Journal of Zhejiang University-SCIENCE B in press
www.jzus.zju.edu.cn; www.springer.com/journal/11585
E-mail: jzus_b@zju.edu.cn

Research Article

https://doi.org/10.1631/jzus.B2600265

Phenolic profiles and antioxidant capacity across 182 mung bean genotypes

Wei CHEN[1*], Zhihua WANG[2*], Jing WANG[3], Xingxing YUAN[4], Wuyang HUANG[2,3,5✉], Ying LI[2,6✉]

[1]*Department of Clinical Nutrition, Department of Health Medicine, Key Laboratory of Diabetes FSMP, State Administration for Market Regulation, Peking Union Medical College Hospital, Chinese Academy of Medical Sciences and Peking Union Medical College, Beijing 100730, China*
[2]*Institute of Agro-Product Processing, Jiangsu Academy of Agricultural Sciences, Nanjing 210014, China*
[3]*College of Chemical Engineering, Nanjing Forestry University, Nanjing 210037, China*
[4]*Institute of Industrial Crops, Jiangsu Academy of Agricultural Sciences, Nanjing 210014, China*
[5]*School of Food and Biological Engineering, Jiangsu University, Zhenjiang 212013, China*
[6]*School of Ocean Food and Biological Engineering, Jiangsu Ocean University, Lianyungang 222005, China*

Abstract: Mung beans (*Vigna radiata* L.) are rich in health-promoting phenolics. This study presents a systematic investigation of the phenolic profiles and antioxidant capacity across 182 diverse mung bean accessions, documenting genotypic variation. Comprehensive analyses revealed that variations in total phenolic content (0.40–1.54 mg GAE/g DW) and total flavonoids (0.78–4.65 mg RE/g DW) are strongly correlated with antioxidant capacity. The measures of antioxidant activity analyzed include ferric reducing antioxidant power (FRAP), DPPH (2,2-diphenyl-1-picrylhydrazyl), and ABTS (2,2-azinobis (3-ethylbenzothiazoline-6-sulfonic acid) radical scavenging. Ultrahigh-performance liquid chromatography with quadrupole time–flight mass spectrometry (UPLC–QTOF–MS) tentatively identified 31 phenolics (including flavonoids, phenolic acids, and coumarins), with the C-glycosyl flavone isovitexin (243–1734 μg/g DW) predominating. Gene-expression analysis of 24 representative genotypes revealed that transcript levels of phenylalanine ammonia-lyase (*PAL*), chalcone synthase (*CHS*), and polyphenol oxidase (*PPO*) are correlated with phenolic accumulation. Significant variations associated with genotype and geographical origin were observed, with genotypes Jinlv 7 (Shanxi) and Sulv 6 (Jiangsu) exhibiting superior phenolic and antioxidant profiles, making them potential candidates for breeding programs. These results provide a scientific basis for breeding highly phenolic mung beans in order to develop functional foods and natural antioxidants.

Key words: Mung bean; Phenolics; Flavonoids; Antioxidant capacity; Genotypic and geographical variation

✉ Wuyang HUANG, wuyanghuang@hotmail.com
Ying LI, liying1981@jaas.ac.cn
* The two authors contributed equally to this work
Wuyang HUANG, https://orcid.org/0009-0004-9601-9925

Received Apr. 18, 2026; Revision accepted July 24, 2026;
Crosschecked xxx. xx, 20xx

1 Introduction

Mung beans, commonly called green gram or lvdou, are the seeds of the leguminous plant *Vigna radiata* L. They contain balanced nutrients, including protein, dietary fiber, minerals, vitamins, and bioactive compounds (Gan et al., 2017). Because of their significant nutritional and medicinal value, mung beans are widely utilized as both food and traditional medicine (Ganesan et al., 2018). Notably rich in protein, they serve as a vital crop for meeting daily intake requirements, particularly in Asia (Nair et al., 2013; Hou et al., 2019). Emerging evidence highlights their health benefits, including antioxidant, anti-inflammatory, antidiabetic, anti-hyperlipidemic, anticancer, hepatoprotective, and immunomodulatory effects (Liyanage et al., 2017; Gupta et al., 2018; Lopes et al., 2018). These functions are primarily associated with an abundance of phytochemicals, particularly phenolics.

Phenolic compounds, the most abundant and ubiquitous plant secondary metabolites, feature hydroxylated aromatic rings (Lattanzio et al., 2013). Based on carbon skeletons, they are categorized into phenolic acids, coumarins, tannins, flavonoids (including flavones, flavonols, isoflavones, flavanones, flavanonols, and anthocyanins), and others. A key bioactivity of phenolics is antioxidant capacity, the ability to scavenge reactive oxygen species or free radicals, thereby protecting against oxidative stress (Hunyadi et al., 2019). This fundamental property underpins their crucial role in maintaining health and normal physiological function, including prevention of cancer and other chronic diseases (Ghasemzadeh et al., 2011). Given these health-promoting properties, phenolics have become a major research focus in nutritional and food science (de Souza et al., 2018).

As mentioned above, mung beans are rich in phenolics, primarily phenolic acids, flavonoids, and tannins (Lee et al., 2011; Shi et al., 2016; Singh et al., 2017a, 2017b), among which isoflavones (e.g., daidzein, genistein) are prominent (Ganesan et al., 2017). The composition and content of these bioactive compounds vary significantly due to multiple factors, including intrinsic factors such as cultivar genotype and seed-coat color; extrinsic factors, i.e. climatic conditions and agronomic practices during cultivation; and methodological factors, e.g. extraction techniques and analytical procedures (Zhang et al., 2013). Mung beans exhibit distinct phenolic profiles influenced by their biosynthetic pathways. Studies suggest that gene-expression patterns such as up-regulation of *PAL* and *CHS* enhance phenolic accumulation, as observed in mango peels and tomatoes (Cheynier et al., 2013; Hoang et al., 2015). These pathways may also contribute to phenolic biosynthesis in mung beans, underscoring their nutritional and commercial value.

Despite the well-documented health benefits of mung bean phenolics, research on the links between genotypic variation, phenolic profiles, and antioxidant activity is still limited. Current screening methods for high-phenolic varieties remain inefficient due to the heterogeneity in phenolic content and composition. In this study, we systematically investigated the total phenolic/flavonoid content, antioxidant activity, and detailed phenolic composition of 182 mung bean genotypes, as well as the gene-expression levels of key enzymes for the biosynthesis and regulation of phenolics, to examine associations between genotypic traits, phenolic accumulation, and antioxidant performance. This work should accelerate the breeding of elite cultivars with superior nutraceutical value and offer a scientific framework for genetic improvement, as well as a pathway toward industrial sustainability.

2 Results and discussion

2.1 Total phenolic and flavonoid content in different genotypes of mung beans

Phenolics in mung beans have garnered significant attention due to their bioactivity (Hou et al., 2019). Total phenolics and flavonoids, key indicators of phenolic content, exhibit antioxidant, anti-inflammatory, hypoglycemic, and antitumor activity (Luo et al., 2016; Randhir et al., 2007). Our analysis of TPC and TFC in

mung bean genotypes from distinct regions revealed inter-varietal differences, with all 182 accessions detailed in Table S1 and 24 representative genotypes in Table 1.

Table 1 Total phenolic content (TPC), total flavonoid content (TFC), and antioxidant capacity of 24 representative mung bean genotypes

