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REVIEW ARTICLE

Comprehensive review of pumpkin (*Cucurbita* spp.): Domestication, global distribution, genetic characterization, breeding strategies, and genomic insights

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Abstract

Cucurbits are a diverse group of plant species grown worldwide for both immature and mature fruits. The fruit is the finest source of beta-carotene, vitamins, and minerals. The crop originated in South America, with Mexico having the most diversity, but it is now scattered worldwide, with Asia Minor serving as a secondary center of diversity. *Cucurbita pepo* and *C. moschata* are the two most extensively cultivated species, demonstrating tolerance to a wide range of environments. The systematic breeding process has resulted in the production of numerous significant cultivars appropriate for a variety of applications. The spontaneous mutation resulted in hull-less seeded cultivars, which allowed for the use of seeds for culinary purposes. Bush growth habit, hull-less seeded, higher beta-carotene, biotic stresses such as fungal (powdery mildew, downy mildew, root or crown rot) and viral (begomovirus and potyviruses) diseases were the primary focus of the breeding. *C. okeechobeensis* and *C. lundelliana* are wild species with the capacity to withstand a variety of diseases. The genomic sequences for the species *C. moschata*, *C. maxima*, *C. pepo* subsp. *pepo*, *C. argyrosperma* subsp. *argyrosperma*, and *C. argyrosperma* subsp. *sororia* is available for use in precision breeding. Saturated genetic maps and the identification of QTLs related to horticulturally important traits will aid in the use of genomic resources for quick improvement and cultivar development with biotic and abiotic stress tolerance.

Keywords: *Cucurbita*, Pumpkin, Squash, Disease, QTLs and Genes.

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Introduction

The new world genus *Cucurbita,* belonging to the family Cucurbitaceae, is believed to have originated in South America. Genetic barriers have preserved the *Cucurbita* species' genetic diversity despite extensive cross-pollination (Whitaker and Bemis 1975, Decker 1988). Squashes and pumpkins are grown for their edible fruits, which are eaten immature (*C. pepo*) or immature and mature (*C. moschata*) (Decker-Walters and Walters, 2000). The thick, firm skin makes the fruits appropriate for long-term preservation and transit. The fruits are rich in vitamins, minerals, carbs, carotenoids, and tocopherols (Batool et al., 2022). Pumpkin seeds are also valued for their oil (70% unsaturated fatty acid), proteins, and zinc. The seeds reduce obesity and early-stage prostate cancer risk (Kalaivani et al., 2018). Pumpkins are widely cross-pollinated but do not show inbreeding depression. Therefore, hybridization, recurrent selection, and backcrossing may improve traits. Pumpkin yields may be severely reduced by begomoviruses, powdery mildew, heat stress, and other environmental factors (Grumet et al., 2021). The development of resistant/tolerant breeding material to reduce these threats is the most dependable and successful technique. Through breeding, genetic resources and variety have been used to increase vine growth, earliness, fruit size, shape, color, quality, yield, and disease and insect resistance. Recent pumpkin and squash breeding enhancement programs have employed biotechnology efficiently. This review summarises pumpkin and squash enhancement efforts with these in mind.

Genetic characterization of *Cucurbita* species

Cucurbitaceae species have been domesticated since ancient times; however, some are still unknown in the wild due to difficulty in tracing their origins (Chomicki et al., 2020). Genetic heterogeneity across species is essential for using plant genetic resources and choosing breeding methods. The first comprehensive genetic research on cucurbits was done by Sinnott and Durham (1922). According to Paris (2001), *Cucurbita* originated in the New World but has long been farmed in the Old World. This genus is most diverse in Mexico, although its species are widespread across Central-North America and South America, from hot, humid tropical to moderate climates (Ferriol and Pico, 2008). *Cucurbita* genus is believed to have 27 species and 2n = 2x = 40 chromosomes (Whitaker, 1974). Five of the genus species *C. pepo* L., *C. moschata* Duchesne, *C. maxima* Duchesne, *C. ficifolia* Bouche, and *C. argyrosperma* Huber have been domesticated and farmed due to improved taxonomic and crossing investigations (Table 1). Domesticated *Cucurbita* species are somewhat crossable but adapted to distinct geographical locations owing to cultivation and selection pressure, making gene transfer difficult. Křistkova et al. (2004) employed plant morphological features such as leaf lamina, flowers, seeds, fruits, crossability, and natural environment to explore *Cucubita* species relatedness. Recent molecular-based phylogenetic studies separated *Cucurbita* species into mesophytic annual and xerophytic perennial clades. Research discovered the genus' primordial xerophytic behavior. Interspecific hybridization barriers among *Cucurbita* species have remained strong, resulting in infertile progenies from xerophytic (*C. foetidissima, C. digitata, C. radicans, and C. pedatifolia*) and mesophytic species (*C. maxima, C. pepo, C. moschata, C. argyrosperma, C. ficifolia, C. ecuadorensis, C. lundelliana, and C. okeechobeensis*). *C. ficifolia* is least compatible with other mesophytic species among grown plants. In the field, *C. lundelliana* is more compatible with other mesophytic species, whereas *C. okeechobeensis* and *C. ecuadorensis* yielded conflicting findings (Robinson and Decker-Walters, 1997). *C. argyrosperma* has been utilised as the female in crossings with *C. moschata*, producing viable offspring (Ortiz-Alamillo et al., 2007). Sibling line cladding in chloroplast and mitochondrial DNA research has also separated xerophytic and mesophytic species (Kistler et al., 2015). However, these new methods have shown outcomes comparable to morphology, interspecific crossability, and natural environment. DNA tests show that *C. argyrosperma* and *C. moschata* are closely related, although *C. okeechobeensis* is the most central species.

