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The Gene Pools of the Grasspea (*Lathyrus sativus* L.)

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With 2 figures and 4 tables

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Abstract

Interspecific hybridization between the grasspea, *Lathyrus sativus*, and 15 wild species in Section *Lathyrus* is reported. Only two species, *L. amphicarpos* and *L. cicera* produced viable F_1 hybrids with low fertility when crossed with *L. sativus* as male parent. Crosses with six other species produced pods following pollination when *L. sativus* was the male, but seedlings were inviable, seeds did not germinate or pods were empty or had totally shrivelled seeds. When *L. sativus* was the female parent, only one cross with *L. gorgoni* produced an F_1, but the seedling was inviable. The germplasm resources of the grasspea are identified, with *L. amphicarpos* and *L. cicera* placed in the secondary gene pool and the other species in the tertiary gene pool. The definition of these germplasm resources is discussed in terms of grasspea improvement through plant breeding.

Key words: *Lathyrus sativus* — wild species Sect. *Lathyrus* — interspecific hybridization — gene pools — germplasm resources — grasspea improvement

Lathyrus sativus L., known as the grasspea, chickling pea or kheshari dhal, is an ancient Old World cultigen, and perhaps one of the first crops to be domesticated in Europe (KISLEV 1989), but its origin is not known (BALL 1968). SMARTT (1984a) noted that even though *L. sativus* has been used as a pulse for a long time, its utilization as a forage crop has resulted in little evolutionary progress as a grain crop. Its wide dispersion is due to its utilization as a forage legume. Its use as a pulse is mainly confined to India where it occupies an area of more than 1 million hectares (LAL et al. 1986). In that country it is one of the most reliable grain crops and may be the only food available in some areas when famines occur. This can result in excessive consumption and may provoke the neurological form of lathyrism (GANAPATHY and DWIVEDI 1961). There has even been a ban on its cultivation by the Indian government (RUTTER and PERCY 1984) in an attempt to reduce the incidence of lathyrism. The neurotoxic principle has been identified as β-N-oxalyl-L-α, β-diaminopropionic acid or ODAP (BELL 1964, MURTI et al. 1964). It has been suggested, however, that there is good scope for selection and development of varieties of low toxicity (KAUL et al. 1986). *L. sativus* is undoubtedly a grain legume with considerable potential for improvement. One of the steps in this process is the identification and characterization of the germplasm resources of the crop, and a study of its evolution.

The genus *Lathyrus* is large with 160 species and 45 subspecies (ALLKIN et al. 1986), divided in 13 sections (KUPICHA 1983). *L. sativus* is placed in Section *Lathyrus* along with 33 other species, including the recently described *L. belinensis* (MAXTED and GOYDER 1988). In earlier classifications, *L. sativus* had been placed in Section *Cicercula*, but KUPICHA (1983) combined this section with Section *Lathyrus*, since the species in these two taxa are very similar in general morphology. The species in Section *Lathyrus* include both annual and perennial forms. The species are all Old World in distribution, principally throughout Europe, North Africa and the Near East, but also reaching as far east as India.

Although there are many *Lathyrus* species, it does not necessarily mean that available germplasm resources outside the biological species will be extensive (SMARTT 1986). The gene pool concept was originally proposed by HARLAN and DE WET (1971) to provide a better classification of crop plants and their wild relatives. Based on the determination of the biological species, this concept has found wide application in the study of the germplasm resources of many crops.

In *L. sativus* it has been suggested that there appears to be a considerable primary gene pool, rather poorly differentiated in terms of morphological characters between what have been reported as a wild form and cultigen in Iraq (TOWNSEND and GUEST 1974). To date there have been no experimental taxonomic studies, and there is little or no information to establish the existence or extent of secondary or tertiary gene pools associated with *L. sativus*. Only a few crossability studies have been reported in the genus *Lathyrus* (MARSDEN-JONES 1919, SENN 1938, SAW LWIN 1956, DAVIES 1958, CRUICKSHANK 1984, YAMAMOTO et al. 1986, KHAWAJA 1988) during the past seventy years. Although a number of hybrids have been obtained between species in Section *Lathyrus* and other sections, only one has been reported between *L. cicera* and *L. sativus* as the female plant (SAW LWIN 1956).

