

#### **ARTICLE**

# Genetic base and origin of cytoplasmic genes of Brazilian cowpea cultivars

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Abstract: The expansion of cowpea (Vigna unguiculata (L.) Walp.) crop has created new demands for its breeding programs. Knowledge of its genetic base is fundamental for choosing progenitors when conducting crosses. This study aimed to estimate the genetic base of Brazilian cowpea cultivars released between 1960 and 2022, in addition to identifying the origin of their cytoplasmic genes. Seventy-three cultivars were released in this period; however, only 41 had information about their original crosses. The ancestors CNC0434, Pitiúba and Seridó were used more frequently in crosses. They have also contributed with the highest frequency to the cultivars' cytoplasmic genes. Therefore, although we found that between 2005 and 2022 there was a 30.95% increase in the contribution of different genotypes, we conclude that the genetic base of cowpea is narrow, and it is necessary to avoid crosses involving CNC0434, Pitiúba and Seridó in future breeding programs of this legume in Brazil.

**Keywords:** Legumes, pedigrees, cytoplasmic genes, relative and accumulated genetic contribution

## **INTRODUCTION**

Vigna unguiculata (L.) Walp, popularly known as "cowpea", among several other names, is a legume belonging to the Fabaceae family (Freire Filho et al. 2011), with relevant nutritional and economic importance, especially for the neediest populations (Neves et al. 2011). It shows great variation in its morphology and adaptive characteristics, in addition to very diverse use and consumption patterns (Freire Filho and Costa 2020). Its cultivation has more rustic aspects, since it tolerates conditions of lower water availability and higher temperatures, such as those found in the Northeast Region of Brazil (Martins et al. 2024).

According to the Food and Agriculture Organization, the world production of cowpea in 2022 was estimated to be about 9,77 million tons (FAOSTAT 2022). The three largest producers were Nigeria (4,13 million tons), Niger (2,86 million tons) and Burkina Faso (829,20 thousand tons) (FAOSTAT 2022). Regarding Brazil, there is a bias in the production data due to the non-separation of the estimates for common bean and cowpea to be accounted for by FAO (Silva 2021). Therefore, Brazil's official position in the world ranking of cowpea production is not available. However, according to Companhia Nacional de Abastecimento (CONAB 2023), Brazil's cowpea production was 588,6 thousand

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<sup>3</sup> Universidade de São Paulo, Escola Superior de Agricultura "Luiz de Queiroz", Departamento de Genética, Avenida Pádua Dias, 11, 13418-900, Piracicaba, SP, Brazil <sup>4</sup> Universidade do Estado de Minas Gerais, Unidade Frutal, Avenida Escócia, 1001, 38202-436, Frutal, MG, Brazil tons, with emphasis on the Northeast region, which produced 411,2 thousand tons, which represents 69.86% of the country's production, followed by the North region with 85,7 thousand tons. Although it is grown mainly in the North and Northeast regions, currently, cowpea cultivation is gaining ground in all Brazilian regions due to the development of cultivars with multiple morpho-agronomic qualities. Breeding programs have been developing cultivars resistant to the main pests and diseases of the crop and adapted to the most different soil and climate conditions (Embrapa 2023). However, there is a frequent need to incorporate genes that increase productivity and meet the demands of consumers and the production chain (Borém and Miranda 2013). More studies are necessary to help obtain improved genotypes, with the choice of progenitors being a crucial step in the progress of improvement, obtaining sustainable genetic gains and reducing the risks of genetic vulnerability caused by the intensive use of related materials (Machado 2014).

Knowledge about the genetic base of the crop, the number of ancestors and their relative genetic contributions give support to avoiding crosses between progenitors belonging to the same gene group (Singh et al. 2022). The relative genetic contribution can be estimated through the average relationship coefficient between all cultivars and an ancestor, and the accumulated genetic contribution can be obtained from these values (Rangel et al. 1996, Silva et al. 1999). This method has been used in many studies and is applicable when records of the pedigrees of each cultivar are available (Wysmierski and Vello 2013). However, in genetic breeding programs, the lack of information about these pedigrees and the scarcity of information related to the origin of cytoplasmic genes are the main limiting factors, which make it difficult to choose contrasting progenitors for conducting crosses.