Mung bean genptype	Origin	TPC (mg GAE/g DW)	TFC (mg RE/g DW)	FRAP (μmol Fe^{2+}/g DW)	DPPH (μmol TE/g DW)	ABTS (μmol TE/g DW)
Bailv 11	BAAS, Baicheng, Jilin	1.11 ± 0.02	2.19 ± 0.68	8.19 ± 0.54	7.80 ± 0.49	5.10 ± 0.25
Bao 20050	Weifang, Shandong	1.28 ± 0.02	1.80 ± 0.03	12.81 ± 0.25	3.26 ± 0.27	3.38 ± 0.08
Baolv 2	Hefei, Anhui	0.97 ± 0.02	1.81 ± 0.07	8.96 ± 0.17	4.84 ± 0.17	3.83 ± 0.14
Binglv 15	SAAS, Taiyuan, Shanxi	1.38 ± 0.06	1.71 ± 0.04	12.16 ± 0.37	3.63 ± 0.38	9.03 ± 0.22
Dayinggelv 925 C5786	BAAS, Baicheng, Jilin	1.54 ± 0.07	1.81 ± 0.17	11.28 ± 1.69	6.53 ± 0.44	8.21 ± 0.09
De 0518	Weifang, Shandong	0.64 ± 0.01	1.48 ± 0.05	12.02 ± 0.37	3.92 ± 0.19	1.74 ± 0.04
Guangrao 1	Weifang, Shandong	1.20 ± 0.01	1.72 ± 0.08	11.31 ± 0.17	3.11 ± 0.41	2.82 ± 0.04
LZL148 Jílv 3	SYAU, Shenyang, Liaoning	1.25 ± 0.07	1.87 ± 0.19	9.50 ± 0.28	2.70 ± 0.15	2.70 ± 0.06
Jìlv 7	Hebei	1.06 ± 0.04	1.97 ± 0.08	9.57 ± 0.08	4.20 ± 0.19	5.41 ± 0.03
Jinlv 7	Shanxi	1.46 ± 0.07	2.25 ± 0.18	16.10 ± 0.79	8.33 ± 0.94	8.82 ± 0.07
Keda 2	NCES, Nanyang, Henan	0.79 ± 0.05	2.08 ± 0.02	10.11 ± 0.21	5.43 ± 0.07	2.22 ± 0.07
Liaolv 5	Liaoning	1.26 ± 0.08	2.33 ± 0.04	7.92 ± 0.79	3.37 ± 0.23	5.38 ± 0.01
Lvfeng 3	SYAU, Shenyang, Liaoning	1.05 ± 0.03	1.79 ± 0.08	8.92 ± 0.16	5.55 ± 0.13	2.86 ± 0.09
Nenlv 10	HAAS, Harbin, Heilongjiang	0.82 ± 0.03	1.80 ± 0.11	9.68 ± 0.21	3.35 ± 0.09	3.66 ± 0.06
Sulv 2	Jiangsu	1.33 ± 0.06	1.94 ± 0.32	13.90 ± 0.30	7.81 ± 0.35	7.25 ± 0.12
Tulv 7	Huhehaote, Neimenggu	0.81 ± 0.02	1.97 ± 0.06	10.53 ± 0.37	5.08 ± 0.12	2.84 ± 0.10
Wanlv 2	ES, Hefei, Anhui	1.06 ± 0.03	2.81 ± 0.14	8.98 ± 0.63	3.95 ± 0.21	4.39 ± 0.19
Wanlv 6	Henan	1.21 ± 0.04	2.99 ± 0.14	12.71 ± 0.36	6.33 ± 0.06	2.64 ± 0.11
Weilv 4	Weifang, Shandong	1.41 ± 0.02	1.89 ± 0.07	10.74 ± 0.91	3.04 ± 0.47	0.57 ± 0.07
Yulv 9	Chongqing	0.99 ± 0.09	1.86 ± 0.13	8.31 ± 0.21	4.19 ± 0.24	4.08 ± 0.15
Zhenglv 17	NCES, Nanyang, Henan	0.77 ± 0.01	1.62 ± 0.07	9.42 ± 0.12	3.31 ± 0.19	1.89 ± 0.10
Zhonglv 5	Beijing	1.10 ± 0.02	2.08 ± 0.05	8.28 ± 0.12	3.76 ± 0.09	4.88 ± 0.22
Jílv 3 × Jìlv 7	JAAS, Jilin, Jilin	0.99 ± 0.06	2.64 ± 0.10	8.59 ± 0.08	3.75 ± 0.17	4.89 ± 0.24
Lvfeng 3 × Sulv 2	JAAS, Jilin, Jilin	0.93 ± 0.07	2.46 ± 0.12	8.68 ± 0.25	5.06 ± 1.02	4.68 ± 0.06

Data are represented as the mean ± standard deviation (SD, n = 3). FRAP, ferric reducing antioxidant power; DPPH, DPPH radical scavenging activity; ABTS, ABTS radical cation scavenging activity; DW, dry weight; GAE, gallic acid equivalent; RE, rutin equivalent; TE, Trolox equivalent; JAAS, Jilin Academy of Agricultural Sciences; BAAS, Baicheng Academy of Agricultural Sciences; SAAS, Shaxi Academy of Agricultural Sciences; ES, Experimental Station; HAAS, Heilongjiang Academy of Agricultural Sciences; SYAU, Shenyang Agricultural University; NCES, Nanyang Comprehensive Experimental Station.

The TPC among the 182 genotypes ranged from 0.40 ± 0.02 mg GAE/g DW (Henanzhenzhulvdou) to 1.54 ± 0.07 mg GAE/g DW (Dayinggelv 925 C5786), with a mean of 0.91 ± 0.23 mg GAE/g DW. The top six accessions (> 1.3 mg GAE/g DW) were LZL035 Bei 2 D0797 (Liaoning), Sulv 2 (Jiangsu), Binglv 15 (Shanxi), Weilv 4 (Shandong), Jinlv 7 (Shanxi), and Dayinggelv 925 C5786 (Jilin). Geographically, Shanxi accounted for two, with the remaining four coming from Liaoning, Jiangsu, Shandong, and Jilin. Most accessions (72%) fell in the moderate range (0.7-1.1 mg GAE/g DW). Black-coated genotypes LZL190 Heizhenzhu 1 and LZL189 Heilvdou 1 exhibited above-average TPC (1.27 ± 0.03 and 1.12 ± 0.05 mg GAE/g DW, respectively). These findings are consistent with previous reports by Shao et al. (2014) on pigmented rice, which demonstrated that black rice contained more phenols than red or white rice varieties**.** Owing to our having just two black-seeded

accessions in this study, attributing higher TPC solely to coat color is untenable, and broader color-balanced studies would be required to dissect genotype from pigmentation.

Similarly, TFC varied markedly, from 0.78 ± 0.06 mg RTE/g DW (Jì 0204) to 4.65 ± 0.21 mg RTE/g DW (Sulv 6), with a mean of 1.88 ± 0.50 mg RTE/g DW. Most accessions (74%) exhibited values within the 1.4-2.2 mg RTE/g DW range. The top four (TFC > 3.0 mg RTE/g DW) were Sulv 6 (Jiangsu), Baolv 200212 × Jilv 7 (Jilin), Wanheilv 1 (Anhui), and Sulv 3 (Jiangsu). All exceeded the mean by 72-148%. Notably, Jiangsu contributed two, including the top-ranked accession.

Our TPC (0.40–1.54 mg GAE/g DW) and TFC (0.78–4.65 mg RE/g DW) ranges are broadly comparable to, but not identical to, early reports. Shi et al. (2016) reported 2.05–2.38 mg GAE/g and 20.08–24.35 mg RE/g across 20 cultivars; Lee et al. (2011) found similar TPC (2.03 ± 0.09 mg GAE/g DW) but different TFC (1.49 ± 0.56 mg CAE/g, using catechin equivalents); Zhang et al. (2013) obtained 1.86–5.07 mg GAE/g and 1.81–5.97 mg RE/g with acetone–water, but much lower values (0.08–0.28 mg GAE/g and 0.74–1.92 mg RE/g) with methanol, underscoring the strong influence of extraction solvent. These discrepancies stem from multiple interrelated factors, including genotype, seed-coat proportion, cultivation conditions, extraction solvent, and analytical methods. Our 182 accessions represent a much broader genetic base than most previous surveys, inherently widening the phenotypic spectrum. Dark-colored seed coats (black or dark green) are richer in phenolics (Shao et al., 2014), and our collection included such pigmented types. Phenolic contents vary dynamically during growth **(**Lu et al., 2019**)** and are significantly affected by geographical origin, cultivar, and processing methods **(**Zhang et al., 2021**).** Although all accessions were grown at a single site to reduce environmental variation, the original seed sources may impose persistent epigenetic or maternal effects (Zuk et al., 2019). In addition, extraction conditions and methodological choices (standards, wavelengths, and reaction times) directly affect absolute values. Collectively, these factors highlight the predominant influence of genetic diversity and the need for standardized protocols in assessing mung bean phenolic profiles.

2.2 *In vitro* antioxidant capacity in different mung bean genotypes

Free radicals damage biomolecules, contributing to inflammation, aging, and cardiovascular disorders (Phaniendra et al., 2015) and are mitigated by antioxidants. Antioxidant capacity is measured by chromogenic detection of radical neutralization with hydrogen donors (e.g., phenolics). To evaluate this key indicator of mung bean functional quality, we assayed *in vitro* antioxidant activity with three complementary assays (FRAP, DPPH, and ABTS) on 182 genotypes. The FRAP assay evaluates reducing power via $Fe^{3+}\rightarrow Fe^{2+}$ conversion (Shen et al., 2022); DPPH assesses lipophilic radical scavenging (Huang et al., 2012); and ABTS determines total capacity in both hydrophilic and lipophilic phases (Cano et al., 2002). It is important to note that these assays reflect chemical scavenging under controlled conditions and do not directly predict *in vivo* bioactivity, which depends on absorption, metabolism, and tissue accumulation of phenolics (Hunyadi, 2019).

The differential rankings of genotypes across the three assays are noteworthy (Table S1). The FRAP ranged from 4.60 ± 0.33 to 16.10 ± 0.79 μmol Fe^{2+}/g DW, with Jinlv 7 (Shanxi) showing the highest value. The DPPH varied from 0.76 ± 0.29 to 8.63 ± 0.24 μmol TE/g DW, with Sulv 5 (Jiangsu) producing the maximum value. However, Sulv exhibited only a moderate FRAP value, implying a phenolic profile favoring hydrogen donation to the lipophilic DPPH radical over Fe^{3+} reduction. The ABTS ranged from 0.41 ± 0.01 to 9.03 ± 0.22 μmol TE/g DW, with Binglv 15 (Shanxi) demonstrating the strongest activity. Notably, four of the top five ABTS performers (Binglv 15, Jinlv 7, Dayinggelv 925 C5786, Sulv 5 and Sulv 2) were also among the highest-TPC accessions, suggesting the role of phenolics as major contributors. The discrepancies arise from the distinct chemical principles of each method and the fact that individual phenolics differ with regard to redox potential and radical-scavenging preferences. Synergistic or antagonistic interactions among coexisting phenolics may further modulate each assay outcome (Hunyadi, 2019). The observed ranges in our study (e.g., ABTS 0.41–9.03 μmol TE/g DW) are comparable with previous reports for Chinese cultivars (3.83-13.44 μmol

TE/g DW; Shi et al., 2016**)** but lower than those for black-seeded varieties (8.76-21.79 μmol TE/g DW; Yao et al., 2013), likely due to genetic differences and variations in extraction and quantification protocols.

