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RESEARCH ARTICLE

Collections of Mungbean [*Vigna radiata*) (L.) R. Wilczek] and urdbean [*V. mungo* (L.) Hepper] in Vavilov Institute (VIR): traits diversity and trends in the breeding process over the last 100 years

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Abstract Mungbean (*Vigna radiata*) (L.) R.Wilczek and urdbean (*V. mungo*) (L.) Hepper are two warm-season legumes that are nutritionally dense and contribute to food security. Despite their value, they have historically been underutilized. The N. I. Vavilov's All-Russian Institute of Plant Genetic Resources *Vigna* germplasm collection is particularly critical for these crops because it includes accessions acquired over a century, from before 1920 into the twenty-first century. Here we evaluate 986 accessions of *V. radiata* (822) and *V. mungo* (164) from the VIR collection to assess historical shifts before and after the Green Revolution in three of the most important traits for breeding: the maturity period, seed productivity per plant, and the weight of 1000 seeds. In addition, for the subset of 200 accessions collected in 1910–1926, another 23 morphological and agronomic traits have been evaluated. This examination allows us to assess differences among these two closely related species, reveals the differences in germplasm from different regions, and trace changes in phenotypic characters in accessions acquired at different times. Indian landraces, in the region of primary domestication and diversification of both crops, are the most phenotypically diverse. It is evident that phenotypic diversity has decayed over time, with shifts towards medium time to maturation and large-seeded types in more recently acquired accessions bred after the start of the Green Revolution. The substantial phenotypic variation in the collection indicates that a number of breeder-desired traits are present in the VIR collection, particularly in the older material pre-dating the advent of Green Revolution breeding.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10722-019-00760-2) contains supplementary material, which is available to authorized users.

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Introduction

Mungbean (*Vigna radiata* (L.) R.Wilczek, green gram) and urdbean (*V. mungo* (L.) Hepper, black gram or black lentil) are often called "minor" crops, due to their restricted global social and economic significance, determined by their place in the world production, their underutilized use, and limited breeding efforts. The term also reflects their relatively narrow regional importance, which has not yet reached a global scale within the range of soil and climatic conditions suitable for them (Chiveng et al. 2015). Meanwhile these crops deserve close attention due to their high nutritional and fodder value, as new sources of ingredients for industry and pharmacology, and their utility in crop rotations. These "underutilized" crops, along with others, are under the constant attention of FAO—the Food and Agriculture Organization with a view to their promotion and large-scale contribution to agricultural production (Williams and Haq 2002).

V. radiata and *V. mungo* are closely related, formerly attributed to the genus *Phaseolus* and classified as one species. Both species have the same chromosome number ($2n = 2x = 22$) and similar karyotypes. There are partially fertile progenies in crosses when *V. radiata* is used as the maternal plant, but the reciprocal crosses have not been found viable (Sen and Ghosh 1963, Chowdhury et al. 1977; Singh 1981). Together with dissimilarities in some morphological features (Burlyaeva et al. 2016), cytological investigations revealed differences of the species in chromosome translocations, deletions and duplications (De Deepesh and Krishnan 1966). *V. radiata* and *V. mungo* have also been placed in separate botanical species by molecular markers (Jaaska and Jaaska 1989; Santala et al. 2006).

Mungbean and urdbean are high in protein, the seeds of which are used mainly for food purposes. To a certain extent, they are also used as fodder crops: as high-protein additives, hay, silage and straw (Fuller 2004; Mogotsi 2006). Like all legumes, due to symbiosis with rhizobial bacteria, they play a significant role in nitrogen cycles and have been used as sedimentary and cover crops. In addition, they have considerable agronomic value for marginal areas of crop production, since they are adapted to extreme conditions of agriculture, in particular, arid and semi-arid regions.

Mungbean occupies 6 million hectares, about 8.5% of the world production area for grain legume crops (without counting the oilseed legume soybean). It is produced throughout the tropical and subtropical belt of the globe. The main world producers are India, China, Indonesia, Thailand, Myanmar, and the Philippines. It is also produced in the Central Asian countries, where, it has likely been grown since the third century BC (Mani 2004). Urdbean, unlike mungbean, is a less common crop. The leading producer is also India, where up to 1.5 million tons of urdbean are produced annually, fully consumed domestically (Ahlawat et al. 2016). The main exporters of urdbean are Myanmar and Thailand (CRN India, 2011).

In the Russian Federation, both species are able to grow in a number of the southern regions of the European part, western Siberia and the Far East (Vishnyakova et al. 2018). The main areas of mungbean cultivation are concentrated in the North Caucasus, in the Caspian lowland and in the south of Primorsky Krai. Both crops are becoming the object of interest as a possibility for diversification of plant industry production in Russian Federation.

Until the middle of the twentieth century, worldwide production of both crops was based on local varieties. Their commercial improvement even in the leading producing countries began relatively recently, and is minor in comparison to other legumes. Furthermore, it is noted that the productivity of modern varieties has grown little with time, which is attributed to the lack of genetic diversity, a low harvest index, the lack of the appropriate varieties for different farming systems, non-simultaneous maturation and susceptibility to diseases and pests (Souframanien and Gopalakrishna 2006). Neither crop has been the beneficiary of the investments of a major breeding program, as has occurred in cereals like wheat, rice, maize, or soybean. The successful development and dissemination of improved mungbean varieties through a research network led by the World Vegetable Center two decades ago significantly increased production and cultivation area (Shanmugasundaram et al. 2009). Since then progress has been limited. Mungbean is a minor pulse crop that is outside of the CGIAR (Consultative Group for International Agricultural Research) mandate system, and up to recently did not attract coordinated research. Increased demand for pulses in South Asia and rising interest of donor organizations in the potential of mungbean as a rotation crop in cereal-based cropping systems has stimulated breeding and research for this crop. The release of a draft whole genome DNA sequence of mungbean provided the basis for genomics- based breeding (Kang et al. 2014) and the development of core collections improved access to genetic resources for breeding (Schafleitner et al. 2015). Nevertheless, to increase production quantity and area, mungbean breeding continuously needs new traits such as heat and cold tolerance, resistance to bacterial diseases and improved nutritive quality of the grain.

The invaluable sources for breeding are plant genetic resources preserved in genebanks. The resources of *V. radiata* and *V. mungo* are quite abundant. The collections of the crops are preserved in many genebanks; the greatest are in the World Vegetable Center (Taiwan), in the National Board for PGR (India), in the Institute of Crop Germplasm Resources (China), the Plant Genetic Resources Conservation Unit (USA), the genebank of the Commonwealth Scientific and Industrial Research Organization (Australia), and Plant Genetic Resources (Pakistan).