Based on calculations related to the genetic contribution of ancestors, studies have revealed narrow genetic base in many crops cultivated in Brazil, such as upland rice cultivars (Montalván et al. 1998, Silva et al. 1999); irrigated rice (Rangel et al. 1996, Rabelo et al. 2015); Brazilian cultivars of soybeans (Hiromoto and Vello 1986, Wysmierski and Vello 2013); and cotton cultivars (Cruz et al. 2023). Regarding cowpea cultivars, as far as we know, only Montalván et al. (2006) studied Brazilian cultivars recommended from 1969 to 2005. All these studies indicated that genetic breeding programs have explored a restricted gene pool. These results highlighted the genetic vulnerability of these crops and provided information about the germplasm that should be avoided in recombination programs.

Considering the hypothesis of a narrow genetic base for cowpea, the present study aimed to i) estimate the genetic base of cowpea cultivars released in Brazil from 1960 to 2020; ii) identify the origin of cytoplasmic genes; and iii) provide support for choosing progenitors in future crosses conducted in cowpea breeding programs.

#### MATERIAL AND METHODS

Information regarding cowpea cultivars recommended in Brazil from 1960 to 2020 used for preparing pedigrees was obtained from cultivar release folders, information from breeders, books and specialized websites, as well as internal reports from teaching and research institutions. Consultations were also conducted in the National Cultivar Registry website (Brasil 2023). The genealogies of cowpea cultivars were examined to identify all their ancestors with the information available. The criteria for analyzing the crosses of the genotypes used followed this order: initially, the crosses of the genotypes described in parentheses were analyzed; subsequently, those present in brackets, followed by those inside keys; finally, the outside of any symbol.

Ancestors were defined as the last parents of cultivar' family tree. The pedigree was constructed until it reached the most distant ancestors that are known or available. The female progenitors, which transmit the cytoplasmic genes, were maintained on the left of their offspring, and with this notation the identification of female ancestors was kept. Backcrosses were represented by the symbol asterisk (\*) followed by the Arabic number corresponding to the many times they were used as recurrent parents.

The calculation of the coefficient of parentage between ancestors was used to estimate the genetic contribution of each ancestor to the genetic constitution of the cultivars. The equation used to calculate the coefficient of parentage was obtained from Falconer and Mackay (1996):  $f(x,y) = \frac{1}{f_{ac}} + \frac{1}{f_{ad}} + \frac{1}{f_{bc}} + \frac{1}{f_{bd}}$ 

where f is the coefficient of parentage between two individuals; x is the individual 1; y is the individual 2; a and b are the parents of x; c and d are the parents of y. It should be noted that, for each cultivar, the contribution of an

ancestor corresponds to the theoretical proportion of genes coming from this ancestor, considering that in each cross, the progeny receives equal proportions from the parents (50% of each) (Falconer and Mackay 1996).

The coefficients of parentage values were used to calculate the percentage of each ancestor's relative genetic contribution (RGC%) to the cultivars' gene pool. The RGC% was calculated as the arithmetic mean of all relatedness coefficients between an ancestor and all cultivars. Successive sums of RGC% of the classified ancestors in a decreasing order formed the accumulated genetic contribution (AGC%) (Rangel 1996, Silva et al. 1999). By the same reasoning, a survey was carried out of ancestors most frequently used as female parents, which are responsible for transmitting the cytoplasmic genes.

### **RESULTS AND DISCUSSION**

Seventy-three Brazilian cowpea cultivars released in the period from 1960 to 2022 were found (Table 1). Of these, 57 were registered in the National Cultivar Registry of the Ministério da Agricultura, Pecuária e Abastecimento of Brazil, and only 41 had available information about their progenitors and respective crosses of origin (Figure 1). The periods with the highest number of releases were between 2000 and 2019 and in the 1980s, with 20 and 19 cultivars registered, respectively. Only two cultivars were released in the 1960s (Seridó and Ipean V-69) and two in the 1970s (Pitiúba and CE-315). Between 2020 and the present day, ten cultivars were released.