Table 2 Qualitative results for major phenolic components in the mung bean extracts by UPLC-QTOF-MS analysis

Compound name	N	Ionization mode	Retention time(min)	Molecular formula	Expected (m/z)	Precursor ion (m/z)	Error (ppm)	Major MS/MS fragments (m/z)
PHENOLIC ACIDS								
4-Hydroxybenzoic acid	181	$[M-H]^-$	7.94	$C_7H_6O_3$	137.0244	137.0246	1.2	93.0357, 65.0428
p-Coumaric acid	36	$[M-H]^-$	12.09	$C_9H_8O_3$	163.0401	163.0401	-0.1	119.0506, 93.0347
Ferulic acid	5	$[M-H]^-$	13.13	$C_{10}H_{10}O_4$	193.0506	193.0505	-0.8	178.0280,134.0373
FLAVONOIDS								
Flavones								
Isoorientin (Luteolin-6-*C*-glucoside)	NA	$[M+H]^+$	11.77	$C_{21}H_{20}O_{11}$	449.1078	449.1077	-0.4	329.0654
Orientin (Luteolin-8-*C*-glucoside)	NA	$[M-H]^-$	12.11	$C_{21}H_{20}O_{11}$	447.0933	447.0919	-3.1	357.0618, 285.0406
Glucosylvitexin (Vitexin-2"-*O*-glucoside)	NA	$[M+H]^+$	12.53	$C_{27}H_{30}O_{15}$	595.1657	595.1656	-0.3	433.1125
Isovitexin (Apigenin-6-*C*-glucoside)	182	$[M+H]^+$	13.00	$C_{21}H_{20}O_{10}$	433.1129	433.1126	-0.8	415.1006, 313.0684
Vitexin-2-*O*-rhamnoside	24	$[M+H]^+$	13.21	$C_{27}H_{30}O_{14}$	579.1709	579.1683	-4.3	433.1117, 415.1000
Vitexin (Apigenin-8-*C*-glucoside)	106	$[M-H]^-$	13.35	$C_{21}H_{20}O_{10}$	431.0984	431.0976	-1.8	341.0635,283.0589, 269.0444
Luteoloside (Luteolin-7-*O*-glucoside)	87	$[M-H]^-$	16.03	$C_{21}H_{20}O_{11}$	447.0933	447.0916	-3.7	285.0395
Luteolin	NA	$[M+H]^+$	18.4	$C_{15}H_{10}O_6$	287.055	287.0545	-1.9	153.0179
		$[M-H]^-$	18.64	$C_{15}H_{10}O_6$	285.0405	285.0396	-2.8	175.0392,151.0023
Diosmetin (Luteolin-4-methyl ether)	NA	$[M-H]^-$	21.35	$C_{16}H_{12}O_6$	299.0561	299.0553	-2.6	284.0318
Isoflavones								
Genistein (4',6,7-Trihydroxyisoflavone)	182	$[M+H]^+$	10.83	$C_{15}H_{10}O_5$	271.0601	271.0597	-1.6	253.0454,243.0654, 153.0188
Puerarin (Daidzein-8-*C*-glucoside)	182	$[M-H]^-$	15.10	$C_{21}H_{20}O_9$	415.1034	415.1022	-3.1	295.0604, 267.0651
Genistin (Genistein-7-*O*-glucoside)	NA	$[M-H]^-$	15.25	$C_{21}H_{20}O_{10}$	431.0984	431.0968	-3.8	269.0453
Daidzein (4',7-Dihydroxyisoflavone)	96	$[M+H]^+$	17.31	$C_{15}H_{10}O_4$	255.0652	255.0646	-2.2	237.0568,199.0956, 137.0233
Flavonols								
Rutin (Quercetin-3-*O*-rutinoside)	15	$[M-H]^-$	13.33	$C_{27}H_{30}O_{16}$	609.1461	609.1458	-0.5	301.0338, 300.0274
Isoquercitrin (Quercetin-3-*O*-glucoside)	141	$[M+H]^+$	13.42	$C_{21}H_{20}O_{12}$	465.1028	465.1003	-5.3	303.0482
Nicotiflorin (Kaempferol-3-*O*-rutinoside)	128	$[M+H]^+$	14.07	$C_{27}H_{30}O_{15}$	595.1657	595.1636	-3.6	287.0547
Isorhamnetin-3-*O*-neohesperidoside	NA	$[M-H]^-$	14.28	$C_{28}H_{32}O_{16}$	623.1617	623.1596	-3.5	315.0458
Astragalin (Kaempferol-3-*O*-glucoside)	91	$[M+H]^+$	14.58	$C_{21}H_{20}O_{11}$	449.1078	449.1066	-2.7	287.0549
Kaempferide (Kaempferol-4'-*O*-methyl ether)	NA	$[M+H]^+$	21.19	$C_{16}H_{12}O_6$	301.0707	301.07	-2.1	286.0463, 258.0517
Flavanones								
Naringin (Naringenin-7-*O*-neohesperidoside)	NA	$[M-H]^-$	14.57	$C_{27}H_{32}O_{14}$	579.1719	579.1698	-3.7	271.0602, 151.0040
Naringenin	19	$[M+H]^+$	15.16	$C_{15}H_{12}O_5$	273.0758	273.0749	-3.3	273.1148, 153.0173
		$[M-H]^-$	20.79	$C_{15}H_{12}O_5$	271.0612	271.0606	-2.2	177.0175,151.0021, 119.0505
Eriodictyol (3',4',5,7-Tetrahydroxyflavanone)	17	$[M-H]^-$	18.30	$C_{15}H_{12}O_6$	287.0561	287.0549	-4.2	151.0024
Flavanonols								
Dihydrokaempferol	NA	$[M+H]^+$	10.83	$C_{15}H_{12}O_6$	289.0707	289.0702	-1.7	153.0191
		$[M-H]^-$	11.83	$C_{15}H_{12}O_6$	287.0561	287.0553	-2.9	243.0657, 125.0257
Dihydroquercetin	161	$[M+H]^+$	11.09	$C_{15}H_{12}O_7$	305.0656	305.0651	-1.5	287.0551, 259.0611,231.0658, 153.0176
		$[M-H]^-$	13.76	$C_{15}H_{12}O_7$	303.051	303.0503	-2.3	285.0388, 125.0242
Anthocyanin								
Cyanidin-3-*O*-glucoside	116	$[M+H]^+$	14.58	$C_{21}H_{20}O_{11}$	449.1078	449.1066	-2.7	287.0549
COUMARIN COMPOUNDS								
Esculin (6,7-Dihydroxycoumarin-6-glucoside)	NA	$[M+H]^+$	7.24	$C_{15}H_{16}O_9$	341.0867	341.0865	-0.8	179.0335
		$[M-H]^-$	7.70	$C_{15}H_{16}O_9$	339.0722	339.0707	-4.3	177.0187, 133.0283
Scopolin (7-Hydroxy-6-methoxycoumarin-β-*D*-glucoside)	NA	$[M+H]^+$	8.86	$C_{16}H_{18}O_9$	355.1024	355.1012	-3.3	193.0484
Esculetin (6,7-Dihydroxycoumarin)	NA	$[M+H]^+$	9.42	$C_9H_6O_4$	177.0193	177.0194	0.4	133.0293

N, the number of mung bean accessions detected in HPLC. NA, not applicable. All compounds were tentatively identified by matching MS/MS data against the SCIEX targeted metabolite library, and identification confidence levels were putative identification.

2.3 Preliminary identification of phenolics in mung beans

Here, we analyzed the phenolic composition of mung beans qualitatively using UPLC-QTOF-MS, a high-resolution platform that enables sensitive and rapid phenolic profiling with excellent reproducibility (Chen et al., 2023). By matching retention time, accurate mass (error < 5 ppm), MS/MS fragmentation patterns, and cross-referencing with the SCIEX library and relevant literature, a total of 31 phenolic compounds were tentatively identified. As detailed in Table 2, these compounds span phenolic acids (4-hydroxybenzoic acid, *p*-coumaric acid, and ferulic acid), coumarins (esculin, scopolin, esculetin), and 25 flavonoids across six subclasses, including nine flavones (vitexin, isovitexin, glucosylvitexin, vitexin-2-*O*-rhamnoside, luteolin, luteoloside, orientin, isoorientin, diosmetin), four isoflavones (daidzein, puerarin, genistein, genistin), six flavonols (rutin, isoquercitrin, nicotiflorin, astragalin, kaempferide, isorhamnetin-3-*O*-neohesperidoside), three flavanones (naringenin, naringin, eriodictyol), two flavanonols (dihydrokaempferol, dihydroquercetin), and one anthocyanin (cyanidin-3-*O*-glucoside); this is consistent with previous reports (Yang et al., 2020).