In this paper we report the first comprehensive study of interspecific hybridization between *L. sativus* and wild species in Section *Lathyrus*, as well as intraspecific crosses within *L. sativus*, in an attempt to define the gene pools of this underexploited pulse.

Materials and Methods

Materials: Fifteen wild species from Section *Lathyrus*, each represented by a single accession, and 11 accessions of *L. sativus* from a wide geographical distribution, were used in the hybridization pro-

Table 1. Accessions of *Lathyrus sativus* and 15 wild *Lathyrus* species used in the hybridization programme

Species	Birmingham No.	Donor	Donor No.
L. amphicarpos	578	Gatersleben	LAT 139/82
L. annuus	185	Siena Bot. Gard.	261
L. basalticus	670	Southampton Univ.	867137
L. cassius	671	Southampton Univ.	867236
L. chloranthus	589		
L. chrysanthus	672	Southampton Univ.	868065
L. cicera	308	Brno Bot. Gard.	
L. gorgoni	216	Gatersleben	LAT 101/78
L. hierosolymitanus	236	Gatersleben	LAT 142/78
L. hirsutus	107	Bordeaux Bot. Gard.	33
L. latifolius	145	Zürich Bot. Gard.	618
L. marmoratus	673	Southampton Univ.	867025
L. odoratus	85	Blanes-Gerona Bot. Gard.	182
L. pseudo-cicera	674	Southampton Univ.	868013
L. tingitanus	463	Vavilov Inst., Leningrad	VIR-1519
L. sativus	404	Madrid — INIA	BG-1441
	429	Izmir Gene Bank	35048
	430	Vavilov Inst., Leningrad	VIR-1321
	434	Vavilov Inst., Leningrad	VIR-1336
	435	Vavilov Inst., Leningrad	VIR-1247
	468	Vavilov Inst., Leningrad	VIR-1516
	507	Vavilov Inst., Leningrad	VIR-1519
	558	NBPGR, India	SEL L-4
	580	Gatersleben	LAT 458/79
	588	Gatersleben	LAT 454/79

gramme (Table 1). Six of the *L. sativus* accessions were used for interspecific hybridization, while 10 were studied for intraspecific crossability. Fourteen of the wild species were annuals, and *L. latifolius* was the only perennial species. In both types of crosses, *L. sativus* was represented by all three flower types described by JACKSON and YUNUS (1984), namely blue, white and a mix of blue and white. The species identify of all plants was verified by reference to published descriptions. The seeds of the wild species were scarified prior to sowing, but this was not necessary for *L. sativus*. At least five plants per accession were used.

Pollinations: On the basis of time to flowering, *L. sativus* and the wild species could be classified into three groups, and this information was important in planning the hybridization programme. Nine species, *L. amphicarpos*, *L. basalticus*, *L. chrysanthus*, *L. cicera*, *L. gorgoni*, *L. hierosolymitanus*, *L. marmoratus*, *L. pseudo-cicera* and *L. sativus*, flowered in less than 8 weeks. Flowering occurred between 8 and 11 weeks in *L. annuus*, *L. cassius*, *L. odoratus* and *L. tingitanus*, and in the three remaining species, *L. chloranthus*, *L. hirsutus* and *L. latifolius*, flowering time was greater than 11 weeks and as long as 16 weeks.

Pollinations were carried out in a glasshouse at the University of Birmingham during the summer months of 1987 and 1988. Buds approaching anthesis were emasculated and then immediately pollinated, as described by CRUICKSHANK (1984). The sepal covering the keel was folded back, the keel excised and the anthers removed. A stigma covered with pollen was removed from the male parent and rubbed on to the stigma of the female parent. After pollination the remaining flower parts were kept intact and covered with parafilm to avoid dehydration, as well as possible contamination by foreign pollen. Developing pods could be seen in successful pollinations after one week, when the parafilm was removed. For each plant an unopened flower was covered with a paper bag to obtain selfed seeds. Each pollination took between 10 and 15 minutes.

A total of 1,055 pollinations was made, comprising 419 interspecific pollinations, 74 intraspecific pollinations of the wild species, 430 intraspecific pollinations between *L. sativus* accessions, and 132 pollinations of all types were made for observation of pollen tube growth. Reciprocal pollinations were made as possible according to availability of flowers only between *L. sativus* and the wild species. Control intraspecific crosses were made with all wild species except *L. latifolius*.