Distribution of cultivated species

Among the cultivated species *C. pepo* is the most variable and adapted to a wide range of habitats, followed by *C. moschata*, which is mostly specific to humid tropics (Hadia et al., 2008). The domestication of pumpkin and squashes dates back to ~10,000 years B.P. from an unidentified wild species in Mexico and many primitive landrace varieties are still grown in Central America and Mexico, constituting a diverse genetic pool of *C. pepo* (Lebeda et al., 2007). The domesticated *C. pepo* was introduced into Asia Minor and Europe during the late 1400s, and subsequently, Asia Minor became its secondary center of diversification (Robinson and Decker-Walters,1997). The economically most important cultivars of *C. pepo* 'zucchini' and 'acorn squash' have European origin. A spontaneous mutant was also observed in Central Europe during 1800's, producing all important hull-less seeds (i.e., seed without outer thick testa layer). The primary gene pool of *C. pepo* constitutes many edible and ornamental cultivars along with wild taxa ssp. *ovifera* var. *texana*, ssp. *fraternal*, and var. *ozarkana*.

Similar to *C. pepo*, genetic diversity for *C. moschata* can be observed among numerous landrace cultivars grown in the American tropics along with hot, humid regions of Asia or Africa. The origin of *C. moschata* is still not clear with reports suggesting Asian origin (Lira-Saade and Montes-Hernandez, 1994). However, the oldest archaeological remains have been found in North-Western Mexico (5000 years B.P), Peru (3000 B.P.), Guatemala (2000 B.P.), and northern Belize (2000 B.P.). *C. moschata* has shown some cross-compatibility with other cultivated species viz., *C. pepo* and *C. maxima,* along with wild species viz., *C. lundelliana* (source of resistance to multiple diseases) enhancing its gene pool. The genetic diversity in some Mexican landraces has been enhanced by introgressions from wide species, including subsp. *sosoria.*

Another cultivated species *viz., C. maxima,* also has maximum diversity in South American temperate zone. It was domesticated about 4000 years ago from the wild progenitor *C. maxima* ssp. *andreana,* which bear small, bitter fruits and is available in Argentina, Bolivia and Uruguay (Decker-Walters and Walters, 2000). *C. ecuadorensis* is another closely related species of *C. maxima,* which is endemic to Ecuador and used as a disease-resistance source in breeding programs. Many landraces can be found in the South American region with traits such as resistance to diseases and long storage. However, landraces with variable characteristics can also be observed in different parts of North America, Australia, Africa, Asia and Europe, with Asia being considered a secondary center of diversity (Ferriol and Pico, 2008).

The species *viz., C. ficifolia* and *C. argyrosperma* have largely remained limited in genetic variability which is observed only for fruit and seed size and color among the landraces of Central Americas and southern U.S.A. The origin of *C. ficifolia* is also not clear, but is considered to be

Table 1: *Cucurbita* species, their origin, distribution, cultivation and usage

Species	*Sub species*	*Origin*	*Wild distribution*	*Cultivation*	*Most common use*
C. pepo L.	*C. pepo* ssp. *pepo*, *C. pepo* ssp. *fraternal,* *C. pepo* ssp. *ovifera var. texana,* *var. ovifera,* *var. ozarkana,*	Mexico (10000 years B.P.)	South-east and central U.S.A., north-east Mexico	Worldwide: Temperate to tropical regions	Mature and immature fruits, Seeds, seed oil
C. maxima Duchesne	*C. maxima* ssp. *maxima*, *C. maxima* ssp. *andreana*	South America (4000 years B.P.)	North and central region of South America	Temperate regions	Mature fruits, seeds
C. moschata Duchesne		Unknown (Mexico, Central or South America) (5000 years B.P.)	Not known	Worldwide: Tropical to sub-tropical, and semi arid regions	Mature and immature fruits
C. foetidissima Kunth			Arid central and west U.S.A., North-Western Mexico		
C. ficifolia Bouché		Unknown (Mexico, Central or South America) (>3000 years B.P.)	Not known	Mountainous Mexico, Central America, Argentina, Northern Chile	Mature fruits
C. digitata Gray			Arid South-West U.S.A., North-West Mexico		
C. radicans Naudin			Central Mexico plateau		
C. argyrosperma Huber	*C. argyrosperma* ssp. *argyrosperma*, *C. argyrosperma* ssp. *sororia*	Southern Mexico (7000 years B.P.)	Pacific coast: central to south Mexico, Gulf coast: North-East Mexico	Mexico, U.S.A., Central America	Seeds
C. okeechobeensis Bailey	*C. okeechobeensis* ssp. *okeechobeensis* *C. okeechobeensis* ssp. *martinezii*		Gulf coast and foothills; North to South Mexico, Florida		
C. lundelliana Bailey			Belize, Guatemala, Lowland: Yucatan		
C. pedatifolia Bailey			Mexican plateau, Queretaro		
C. ecuadorensis Cutler and Whitaker			Pacific coast: Ecuador		

Source: Nee (1990), Dhatt et al. (2020)

originated in Asia or, Central America or southern Mexico (Andres, 1990; Lira-Saade and Montes-Hernandez, 1994). However, archaeological studies have found domestication evidence in the Andean regions of South America (Andres, 1990). *C. ficifolia* is not closely related to any of the wild *Cucurbita* species, therefore, phylogenetic studies have also remained unclear to support the domestication hypotheses. The species *C. argyrosperma* was domesticated in Mexico, with archaeological evidence dating back to 7000 years B.P. (Smith, 2006). This species is primarily cultivated in Mexican and Central American regions, with some minor cultivation in Asian countries. There are reports of high levels of gene flow between and wild taxa and cultivated *C. argyrosperma*.