Phytoestrogens, including genistein, daidzein, and glycitein, are bioactive compounds exhibiting weak estrogen-like effects that predominantly accumulate in leguminous plants, especially soybeans and mung beans (Zaheer et al., 2017). Mazur et al. (1998) isolated daidzein (9.7 μg/100 g DW) and genistein (365 μg/100 g DW) from soybeans, while Tang et al. (2014) identified genistein and its glycoside compounds in mung beans. We successfully detected the aglycone forms of daidzein and genistein, as well as a glycosylated conjugate, genistin, all of which belong to the isoflavones subclass. It is noteworthy that while flavonoids predominantly exist as glycosylated or esterified conjugates (Hou et al., 2019), our results confirm that the free aglycone forms can also be detected in certain cases.

2.4 Quantification analysis of phenolics in different mung bean genotypes

We performed further quantitative analysis of 18 phenolics across the 182 genotypes using HPLC, which brought their content variability to light. Of the compounds analyzed, six (ferulic acid, rutin, eriodictyol, naringenin, vitexin-2-*O*-rhamnoside, and *p*-coumaric acid) were detected in < 40 accessions (Table 2) with means < 10 μg/g DW. Astragalin occurred in 91 accessions at a moderate level (13.23 ± 12.07 μg/g DW). The remaining 11 major phenolics (mean values > 50 μg/g DW or present in > 100 accessions) are detailed in Table S4 (full dataset) and Table 3 (24 representative genotypes). These major compounds belong primarily to the flavone (e.g., isovitexin, luteoloside), isoflavone (e.g., genistein, puerarin), and phenolic acid (e.g., 4-hydroxybenzoic acid) subclasses.

Isovitexin (759.53 ± 249.61 μg/g DW) and puerarin (227.31 ± 77.43 μg/g DW) were the most abundant flavonoids distributed in all accessions, while 4-hydroxybenzoic acid (302.90 ± 134.27 μg/g DW) dominated in 181 accessions. They collectively accounted for > 69% of the total quantified phenolics. Widely distributed minor compounds included genistein (39.09 ± 36.90 μg/g DW, all), isoquercitrin (23.58 ± 7.26 μg/g DW, n = 141), and dihydroquercetin (5.53 ± 2.67 μg/g DW, n = 161). Isovitexin ranged from 243.39-1734.13 μg/g DW, peaking in Jinlv 7 (Shanxi, 1734.13 ± 0.27 μg/g DW), Liaolv 5 (Liaoning, 1675.30 ± 11.09 μg/g DW), and Binglv 9 (Shanxi, 1468.39 ± 1.83 μg/g DW). Notably, Zhonglv 5 (Beijing) contained exceptionally high 4-hydroxybenzoic acid (709.10 ± 2.64 μg/g DW) and luteoloside (855.36 ± 5.94 μg/g DW). Conversely, Weilv 12 had the lowest isovitexin (243.39 ± 4.92 μg/g DW) and 4-hydroxybenzoic acid (165.36 ± 11.64 μg/g DW), while C0925 had the lowest luteoloside (4.14 ± 7.20 μg/g DW); both of these bean varieties were from Weifang. Hybrids (Jílv 3 × Jìlv 7 and Lvfeng 3 × Sulv 2) exhibited intermediate levels, suggesting heterosis. Luteoloside, detected in 87 accessions, showed huge variation (mean 367.77 ± 317.84 μg/g DW). Cyanidin-3-*O*-glucoside was absent (ND) in 66 genotypes, with a very low mean (3.42 ± 0.91 μg/g DW). Daidzein (ND–138.11 ± 1.64 μg/g DW), nicotiflorin (ND–113.70 ± 8.16 μg/g DW), and vitexin (ND–70.01 ± 4.37 μg/g DW) also varied substantially. The extensive variability suggests genetic or regional influences on phenolic biosynthesis (Boudet et al., 2007).

Table 3 Quantitative results for major phenolic components in the extracts of 24 representative mung bean genotypes by HPLC analysis

Mung bean genptype	Content（μg/g DW）										
	4-Hydroxybenzoic acid	Isovitexin	Vitexin	Luteoloside	Genistein	Puerarin	Isoquercitrin	Nicotiflorin	Dihydroquercetin	Daidzein	Cyanidin-3-*O*-glucoside
Bailv 11	486.95 ± 41.87	778.35 ± 5.21	42.51 ± 24.54	830.81 ± 5.23	26.77 ± 0.07	119.67 ± 11.92	30.22 ± 0.91	27.73 ± 17.59	1.42 ± 1.32	ND	ND
Bao 20050	273.60 ± 1.74	807.31 ± 47.34	0.02 ± 0.03	32.91 ± 0.73	27.87 ± 0.13	186.96 ± 5.41	16.39 ± 0.18	113.70 ± 8.16	6.22 ± 0.90	135.44±0.60	2.44 ± 0.11
Baolv 2	386.44 ± 0.39	991.81 ± 0.67	ND	ND	30.50 ± 0.04	215.22 ± 0.13	27.87 ± 0.04	24.30 ± 0.79	5.41 ± 1.37	2.70 ± 0.02	ND
Binglv 15	544.11 ± 16.55	1253.39 ± 7.28	ND	29.91 ± 14.04	33.11 ± 4.04	362.43 ± 5.70	37.34 ± 5.61	28.04 ± 19.29	6.93 ± 5.53	0.12 ± 0.04	2.28 ± 1.35
Dayinggelv 925 C5786	574.63 ± 64.23	1195.90 ± 6.51	63.04 ± 24.80	ND	41.58 ± 0.08	226.96 ± 0.24	7.07 ± 12.24	52.14 ± 16.55	6.92 ± 0.74	0.13 ± 0.01	ND
De 0518	113.57 ± 33.98	617.22 ± 40.66	8.53 ± 5.28	ND	31.51 ± 0.12	258.28 ± 4.59	ND	5.69 ± 3.28	0.97 ± 0.46	ND	ND
Guangrao 1	360.54 ± 11.06	889.37 ± 6.82	ND	5.95 ± 5.21	27.59 ± 0.21	194.92 ± 3.97	28.57 ± 6.10	0.03 ± 0.02	4.31 ± 0.74	135.98±0.64	3.41 ± 0.04
LZL148 Jílv 3	389.19 ± 0.92	1046.39 ± 0.54	0.05 ± 0.00	9.37 ± 0.08	30.27 ± 0.02	412.07 ± 0.42	23.99 ± 0.21	ND	8.20 ± 0.60	74.46 ± 0.05	3.12 ± 0.01
Jìlv 7	535.07 ± 0.75	784.10 ± 1.31	ND	780.85 ± 7.79	30.87 ± 0.08	279.22 ± 13.03	23.97 ± 0.38	ND	6.65 ± 0.62	0.19 ± 0.01	1.64 ± 0.07
Jinlv 7	589.96 ± 2.44	1734.13 ± 0.27	56.38 ± 4.11	7.48 ± 0.15	148.60 ± 0.21	236.44 ± 11.57	35.93 ± 0.63	78.44 ± 4.16	10.20 ± 0.06	ND	1.39 ± 1.48
Keda 2	383.25 ± 23.13	913.43 ± 2.83	4.00 ± 3.69	ND	160.62 ± 9.09	227.95 ± 4.83	11.36 ± 19.67	0.04 ± 0.01	4.38 ± 0.25	ND	1.45 ± 0.03
Liaolv 5	453.50 ± 99.11	1675.30±11.09	56.40 ± 6.69	ND	33.27 ± 0.08	338.52 ± 0.97	31.40 ± 13.70	67.85 ± 31.92	12.94 ± 1.78	ND	1.97 ± 0.17
Lvfeng 3	289.46 ± 6.57	894.30 ± 3.76	ND	ND	35.23 ± 0.05	235.20 ± 2.84	ND	0.03 ± 0.01	5.60 ± 0.09	75.46 ± 0.06	ND
Nenlv 10	339.99 ± 18.66	1008.86±13.94	18.13 ± 10.44	11.47 ± 5.48	44.11 ± 1.36	165.70 ± 1.89	21.62 ± 1.46	ND	3.79 ± 2.28	10.89 ± 6.29	1.57 ± 0.91
Sulv 2	624.62 ± 0.10	607.35 ± 1.49	2.25 ± 0.06	624.22 ± 2.61	41.67 ± 0.08	282.97 ± 1.67	22.52 ± 0.13	17.41 ± 1.11	5.89 ± 0.01	0.22 ± 0.01	ND
Tulv 7	457.38 ± 9.49	867.99 ± 6.49	1.07 ± 1.59	ND	272.03 ± 12.28	310.23 ± 2.45	ND	0.03 ± 0.01	4.49 ± 0.94	ND	1.76 ± 0.02
Wanlv 2	248.81 ± 0.09	1015.67 ± 0.22	31.97 ± 0.35	ND	35.10 ± 0.04	217.26 ± 0.32	8.47 ± 0.11	35.86 ± 1.01	3.53 ± 0.02	2.60 ± 0.02	ND
Wanlv 6	545.95 ± 0.92	1155.15 ± 4.41	ND	ND	44.78 ± 0.10	534.33 ± 1.34	29.70 ± 0.18	68.99 ± 5.81	5.17 ± 1.82	ND	2.15 ± 0.07
Weilv 4	400.90 ± 36.76	1027.41 ± 7.23	15.68 ± 9.05	ND	34.22 ± 0.27	471.51 ± 7.06	ND	33.92 ± 22.21	0.97 ± 0.04	110.71±0.12	ND
Yulv 9	372.98 ± 0.27	1145.66 ± 1.08	ND	ND	23.56 ± 0.04	324.59 ± 0.39	26.06 ± 0.06	39.04 ± 0.08	4.45 ± 1.21	0.17 ± 0.01	ND
Zhenglv 17	269.30 ± 3.66	981.28 ± 6.90	0.05 ± 0.01	ND	152.93 ± 1.69	172.88 ± 3.94	37.06 ± 1.34	0.03 ± 0.01	6.84 ± 0.66	ND	0.82 ± 0.50
Zhonglv 5	709.10 ± 2.64	869.22 ± 23.97	0.05 ± 0.01	855.36 ± 5.94	30.33 ± 0.06	253.64 ± 6.18	29.09 ± 0.59	5.15 ± 2.97	8.05 ± 0.06	0.07 ± 0.01	1.39 ± 0.01
Jílv 3 × Jìlv 7	404.94 ± 109.86	690.99 ± 18.14	70.01 ± 4.37	644.00 ± 32.09	36.24 ± 0.19	241.46 ± 2.22	12.61 ± 10.74	3.75 ± 2.13	4.72 ± 0.05	ND	2.97 ± 0.09
Lvfeng 3×Sulv 2	211.50 ± 4.41	607.76 ± 8.69	43.80 ± 2.83	675.69 ± 19.44	31.29 ± 0.06	192.79 ± 5.59	6.57 ± 0.22	0.05 ± 0.01	4.40 ± 0.06	ND	3.02 ± 0.01