Pollen counts and stainability: Fresh pollen was taken from at least two plants per accession immediately prior to anthesis to determine the pollen count and stainability. Pollen was mixed with 0.5 ml of acetocarmine (0.5 % carmine in 45 % acetic acid) in order to have comparative estimates between accessions. Total pollen and percentage stainability were determined using a haemocytometer.

Pollen tube growth: Studies of *in vivo* pollen tube growth under ultraviolet fluorescence microscopy were carried out using the method described by MARTIN (1959), but with the following modifications. Excised pistils were fixed in Carnoy's solution for 24 hours, cleared in 2M sodium hydroxide for 2 hours at 60 °C, and stained in 0.4 % aniline blue in 0.1 M potassium phosphate buffer. The stained pistils were mounted in glycerine and observed using a Leitz Orthoplan microscope under ultraviolet light with a HBO 200 high pressure mercury lamp at a wavelength of 400 nm.

Meiosis: Chromsome pairing at metaphase I was observed in putative interspecific hybrids and the intraspecific hybrids in *L. sativus*. Buds about 2 mm long were collected, and 3—5 anthers macerated in acetic orcein (1 % orcein in 45 % acetic acid) without fixation. Each preparation was heated for five seconds, and left to stain for a further three minutes, and then squashed.

Results

Pollen viability

Pollen stainability ranged from as low as 53 % in *L. sativus* (accession 507) to more than 98 % in *L. cassius* (Table 2). Most were in excess of 80 %. However, when the total pollen count was taken into consideration, the actual viable pollen could be estimated. *L. latifolius* had the lowest pollen stainability, but because the total pollen count was high, viable pollen was estimated at 42.2×10^4. The highest viable pollen count, at 60.3×10^4 was recorded in *L. odoratus*, even though pollen stainability was as low as 74 %. The lowest viable pollen count was recorded in *L. marmoratus*, at 3.6×10^4.

Interspecific hybridization

Successful crosses were indicated by the formation of pods and seeds. However, in only two combinations, namely *L. amphicarpos* × *L. sativus* and *L. cicera* × *L. sativus*, were verified hybrids obtained (Table 3). Generally the crosses were more successful when the wild species was the female. Ten of the interspecific combinations were successful in these cases, in terms of pod formation, but only six were

Table 2. Mean pollen viability in *Lathyrus sativus* and 15 wild *Lathyrus* species, and two interspecific hybrids

Species	% pollen stainability	Total viable pollen ($\times 10^4$)
L. amphicarpos	82.1	4.6
L. annuus	95.5	17.1
L. basalticus	92.0	8.1
L. cassius	98.3	22.6
L. chloranthus	70.4	17.8
L. chrysanthus	93.9	29.4
L. cicera	75.4	4.6
L. gorgoni	87.2	12.3
L. hierosolymitanus	91.7	17.6
L. hirsutus	84.8	7.8
L. latifolius	57.2	42.4
L. marmoratus	83.7	3.6
L. odoratus	74.5	60.3
L. pseudo-cicera	89.2	16.5
L. tingitanus	89.5	32.3
L. sativus	89.3	24.9
	69.3	15.8
	82.4	20.6
	64.7	14.3
	53.2	15.1
	64.2	15.6
Interspecific hybrids		
L. amphicarpos		
× *L. sativus* 433	1.9	0.10
× *L. sativus* 434	5.2	0.40
× *L. sativus* 435	1.7	0.15
× *L. sativus* 468	7.5	0.80
L. cicera		
× *L. sativus* 435	2.3	0.30
× *L. sativus* 507	1.0	0.07
× *L. sativus* 588	0.3	0.03

successful when *L. sativus* was the female. Seeds were obtained from the crosses *L. sativus* × *L. gorgoni* and *L. latifolius* × *L. sativus*, but following germination, the F_1 hybrids were inviable. In the cross *L. chloranthus* × *L. sativus*, the F_1 seed failed to germinate.

In crosses with five species, *L. sativus* as female produced only empty pods with shrivelled seeds. The reciprocals of these crosses gave very different results. Both *L. amphicarpos* and *L. cicera* produced viable hybrids, but with *L. hierosolymitanus* and *L. hirsutus*, the pollinations failed completely when *L. sativus* was the male parent. The opposite result was obtained in reciprocal crosses of *L. annuus*, *L. marmoratus*, *L. pseudo-cicera* and *L. tingitanus* with *L. sativus*. These failed completely when *L. sativus* was the female, but pods with shrivelled seeds or empty pods were formed with *L. sativus* as the male parent.