A total of 70 cultivars, around 96%, were recommended for the North and/or Northeast regions of Brazil, with 18 being recommended specifically for the North region and 38 for the Northeast region (Table 1). In addition to being

**Table 1.** Cowpea cultivars released in Brazil in the period between 1960 and 2022, including the institution responsible for obtaining them, the Brazilian region and state where they were recommended and the year of release

Cultivars	Institutions <sup>2</sup>	Regions	States <sup>3</sup>	Years
EMAPA 1*	EMAPA	-	-	-
Seridó	UFC	Northeast	CE	1968
IPEAN V-69 <sup>1</sup>	IPEAN	North	AM	1969
Pitiúba¹	UFC	Northeast	CE	1970
CE-315 <sup>1</sup>	UFC	Northeast	CE, PI	1978
Quarenta Dias¹	EMBRAPA	Northeast	PI	1981
Sempre Verde <sup>1</sup>	EMBRAPA	Northeast	PI	1981
Manaus	EMBRAPA	North	AM	1981
/ita 3¹	EMBRAPA	Northeast	PI, MA	1982
BR1 Poty*	EMBRAPA	Northeast	MA, PI, CE, RN, PE, BA	1984
BR2 Bragança¹	EMBRAPA	North	PA	1985
BR3 Tracuateua¹	EMBRAPA	North	PA	1985
BR4 Rio Branco*	EMBRAPA	North	AC	1985
BR5 Cana Verde*	EMBRAPA	North	AC	1985
3R6 Serrano*	EMPARN	Northeast	RN	1985
CNC 0434	EMBRAPA	North	AM	1985
BR7 Parnaíba*	EMBRAPA	Northeast	PI	1986
R8 Caldeirão*	EMBRAPA	North	AM	1986
BR9 Longá¹	EMBRAPA	Northeast	PI	1987
BR10 Piauí*	EMBRAPA	Northeast	PI	1987
PA-205 <sup>1</sup>	IPA	Northeast	PE	1988
3R12 Canindé*	EMBRAPA	Northeast	PI	1988
EPACE-10*1	EPACE	Northeast	CE	1988
Setentão*1	UFC	Northeast	CE	1988
PA-206 <sup>1</sup>	IPA	Northeast	PE	1989
Riso do ano¹	EMPARN	Northeast	RN	1990
BR14 Mulato*1	EMBRAPA	Northeast	PI	1990
BR15 Asa Branca*1	EMPARN	Northeast	RN	1990