Data are represented as the mean ± standard deviation (SD, n = 3). DW, dry weight; ND, not detected.

The phenolic profile of mung beans exhibits a distinct compositional hierarchy. Flavones (especially C-glycosyl flavones, mainly isovitexin and luteoloside) are the most abundant subclass, followed by phenolic acids (notably 4-hydroxybenzoic acid) and isoflavones (particularly genistein). Other flavonoid subclasses (flavonols, flavanones, flavanonols, and anthocyanins) occur at lower levels. Mung bean flavonoids, especially flavones, play a core defensive role through antioxidant activity, pathogen inhibition, and stress signaling, while influencing nutritional quality (Das et al., 2024). Phenolic acids contribute to antioxidant, anti-inflammatory, and hypoglycemic effects, and their levels are enhanced during germination (Tomé-Sánchez et al., 2020). Isoflavones are involved in hormone modulation and anticancer activity, though they require fermentation or germination for bioactivation (Aboushanab et al., 2022). The differences in abundance among subclasses reflect their distinct biosynthetic pathways and physiological functions, illustrating the complex interplay between mung beans' chemical-defense and nutritional applications.

2.5 Genotypic and regional variations of phenolics in mung beans

The phenolic-compound content of food crops is influenced by genotype (variety or accession) and agronomic practices, as well as post-harvest and climatic conditions (Zuk et al., 2019). In our study, all 182 mung bean genotypes were cultivated under identical agronomic conditions at a single site to minimize environmental variation. This controlled cultivation revealed that the observed differences in phenolic distribution were associated with genotypic variation and geographical origin. However, a common-garden experiment cannot eliminate all confounders from original seed sources. The observed geographical differences likely reflect the genetic composition of the accessions, not direct environmental effects at their origin.

Significant genetic variation exists among mung bean accessions with regard to TPC, TFC, and key individual phenolics. Ten major variety series are shown in Fig. 1. Notably, Sulv, Jinlv, Liaolv, and Binglv displayed significantly higher TPC, with means exceeding 1.0 mg GAE/g DW (Fig. 1a, $p < 0.05$ *vs.* Weilv). Among these, Sulv stood out as having the highest levels of TPC, TFC, and 4-hydroxybenzoic acid, consistent with its superior DPPH radical-scavenging capacity. Jinlv ranked second in both TPC and isovitexin content, which correlated with its high FRAP activity, while Binglv exhibited the greatest puerarin accumulation, corresponding to its exceptional ABTS scavenging performance. In contrast, Bailv exhibited the highest luteoloside concentration but the lowest FRAP value (Fig. 1b-f). We observed notable differences even among genotypes of the same variety series, with certain accessions exhibiting markedly higher TPC and TFC compared to others within their group (e.g., Binglv 9 *vs*. Binglv 18**)**. Similarly, genotypes originating from the same geographical region displayed significant divergence in phenolic and flavonoid accumulation. For instance, within the Shanxi-derived accessions, Jinlv 7 demonstrated substantially elevated TPC and TFC levels relative to Dayanglvdou C0385, another accession from the same locality (Table S1), highlighting the influence of genetic background over environmental factors.

Individual phenolic content also exhibited a significant association with geographical origin, as shown in Table S5**.** Jiangsu accessions demonstrated the highest average TPC (1.13 ± 0.25 mg GAE/g DW), TFC (2.88 ± 1.11 mg RE/g DW), and 4-hydroxybenzoic acid (610.91 ± 193.1 μg/g DW), along with superior DPPH (6.28 ± 2.21 μmol TE/g DW); this is likely due to local adaptation. The Thailand genotype had remarkably high values, whereas Gansu accessions had the lowest. However, the limited sample size warrants caution. Regional variation was observed. For instance, Jilin and Hebei accessions had elevated levels of luteoloside and vitexin (696.51 ± 83.82 μg/g DW, 40.56 ± 12.57 μg/g DW; 648.58 ± 75.65 μg/g DW, 38.59 ± 22.28 μg/g DW), while Shanxi and Chongqing accessions had higher isovitexin (918.64 ± 436.45 μg/g DW; 993.07 ± 156.69 μg/g DW). Liaoning (101.25 ± 42.59 μg/g DW) and Shandong accessions (105.51 ± 52.72 μg/g DW) had significantly higher daidzein than beans from other regions (mostly < 1 μg/g DW or ND). Ferulic acid was detected only in Jilin (7.39 ± 3.21 μg/g DW), Jiangsu (6.08 ± 0.54 μg/g DW), and Anhui (2.81 ± 0.19 μg/g DW). This geographical variability suggests that the genetic background of accessions originating from different regions may

be associated with distinct phenolic biosynthesis characteristics (Cheynier et al., 2013; Joët et al., 2010). Notably, potential genotype-by-environment interactions could further modulate phenotypic expression, although assessing such interactions would require multi-environment trials with replication across sites and years. These findings underscore the importance of considering both genetic background and geographical origin when selecting mung bean genotypes with optimal phenolic content for nutritional and functional food applications.

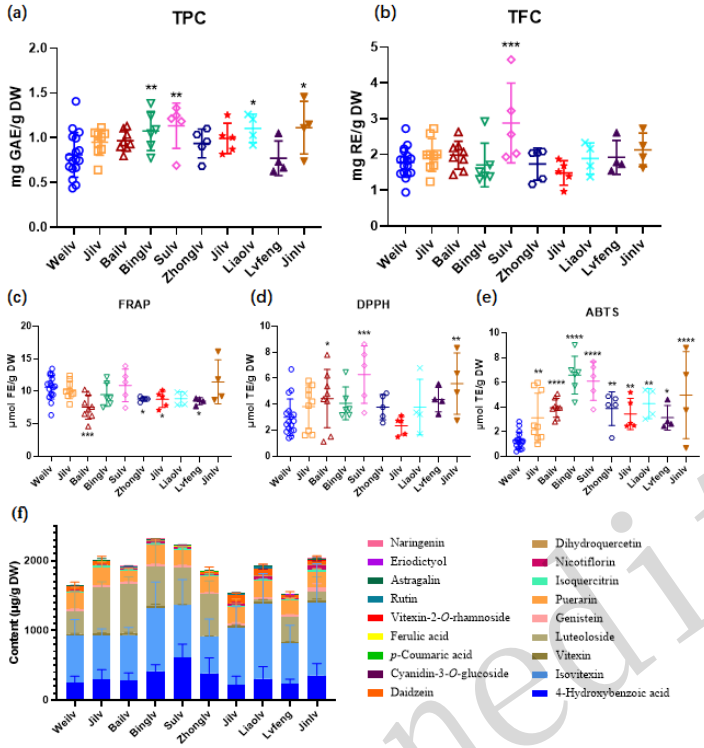

Fig. 1 (a) Total phenolic content, (b) total flavonoid content, (c) ferric reducing antioxidant power, (d) DPPH radical-scavenging activity, (e) ABTS radical-cation-scavenging activity, and (f) distribution of the corresponding contents of 18 phenolics in different mung bean genotypes from nine representative variety series. Data are represented as the mean ± SD (n = 4-18, the number of accessions). One-way analysis of variance with the Tukey's multiple comparisons test was used for multiple comparisons. Differences were considered significant at *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, and ****$p < 0.0001$ compared with the Weilv variety series.