In crosses between *L. gorgoni* and *L. basalticus* with *L. sativus* as the female the hybrid origin of the progenies must be regarded as suspect. In the reciprocal crosses, even though seed set was extremely low in both instances, a morphological comparison of the progeny indicated that they may have resulted from selfing, and in these cases.

Plants from the crosses *L. amphicarpos* × *L. sativus* and *L. cicera* × *L. sativus* were verified as hybrids with low fertility (Table 2) on the basis of morphological characters. The differences between the hybrids and female parents were more distinct in the case of *L. amphicarpos* than *L. cicera*, because the former was morphologically very different from *L. sativus*. Hybrid flowers were intermediate in size in both combinations, and the flower colour was also different from the female parent. In both combinations the hybrid flowers ranged from light red to slightly bluish-red. Both *L. amphicarpos* and *L. cicera* have brick red flowers. Intermediate characters were observed with respect to the size and shape of pods in the hybrids, as well as the length of the leaflets, petioles and tendrils. In both combinations the F_1 plants grew vigorously and flowered profusely. Most flowers aborted at an early stage of development, and those that remained only produced empty pods.

Pollen tube growth

Observations of pollen tube growth were made on 82 pollinations representing 26 interspecific combinations involving 14 species. In those pollinations which failed completely (Table 3), alien pollen failed to germinate on the stigma. In a compatible combination, such as *L. cicera* × *L. sativus*, abundant pollen tubes could be seen in the style and ovary, and within 24 hours after pollination, the pollen tubes had

Table 3. Interspecific hybridization between *Lathyrus sativus* and 15 wild species in Section *Lathyrus*

Cross	Polli-nations	Pods	Pods with seeds	Remarks
L. sativus × *L. gorgoni*	33	3	1	Seed germinated, but seedling inviable
L. sativus × *L. amphicarpos*	12	1	0	Empty pods or totally shrivelled seeds
× *L. basalticus*	10	3	0	
× *L. cicera*	31	1	0	
× *L. hierosolymitanus*	27	1	0	
× *L. hirsutus*	13	1	0	
L. sativus × *L. annuus*	6	0	0	Pollinations failed completely
× *L. cassius*	7	0	0	
× *L. chloranthus*	13	0	0	
× *L. chrysanthus*	10	0	0	
× *L. latifolius*	8	0	0	
× *L. marmoratus*	13	0	0	
× *L. odoratus*	25	0	0	
× *L. pseudo-cicera*	11	0	0	
× *L. tingitanus*	16	0	0	
L. amphicarpos × *L. sativus*	17	11	11	Verified hybrids obtained
L. cicera × *L. sativus*	15	15	6	
L. latifolius × *L. sativus*	10	1	1	Seed germinated, but seedling inviable
L. chloranthus × *L. sativus*	11	1	1	Seed obtained, but did not germinate
L. annus × *L. sativus*	3	2	0	Empty pods or totally shrivelled seeds
L. marmoratus × *L. sativus*	18	15	0	
L. pseudo-cicera × *L. sativus*	14	6	0	
L. tingitanus × *L. sativus*	19	1	0	
L. cassius × *L. sativus*	5	0	0	Pollination failed completely
L. chrysanthus × *L. sativus*	8	0	0	
L. hierosolymitanus × *L. sativus*	16	0	0	
L. hirsutus × *L. sativus*	8	0	0	
L. odoratus × *L. sativus*	12	0	0	
L. basalticus × *L. sativus*	7	1	1	F_1 suspected as being selfed progeny
L. gorgoni × *L. sativus*	20	9	1	

already effected fertilization. A similar pattern of pollen growth was seen in the cross *L. amphicarpos* × *L. sativus*. In these crosses, callose plugs were abundant, but in less compatible crosses such as *L. sativus* × *L. hirsutus* and *L. chloranthus* × *L. sativus*, callose plugs were scarce.

The only combination that formed pods with seeds when *L. sativus* was the female was the cross with *L. gorgoni*. Pollen tubes could be seen entering the micropyle of the ovules 48 hours after pollination. Although no seeds were obtained from the cross *L. marmoratus* × *L. sativus*, pod formation was high (83 %).

