the triploid *C. comosa* (**Figure 3h, i**) and the triploid *C. elata* (**Figure 3j, k**). In addition, the meiotic figure obtained from the triploid cytotype of *C. comosa* comprises of 21 trivalents; each is a pairing of three homologous chromosomes (**Figure 3f**). Cytogenetic characteristics of triploidy have been observed in other *Curcuma* species, such as *C. longa* [60] and *C. zedoaria* [71].

This triploidization is likely to be the outcome of hybridization between unreduced ($2n$) and normal ($1n$) gametes within or between the diploid populations. Such mechanism has been well documented [72, 73]. In Zingiberaceae, multiple occurrences of triploid formation have been shown in the ornamental ginger genus *Globba* L. from Southeast Asia, based on molecular phylogenetic analysis of both chloroplast and nuclear genes [74]. The situation with *Curcuma*—wan-chak-motluk—is similar to that of *Globba* in that tetraploids ($2n = 84$) are extremely rare (**Table 1**) and the triploids are variable both morphologically and cytogeographically [51]. The molecular study by Zaveska et al. [75] has shown that in *Curcuma*, the genus of palaeopolyploid origin, its evolution is most likely driven by hybridization and polyploidization.

Once a triploid has arisen, it could easily survive because *Curcuma*, like other genera in Zingiberaceae, reproduces predominantly by vegetative means, i.e. the plants often propagate by rhizomes and numerous bulbils produced on the inflorescence. In the context of cultivation and utilisation of wan-chak-motluk, triploid cultivars (with $2n = 63$) are indeed very popular among the growers, for example, for having larger rhizomes. We have also found that triploid and tetraploid plants do have proportionally larger genome sizes compared with the diploid plants [59]. Polyploidization in plants often increases cell size as well as growth rates, giving rise to plant phenotypes having higher physiological capacity and productivity [76]. Increasing the ploidy level is known to be positively correlated with plant production, both biomass and yield [69]. Furthermore, polyploids are often said to have a broader ecological tolerance than their diploid progenitors [77]. This is thought to be due to the effects of increased heterozygosity providing metabolic flexibility to cope with wider arrays of conditions [76]. In addition, the advantages of having more copies of the genes should allow polyploids to thrive in environments that pose challenges to their diploid progenitors [78]. In Zingiberaceae, triploids are highly successful in cultivation, mainly due to their productive rhizomes. In natural environments, triploids may be superior as a likely result of the plant's fitness as described above. *Curcuma* triploids are indeed common and widespread over a vast geographical range throughout Asia [9, 10, 62, 63, 70, 71]. Future studies combining cytogenomics, genetics, physiology and ecology should shed light onto the underlying physiological mechanism and its genetic basis of such gains in polyploidy.

6. Conclusion

The most widely cultivated plants belong to the two largest genera of this family, the ginger genus (*Zingiber*) and the turmeric genus (*Curcuma*). They are also the best researched plants from this family, and the most researched topics concern medicinal properties and health benefits, pharmaceutical, biochemical and molecular characterisation, as well as applications in food science and technology. The present study identifies numerous polyploid species in the turmeric genus (*Curcuma*) from Thailand. In particular, triploid species and/or cultivars are popular for a large-scale cultivation. The plants are easily propagated via underground rhizomes, which are also the part of the plant that contains bioactive compounds with medicinal properties. Rhizomes of triploid cultivars are bigger than those of the diploid, wild relatives and thus are more economically valuable. Triploids are also the most adaptable plants in diverse environments. On the other hand, the overharvesting of wild plants, in search for novel or better bioactive compounds, poses a serious risk of species extinction. Cytogenetic research, such as that presented here, can provide useful information for both types of activities, i.e. in the plant improvement for cultivation and in the conservation of natural biodiversity.

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