2.6 Genetic analysis of key enzymes for the biosynthesis and regulation of phenolics

Phenolic content variation in mung bean is largely determined by polymorphisms in structural genes, their transcription factors, and seed-coat pigment genes. Darker-seeded genotypes generally accumulate more phenolics, which influence color and taste (Chai et al., 2021; Alcaraz-Mármol et al., 2017). Biosynthesis of phenolic compounds involves key enzymes such as *PAL* and *CHS*. In the phenylpropanoid–flavonoid pathway, PAL catalyzes the first committed step, converting phenylalanine to cinnamic acid (Kong et al., 2015), while CHS initiates flavonoid-backbone biosynthesis by condensing malonyl-CoA and coumaroyl-CoA to form naringenin chalcone (Tong et al., 2021). Subsequent steps involve a series of downstream enzymes, such as CHI, F3H, F3'H, FLS, DFR, ANS, LAR, ANR, UGTs, and MYB/bHLH/WD40 transcription factors. (Ren et al., 2026). Polyphenol oxidase, though not directly involved in biosynthesis, oxidizes phenolics to quinones, causing enzymatic browning and reduced phenolic content in harvested tissues, while also contributing to pathogen defense by generating toxic products (Daayf et al., 2012). So, higher PPO expression typically correlates with reduced phenolic stability, not enhanced accumulation.

Twenty-four representative genotypes were selected for qRT-PCR analysis of three key genes from *V. radiata*, including 22 accessions from different variety series and two hybrids (Fig. 2). *PAL* levels were highest in De 0518 (32.80 ± 20.76 fold change, $p < 0.001$), but lowest in Binglv 15 (0.11 ± 0.08 fold change). Despite moderate *CHS* (3.01 ± 1.89 fold change) and very low *PPO* (0.03 ± 0.01 fold change), Binglv 15 retained high phenolic content and antioxidant capacity. Keda 2 showed the highest *CHS* and *PPO* transcript levels (41.84 ± 14.52 and 18.06 ± 2.31 fold change, respectively, both $p < 0.001$), yet only moderate phenolic values. The lowest *CHS* levels were observed in Guangrao 1, Jilv 7 and Dayinggelv 925 C5786, while the lowest *PPO* levels were in Yulv 9 and Binglv 1. Compared with its hybrid (Lvfeng 3 × Sulv 2), Sulv 2 had higher *PAL* and *CHS* (both $p < 0.05$) but lower *PPO* expression, consistent with its elevated phenolic values.

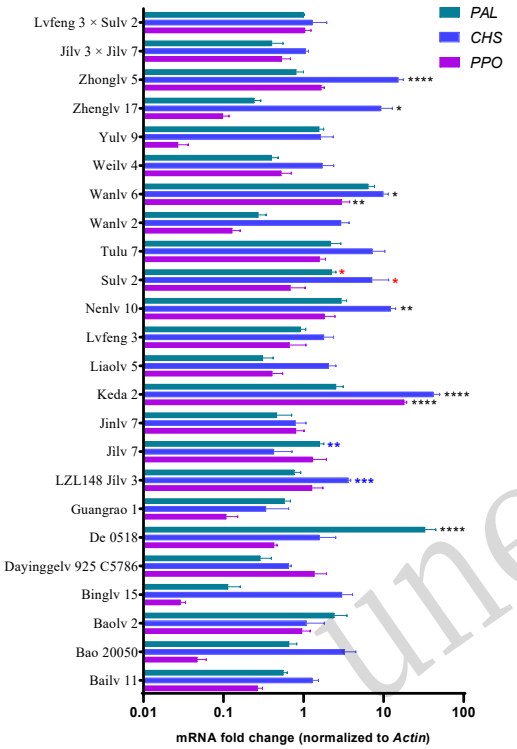

Fig. 2 Expression of *PAL*, *CHS*, and *PPO* mRNA in 24 representative mung bean genotypes. *PAL*, phenylalanine ammonia-lyase; *CHS*, chalcone synthase; *PPO*, polyphenol oxidase. Data are represented as the mean ± SD (n = 3-4). One-way analysis of variance with Tukey's multiple comparisons test was used for multiple comparisons. Differences were considered significant at *$p < 0.05$, **$p < 0.01$, and ****$p < 0.0001$ compared with the sample Lvfeng 3 × Sulv 2. Statistical significance between the two groups was conducted using unpaired two-tailed Student's *t*-tests. *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$ compared with the hybrid sample (red for Lvfeng 3 × Sulv 2, blue for Jílv 3 × Jìlv 7).

Previous studies have shown that *PAL* upregulation is associated with increased phenolic compound synthesis (Kumar et al., 2023), while higher CHS activity correlates with elevated flavonoid accumulation and antioxidant capacity (Pham et al., 2017). Lower *PPO* expression has been associated with better phenolic-content retention (Tomás-Barberán et al., 2001). Pearson correlation analysis showed that *CHS* and *PPO* expression were negatively correlated **(**Fig. S1, $p < 0.001$**).** Most individual gene–phenolic correlations were non-significant, except for *CHS* vs. genistein, *PAL* vs. TPC, and *PAL* vs. 4-hydroxybenzoic acid (Table S6). Overall, phenolic accumulation does not appear to be controlled by any single gene but may involve complex interactions, although the correlative nature of these data and the limited sample size (n = 24) preclude strong mechanistic conclusions.

2.7 Correlation between phenolics and antioxidant capacity

Pearson correlation analysis of 10 key indicators across 182 genotypes (Fig. 3a) revealed significant ($p < 0.05$) positive correlations between antioxidant indices (FRAP, DPPH, and ABTS) and TFC/TFC/4-hydroxybenzoic acid/isovitexin. Specifically, TPC exhibited the strongest positive correlations ($p < 0.001$) with all measured traits except genistein**.** It is important to note that these correlations only reflect statistical associations, not causation. To further identify the main phenolic contributors, we performed multiple linear regression (MLR) with 20 phenolic predictors (TPC, TFC, and 18 individual compounds) for each antioxidant index (Table S7). All MLR models were highly significant ($p < 0.0001$), with TPC emerging as the strongest positive predictor ($\beta = 3.92$, 6.41, and 5.97 for FRAP, DPPH, and ABTS, respectively; all $p < 0.01$), which confirmed total phenolics as the primary driver **(**Zhang et al., 2021**)**. Specific individual compounds showed assay-dependent contributions: dihydroquercetin, naringenin, isoquercitrin, and 4-hydroxybenzoic acid for ABTS; genistein and nicotiflorin for DPPH; and vitexin-2-*O*-rhamnoside for FRAP. In contrast, isovitexin and daidzein exhibited negative coefficients in certain models. Therefore, different phenolic compounds with distinct chemical properties may contribute differently to each assay. Together, these findings demonstrate that antioxidant capacity reflects the combined and differential effects of multiple phenolic components beyond TPC/TFC alone.

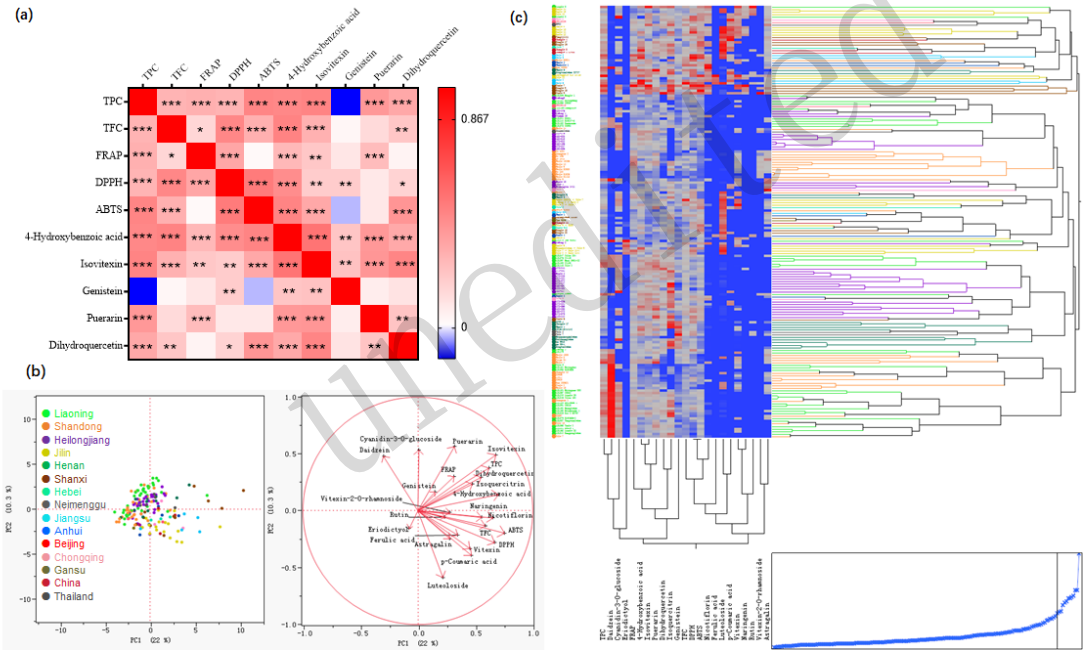

Fig. 3 (a) Pearson correlation analysis between the 10 key indicators (total phenolic/flavonoid content, three antioxidant indicators, five main phenolics; red and blue represent a positive or negative correlation, respectively), (b) principal component analysis and (c) cluster analysis involving the 23 variables of 182 mung bean genotypes from 15 original places (marked with different colors). Differences were considered significant at *$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$.