This can be explained by the fact that pollen tubes were abundant and comparable to the compatible cross, *L. cicera* × *L. sativus*.

Meiosis

Chromosome pairing was observed in both interspecific and intraspecific hybrids. Regular pairing of 7 bivalents was seen in all intraspecific hybrids of *L. sativus* (Figs. 1 a and 1 b). In the hybrid *L. cicera* × *L. sativus*, 6 bivalents and 2 univalents or 7 bivalents were observed (Figs. 1 c and 1 d). In the hybrid *L. amphicarpos* × *L. sativus*, meiotic irregularities such as multivalents and univalents were seen (Figs. 1 e and 1 f).

Intraspecific hybridization

Wild species: Although the number of pollinations of each type was rather small (from 1 to 12), all but four species showed normal fertility in sib-matings. The proportion of pods with seeds was lower in *L. gorgoni* (9/10), *L. hierosolymitanus* (3/5), *L. odoratus* (2/5) and *L. chloranthus* (1/5). Only one pollination was made for *L. annuus*, but this was successful.

L. sativus: The level of success of crosses between different *L. sativus* accessions was much higher than achieved in the interspecific crosses, but some genetic barriers do apparently exist between them (Fig. 2). Some pollinations failed completely, and the level of compatibili-

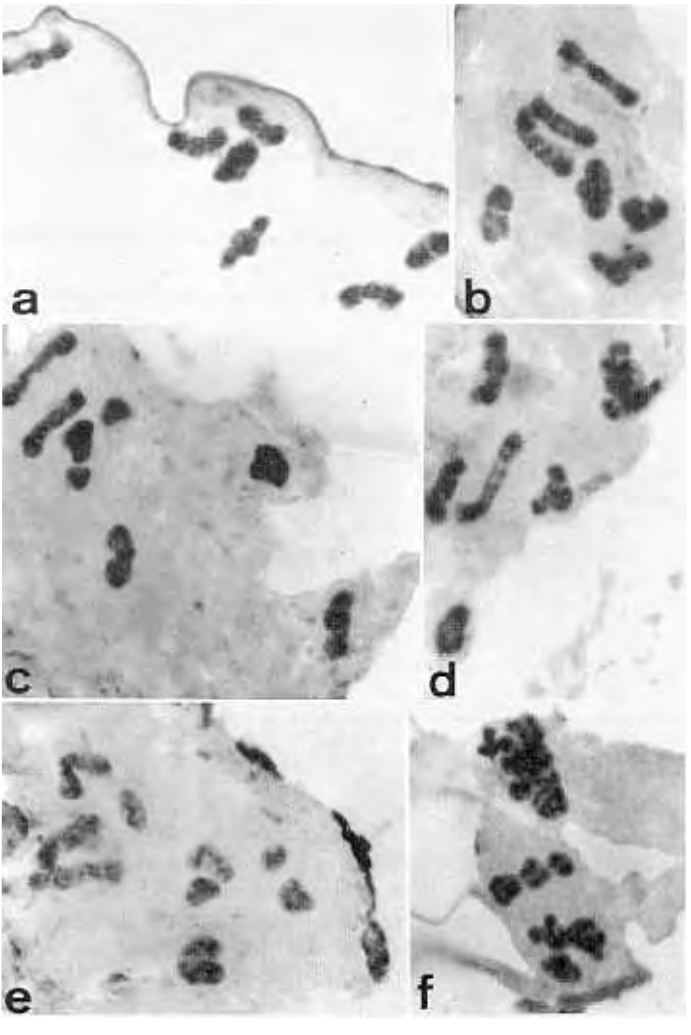

Fig. 1. Metaphase chromosome pairing in F_1 intraspecific and interspecific hybrids in *Lathyrus* Section *Lathyrus*: a and b, *L. sativus* (434) × *L. sativus* (429); c and d, *L. cicera* (308) × *L. sativus* (507); e, *L. amphicarpos* (578) × *L. sativus* (433); and f, *L. amphicarpos* (578) × *L. sativus* (468)