Vavilov Institute's (VIR's) collection contains 1478 accessions of *V. radiata* and 230 of *V. mungo*. The beginning of *Vigna* collection in VIR was initiated in 1910 (Vishnyakova et al. 2018). The first introductions came from Manchuria and the Central Asian Syr-Darya river region (Kyrgyzstan, eastern Uzbekistan, and Southern Kazakstan). Later the collection was expanded by VIR expeditions and additions from other world genebanks. The most valuable old landraces were collected at the beginning of twentieth century by NI Vavilov, IP Borodin, EN Sinskaya, AD Voeikov and in the 1950–1960s by DV Ter-Avanesyan (Vishnyakova et al. 2018).

VIR collections of mungbean and urdbean have been successfully grown in the Astrakhan region to study and maintain the viability of the seeds. It has been shown that seed productivity there could achieve 41–60 g/plant in the varieties maturated for 69–80 days, and more than 80 g/plant when they ripen in 81–90 days (Burlyaeva et al. 2014). As predominantly selfing crops, they can be maintained without genetic loss over time with these amplification and line maintenance practices. This is ideal for examining the potential for loss of diversity in accessions that were added to the collection over the past century.

Here we present the analysis of the ecological and geographical diversity of mungbean and urdbean from the VIR collection and trends in the variability of the main economically valuable traits (maturity period, plant productivity and seed weight) during the breeding process for 100 years. This is the most extensive phenotyping effort for these crops in a northern location performed to date of which we are aware. The objectives of the current study are 1) evaluation of the diversity of accessions by biological and agronomic traits in the VIR collection, 2) analysis of interspecific and intraspecific variability of biological and agronomic traits, and 3) evaluation of changes in the main breeding characters occurred over the past 100 years. The third aim is particularly critical for justifying the preservation of old accessions in genebanks.

Materials and methods

Germplasm

A long-term field evaluation of 986 accessions of *V. radiata* (822) and *V. mungo* (164) from VIR collection originating in 54 countries was carried out at the VIR branch of the Astrakhan experimental station located in the southeastern part of the Astrakhan region, in the zone of the Caspian deserts and the Volga delta (46°07′N, 41°01′E). Most accessions came from India (353), China (158), Kenya (83), Uzbekistan (123), and Afghanistan (101). These are mainly landraces from the centers of origin and from the countries traditionally cultivating these species; about 8% are commercial varieties and about 1% are wild accessions. Of the 986 accessions studied, 200 old landraces originating from 14 countries were introduced into the collection during 1910–1926.

Experimental location

The climate of the Astrakhan region is dry and sharply continental; it is second only to Central Asian deserts and semi-deserts according to the degree of aridity within the Russian Federation. The soils in the experimental field were alluvial-meadow, heavy loam, slightly saline (chloride-sulfate type of salinity), slightly acidified and with a low humus content. The weather conditions during the years of evaluation differed in their parameters. The sum of air temperatures above 10 °C during the vegetation period reached a cumulative 3500–3600 growing degree days (°C). The annual amount of precipitation ranged between 180 and 290 mm.

Evaluation conditions

The sowing was carried out in a moist, warmed-up soil layer not earlier than first or second week of May, when the average daily air temperature reached 14–16° C. Method of sowing is wide-row. Seeds were sown manually, the width between rows was 70 cm, and the distance between seeds in the row was 10 cm. The depth of seeding was 3–5 cm when planted in moist soil and up to 6 cm at lower humidity. Accessions were cultivated under irrigated conditions: during the growing season, six irrigations were provided by sprinklers with an average of 250–300 m^3/ha.

Measurement details

The evaluation of the accessions (phenological observations, morphological and biological descriptions) have been carried out in accordance with the VIR "Guidelines" (Vishnyakova et al. 2010). Each accession was evaluated during 3 years by a single researcher (M Burlyaeva). Six plants of each replicate plot were analyzed. "Descriptors for Mung Bean" (1980), "Descriptors for *Vigna mungo* and *V. radiata*" (1985), and "The international descriptors for species of the genus Vigna (Savi)." (2016) have been used. The most significant traits for breeding have been analyzed in the total sample of 986 accessions: the maturity period, seed productivity of one plant, and the weight of 1000 seeds. In addition, in 200 accessions from 1910 to 1926, we evaluated 23 more traits (26 in total, all listed in Supplemental Table 1). Raw data is available as Supplemental Table 2.

Statistical analysis

Our statistical analysis was performed in Statistica 7 software package (TIBCO.com). We performed Descriptive Statistics to assess means of each trait (Supplemental Tables 1, 2, 3, 4) in each species, each origin and in each period of collection (1910–1926, 1946–1970, post 1970). ANOVA (one-way and main effects analysis of variance) was used to assess the significance of differences among the two species, across different geographic origins of the accessions, and across periods of time introduction in the collection. Correlation analysis to assess the relationships among the VIR traits for all accessions was also performed.

The analysis of the traits was carried out by mean values obtained as a result of 3–4 years of research. The evaluation in different years had been carried out at the same stages of development: seed productivity and seed weight measured during the stage of full maturity. The duration of maturation period in our analysis had been truncated at 140 days, as it is the most appropriate time for harvesting in Astrakhan—during September–October. For the accessions with longer period of maturation in Astrakhan environment there were no chance to ripe.

Each accession was studied on 6 randomly selected plants from the plot. When carrying out the variance analysis, all the necessary requirements were met: the normality of the distribution of the values of the trait under study; equality of variances in the samples being compared; random and independent sampling. To confirm the equality of variance, the Levene's test and the Brown & Forsy test were used. In addition to estimating the mean, the variance analysis included the determination of the η^2% (intraclass correlation) determination coefficient, which indicates what proportion of the total variability is attributed to this factor. The Pearson correlation coefficients was calculated for the most important traits in mungbean breeding. The values of the correlation coefficient $r < 0.5$ were considered as low, $0.7 > r \geq 0.5$ as average, $0.9 > r \geq 0.7$ as high, and $r \geq 0.9$ as very strong (Sokal and Rohlf Sokal and Rohlf 1995).