Principal component analysis of 182 genotypes from 15 origins (Fig. 3b) revealed suggestive chemo-geographic patterns, with PC1 (22%) and PC2 (10.3%) collectively explaining 32.3% of total variance**.** This relatively low proportion indicates substantial data complexity. Nevertheless, these two dimensions represent the main directions of variation. Partial geographic tendencies were observed, with Jiangsu/Jilin/Shanxi genotypes loaded positively on PC1 while Shandong/Gansu accessions loaded negatively. Jinlv7 (Shanxi) stood out as an extreme chemotype with high isovitexin content and FRAP activity (PC1 > 0, PC2 > 0). The PC1 positively correlated antioxidant metrics and most phenolics, while daidzein and eriodictyol loaded negatively.

Along PC2, distinct separation patterns between compound classes further indicated that individual phenolics differ in their contribution profiles. Although these patterns are suggestive rather than definitive, they may offer preliminary guidance for cultivar selection.

Hierarchical clustering of 182 genotypes (Fig. 3c; Fig. S1 for 24 representative genotypes) revealed distinct groupings based on phenolic profiles and antioxidant properties. Accessions from the same origin or variety series often clustered together, suggesting potential genetic or geographical influences (Nurzyńska-Wierdak et al., 2023). Antioxidant parameters and phenolic compounds separated into two major clusters, broadly corresponding to the positive and negative loadings on PC2 of the PCA. Notably, Jinlv 7 had high levels of flavonoids and antioxidant activity and formed a distinct cluster, while hybrids (e.g., Jílv 3 × Jìlv 7 and Lvfeng 3 × Sulv 2) occupied intermediate positions**,** consistent with the PCA results**.** These multivariate analyses collectively highlight the functional diversity among genotypes for potential applications in nutrition and agriculture.

3 Conclusions

This study demonstrates substantial genotype-associated variation in phenolic profiles and antioxidant capacity among mung bean genotypes, indicating associations between genotypic differences and phenolic accumulation. Antioxidant activities correlate strongly with phenolic contents. Key components, such as the C-glycosyl flavone isovitexin and 4-hydroxybenzoic acid, are tentatively identified as major contributors. There are distinct accumulation patterns for different phenolic subclasses, including phenolic acids, flavones, and isoflavones. These findings should facilitate targeted breeding of nutritionally-enhanced mung bean cultivars and support their utilization in functional foods. Additionally, the established correlations between genotypic traits and phenolic profiles could provide a scientific basis for selecting superior germplasm for industrial applications. However, it should be acknowledged that the gene-expression analysis was limited to mature seeds and only three genes, which may not fully capture the biosynthetic dynamics of seed development or the complexity of the regulatory network. Further research, including multi-environment trials and genetic analyses (e.g. genotyping, QTL mapping, marker-trait association or genome-wide association study), is needed to assess the environmental stability of these traits and to better understand the genotypic contributions to phenolic accumulation.

Materials and methods

The detailed methods are provided in the electronic supplementary materials of this paper.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Acknowledgments

This work was supported by Jiangsu Provincial Agricultural Science and Technology Independent Innovation Fund (cx(23)1014) and National High Level Hospital Clinical Research Funding (2025-PUMCH-C-004).

Author contributions

Wei CHEN performed the experimental research, funding acquisition. Zhihua Wang performed the experimental research and data analysis, wrote original draft manuscript. Jing WANG performed the data analysis. Xingxing YUAN contributed to the study design and resources. Wuyang HUANG contributed to the experimental supervision, data analysis, reviewing and editing of the manuscript. Ying LI contributed to the study design, project administration, and funding acquisition. All authors have read and approved the final manuscript, and therefore, have full access to all the data in the study and take responsibility for the integrity and security of the data.

Compliance with ethics guidelines

Sample: Wei CHEN, Zhihua WANG, Jing WANG, Xingxing YUAN, Wuyang HUANG, and Ying LI declare that they have no conflicts of interest.

Declaration on the use of generative AI tools

No generative AI tools were used in the preparation of this manuscript.

References

Aboushanab SA, Khedr SM, Gette IF, 2022. Isoflavones derived from plant raw materials: Bioavailability, anti-cancer, anti-aging potentials, and microbiome modulation. *Crit Rev Food Sci*, 63(2): 261-287. https://doi.org/10.1080/10408398.2021.1946006

Alcaraz-Mármol F, Nuncio-Jauregui N, Garcia-Sanchez F, et al., 2017. Characterization of twenty pomegranate (*Punica granatum* L.) cultivars grown in Spain: Aptitudes for fresh consumption and processiong. *Sci Hortic*, 219(17): 152-160. https://doi.org/10.1016/j.scienta.2017.03.008

Boudet AM, 2007. Evolution and current status of research in phenolic compounds. *Phytochemistry*, 68(22-24): 2722-2735. https://doi.org/10.1016/j.phytochem.2007.06.012

Cano A, Alcaraz O, Acosta M, 2002. On-line antioxidant activity determination: comparison of hydrophilic and lipophilic antioxidant activity using the ABTS•+ assay. *Redox Rep*, **7**(2): 103-109. https://doi.org/10.1179/135100002125000334

Chai Z, Herrera-Balandrano DD, Yu H, et al., 2021. A comparative analysis on the anthocyanin composition of 74 blueberry cultivars from China. *J Food Composit Anals*, 102: 104051. https://doi.org/10.1016/j.jfca.2021.104051

Chen CY, Li YH, Li Z, 2023. Characterization of effective phytochemicals in traditional Chinese medicine by mass spectrometry. *Mass Spectrom Rev*, 42(5): 1808-1827. https://doi.org/10.1002/mas.21782

Cheynier V, Comte G, Davies KM, et al., 2013. Plant phenolics: Recent advances on their biosynthesis, genetics, and ecophysiology. *Plant Physiol Biochem*, 72: 1-20. https://doi.org/10.1016/j.plaphy.2013.05.009

Daayf F, El Hadrami A, El Bebany AF, 2012. Phenolic compounds in plant defense and pathogen counter defense mechanisms. *Recent Adv Polyphenol Res*, 3: 191-208. https://doi.org/10.1002/9781118299753.ch8

Das A, Choudhury S, Gopinath V, et al., 2024. Functions of flavonoids in plant, pathogen, and opportunistic fungal interactions. In: Akhtar MS (Eds.), Opportunistic Fungi, Nematode and Plant Interactions: Interplay and Mechanisms. Springer, Singapore. https://doi.org/10.1007/978-981-97-2045-3_6

De Souza EL, de Albuquerque TMR, dos Santos AS, et al., 2018. Potential interactions among phenolic compounds and probiotics for mutual boosting of their health-promoting properties and food functionalities – A review. *Crit Rev Food Sci*, 59(10): 1645-1659. https://doi.org/10.1080/10408398.2018.1425285

Ganesan K, Xu B, 2018. A critical review on phytochemical profile and healthpromoting effects of mung bean (*Vigna radiata*). *Food Sci Hum Wellness*, **7**(1): 11-33. https://doi.org/10.1016/j.fshw.2017.11.002

Gan R-Y, Lui W-Y, Wu K, et al., 2017. Bioactive compounds and bioactivities of germinated edible seeds and sprouts: An updated review. *Trends Food Sci Technol*, 59: 1-14. https://doi.org/10.1016/j.tifs.2016.11.010

Ghasemzadeh A, Ghasemzadeh N, 2011. Flavonoids and phenolic acids: Role and biochemical activity in plants and human. *J Med Plants Res*, 5: 6697-6703. https://doi.org/10.5897/jmpr11.1404

Giusti F, Caprioli G, Ricciutelli M, et al., 2017. Analysis of 17 polyphenolic compounds in organic and conventional legumes by high-performance liquid chromatography-diode array detection (HPLC-DAD) and evaluation of their antioxidant activity. *Int J Food Sci Nutr*, 69(5): 557-565. https://doi.org/10.1080/09637486.2017.1399258

Gupta N, Srivastava N, Bhagyawant SS, 2018. Vicilin—A major storage protein of mungbean exhibits antioxidative potential, antiproliferative effects and ACE inhibitory activity. *PLoS One*, 13(2): e0191265. https://doi.org/10.1371/journal.pone.0191265

Hoang VLT, Innes DJ, Shaw PN, et al., 2015. Sequence diversity and differential expression of major phenylpropanoid-flavonoid biosynthetic genes among three mango varieties. *BMC Genomics*, 16: 1-12.

https://doi.org/10.1186/s12864-015-1784-x

Hou D, Yousaf L, Xue Y, et al., 2019. Mung bean (*Vigna radiata* L.): Bioactive polyphenols, polysaccharides, peptides, and health benefits. *Nutrients*, 11(6): 1238.
https://doi.org/10.3390/nu11061238