Genetic resources

Improvement initiatives should aim to collect, characterize, and safeguard agricultural genetic resources, particularly for neglected and underutilized crop species (Salgotra and Chauhan, 2023). Pumpkin genetic diversity—landraces, wild relatives, and conventional cultivars—provides a foundation for creating novel varieties. Many approaches have been explored to evaluate crop genetic diversity, including morphological, biochemical, and molecular traits (Soltani et al., 2017). However, fruit shape and size variations have remained the major approach, leading to cultivar classification of *Cucurbita* species. The cultivars in *C. pepo* have been classified into eight groups based on fruit shape and length/width ratio, with four (Zucchini, Vegetable Marrow, Pumpkin and Cocozelle) belonging to ssp. *pepo* and the remaining (Straightneck, Scallop, Crookneck and Acorn) to ssp. *texana* (Paris, 1986). In *C. maxima* seven horticultural groups (Delicious, Hubbard, Orange Marrows, Banana, Turban, Show or Display, Warty or Pebbled) were proposed by Castetter (1925), while Grebenščikov (1958) gave a classification of six varieties (*Bananina*, *Turbaniformis*, *Maxima*, *Parvifructina*, *Hubbardiana*, and *Zapallitina*). Goldman (2004) presented a grouping into seven cultivar groups (Hubbard, Australian, Buttercup, Turban, Mammoth, Banana, and Zapallito). In the contrary, for *C. moschata*, no satisfactory sub-specific classification has been reported, and cultivars are grouped based on geographical origin into two assemblages viz., Caribbean-Colombian (short-day flowering, brown seeds); and Mexican (long-day flowering induction and light tan-colored seeds). The gene(s) governing the majority of these traits are known (Table 2) and are available in primary or secondary gene pools but need to be introduced into new cultivars with the use of a suitable breeding method, including interspecific hybridization. The interspecific hybridizations has been successfully used to introgress zucchini yellow mosaic virus (ZYMV) and cucumber mosaic virus (CMV) resistance from *C. moschata* to *C. pepo.* Similarly, resistance against powdery mildew has been transferred from *C. okeechobeensis* to *C. pepo* and *C. moschata* (Holdsworth et al., 2016).

Breeding for genetic improvement of traits

Highly cross-pollinated *Cucurbita* species have monoecious flowering, numerous flowers, seeds, yield and quality variation. Thus, hybridization breeding methods are popular worldwide because to their homogeneity, earliness, and better yield, which traditional breeding methods cannot attain (Thakur et al., 2016). Figure 1 shows several *C. pepo* and *C. moschata* fruit varieties at PAU, Ludhiana. Pumpkin and squash breeding focuses on total fruit production, where fruit number and weight are key. Table 3 lists heterosis exploitation studies for fruit production and contributing characteristics, whereas trait-wise breeding achievements are below.

Bush growth habit

Along with total fruit yield, harnessing early yield with a high harvest index has remained a top priority in vegetable breeding and bush growth habit has been closely associated with these characteristics in pumpkins (El-Sayed et al., 2011). In *Cucurbita* species, bush growth habit has been characterized as dominant over vine growth and many breeding methods, including interspecific hybridization, have been followed to develop bush or semi-bush pumpkin cultivars. In *C. maxima*, bush growth habit has been linked to three QTLs present in linkage groups 1, 3 and 4. A QTL on LG 3 *viz.*, qCmB2 explained 21.4 % of the total phenotypic variations and a gene (Cma-004516) encoding for gibberellin (GA) 20-oxidase was found associated with a bush trait. In *C. pepo*, a dominant locus (*CpDw,*) governing the dwarf phenotypic appearance was reported by Ding et al. (2021).

Figure 1: Variability in the germplasm at PAU, Ludhiana. *C. pepo* (zucchini, A-D); *C. moshata* (E-G)

Table 2: List of traits, genes governing them and their sources

Trait	*Specie*	*Gene symbol*	*Description*	*Source*	*Reference*
Sex					
androecious	*C. pepo*	*a*	Produces only male flowers	Greckie	Kubicki (1970)
Androecy enhancer	*C. pepo*	*Ae*		Cross among 'Vegetable Spaghetti' (*ae/ae)* and Bolognese *(Ae/Ae)*	Manzano et al. (2008)
Male sterility					
	C. pepo	*ms1*	Abortion of male flower before anthesis	Cross involving 'Golden Hubbard'	Scott and Riner (1946)
	C. pepo	*ms2*	Abortion of male flowers (shrivelled androecium turns brown)	Eskandarany	Eisa and Munger (1968)
Fruit pigmentation					
Yellow	*C. pepo*	*B*		Ornamental gourd: 'Vaughn's Pear Shaped'	Paris (1988)
	C. moschata	B		'Precocious'	
	C. maxima	B^{max}*/ B-2*		*C. maxima* subsp. *andreana*	Shifriss (1989)
Plain fruit colour	*C. pepo*	*Pl*		'Beirut' vegetable marrow and 'Fordhook Zucchini'	Paris (1992)
White flesh	*C. pepo*	*Wf*		*Scallop squash (Wf), straightneck (wf) squash*	Loy (2012-2013)
Colour inhibitor	*C. pepo*	*I-mc*		Scallop squash	Clayberg (1992)
Bitterness					
	C. maxima, C. maxima × C. ecuadorensis	Bi^{max}	High concentration of cucurbitacin	*C. maxima* subsp. *andreana* and *C. ecuadorensis*	Contardi (1939), Herrington and Brown (1988)
Fruit Shape					
Butternut	*C. moschata*	*Bn*	Butternut fruit	'New Hampshire Butternut'	Mutschler and Pearson (1987)
Disc shape	*C. pepo*	*Di*	Disc fruit shape	Scallop squash	Sinnott and Durham (1922)
Growth habit					
Bush	*C. pepo*	*Bu*	Bush *habit. Short internodes*	'Giant Yellow Straightneck' and NIL 'Table Queen'	Wu et al. (2007)
	C. maxima			*Bu* from inbred line, *bu* from Delicious	
	C. moschata,			*Bu* (From inbred line), *bu* from undisclosed parent.	
Flowering					
Multiple flowering	*C. pepo*	*Mf*	Differentiation of more than one flower bud at a leaf axil	Near-isogenic line of the 'True French' zucchini.	Paris and Hanan (2010)