Results

Species differences

We observed reliable differences between the two species (means in Supplemental Table 3) based on one-way analysis of variance in the full set of 986 lines, namely the maturity period ($F_{1,973} = 8.361$, $p = 0.0039$, Fig. 1a), seed productivity per plant ($F_{1,977} = 52.47$; $p < 0.001$, Fig. 1b), and 1000 seed weight ($F_{1,\ 984} = 5.985$, $p = 0.0146$; Fig. 1c). In the smaller set of 200 lines for which we could measure 26 traits in total, we observed significant differences among the species in terms of: growth habit, mature pod color, pod shattering in the field, 1000 seed weight (Fig. 1 d–g, Table 1). The remaining traits studied did not show significant differences between the species in the set of 200 lines.

Differences in lines among geographic origins and trait correlations

We noted differences among accessions based on the country of origin in the complete 986 accession dataset in all three traits studied. In the 794 *V. radiata* accessions (after removing countries for which only one or two accessions were available), there were differences among origin countries in 1000 seed weight ($F_{25,792} = 6.528$, $p < 0.0001$), maturity period ($F_{25,792} = 3.33$, $p < 0.0001$), and seeds per plant ($F_{25,792} = 6.539$, $p < 0.001$). In the accessions 153 *V. mungo* accessions (after removing countries for which only one or two accessions were available), there were differences among origin countries in 1000 seed weight ($F_{7,151} = 5.84$, $p < 0.0001$), maturity period ($F_{7,151} = 2.92$, $p < 0.01$), and seeds per plant ($F_{7,151} = 4.06$, $p < 0.001$). In the 200-landrace dataset, we observed variability also of the traits growth habit, color of petiole, mature pod color, leaflet shape, leaf pubescence, pod length, pod shattering, number of seeds per pod, days to maturity, seed weight based on the geographic origin of the landraces (Fig. 2, Table 2).

As an example of regional variation for *V. radiata,* Indian accessions have been characterized by an erect bush form, small pods and predominated dark seeds (with a weight of 1000 seeds of 30.2 g) compared to landraces of both species from other regions. Among Indian accessions there are both early and late-maturated forms. The latter do not bloom in Astrakhan region environment where we phenotyped them. Chinese, Korean, and Japanese landraces were characterized by early maturation, large beans and seeds (with a weight of 1000 seeds up to 80 grams) with light green and yellow seed coat color. Mungbeans from Iran, Afghanistan, and Central Asia are medium-ripening, medium-sized, and have curly branches. Landraces from other countries were close to either Indian, Chinese, or Iranian accessions (Table 2, Supplemental Table 4). Figure 3 shows that India and Chinese accessions has the largest phenotypic range in seed weight per plant (a) and 1000 seed weight (b) in the whole dataset of 986 accessions. Afghan and Uzbek accessions are less diverse in all the traits studied and early-maturated and high-productive forms are nearly absent in this region.

The analysis of correlations between traits in the full 986 accession collection did not reveal significant interrelations (Table 3). Apparently at the edge of the cultivation area (Astrakhan region), the duration of maturity period and seed weight are not strongly related to plant productivity. We can assume that in our experiments these characters were more dependent on climatic conditions.

Differences in accessions collected over time

The historical length of the VIR collection makes it ideal for examining changes in landrace characteristics over time. The century period over which the VIR collection was assembled allowed us to study not only the variability of traits valuable for breeding (maturity period, plant productivity and seed weight) in *V. radiata* and *V. mungo*, but also the changes that occurred with these traits during the breeding process of the past 100 years (Supplemental Table 5).

Furthermore, among the old landraces collected in the early 1900s, there are accessions with different combinations of many valuable traits. There are forms from early maturing to late maturing, from small-seeded to large-seeded, with shrubby and unfinished growth, with seeds of various shades of black, brown, green and yellow, with different degree of pods shattering, etc. Using the potential of this gene pool will contribute to a more effective mungbean and urdbean breeding.

One-way ANOVA showed the significant effect of the date of introduction into the VIR collection for the