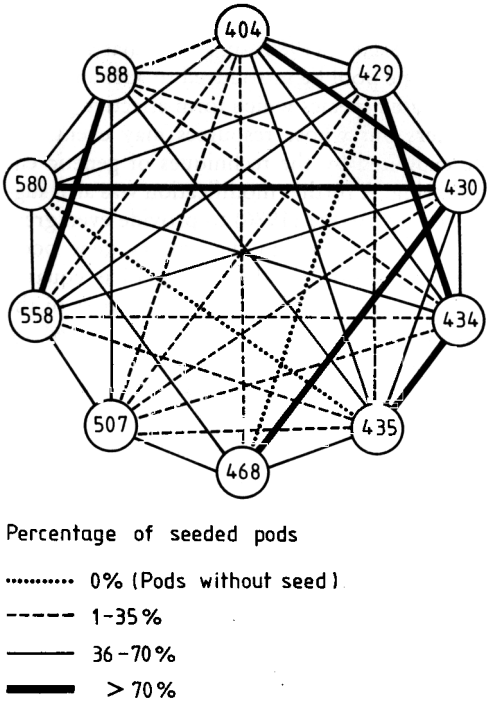

Fig. 2. Crossing polygon of ten accessions of *Lathyrus sativus*, based on the percentage of pods formed with seeds following intraspecific hybridization

ty varied considerably between accessions. The results of intraspecific hybridization gave no evidence of geographical origin as a factor in the success or failure of hybridization within *L. sativus*. Only a limited sample of intraspecific hybrids was grown. All plants grew vigorously, flowered profusely and produced mature pods with seeds, as expected on the basis of the normal meiosis observed. Fifty samples from the intraspecific pollinations representing most of the combinations between the 10 accessions were observed for pollen tube growth. In almost all cases, pollen tubes could be seen in the ovary within 24 hours of pollination. There was no evidence of inhibition of pollen tube growth in the pistil.

Discussion

HARLAN and DE WET (1971) considered that the gene pool concept could usefully be applied to ease the difficulties in producing satisfactory taxonomies for cultivated plants and their wild relatives. It is clear, as SMARTT (1990) has pointed out, that the Harlan and de Wet system is of equal value in consideration of genetic resources, for purposes of their classification, evaluation and documentation. In contrast, MARSHALL (1990) has argued that the value of this system, based as it is on crossability and ease of gene transfer, was its direct relevance to plant breeding, but that developing molecular genetic technologies may make this system obsolete. The prospect in the future is that the potential gene pool of any species will include all life forms. Whilst this prediction may well apply to the major food crops, such as wheat, maize, rice and potatoes to name but a few, it is highly unlikely that an underexploited crop such as the grasspea will attract such high biotechnological priority. In the meantime, therefore, the identification of the gene pools of this cultigen remains important, since an adequate knowledge of interspecific hybridization capability of *L. sativus* is an essential prerequisite to effective evaluation of the broader range of genetic resources which might be exploited in the improvement of this crop (SMARTT 1990).

On the basis of morphological variation, 10 species were considered as being more closely related to *L. sativus* (YUNUS 1990). Seven of them were included in the crossability study, but seeds were not available for *L. blepharicarpus*, *L. hirticarpus* and *L. stenophyllus*. Only two of the 15 wild species in Section *Lathyrus*, namely *L. amphicarpos* and *L. cicera*, have a reasonably close biological relationship with *L. sativus*. Morphological data from DAVIS (1970), JACKSON and YUNUS (1984) and YUNUS (1990) have indicated the close relationship of these two species to *L. sativus*. However, the degree of interspecific crossability and the fertility of the F_1 hybrids is not sufficiently high, according to the HARLAN and DE WET (1971) gene pool concept, to consider that they and *L. sativus* belong to the same biological species.

Cytological studies carried out by YUNUS (1990) also showed that there is a correlation between karyotypes and the relationship between species in Section *Lathyrus*. In particular, the karyotype of *L. sativus* was similar to *L. amphicarpos* and *L. cicera*, with which F_1 hybrids were formed, as well as *L. basalticus*, *L. gorgoni* and *L. marmoratus* but which

showed a lesser degree of relationship with *L. sativus*.

Interspecific hybridization in the genus *Lathyrus* (SENN 1938, HITCHCOCK 1952, DAVIES 1958) and also in other legumes (SMARTT 1979) is considered difficult and rare. One of the factors for incompatibility between *Lathyrus* species was considered by SIMOLA (1967) to be due to dissimilar non-protein amino acid pools which influence pollen germination and growth, thus forming an effective hybridization barrier. *Lathyrus* species which hybridize have been reported to be chemically related (BELL and FOWDEN 1964, SIMOLA 1966). It is clear from this study that embryo abortion is an important barrier to interspecific hybridization, confirming the findings of DAVIES (1958). There have been conflicting reports whether the length of the style is an effective barrier to hybridization (DAVIES 1957, KHAWAJA 1988). Time to flowering must also be an important isolating mechanism in sympatric species.