Leafy tendril	*C. pepo*	*Lt*	Tendrils with laminae	Ornamental gourd	Scarchuk (1974)
Tendrilless plants	*C. pepo*	*td*	*tendrilless* plants	Mutant from ornamental pumpkin	Loy (2012-13)
White corolla	*C. maxima*	*wc*		*'Ispanskaya' × 'Emerald'.*	Korzeniewska (1996)
Seed					
Hull-less seed	*C. pepo, C. moschata*	*h/n*	Hull-less (naked) seeds. Lacks lignified seed coat	Oilseed pumpkin	Zraidi et al. (2003)

The locus was mapped to an approximate region of 24.6 kb on chromosome 10 with five annotated genes. Among them, GA 2-12 oxidase gene *'Cp4.1LG10g05910.1'* was categorized as a candidate gene for *CpDw*. Thus, the genetic analysis of bush growth habit in most of *Cucurbita* species rendered it as a dominant trait with varying levels of expression that vary with environmental conditions. The benefits offered by bush growth habit have prompted the development of cultivars/hybrids for general cultivation in the region viz., PPH-1, PPH-2 (*C. moschata*), PCK-1 (*C. pepo*) by Punjab Agricultural University (PAU), Ludhiana, India (Dhatt and Sidhu, 2017).

Hull-less seed

Pumpkin seeds are rich in nutrients and contain 35 to 45% oil, having fatty acids like oleic, stearic, palmitic and linoleic acid. However, the thick, leathery seed coat (hull) developed due to lignified testa requires an expensive process of dehulling prior to use. This problem has been evaded with the use of a natural mutant originated from Austria (*C. pepo* var. *styriaca*, hull-less seeded pumpkin), which has been used worldwide to breed hull-less seeded cultivars (i.e., cultivars without hard seed coat layers) (Latifi et al., 2012). The hull-less landraces were used for breeding the first Austrian oil-seeded variety 'GleisdoferOlkurbis' while other varieties recommended for cultivation in Western countries and the USA were *Lady Godiva*, *Eat All*, *Baby Bear*, *Snack Jack*, and *Triple Treat* (Ferriol and Pico, 2008). In India, the first hull-less seeded variety, *viz.*, '*PAU Magaz Kadoo*-1' in *C. pepo* background, was released by the PAU in 2018 (Dhatt, 2019). Recently, using QTL-seq techniques, a genomic region governing the hull-less seed trait on chromosome 12 of *C. pepo* was identified, along with a potential candidate gene *viz.*, NST1 (*Cp4.1LG12g04350*).

Fruit quality and nutritional traits

Growers usually favor high-yielding quality fruit types or hybrids. High nutritional and pharmacological characteristics have been the subject of research for decades. In China, India, Argentina, Brazil, Mexico, and America, *Cucurbita* species have been used as antihypertension, antidiabetic, anti-hypercholesterolemia, immunomodulation, antitumor, antibacterial, antiinflammation, intestinal antiparasitic, and antalgic agents. The Indian market prefers mottled green skin thus multiple varieties and hybrids have been developed. Fruit flesh contains carbohydrates and sugars, but quality, fruit size, and yield have been correlated negatively (Loy, 2012). Pumpkins are an essential source of vitamin A since they retain up to 100% of their carotene when cooked. Fruit flesh carotenoid concentration varies greatly among *Cucurbita* accessions. A complementary interaction between the dominant alleles B and L-2 gives *C. pepo* orange fruit flesh.

Biotic stresses

Pumpkin and squashes are prone to various fungal (powdery mildew, downy mildew, root or crown rot) and viral (begomovirus and potyviruses) diseases, which cause yield losses up to 100% (Nagendran et al., 2017, Sagar et al., 2020). The most promising method to manage these diseases is the breeding of resistant cultivars, which requires extensive screening of cultivated and wild germplasm for resistance (Saez et al., 2020). Wild species *viz.*, *C. okeechobeensis* and *C. lundelliana* have the potential of resistance against different diseases. Powdery mildew (PM) resistance was introduced from *C. moschata via* bridge cross into the *C. pepo* background, which revealed a dominant gene inheritance of resistance in *C. lundelliana*. However, genotypes identified with these introgressions showed linkage drag and incomplete resistance, preventing them from being commercialized. A breakthrough occurred when powdery mildew resistance was transferred into *C. pepo* from *C. okeechobeensis*, and then resistant hybrids of *C. pepo* were commercialized. Currently, PM resistance in almost all commercial varieties/cultivars of *C. pepo* and *C. moschata* is due *to Pm-0* gene (Holdsworth et al., 2016). Germplasm showing resistance to *Phytophthora* crown rot induced by *Phytophthora capsici* in the genetic background of *C. moschata* and *C. pepo* has also been identified (Ramos et al., 2020; Vogel et al., 2020).