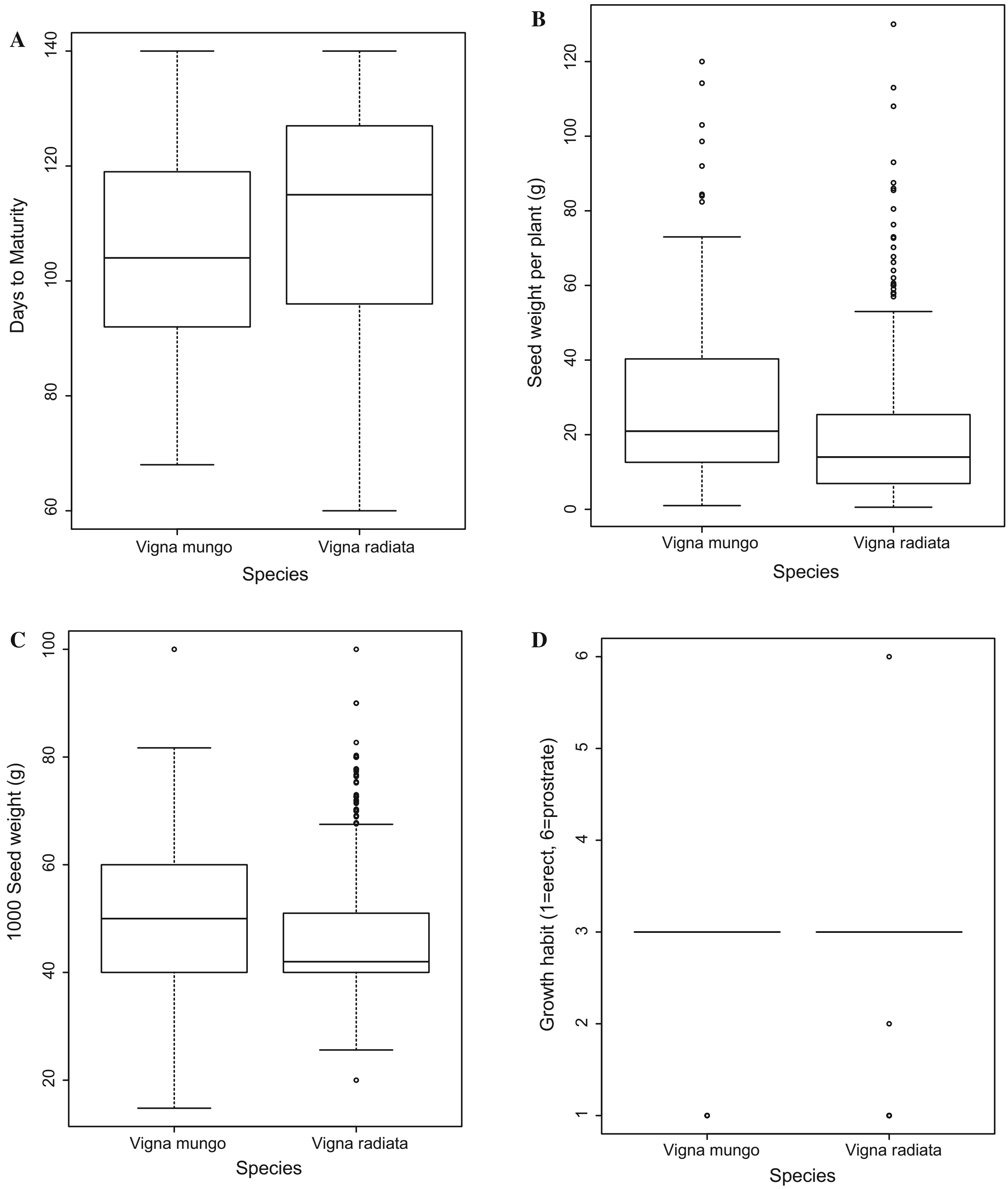

Fig. 1 Variability of several traits in both the complete 986 accession dataset (**a**–**c**) and the smaller 200 accession dataset (**d**–**g**) between *V. radiata* and *V. mungo*. Variation in days to maturity (**a**), seeds per plant (**b**), 1000 seed weight (g) (**c**), growth habit (1 = erect, 6 = prostrate) (**d**), mature pod color (1 = white, 10 = black) (**e**), pod shattering in the field (0 = dehiscient, 10 = indehiscient) (**f**), seed weight (g) (**g**)

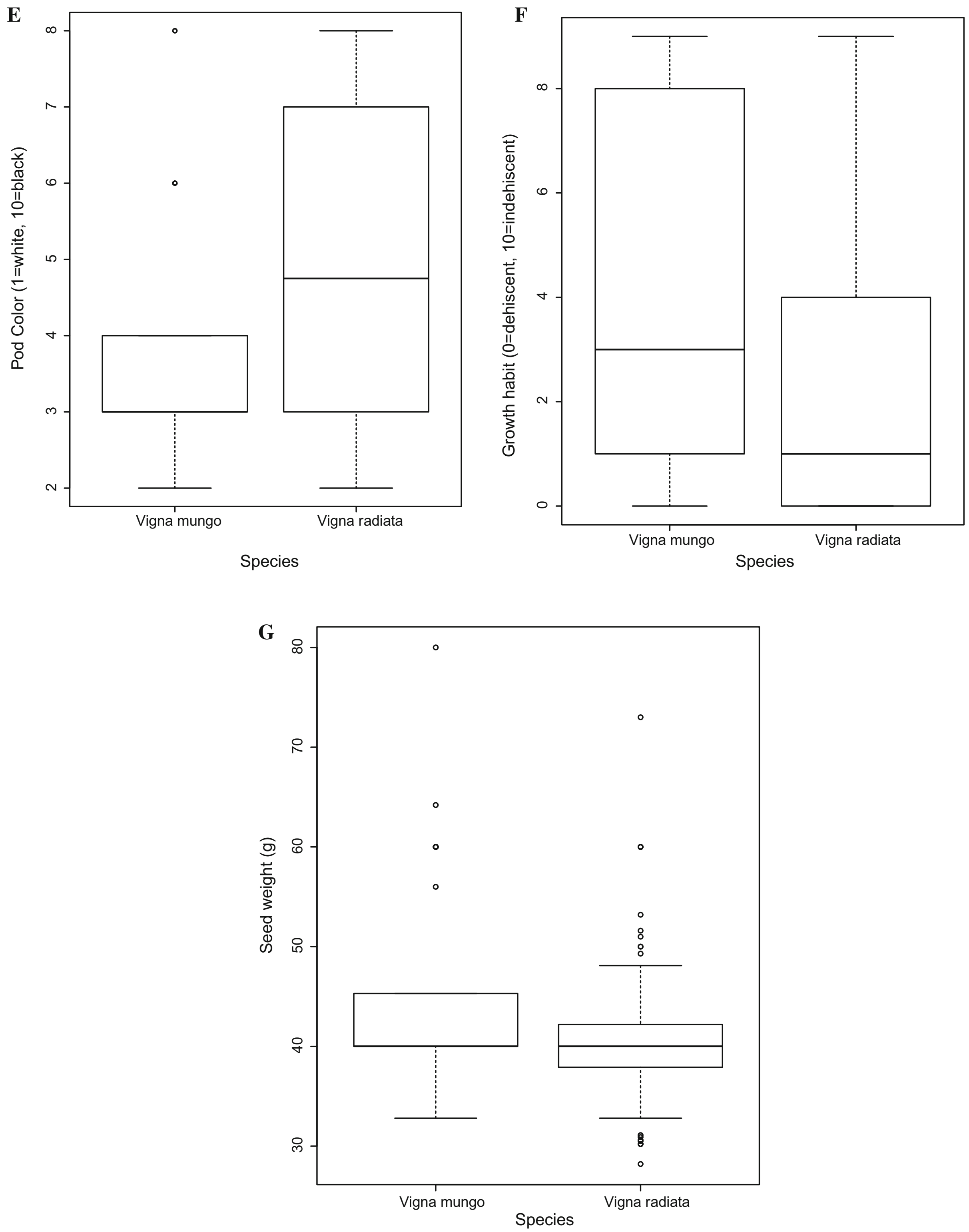

Fig. 1 continued

Table 1 The results of ANOVA (one-way analysis of variance) to identify the association between the variability of morphological and agronomic traits and belonging to the species *Vigna radiata* or *V. mungo* from 200 old landraces acquired between 1910 and 1926

Effect	Df	Growth habit				Mature pod color				Pod shattering in the field				Seed weight			
		SS	MS	F	*p*	SS	MS	F	*p*	SS	MS	F	*p*	SS	MS	F	*p*
Species	1	0.32	0132	4.06	0.045	34.61	34.61	8.49	0.0040	80.58	80.58	8.09	0.0049	730.7	730.7	14.51	0.0002
Error	189	14.83	0.08			770.63	4.08			1882.90	9.96			9518.1	50.4		
Total	190	15.15				805.25				1963.48				10248.7			

SS sum of squares, *MS* mean square, *F* test, *p* significance level, *df* degrees of freedom

Fig. 2 Trait variability in the dataset of 200 old *V. mungo* and ▶ *V. radiata* landraces sampled at different geographic locations. **a**–**j** present data for growth habit, color of petiole, mature pod color, leaflet shape, leaf pubescence, pod length, pod shattering, number of seeds per pod, days to maturity, and seed weight

variability of traits: days to maturity, seed weight per plant, seed weight (Table 4a, b). The force of influence of η^2% (intraclass correlation) of the year of introduction for days to maturity, for seed weight per plant, and for seed weight were 20.00%, 28.54% and 32.64%, respectively. Thus, the greatest change in the breeding process occurred on seed weight.