BR16 Chapéu de Couro*1	EMPARN	Northeast	RN	1990
EPACE11 Jaguaribe*	EPACE	Northeast	CE	1991
BR17 Gurguéia*¹	EMBRAPA	Northeast	PI	1994
BRS Amapá*¹	EMBRAPA	North	AP	1997
BR18 Pericumã*	EMAPA	Northeast	MA	1998
Monteiro <sup>1</sup>	EMBRAPA	Northeast	PI	1998
Patativa*1	EMBRAPA	Northeast	CE	1999
EPACE V-96*	EMBRAPA	Northeast	CE	1999
BRS Mazagão¹	EMBRAPA	North	AP	2000
BRS Rouxinol*1	EBDA	Northeast	BA	2001
BRS Paraguaçu*1	EBDA	Northeast	BA	2002
De Metro¹	Hortivale	-	-	2003
Poços de Caldas¹	EPAMIG	Southeast	MG	2003
BRS Guariba*1	EMBRAPA	Northeast	PI, MA	2004
BRS Marataoã*	EMBRAPA	Northeast	PI, PB, BA	2004
BRS Urubuquara¹	EMBRAPA	North	PA	2005
BRS Milênio <sup>1</sup>	EMBRAPA	North	PA	2005
BRS Potiguar <sup>1</sup>	EMPARN	Northeast	RN	2005
BRS Novaera*1	EMBRAPA	North, Northeast, Central-West	RO, RR, PA, AP, AM, MA, RN, MS	2007
BRS Pujante*1	EMBRAPA	Northeast	PE, BA	2007
BRS Xiquexique*1	EMBRAPA	North, Northeast, Central-West	AP, AM, PA, RO, RR, AL, BA, MA, PE, PI, RN, SE, MT, MS	2008
BRS Cauamé*1	EMBRAPA	North, Northeast, Central-West	RO, RR, AP, AM, PA, PE, AL, SE, MS	2009
BRS Tumucumaque*1	EMBRAPA	North, Northeast, Central-West	RO, AM, RR, PA, AP, MA, PI, RN, PE,	2009
BRS Pajeú*1	EMBRAPA	North, Northeast, Central-West	AL, SE, MT, MS RR, RO, RR, AM, MA, PI, PE, AL, SE, MT. MS	2009
BRS Potengi*1	EMBRAPA	Northeast, Central-West	MA, PI, RN, PE, MT, MS	2009
BRS Itaim*1	EMBRAPA	North, Northeast	RR, PA, TO, PI	2009
BRS Juruá*1	EMBRAPA	North, Northeast, Central-West	RR, PA, TO, PI, SE, BA, MT	2009
BRS Aracê*1	EMBRAPA	North, Northeast, Central-West	RR, PA, TO, PI, SE, BA, MT	2009
BRS Acauã*1	EMBRAPA	Northeast	BA, PE, PI	2010
BRS Carijó*1	EMBRAPA	Northeast	BA, PE, PI	2010
BRS Tapaihum*1	EMBRAPA	Northeast	BA, PE, PI	2011
Miranda IPA 207*1	IPA	North, Northeast, Central-West	PA, PI, MA, MT	2016
BRS Imponente*1	EMBRAPA	North, Northeast, Central-West	PA, PI, MA, MT	2016
BRS Abiru <sup>1</sup>	EMBRAPA	Northeast	BA, CE, PE, PI	2017
BRS Batarra <sup>1</sup>	EMBRAPA	Northeast	BA, CE, PE, PI	2017
BRS Bené¹	EMBRAPA	North	PA	2020
BRS Guirá	EMBRAPA	North	PA	2022
BRS Lauré <sup>1</sup>	EMBRAPA	North	PA	2020
BRS Natalina <sup>1</sup>	EMBRAPA	North	PA	2020
BRS Raira <sup>1</sup>	EMBRAPA	North	PA	2020
BRS Utinga*1	EMBRAPA	North	PA	2020
BRS Olho Negro <sup>1</sup>	EMBRAPA	North, Northeast, Southeast, Central-West	RR, AP, AM, PA, TO, MA, PB, PE, PI, MG, RJ, SP, MS, MT	2021
BRS Verdejante <sup>1</sup>	EMBRAPA	Northeast	CE, PI, RN	2021
			RO, RR, AM, PA, AL, CE, MA, PE, PI,	
BRS Exuberante <sup>1</sup>	EMBRAPA	North, Northeast	RN, SE RO, RR, AM, PA, AL, CE, MA, PE, PI,	2022

<sup>&</sup>lt;sup>1</sup> Cultivars registered with the Ministério de Agricultura, Pecuária e Abastecimento. National Cultivar Registry (RNC). Available at

<sup>&</sup>lt;a href="https://sistemas.agricultura.gov.br/snpc/cultivarweb/cultivares\_registradas.php">https://sistemas.agricultura.gov.br/snpc/cultivarweb/cultivares\_registradas.php</a> Accessed on May 23, 2024.

<sup>&</sup>lt;sup>2</sup> Exposição Municipal Agropecuária e Industrial de Avaré (EMAPA); Universidade Federal do Ceará (UFC); Instituto de Pesquisas e Experimentações Agropecuárias do Norte (IPEAN); Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA); Empresa de Pesquisa Agropecuária do Rio Grande do Norte (EMPARN); Instituto de Pesquisas Agronômicas (IPA); Empresa de Pesquisa Agropecuária do Ceará (EPACE); Empresa Baiana de Desenvolvimento Agrícola (EBDA); Empresa de Pesquisa Agropecuária de Minas Gerais (EPAMIG).