Cucurbita species are known to be infected by various potyviruses {ZYMV (Zucchini yellow mosaic virus), PRSV (Papaya ring spot virus), WMV (Watermelon mosaic virus), CMV (Cucumber mosaic virus) and begomoviruses {(SLCCNV (Squash leaf curl China virus), ToLCNDV (Tomato leaf curl New Delhi virus)} (Sagar et al., 2020; Martín-Hernández and Pico, 2021). The virus resistance reaction of three main domesticated *Cucurbita* species is quite different. Screening of germplasm for resistance against different viruses disclosed *C. maxima* and *C. pepo* to be highly susceptible,

Table 3: Heterosis for fruit traits in *Cucurbita*

Traits	*No. of hybrids*	*Standard heterosis (%)*	*Heterobeltosis (%)*	*References*
No. of fruits per plant	36	-79.07 to 37.21	–73.68 to 70.00	Tamil Selvi et al. (2014)
	15		-62.30 to 65.00	Ahmed et al. (2017)
	21	14.29 to 107.14	-6.59 to 35.82	Singh et al. (2019)
		-44.17 to 28.08	-56.42 to 44.44	Mohsin et al. (2022)
		-30.05 to 88.00	-39.05 to 74.11	Hosen et al. (2022)
Fruit polar diameter	36	-46.51 to 26.30	–25.59 to 22.58	Tamil Selvi et al. (2014)
	15	–4.56 to 13.94	–4.56 to 21.87	Kumar et al. (2018)
	21	-0.39 to 29.99	-9.44 to 20.99	Singh et al. (2019)
		-27.74 to 129.01	-32.13 to 34.33	Mohsin et al. (2022)
Fruit equatorial diameter	21	1.56 to 44.31	-16.57 to 10.40	Singh et al. (2019)
	15	–5.30 to 15.01	–5.30 to 26.41	Kumar et al. (2018)
	36		-37.89 to 90.32	Singh et al. (2019)
		-27.83 to 25.43	-27.59 to 13.94	Mohsin et al. (2022)
Fruit weight		-3.33 to 198.95	-45.56 to 64.24	Mohsin et al. (2022)
		-38.39 to 78.93	-33.84 to 86.51	Hosen et al. (2022)
Fruit yield per plant	36	-50.98 to 96.44	-52.53 to 77.65	Tamil Selvi et al. (2014)
	15		-43.40 to 152.40	Ahmed et al. (2017)
	21		-68.20 to 68.20	Pandey et al. (2010)
	21	20.87 to 123.48	-27.98 to 56.20	Singh et al. (2019)
		-28.06 to 251.32	-64.62 to 164.74	Mohsin et al. (2022)
		-43.58 to 160.46	-39.68 to 178.46	Hosen et al. (2022)

Table 4: Resistant sources against different biotic stresses in genus *Cucurbita* and their genetic control

Species	*Biotic stress*	*Source of resistance/tolerance*	*Genetic control*	*References*
C. moschata	Phytophthora crown rot	#394-1-27-12	Three Dominant genes	Ramos et al. (2020)
	Zucchini yellow mosaic virus	Nigerian Local	Monogenic dominant	Brown et al. (2003)
		Menina	Polygenic dominant	Paris et al (2000)
		Sole	Recessive gene	Wessel-Beaver (2005)
		Bolina	-	Paris et al. (1988)
	Watermelon mosaic virus	Nigerian Local	Monogenic dominant	Brown et al. (2003)
		Menina	Single dominant	Brown et al. (2003)
	Papaya ringspot virus W	Nigerian local	Monogenic recessive	Brown et al. (2003) Miranda-Vélez et al. (2019)
	Cucumber mosaic virus	Nigerian local	Monogenic dominant	Brown et al. (2003)
	Squash leaf curl virus	-	slc-2 Recessive	Vilmorin and Cie (2010)
		AVPU1426	Single recessive gene	Dhillon et al. (2021)
		PVR-1343 (Punjab Nawab)	Digenic recessive genes	Dhatt et al. (2020)
	Tomato leaf curl New Delhi Virus (ToLCNDV)	PI 604506, PI 381814	Single recessive	Sáez et al. (2020)
		BSUAL-252, BSUAL-256, BSUAL-264	Single dominant	Romero-Masegosa et al. (2020)
		AVPU1426	Single recessive	Dhillon et al. 2021
		PVR-1343 (Punjab Nawab)	Digenic recessive	Dhatt et al. (2020)
C. pepo	*Squash leaf curl virus*	-	Slc 2	Montes-Garcia et al. (1998)
C. maxima	WMV	PI 419081	-	Provvidenti et al. (2000)
	PRSV	Zapatillo redondo	-	

Table 5: Genome sequencing in *Cucurbita* genus

Genus	*Species*	*Variety*	*Chromosome*	*Gene*	*mRNA*	*Protein*	
Cucurbita	*maxima*	Rimu	20	32,076	32,076	32,076	*Cucurbit* genomic database
	moschata	Rifu	20	32,205	32,205	32,205	
	pepo	MU-CU-16	20	27,868	27,868	27,868	
	argyrosperma	SMH-JMG-627	-	28,298	28,298	-	

while resistance was observed in *C. moschata*. Among potyviruses, ZYMV is a most common and damaging pathogen of *Cucurbita* group. Different resistant sources from Nigeria, Puerto Rico and Portugal have been identified against different ZYMV strains in *C. moschata* (Brown et al., 2003; Pachner et al., 2011). Seven genes *viz.*, *Zym-0, Zym-1, Zym-2, Zym-3, Zym-4, zym-5, zym-6* governing resistance to ZYMV have been reported in *C. moschata* background (Pachner et al., 2011). Monogenic dominant resistance to WMV and CMV, while monogenic recessive gene resistance to PRSV, has also been recognized in the background of *C. moschata*. Different begomovirus resistance sources from diverse origins, namely US, India, Japan, Nigeria and Spain have been identified (Saez et al., 2016). Recently, two inbred lines *viz.*, AVPU1426 and PVR-1343 of *C. moschata* identified at World Vegetable Centre and PAU Ludhiana Punjab possess resistance to SLCCNV (Verma et al. 2022). In contrast to SLCCNV, genetic control of resistance to ToLCNDV has identified in six lines of *C. moschata* from diverse regions: PI 604506 (USA), PI 381814 (India; Saez et al. 2020), AVPU1426 (Bangladesh; Dhillon et al., 2021), BSUAL-252, BSUAL-256, BSUAL-264 (Japan), PVR-1343 (India; Verma et al., 2022, Dhatt & Sharma, 2019). Table 4 summarizes the information regarding breeding for biotic resistance in *Cucurbita* species.