It is evident from the historical pattern in Figs. 4a, d that there was a wider range of variability of the maturity period duration in *V. radiata*, received in the collection in before 1940, than in accessions collected in the period from 1940 to 1970. A Levene's test of homogeneity of variances shows a significant difference in variances of days to maturity over the length of the collection (Test statistic = 3.47, $p = 0.015$). In the 1970–1990s diversity of the accessions remains similar as in previous years, i.e. breeders and farmers preferred mid-ripening varieties. By the 2000s and in subsequent years there is a further narrowing of the amplitude over the duration of the growing season for the varieties used in the farms, as the breeders bred varieties with a period of maturation from 90 to 120 days. At the beginning of twenty-first century this range became much narrower. In *V. mungo*, for which the collection is substantial smaller, particularly after 1991 (three accessions), the Levene's test was not significant over time of acquisition (Test statistic = 1.0232, $p = 0.384$).

We observed a different pattern of historical change for seed productivity and seed weight (Fig. 4b, c, e, f, 5a–c). We note that up to the middle of the twentieth century there were only small-seeded forms in both species, with the 1000 seed weight much less then 20 g (Fig. 4b, e). Since the 1950s, as the stock of cultivated forms has been expanding, more highly productive accessions of *V. radiata* and *V. mungo* with greater seed weight have appeared. The accessions with the variability of the trait 40.0–100.0 g began to enter into the collection, compared with the total diversity of gene pool 14.8–100.0 g. (Figure 4b, e, 5a). Then breeding was stabilized on the middle-seeded varieties with an average 1000 seed weight of 40 g in *V. radiata* (Fig. 4 b, e, 5a) and 45 g in *V. mungo*.

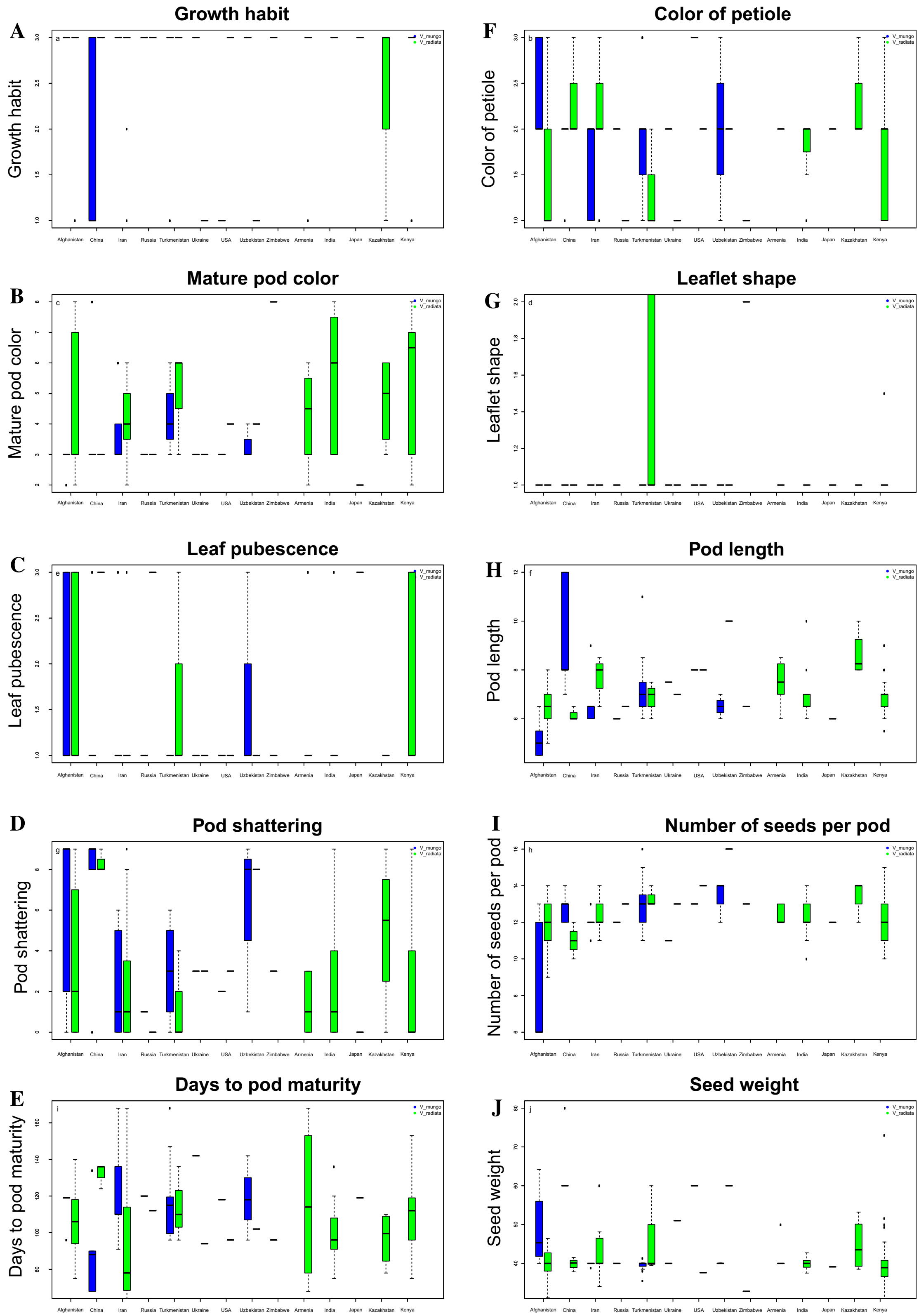
A
Growth habit
Growth habit
F
Color of petiole
Color of petiole
B
Mature pod color
Mature pod color
G
Leaflet shape
Leaflet shape
C
Leaf pubescence
Leaf pubescence
H
Pod length
Pod length
D
Pod shattering
Pod shattering
I
Number of seeds per pod
Number of seeds per pod
E
Days to pod maturity
Days to pod maturity
J
Seed weight
Seed weight
V_mungo
V_radiata
Afghanistan China Iran Russia Turkmenistan Ukraine USA Uzbekistan Zimbabwe Armenia India Japan Kazakhstan Kenya