Huang WY, Zhang HC, Liu WX, et al., 2012. Survey of antioxidant capacity and phenolic composition of blueberry, blackberry, and strawberry in Nanjing. *J Zhejiang Uni Sci B*, 13(2): 94-102.
https://doi.org/10.1631/jzus.B1100137

Hunyadi A, 2019. The mechanism(s) of action of antioxidants: From scavenging reactive oxygen/nitrogen species to redox signaling and the generation of bioactive secondary metabolites. *Med Res Rev*, 39: 2505-2533. https://doi.org/10.1002/med.21592

Joët T, Salmona J, Laffargue A, et al., 2010. Use of the growing environment as a source of variation to identify the quantitative trait transcripts and modules of co-expressed genes that determine chlorogenic acid accumulation. *Plant Cell Environ*, 33(7): 1220-1233.
https://doi.org/10.1111/j.1365-3040.2010.02141.x

Kong JQ, 2015. Phenylalanine ammonia-lyase, a key component used for phenylpropanoids production by metabolic engineering. *RSC Adv*, 5(77): 62587-62603.
https://doi.org/10.1039/C5RA08196C

Kumar K, Debnath P, Singh S, et al., 2023. An overview of plant phenolics and their involvement in abiotic stress tolerance. *Stresses*, 3: 570-585.
https://doi.org/10.3390/stresses3030040

Lattanzio V, 2013. Phenolic compounds: Introduction. In: Ramawat K, Mérillon JM (Eds.) Natural Products. Springer-Verlag, Berlin, Heidelberg.
https://doi.org/10.1007/978-3-642-22144-6_57

Lee JH, Jeon JK, Kim SG, et al., 2011. Comparative analyses of total phenols, flavonoids, saponins and antioxidant activity in yellow soy beans and mung beans. *Int J Food Sci Tech*, 46: 2513-2519.
https://doi.org/10.1111/j.1365-2621.2011.02775.x

Liyanage R, Kiramage C, Visvanathan R, et al., 2017. Hypolipidemic and hypoglycemic potential of raw, boiled, and sprouted mung beans (*Vigna radiata* L. Wilczek) in rats. *J Food Biochem*, 42(1): e12457.
https://doi.org/10.1111/jfbc.12457

Lopes L, Martins M, Farias L, et al., 2018. Cholesterol-lowering and liver-protective effects of cooked and germinated mung beans (*Vigna radiata* L.). *Nutrients*, 10(7): 821.
https://doi.org/10.3390/nu10070821

Luo J, Cai W, Wu T, 2016. Phytochemical distribution in hull and cotyledon of adzuki bean (*Vigna angularis* L.) and mung bean (*Vigna radiate* L.), and their contribution to antioxidant, anti-inflammatory and anti-diabetic activities. *Food Chem*, 201: 350-360.
https://doi.org/10.1016/j.foodchem.2016.01.101

Lu Y, Chang X, Guo X, 2019. Dynamic changes of ascorbic acid, phenolics biosynthesis and antioxidant activities in mung beans (*Vigna radiata*) until maturation. *Plants*, 8: 75.
https://doi.org/10.3390/plants8030075

Mazur WM, Duke JA, Wähälä K, 1998. Isoflavonoids and lignans in legumes: nutritional and health aspects in humans. *J Nutr Biochem*, 9(4): 193-200.
https://doi.org/10.1016/S0955-2863(97)00184-8

Nair RM, Yang R-Y, Easdown WJ, et al., 2013. Biofortification of mungbean (*Vigna radiata*) as a whole food to enhance human health. *J Sci Food Agric*, 93(8): 1805-1813.
https://doi.org/10.1002/jsfa.6110

Nurzyńska-Wierdak R, 2023. Phenolic compounds from new natural sources—Plant genotype and ontogenetic variation. *Molecules*, 28(4): 1731.
https://doi.org/10.3390/MOLECULES28041731

Phaniendra A, Jestadi DB, Periyasamy L, 2015. Free radicals: properties, sources, targets, and their implication in various diseases. *Indian J Clin Biochem*, 30(1): 11-26.
https://doi.org/10.1007/s12291-014-0446-0

Pham HNT, Vuong QV, Bowyer MC, et al., 2017. Optimum conventional extraction conditions for phenolics, flavonoids, and antioxidant capacity of *Helicteres hirsuta* Lour. Asia-Pac. *Asia-Pac J Chem Eng*, 12: 332-347.
https://doi.org/10.1002/apj.2076.

Randhir R, Shetty K, 2007. Mung beans processed by solid-state bioconversion improves phenolic content and functionality relevant for diabetes and ulcer management. *Innov Food Sci Emerg*, 8(2): 197-204.

https://doi.org/10.1016/j.ifset.2006.10.003

Ren S, Cui J, Wang L, et al., 2026. Plant flavonoids: Biosynthesis, regulation, and roles in biotic and abiotic stresses. *Plant Cell Environ*, 49: 5664-568.
https://doi.org/10.1111/pce.70540

Shao YF, Xu FF, Sun X, 2014. Identification and quantification of phenolic acids and anthocyanins as antioxidants in bran, embryo and endosperm of white, red and black rice kernels (*Oryza sativa* L.). *J Cereal Sci*, 59(2): 211-218. https://doi.org/10.1016/j.jcs.2014.01.004

Shen N, Wang T, Gan Q, et al., 2022. Plant flavonoids: Classification, distribution, biosynthesis, and antioxidant activity. *Food Chem*, 383: 132531. https://doi.org/10.1016/j.foodchem.2022.132531

Shi ZX, Yao Y, Zhu YY, 2016. Nutritional composition and antioxidant activity of twenty mung bean cultivars in China. *Crop J*, 4(5): 398-406.
https://doi.org/10.1016/j.cj.2016.06.011

Singh B, Singh JP, Kaur A, et al., 2017. Phenolic composition and antioxidant potential of grain legume seeds: A review. *Food Res Int*, 101: 1-16.
https://doi.org/10.1016/j.foodres.2017.09.026

Singh B, Singh JP, Singh N, et al., 2017. Saponins in pulses and their health promoting activities: A review. *Food Chem*, 233: 540-549.
https://doi.org/10.1016/j.foodchem.2017.04.161

Tang DY, Dong YM, Ren HK, 2014. A review of phytochemistry, metabolite changes, and medicinal uses of the common food mung bean and its sprouts (*Vigna radiata*). *Chem Cent J*, 8: 4.
https://doi.org/10.1186/1752-153X-8-4

Tomás-Barberán FA, Espín JC, 2001. Phenolic compounds and related enzymes as determinants of quality in fruits and vegetables. *J Sci Food Agric*, 81: 853-876.
https://doi.org/10.1002/jsfa.885

Tomé-Sánchez I, Martín-Diana AB, Peñas E, 2020. Soluble phenolic composition tailored by germination conditions accompany antioxidant and anti-inflammatory properties of wheat. *Antioxidants*, 9(5): 426.
https://doi.org/10.3390/antiox9050426

Tong Y, Lyu Y, Xu S, 2021. Optimum chalcone synthase for flavonoid biosynthesis in microorganisms. *Crit Rev Biotechnol*, 41(8): 1194-1208.
https://doi.org/10.1080/07388551.2021.1922350

Xie J, Du M, Shen M, et al., 2019. Physico-chemical properties, antioxidant activities and angiotensin-I converting enzyme inhibitory of protein hydrolysates from Mung bean (*Vigna radiate*). *Food Chem*, **270**, 243-250.
https://doi.org/10.1016/j.foodchem.2018.07.103

Yang QQ, Ge YY, Gunaratne A, 2020. Phenolic profiles, antioxidant activities, and antiproliferative activities of different mung bean (*Vigna radiata*) varieties from Sri Lanka. *Food Biosci*, 37: 100705.
https://doi.org/10.1016/j.fbio.2020.100705

Yao Y, Yang XS, Tian J, 2013. Antioxidant and antidiabetic activities of black mung bean (*Vigna radiata* L.). *J Agric Food Chem*, 61(34): 8104-8109.
https://doi.org/10.1021/jf401812z

Zaheer K, Akhtar MH, 2017. An updated review of dietary isoflavones: Nutrition, processing, bioavailability and impacts on human health. *Crit Rev Food Sci*, 57(6): 1280-1293.
https://doi.org/10.1080/10408398.2014.989958

Zhang S, Feng Y-C, Fu T-X, et al., 2021. Effect of processing on the phenolics content and antioxidant properties of mung bean. *Cereal Chem*, 98: 355-366.
https://doi.org/10.1002/cche.10375

Zhang X, Shang P, Qin F, et al., 2013. Chemical composition and antioxidative and anti-inflammatory properties of ten commercial mung bean samples. *LWT Food Sci Technol*, 54: 171-178.
https://doi.org/10.1016/j.lwt.2013.05.034

Zuk M, Szperlik J, Hnitecka A, 2019. Temporal biosynthesis of flavone constituents in flax growth stages. *Plant Physiol Biochem*, 142: 234-245.
https://doi.org/10.1016/j.plaphy.2019.07.009

Supplementary information

Sample: Materials and methods; Tables S1 and S2; Figs. S1 and S2