<sup>&</sup>lt;sup>3</sup> Brazilian States: Ceará (CE), Amazonas (AM), Piauí (PI), Maranhão (MA), Rio Grande do Norte (RN), Pernambuco (PE), Bahia (BA), Pará (PA), Acre (AC), Amapá (AP), Minas Gerais (MG), Paraíba (PB), Rondônia (RO), Roraima (RR), Mato Grosso do Sul (MS), Alagoas (AL), Sergipe (SE), Mato Grosso (MT), Tocantins (TO), Rio de Janeiro (RJ), São Paulo (SP). \* Cultivars that have information about crosses in the literature and are therefore used in genetic contribution calculations.

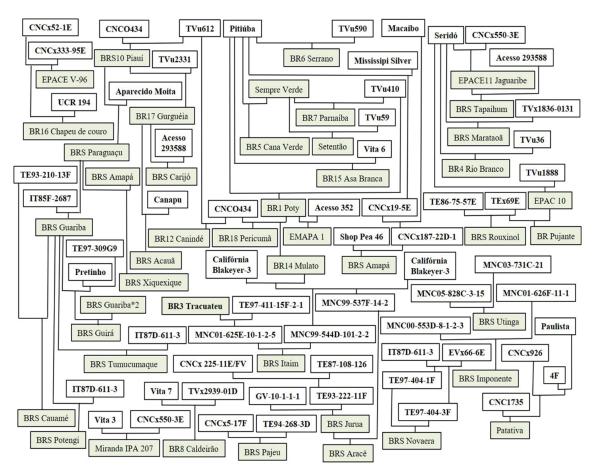


Figure 1. Genealogy of cowpea cultivars used to obtain the relative (RGC) and accumulated (AGC) genetic contributions of ancestral genotypes. Shaded genotypes are cultivars released in the period between 1960 and 2022 and which have information about their crosses in the literature, and those highlighted in bold represent the ancestors.

recommended for these regions, BRS-Novaera, BRS-Xiquexique, BRS-Cauamé, BRS-Tumucumaque, BRS-Pajeú, BRS-Potengi, BRS-Juruá, BRS-Aracê, Miranda IPA 207, BRS-Imponente, and BRS Olho Negro were also recommended for the Central-West region. The BRS-Olho Negro cultivar, released by Embrapa in 2021, was the only one with greater national coverage, being recommended for the North, Northeast, Central-West and Southeast regions of Brazil; however, information about its parents was not found.

Regarding the cultivars with available information about crosses, 55 ancestors made up their genealogies (Figure 1), which were used to calculate the relative (RGC) and accumulated (AGC) genetic contribution (Table 2). Cultivar CNC0434 alone contributed 8.30% to the formation of the genetic base of cowpea cultivars. This ancestor was obtained from selection carried out at the Empresa Brasileira de Pesquisa Agropecuária (Embrapa), within an  $F_2$  generation from the International Institute of Tropical Agriculture (IITA), and has good tolerance to the attack of severe mosaic, root-knot nematodes and green leafhopper (Nogueira 1985). Next are Pitiúba, Seridó, Tvu612 and Tvu410, each contributing 7.31, 6.10, 5.35 and 4.21%, respectively. Also noteworthy are IT85F-2687, Aparecido Moita, Sempre verde, IT87D-611-3, Tvu2331, Acesso 293588 and Tvu590, which had contribution between 2.43 and 3.85%. All these ancestors together, 12 in total, which contributed around 52.62% to the cultivars' gene pool, are from Africa, most often from Nigeria, or obtained from crosses between African and Brazilian materials, with the exception of Tvu410 (breeding material) and Tvu2331 (traditional cultivar/landrace), from the United States of America and India, respectively (IITA 2024). The other ancestors contributed around 0.50 to 1.81, except for Mississipi Silver, 4F, Paulista, TE97-309G9 and Pretinho, the ancestors that contributed least to the formation of the cultivars' gene pool with a value equal to 0.30%. It is worth

Table 2. Relative (RGC) and accumulated (AGC) genetic contribution from the ancestors of cowpea cultivars