Table 2 The results of ANOVA (one-way analysis of variance) to identify the association between the variability of morphological, agronomic characters and the origin in 200 old landraces

Effect	df	Growth habit				Color of petiole				Mature pod color				Leaflet shape				Leaf pubescence			
		SS	MS	F	*p*	SS	MS	F	*p*	SS	MS	F	*p*	SS	MS	F	*p*	SS	MS	F	*p*
Origin	13	2.73	0.21	2.93	0.001	8.89	0.68	2.02	0.021	92.84	7.14	1.79	0.047	44.61	3.43	3.16	0.0003	19.10	1.47	2.01	0.022
Error	186	13.32	0.07			61.29	0.34			720.68	3.98			199.03	1.09			133.99	0.73		
Total	199	16.05				70.18				813.52				243.64				153.10			
Effect	df	Pod length				Pod shattering				Number of seeds per pod				Seed weight				Days to pod maturity			
		SS	MS	F	p	SS	MS	F	p	SS	MS	F	p	SS	MS	F	p	SS	MS	F	p
Origin	13	77.10	5.93	5.64	0.000	229.41	17.65	1.84	0.041	71.16	5.47	2.98	0.001	2751.78	211.68	5.09	0.000	9993.17	768.71	1.93	0.029
Error	186	192.39	1.05			1759.35	9.61			332.91	1.84			7528.23	41.59			72130.32	398.51		
Total	199	269.49				1988.76				404.07				10280.02				82123.49			

SS sum of squares, *MS* mean square, *F* test, *p* significance level, *df* degrees of freedom

Furthermore, an increase in seed productivity is also evident. In the beginning of the twentieth century the collection received the accessions with seed productivity indicators from 11.0 to 32.0 g per plant in average, while by twenty-first century yield reached up to 100 g per plant with the average about 80 g per plant in both crops (Fig. 4c,f, 5a). The total diversity of this trait in gene pools is 1.0–130.0 and 0.1–130.0 g/plant for *V. radiata* and *V. mungo* respectively.

Discussion

We find differences in days to maturity, seed size, and seeds per plant among accessions of *V. radiata* (mungbean) and *V. mungo* (urdbean) based on which species they are, their geographic origin, and the year they were acquired by the VIR collection in a set of 986 phenotyped accessions. For the first time we showed the significant differences between *V. radiata* and *V. mungo* in the following traits: growth habit, pod shattering in the field, mature pod color, days of maturity, 1000 seed weight and seed weight per plant. These phenotypic differences are in addition to the known morphological, cytological, biochemical and molecular characters that have separated *V. radiata* and *V. mungo* into distinct taxa (De Deepesh and Krishnan 1966; Jaaska and Jaaska 1989; Santala et al. 2006; Dikshit et al. 2007; Burlyaeva et al. 2016).

It is also known that there are several differences in agronomic characteristics of the crops. For instance, mungbean prefers fertile loamy, well drained soil with pH = 5.5–8.2 (Krishna 2010). As for urdbean it prefers lighter soils with a pH of 4.7–7.5 (Baligar and Fageria 2007; Jansen 2006). With respect to precipitation, a distinct intra-species differentiation exists in both crops. Early ripening varieties can grow in semi-arid conditions with 60–90 cm of precipitation a year; medium-ripening varieties require a more substantial annual rainfall of 90–150 cm (Tomooka et al. 2002). All these data are useful tools for the choice of the genotypes for the planting in specific soil and climatic conditions, both at the species and intraspecific levels. The differences in soil preferences may create a useful system in which to dissect the genetic basis of soil type preferences in warm season legumes. Furthermore, introgression lines between the two species are likely promising sources of disease

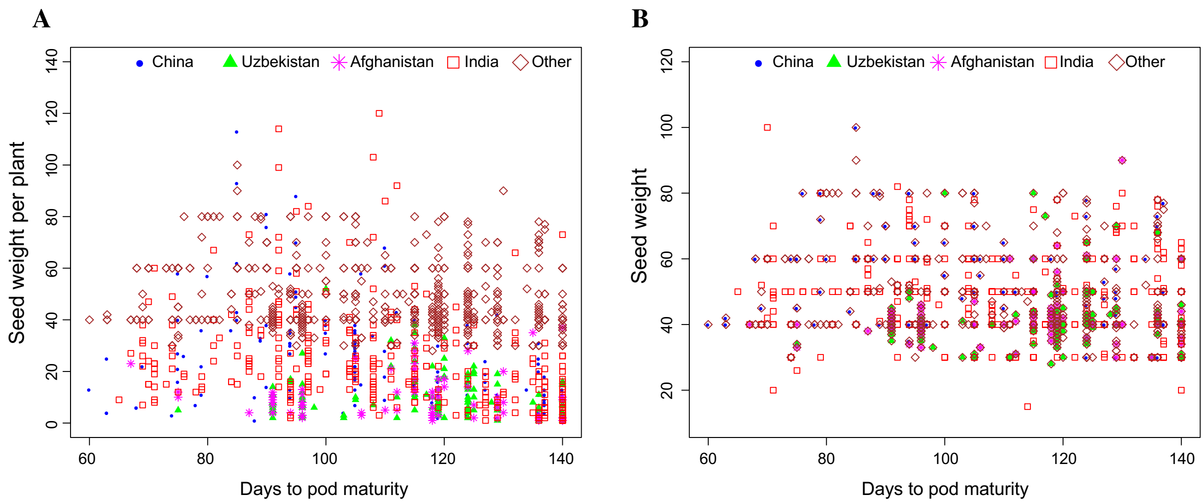

Fig. 3 Regional variation in seed weight per plant (**a**) and seed weight (**b**) in different maturity groups of accessions from the whole dataset of 986 landraces

Table 3 Correlations of the traits in *Vigna radiata* and *V. mungo* in the full collection of 986 accessions

Variable	Days to maturity	Seed weight per plant	1000 Seed weight
Days to maturity	1.00	0.39	0.44
Seed weight per plant	− 0.35	1.00	0.61
1000 Seed weight	− 0.18	0.30	1.00

R values are on the bottom triangle of the matrix, and *p*-values on the upper portion of the matrix

resistance, such as *V. mungo* as a source of resistance for mungbean yellow mosaic virus (Gil et al. 1983) and for more balanced amino acid content, specifically the higher methionine content of the grain (Nair et al. 2013).