Abiotic stresses

Cucurbita is sensitive to environmental extremes that fluctuate constantly, thus, cultivars that can adapt to a variety of stress situations must be developed. The main abiotic factors impacting pumpkin and squash productivity include drought, temperature extremes, and salt. Some *Cucurbita moschata* accessions tolerate abiotic stress. Complex genetics of abiotic stressors make traditional breeding difficult to identify and generate resistant lines. Pumpkin has been used more as rootstock for grafting in cucurbits to enhance salt tolerance, low temperature or freezing tolerance, alkalinity stress, and cadmium toxicity. Pumpkin tolerance to abiotic stresses is little studied at the molecular level.

Molecular breeding approaches

Genomic studies in Cucurbita group

The availability of genome sequences of diverse *Cucurbita* species *viz.*, *C. moschata*, *C. maxima*, *C. pepo* subsp. *pepo*, *C. argyrosperma* subsp. *argyrosperma, C. argyrosperma* subsp. *sororia* has been a major breakthrough in *Cucurbita* group research (Table 5). A family-wide genomics database of cucurbit (CuGenDB, http://www.icugi.org), which integrates genomic sequences and gene annotation data has been developed to enable the utilization and application of genomics in cucurbits (Yu et al., 2023). The genomes of *C. maxima, C. pepo,* and *C. moschata,* with an assembly size of 263, 269.9 and 271.4 Mb, respectively are available on NCBI (https://www.ncbi.nlm.nih.gov/genome) and CucuGenDb (http://cucurbitgenomics.org). The genome sequences of these species facilitate the development of saturated genetic maps and identify QTLs associated with horticulturally important traits. The enormous amount of genomic data makes it feasible to dissect these complex traits and characterize the underlying genes. Therefore, the breeding programs in genus *Cucurbita* will be hastened via accessing these genomic resources.

Transcriptomics

The transcriptome profiling technique is powerful and widely used, allowing cost-efficient in-depth analysis of *Cucurbita* genome transcribed regions (Wang et al., 2009). Further, the sequenced transcripts are utilized for gene(s) prediction. This technique has been extensively used to identify the genes responsible for improving production and quality as well as abiotic and biotic stress tolerance. In pumpkin and squashes, numerous studies have reported the differential gene expression in different tissues at various stages of growth and development under distinct environmental conditions (Zhao et al., 2022; Xue et al., 2022). The first *Cucurbita* transcriptome was reported in *C. pepo* by utilizing 454 GS Titanium technology (Blanca et al., 2011). These transcriptomes epitomize key advances in the genomics of *C. pepo*, showing the gene repertoire expressed during plant, flower and fruit development. Some of the genes in the transcriptome have been characterized functionally in squashes for the determination of sex, parthenocarpy and fruit set (Martinez et al., 2014). A fruit and seed transcriptomes of oilseed pumpkin (Lady Godiva) and acorn squash cultivar (Sweet Reba) were developed over five different developmental stages, and candidate gene(s) associated with carbohydrate metabolism and carotenoid were reported (Wyatt et al., 2015, 2016). Subsequently, many

Table 6: Next generation sequencing integrated with linkage mapping for identification of QTL governing different horticultural traits in *Cucurbita* genus

Sequencing approach	*Mapping population type and parentage*	*Trait of interest*	*Identified QTL(s)*	*Linkage group/ Chromosome number*	*Statistical method used*	*R² (%)*	*References*
Genotyping by-sequencing (GBS)	*C. maxima* 186 F_2 derived from Rimu×SQ026 cross	Dwarf vine	1(*qCmB2, qCmB1, qCmB*)	LG3, LG1, LG 4	Inclusive composite interval mapping (ICIM)	7.65-21.39	Zhang et al. (2015)
	C. pepo 120 F_8 RILs derived from zucchini × scallop cross	Leaf incision	1(Li)	LG10	Composite Interval Mapping (CIM)	50.00	Montero Pau et al. (2017)
		Silver leaf	*3(Sl_12, Sl_1, Sl_16)*	LG1, LG12, LG16		3.83-23.32	
		Days to female flowering	*2(DFeF_12, DFeF_9)*	LG12, LG9		2.61-7.87	
		Immature Fruit shape	*2(IFSh_3, IFSh_12)*	LG12, LG3		6.73-17.83	
		Immature Fruit length	*3(IFLe_3, IFLe_15, IFLe_12)*	LG3, LG15, LG 12		6.72-31.79	
		Mature Fruit shape	*3(MFSh_3, MFSh_4, MFSh_5)*	LG3, LG4, LG5		3.02-10.99	
		Mature Fruit length	*4(MFLe_3, MFLe_12, MFLe_6, MFLe_9)*	LG3, LG12, LG6, LG9		3.55-38.71	
		Mature Fruit width	*2(MFWi_3, MFWi_12)*	LG3, LG12		7.42-15.14	
		Mature flesh color	*4(MbFCo_19, MaFCo_19, MaFCo_10, MaFCo_13)*	LG19, LG10, LG13		1.49-62.93	
	C. moschata F_2 population derived from TG201 (susceptible) ×TG10 (resistant) cross	Powdery Mildew Resistance	1	Chr3	Composite Interval mapping	-	Park et al. (2020)
	C. moschata BC_1 individuals derived from Shima×Taina Dorada cross	Insect damage and red color intensity	1	LG1	Haldane mapping function	18.00	Del Valle Echevarria et al. (2020)
		Cavity width	1			16.47	
	C. moschata F_2 population derived from N137×N29 cross	Fruit Length	*3(fl2.1, fl6.1, fl14.1)*	LG2, LG6, LG14	Composite Interval Mapping (CIM)	3.45-8.02	Han et al. (2022)
		Fruit Diameter	*5(fd1.1, fd5.1, fd12.1, fd15.1, fd19.1)*	LG1, LG5, LG12, LG15, LG19		3.26-6.66	
		Fruit Shape Index	*3(fsi2.1, fsi6.1, fsi15.1)*	LG2, LG6, LG15		4.95-8.46	
		Fruit thickness	*6(fth1.1, fth4.1, fyh5.1, fh6.1, fth14.1, fth16.1)*	LG1, LG4, LG5, LG6, LG14, LG16		2.55-4.88	
		Seed Cavity Size	*2(scs5.1, scs12.1)*	LG5, LG12		3.52-5.23	
		Fruit Weight	*4(fw1.1, fw2.1, fw12.1, fw16.1)*	LG1, LG2, LG12, LG16		4.01-5.05	
		TSS	*7(tss2.1, tss3.1, tss4.1, tss5.1, tss7.1, tss8.1, tss9.1)*	LG2, LG3, LG4, LG5, LG7, LG8, LG9)		2.60-6.58	