N°	Ancestors	RGC%	AGC%	N°	Ancestors	RGC%	AGC%
1	CNC0434	8.30	8.30	29	Vita 6	1.02	78.65
2	Pitiúba	7.31	15.61	30	Vita 3	1.02	79.67
3	Seridó	6.10	21.71	31	CNCx11-9D	1.02	80.69
4	TVu612	5.35	27.06	32	UCR194	1.02	81.71
5	TVu410	4.21	31.27	33	MNC99-537F-14-2	1.02	82.73
6	IT85F-2687	3.85	35.12	34	EVx66-6E	1.02	83.75
7	Aparecido Moita	3.51	38.63	35	CNC1735	1.02	84.77
8	Sempre Verde	3.35	41.98	36	Acesso 352	1.02	85.79
9	IT87D-611-3	3.35	45.33	37	Vita 7	1.02	86.81
10	TVu2331	2.43	47.76	38	TVx2939-01D	1.02	87.83
11	Acesso 293588	2.43	50.19	39	CNCx5-17F	1.02	88.85
12	TVu590	2.43	52.62	40	TE94-268-3D	1.02	89.87
13	CNCx 252-1E	1.81	54.43	41	MNC00-553D-8-1-2-3	1.02	90.89
14	Snop Pea 46	1.81	56.24	42	MNC01-626F-11-1	1.02	91.91
15	CNCx187-22D-1	1.81	58.05	43	MNC05-828C-3-15	1.02	92.93
16	TVu1888	1.81	59.86	44	MNC03-731C-21	1.12	93.95
17	Califórnia Blackeye-3	1.81	61.67	45	CNCx19-5E	0.90	94.85
18	GV-10-1-1-1	1.81	63.48	46	Macaibo	0.90	95.75
19	TE93-222-11F	1.81	65.29	47	CNCx225-11E/FV	0.80	96.55
20	TE86-75-57E	1.81	67.1	48	TE87-108-126	0.80	97.35
21	TEx69E	1.81	68.91	49	TE97-411-15F-2-1	0.50	97.85
22	CNCx550-3E	1.81	70.72	50	CNCx926	0.50	98.35
23	CNCx333-95E	1.81	72.53	51	Mississipi Silver	0.30	98.75
24	TE93-210-13F	1.02	73.55	52	4F	0.30	99.05
25	Canapu	1.02	74.57	53	Paulista	0.30	99.35
26	TVu36	1.02	75.59	54	TE97-309G9	0.30	99.65
27	TVx1836-0131	1.02	76.61	55	Pretinho	0.30	100
28	MNC99-544D-101-2-2	1.02	77.63				

noting that the center of diversity of cultivated cowpea is in West and Central Africa, while that of wild relatives is in southern Africa (Boukar et al. 2020). Seeds from several of these wild relatives were collected and preserved at IITA, where breeders conducted crosses to obtain lines with genes for pest resistance and drought tolerance, among other traits (Boukar et al. 2019).

The results obtained in our study demonstrate an increase in the number of ancestors in formation of cowpea cultivar compared to the results obtained by Montalván et al. (2006), going from 35 to 55 ancestors. The contributions of these ancestors to the genetic base in our research ranged from 0.30% (Mississipi Silver, 4F, Paulista, TE97-309G9 and Pretinho) to 8.30% (CNC0434), different from the variation found by Montalván et al. (2006), which ranged from 0.29% (TVx4569-03E) to 15.04% (TVu1190). Quantitatively, there was an expansion in the genetic base of cowpea, since ten main ancestors in Montalván et al. (2006) study contributed 62.54% of the genes, while in our study, the first ten ancestors represented only 47.76%. Therefore, there was an increase of about 30.95% in the contribution of different genotypes to the cowpea genetic base.

In a similar study with soybeans in Brazil, Hiromoto and Vello (1986) observed that cultivars were derived from only 26 ancestors, with only four contributing approximately 50% to the gene pool, indicating a very narrow genetic base for this crop. Wysmierski and Vello (2013) also studied the genealogy of Brazilian soybean cultivars and concluded that their genetic base is quite narrow, as despite being made up of 60 ancestors, only four of them represented 55.3% of the gene pool. Similar conclusions were also obtained in studies conducted on soybean varieties cultivated in the United States (Delannay et al. 1983, Sneller 1994), China (Cui et al. 2000), Japan (Zhou et al. 2000) and India (Bharadwaj 2002).