We found patterns of eco-geographic differentiation in both species, but more pronounced in *V. radiata*. Indian accessions had climbing and erect habitus, small pods and seeds in both species. They showed a great diversity in dates of maturity. They are characterized mainly by dark seeds (Burlyaeva et al. 2014). India is recognized as the center of origin of both species (Fuller and Harvey 2006). Indian accessions in our study exhibit the greatest diversity in all of traits, which is also typical for centers of origin and diversity. In addition, such a pattern is consistent with limited breeding efforts. The second group of accessions is comprised by the mungbean accessions from China, Japan and Korea. They are short-maturated and have large pods and seeds and mainly light-seeded (Burlyaeva et al. 2014). We assume this is evidence of selection from the gene pool when it moved to the North from the center of origin. A third group is comprised by Iranian, Afghan and Middle-Asian landraces with average manifestation of the traits both in dates of maturity and seed weight. These peculiarities for Middle-Asian landraces of mungbean had been marked also by NI Vavilov (1929).

These data in *V. radiata* are in the accordance of classification created in VIR in 1930s (Ditmer 1937), where three subspecies were recognized: *indicus, chinensis* and *iranicus*. Therse groups are connected with broad geographic regions. Sinskaya (1948) proposed to consider them as regional or climatic ecotypes. The ecologo-geographic differentiation of gene pool is supported in our research, and corresponds to the major geographic and climatic zones in which *V. radiata* was domesticated and diverged early in its cultivation history.

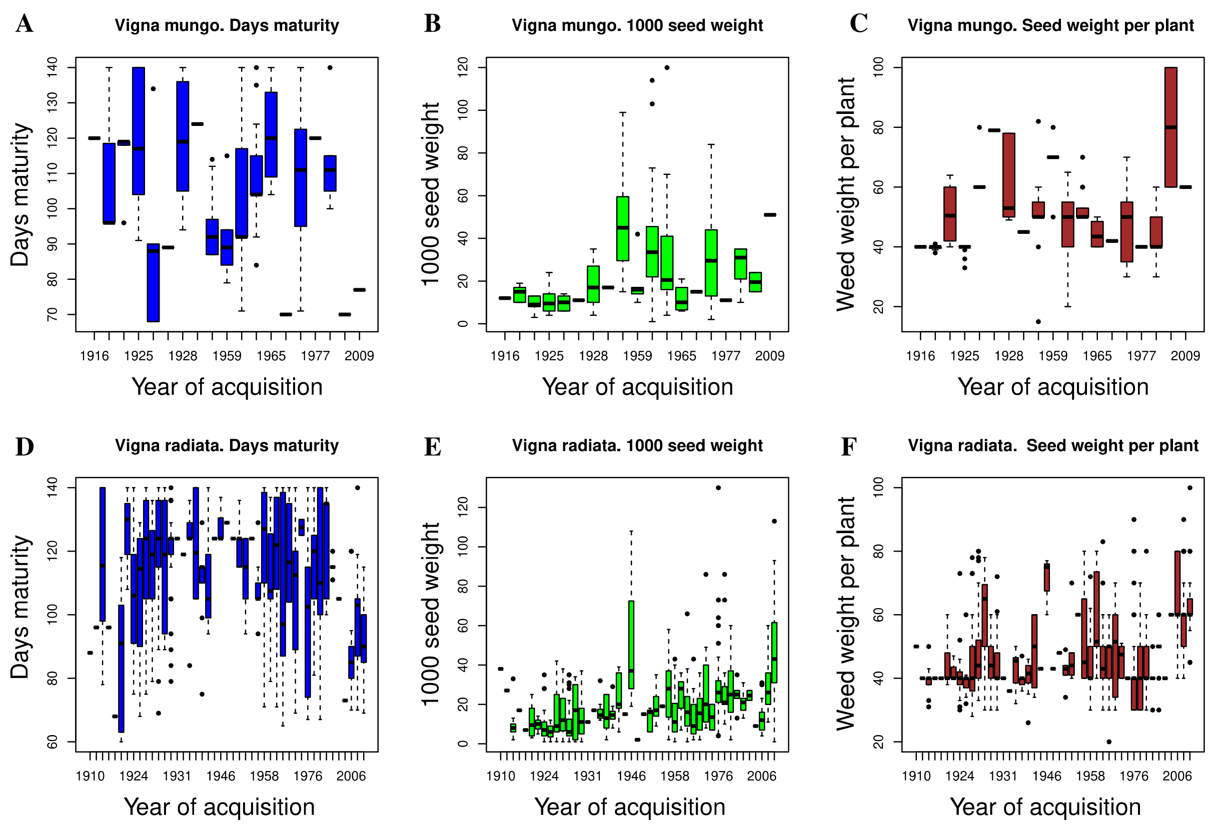

Fig. 4 Variability of the traits: days to maturity, seed weight per plant, seed weight of *Vigna radiata* and *V. mungo* accessions, introduced into the collection in different periods during 1910–2009 years. **a** *V. mungo* days to maturity, **b** *V. radiata* days to maturity, **c** *V. mungo* 1000 seed weight (g), **d** *V. radiata* 1000 seed weight (g), **e** *V. mungo* seed weight per plant (g), **f** *V. radiata* seed weight per plant (g)

Table 4 a-b. The results of ANOVA (one-way analysis of variance) to identify the association between days to maturity, seed weight per plant, seed weight and the date of introduction into collection (Acqdate), using the full 986 accessions

Effect	Df	Days to pod maturity				Seed weight per plant				1000 Seed weight			
		SS	MS	F	*p*	SS	MS	F	*p*	SS	MS	F	*p*
(a)													
Acqdate	1	27391	27391	73.61	< 0.0001	44322	44322	232.5	< 0.0001	9087	9087	60.46	< 0.0001
Error	819	302149	372			156145	191			123390	150		
Total	823	329440				200467				122477			
(b)													
Acqdate	1	953	952.9	2.457	0.0405	5528	5528	10.91	< 0.0001	31	30.96	0.207	0.65
Error	159	61661	387.8			79037	507			24115	149.79		
Total	165	62614				84565				24146			

Dates were placed into four bins, with those acquired before 1940 in the first bin, 1941–1970 in the second, 1971–1991 in the third, and those after 1991 in the fourth. A. *V. radiata*. B. *V. mungo*