Double-digest restriction site-assoc. DNA sequencing	*C. moschata* F_2 derived from CMO-1×CMO-97 cross	Fruit	Pericarp colour	1 (*qpc8-a*)	LG8	Multiple QTL mapping	93.6	Zhong et al. (2017)
			Pericarp strip	1 (*qps8-a*)			90	
		Carotenoid	Lutein content	5 (*qlut8-a, qlut8-b, qlut11-a, qlut11-b, qlut20-a*)	LG8, LG11, LG20,		15.1-25.6	
			α-carotene content	2 (*qacr8-a, qacr17-a*)	LG8, LG17		12.6-19.1	
			β-carotene content	3 (*qβcr11-a, qβcr15-a, qβcr20-a*)	LG11, LG15, LG20		10.5-23.2	
			Total carotenoid content	4 (*qcar8-a , qcar11-a , qcar11-b , qcar20-a*)	LG8, LG11, LG20		13.2-28.6	
		Sugar	Glucose and sucrose content	2 (*qglu19-a , qsuc10-a*)	LG19 and LG10		11.4-11.3	
			Sucrose vs glucose ratio	1(*qs/g19-a*)	LG19		12.4	
		Fruit morphology	Fruit tuberculate	2(*qtf8-a , qtf11-a*)	LG8, LG11		12.3-16.9	
			Hollow fruit	2(*qfh8-a,qfh11-a*)	LG8, LG11		10.3-16.9	
			Diameter of fruit	2 (*qfd8-a , qfd13-a*)	LG8, LG13		11.1-19.0	
			Thickness of fruit	3 (*qpt8-a, qpt8-b, qpt9-a*)	LG8, LG9		10.3-15.2	
			Chamber width	3(*qcw8-a , qcw8-b , qcw13-a*)	LG8, LG13		9.6-11.4	
RAD-seq	*C. moschata* population derived from cross of Bí Hồ Lô TN6×Shishigatani	Brix		1	LG6	Composite interval mapping	23.1	Hashimoto et al. (2020)
		Chroma of flesh color		1	LG2		28.8	
		Flowering time of female flower		1	LG7		23	
		Fresh weight		1	LG20		25	
		Fruit Height		1	LG20		16.8	
SLAF-seq method	*C. maxima* F_2 individual derived from cross of 2013-12× 9-6	Seed length		4(*SL4-1, SL6-1,SL17-1, SL18-1*)	LG4, LG6, LG17, LG18	Composite interval mapping	13-38.6	Wang et al. (2020)
		Seed width		4(*SW4-1,SW5-1,SW6-1,SW8-1*)	LG4, LG5, LG6, LG8		6.9-28.9	
		Hundred seed weight		2(*HSW6-1, HSW17-1*)	LG6, LG17		13.2-17.2	
	C. moschata Duch F_2 population derived from PPIS (photoperiod-insensitive) and PPS (photoperiod-sensitive) inbred lines	1st female flowering node		*1(qfffn6)*	LG6	-	30.5	Abbas et al. (2022)
		No. of female flower		*1(qnff6.1)*	LG6	-	22.9	

	C. moschata F_2 population derived from resistant (394-1-27-12)× susceptible (Butter Bush) cross	Resistance to Phytophthora crown rot	3 (*QtlPC-C04, QtlPC-C11,QtlPC-C14*)	LG4, LG11, LG14	Interval mapping	-	Ramos et al. (2020)
	C. pepo F_2 individuals derived from Dunja(S)× PcNY-21(R) cross	Resistance to Phytophthora root and crown rot	6	Chr4, Chr5, Chr8, Chr12, Chr16, Chr19	-	1.92-9.82	Vogel et al. (2020)
	F_2 population of *C. moschata* derived from Nigerian Local (R) and Butterbush (S) cross	Resistance to ZYMV	4 (*QtlZYMV_C02;QtlZYMV_C04; QtlZYMV_C08; QtlZYMV_C20*)	Chr2, Chr4, Chr8, Chr20	-	-	Shrestha et al. (2021)
QTL-seq Bulk Segregant Analysis	*C. pepo* $F_{2:3}$ progenies derived from HP111 (hulled) and HLP36 (hull-less) cross	Hull-less seed trait	1(*Cphl-1*)		-	-	Kaur et al. (2022)
	C. pepo F_2 population derived from X10 and JIN234 cross		1(*CpNST1*)	Chr12	-	-	Lyu et al. (2022)
	C. pepo F_2 population derived from Kakai (hull-less) × Table Gold Acorn (hulled) cross		1(*Qtlhull-less-C12*)		Interval mapping	-	Meru et al. (2022)
	C. moschata $F_{2:3}$ progenies derived from PVR-1343(R)×P-135(S) cross	Resistance to Begomovirus (SLCCNV and ToLCNDV)	2(*qMI-Sq/To7.1, qMI-Sq/To17.1*)	Chr7, Chr17	Inclusive composite interval mapping	59.84	Verma et al. (2023)

differentially expressed genes associated with seed coat development (Xue et al., 2022), flowering, fruit morphology (Wyatt et al., 2015; Huang et al., 2019), disease resistance (Amoroso et al., 2022), and postharvest cold storage (Benitez et al., 2022) were determined using RNA-seq.