Table 3. List of ancestors that contributed to the cytoplasmic genes of cowpea cultivars

Source of cytoplasmic genes	Number of favored cultivars	Source of cytoplasmic genes	Number of favored cultivars
CNC0434	16	Pretinho	1
Pitiúba	11	TVu612	1
Seridó	7	MNC01-625E-10-1-2-5	1
IT85F-2687	5	BR3 Tracuateua	1
Snop Pea 46	2	Vita 3	1
CNCx19-5E	2	Vita 7	1
Califórnia Blackeye-3	2	TE97-404-1F	1
Sempre Verde	2	CNC1735	1
CNCx252-1E	2	CNCx926	1
GV-10-1-1-1	2	4F	1
CNCx225-11E/FV	2	CNCx5-17F	1
TE86-75-57E	2	MNC00-553D-8-1-2-3	1
IT87D-611-3	2	MNC05-828C-3-15	1
TE98-210-13F	1		

In upland rice, similar results were obtained by Silva et al. (1999), who through AGC, observed that only three ancestors contributed 42.61% of the gene pool of the 34 cultivars with known genealogy, and that only the first nine ancestors contributed 69.88% of the gene pool of this crop. The authors considered the genetic base of upland rice to be narrow, revealing the need for its expansion. In irrigated rice, Rabelo et al. (2015) analyzed the genealogical information of 110 Brazilian cultivars and found 123 ancestors, whose relative genetic contributions ranged from 0.0018% to 14.6351%. Despite the large number of ancestors, the genetic base of Brazilian irrigated rice cultivars was considered narrow due to the use of the same genotypes as parents in several crosses. In cotton, Cruz et al. (2023) estimated the genetic base of 109 Brazilian cultivars. Twelve of the 68 ancestors identified contributed 52.03% of the genes, and 33% of the cultivars resulted from direct selection of local breeds or ancient cultivars, also demonstrating a narrow genetic base.

Regarding the origin of cytoplasmic genes, 27 of 55 ancestors were used as female parents in the crosses for the development of cowpea cultivars (Table 3). The ancestors CNC0434, Pitiúba and Seridó, all of Brazilian origin, were the most significant cytoplasmic ancestral sources, as they provided cytoplasmic genes for 16 (39.02%), 11 (26.83%) and 7 (17.07%) cultivars, respectively. Next, IT85F-2687 stands out, of Nigerian origin, providing cytoplasmic genes for five cultivars. All other ancestors contributed to the formation of one to two cultivars. Previous studies in this regard were not found for cowpea; however, for upland rice, Silva et al. (2002) recorded 16 ancestors in the cytoplasmic genes of 39 Brazilian cultivars. Thus, the cowpea ancestors most used in Brazil as female parents observed in our study have a common maternal origin and, therefore, the cytoplasmic genes are more uniform, considering the wide diversity of the germplasm of the species. Genetic uniformity may increase the vulnerability of the cowpea crop to biotic and abiotic stresses (Adewale et al. 2011). This demonstrates once again the importance of using germplasm with a wider genetic base to provide buffer and resilience to the cowpea crop against climatic and other environmental changes, ensuring sustainable food security.

From the results obtained in our study, we can infer that the genetic base of cowpea in Brazil is narrow, corroborating our hypothesis, as among the 55 ancestors of the 73 cultivars released in Brazil between 1960 and 2022, only five (CNC0434, Pitiúba, Seridó, Tvu612 and Tvu410) were used more frequently in crosses. Among these, except for Tvu612 and Tvu410, all the aforementioned ancestors were also those that contributed the most to mitochondrial and plastid genes, and thus confer the characteristics of maternal inheritance in the crop's gene pool. To reduce the cytoplasmic uniformity of cowpea cultivars, we recommend avoiding crosses involving CNC0434, Pitiúba and Seridó, and those derived from these genotypes.

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### **DATA AVAILABILITY**

The datasets generated and/or analyzed during the current research are available from the corresponding author upon reasonable request.

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