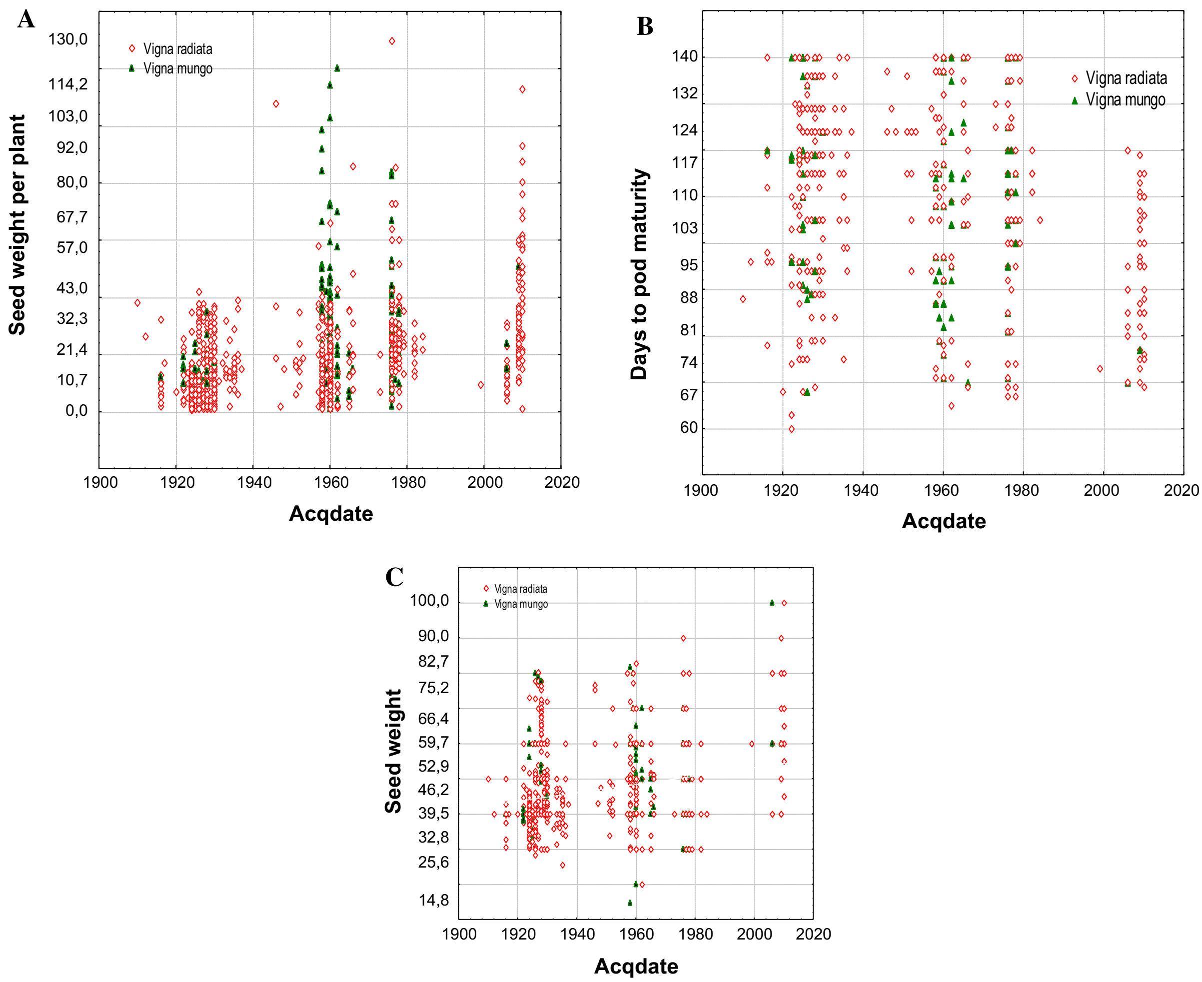

Fig. 5 Variability of the traits days to maturity (**a**), seed weight (**b**) and seed weight per plant (**c**) in *V. radiata* and *V. mungo* in different periods of introduction into collection

The existence of century-old accessions in the collection allowed us to trace some peculiarities in breeding both local and commercial varieties for a period of 100 years. For the changes of traits we have studied, a general trend is evident—a significant decrease in the phenotypic diversity of the gene pool. There were some specific features during different periods. The most productive, large-seeded varieties were created in 1960-1980. Before 1960 the seed weight character was the most diverse (Fig. 4b, e). At that time varieties have been bred with both the smallest and the largest seeds. By 1980s, forms with very large seeds (weight of 1000 seeds 90 g) appeared, and small-seeded samples (14–20 g) decreased in number. In 2000s, there was a decrease in diversity due to elimination of small-seeded forms, and they produced presumably the varieties with a weight of 1000 seeds from 40 to 60 g. At the present time, mainly medium-sized, medium-ripening, medium-productive varieties have been added to the collection. Over the past 100 years, there has been a sharp decline in the use of late-maturing forms in agricultural production. It is worth noting that in the Astrakhan environment the most productive were medium-ripening accessions of both species mostly from the group of China, Japan and Korea. The accessions with long maturation period had no chance to mature in this region. As the most extensive phenotyping effort for these crops, this shows the value of northern landraces (those from temperate East Asia) as a starting point for breeding new temperate varieties, and the importance of phenology for success in seasonal temperate regions.

Our analysis shows that the VIR collection is an important repository of variation for minor crops like mungbean and urdbean, which could be effectively deployed in international breeding programs. Both crops have become objects of intensive molecular characterization and genomic research in recent years (for review see Kang et al. 2014; Kim et al. 2015; Nath et al. 2017). Certain features make them well-suited model organisms of legume plants because of their small genome size, short life-cycle, self-pollinating, and close genetic relationship to other legumes (Kim et al. 2015). An International Mungbean Improvement Network—IMIN has been created to coordinate the research activities between the different research groups (AVRDC 2015). These developments will benefit from the unique diversity of older collections like those at the VIR, which possess diversity that has eroded in more recently assembled collections like those of the World Vegetable Center or national collections in Australia, Japan, or South Korea. At a time when resources for maintaining genebanks are often very limiting, particularly in middle income or lower income countries, our results show the critical importance of maintaining collections of substantial historical duration like the VIR collection.

Conclusion

The VIR collection is an important repository of variation for mungbean and urdbean. Collected accessions comprised pre-dominantly of old landraces fully reflecting the range of variability of morphological and phenological characters of these crops. Harnessing genotypes possessing early maturity, high productivity and traits of adaptability in breeding of new varieties will contribute to the improvement of the gene pool and the expansion of the production of these crops. Ensuring the long term preservation and utilization of this collection is important for improving these two crops to handle changing climates, for cultivation in new geographic areas, including greater areas in Russia, and for shifting consumer preferences. Although genebanks often face many challenges and difficult choices in a time of limited funding, preserving the unique diversity of historical collections should remain an important priority.

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Compliance with ethical standards

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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