C. moschata first transcriptome assembled into 62,480 unigenes (Wu et al., 2014). Utilizing this transcriptome, researchers identified differences in transcriptional expression of *Cm-PIE1*, *Cm-LWD1*, *Cm-TIC*, *Cm-FIO1, Cm- ELF6*, *Cm-APRR5* and *CmFBH3* genes in pumpkin photoperiod insensitive lines. Furthermore, complete transcriptome analysis of *C. moschata* two germplasm lines viz., CMO-X and CMO-E revealed that carotenoid isomerase, phytoene desaturase, zeaxanthin epoxidase, phytoene synthase and hexokinase, sucrose phosphate synthase and fructokinase were strongly correlated with production of carotenoids and metabolites of sucrose, respectively (Abbas et al., 2020).

In pumpkin, the candidate disease-resistance genes viz., *WRKY21*, *MLO3*, and *SGT1*, imparting resistance to powdery mildew, were identified (Guo et al., 2018). Transcriptional changes in pumpkin tolerance to *Fusarium wilt* were studied in different tissues (root, stem, leaf and fruit) and identified 16 key genes related to pathogenesis-resistance (PR), transcription factors, secondary metabolism, and signal binding (Xu et al., 2022). Furthermore, comparative transcriptomic analysis of *C. pepo* ZYMV susceptible (TF) and tolerant (381e) lines revealed 146 genes that were expressed differentially in 381e, which involved in transcription, photosynthesis, callose synthesis and organization of cytoskeleton (Amoroso et al., 2022). A recent study on pumpkin chilling tolerance showed that the transcription factors viz., *ZAT10*, *MYB76*, *AP2/ ERF* domain and *DELLA* protein *GAIP* controlled chilling tolerance in zucchini (Liu et al., 2021).

Marker-assisted breeding (MAB)

The availability of genomic resources, viz., genomic library, EST database, transcriptome assembly, genome sequences, etc., hastened the molecular-assisted breeding program of pumpkin and squashes. The identified molecular markers are being utilized for genetic diversity, genetic mapping, and marker-assisted breeding (Dhatt et al., 2020). Different DNA markers viz., AFLP (Amplified fragment length polymorphism), RAPD (Random amplified polymorphic DNA), ISSR (Inter Simple Sequence Repeat), SRAP (Sequence related amplified polymorphism), and SSR (Simple sequence repeat) have been used in genetic diversity studies to evaluate inter- and intra-species genetic relationships among *C. moschata, C. pepo* and *C. maxima* accessions. *Cucurbita* genetic maps have been constructed using RAPD, AFLP, SSR and SNP markers (Esteras et al., 2012). High throughput SNP markers showed successful QTL mapping of various traits in *C. pepo* (Holdsworth et al., 2016; Capuozzo et al., 2017; Kaur et al., 2022), *C. moschata* (Zhong et al., 2017;

Verma et al., 2023) and *C. maxima*. The details of NGS-based QTL discovery in genus *Cucurbita* are given in Table 6.

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सारांश

कद्दू, दुनिया भर में अपरिपक्व और परिपक्व दोनों फलों के लिए उगाया जाता है। इसके फल बीटा-कैरोटीन, विटामिन और खनिजों के बेहतरीन स्रोत हैं। कद्दू की उत्पत्ति दक्षिण अमेरिका में हुई, जिस कारण मेक्सिको में सबसे अधिक विविधता पाई जाती है। लेकिन अब यह दुनिया भर में उगाया जाता है और एशिया माइनर विविधता के द्वितीयक केंद्र के रूप में पहचाना जाता है। *Cucurbita pepo* और *C. moschata,* कद्दू की दो सबसे व्यापक रूप से खेती की जाने वाली प्रजातियां हैं, जो वातावरण की एक विस्तृत श्रृंखला के प्रति सहिष्णुता का प्रदर्शन करती हैं। व्यवस्थित प्रजनन प्रक्रिया के परिणामस्वरूप विभिन्न प्रकार के अनुप्रयोगों के लिए उपयुक्त कई महत्वपूर्ण किस्मों का उत्पादन किया गया। सहज उत्परिवर्तन के परिणामस्वरूप उपजी छिलका रहित बीज वाली किस्में, मिष्ठान्न, बेकिंग और स्नैक्स उद्योगों में सफल उपयोग में लाई जा रही हैं। कद्दू का प्रजनन मुख्य रूप से बुश की वृद्धि की आदत, छिलका रहित बीज, उच्च बीटा-कैरोटीन, जैविक तनाव जैसे फंगल (पाउडरी मिल्ड्यू, डाउनी मिल्ड्यू, जड़ या तना सडन) और वायरल (बेगोमोवायरस और पोटीवायरस) रोग पर केंद्रित है। *C. okeechobeensis* और *C. lundelliana* जैसी जंगली प्रजातियां विभिन्न प्रकार की बीमारियों का सामना करने की क्षमता रखती हैं। *C. moschata, C. maxima, C. pepo subsp. pepo, C. argyrosperma subsp. argyrosperma* और *C. argyrosperma* subsp. *sororia* प्रजातियों के जीनोमिक अनुक्रम सटीक प्रजनन में उपयोग के लिए उपलब्ध हैं। संतृप्त आनुवंशिक मानचित्र और बागवानी रूप से महत्वपूर्ण लक्षणों से संबंधित क्यूटीएल की पहचान जैविक और अजैविक तनाव सहिष्णुता के साथ त्वरित सुधार और खेती के विकास के लिए जीनोमिक संसाधनों के उपयोग में सहायता करेगी।