In terms of defining the gene pools of *L. sativus* on the basis of interspecific hybridization reported in this paper, we suggest that the gene pool concept of HARLAN and DE WET (1971) is inadequate to encompass the range of interspecific relationships between *Lathyrus* species. SMARTT (1980) suggested that a quaternary gene pool be introduced to accommodate the related species which form effective genetic barriers but whose resources may eventually be exploited by the techniques of genetic engineering. A further modification was also suggested by SMARTT (1986) to provide even greater distinction within the tertiary gene pool, where the order of the gene pool is equated with the relative degree of effectiveness of the interspecific isolating mechanisms. Based on our studies, we can assign the different *Lathyrus* species to the three gene pools, as shown in Table 4.

The primary gene pool in *L. sativus* was described by TOWNSEND and GUEST (1974) as considerable and poorly differentiated in morphological characters between wild forms and the cultigen in Iraq, but may be differentiated in areas where it is cultivated and not established in the wild (SMARTT 1984b). VAVILOV (1951) described the highly selected form of *L. sativus* as having white flowers and white seeds, and it was postulated by JACKSON and YUNUS (1984) that the primitive form has blue flowers and speckled seeds. The rare pink form

Table 4. The germplasm resources of *Lathyrus sativus*, based on the gene pool concept of HARLAN and DE WET (1971), and ordination suggested by SMARTT (1986)

Gene pool	Ordination	Constituents	Species
I 1A	1st order	Cultigen	*L. sativus*
1B	2nd order	Wild counterpart	Unknown
II	3rd order	Cross compatible species producing more or less fertile hybrids	*L. amphicarpos*
			L. cicera
III	4th order	Cross compatible species producing viable but sterile hybrids	*L. gorgoni*
			L. latifolius
	5th order	Cross compatible species producing inviable hybrids	*L. chloranthus*
	6th order	Other related species not producing any hybrids	*L. annuus*
			L. basalticus
			L. cassius
			L. chrysanthus
			L. hierosolymitanus
			L. hirsutus
			L. marmoratus
			L. odoratus
			L. pseudo-cicera
			L. tingitanus
			Other Section *Lathyrus* species (?)
	7th order	Distantly related species	Other *Lathyrus* sections

of *L. sativus* reported by VAVILOV (1951) and KAUL et al. (1986) was found only once in our seed materials and was not used in the crossability programme.

Is *L. cicera* or *L. amphicarpos* the wild progenitor of *L. sativus*? On the basis of the data presented here, this hypothesis is unlikely. ALLKIN et al. (1985) reported the wild origin of *L. sativus* as unknown. The only report on the wild form of *L. sativus* was by TOWNSEND and GUEST (1974) but there has been no clarification as to whether these plants were truly wild or escapes from cultivation. The studies by JACKSON and YUNUS (1984) gave no indication of conspecific wild forms, and until the reports of wild *L. sativus* from Iraq are confirmed, the existence of a wild form must be regarded as doubtful. Simple tests on accessions of hard-seededness and observations on seed coat colour and seed size could narrow the field, plus studies of relative reductions of pod dehiscence at or near maturity.

The germplasm resources profile of *L. sativus* shows a tertiary gene pool that is most extensive, but with a restricted secondary gene pool, with which transfer of genes will be difficult. Without the identification of gene pool 1B (wild conspecific races), it is clear that exploitation of germplasm resources for the improvement of the grasspea must be concentrated in gene pool 1A including the landrace materials. There is good evidence from isozyme polymorphisms (YUNUS et al. 1990) that the landraces are genetically heterogeneous and even heterozygous at some loci. If this level of detected heterozygosity is a reflection of wider heterozygosity in the species, this is an interesting finding, since the indications in our work were that *L. sativus* is predominantly autogamous. Consequently, exploitation of this variable gene pool 1A through hybridization between different lines should result in considerable heterosis and prospects for selection of favourable characters which might lead to a wider utilization of this grain legume.

Zusammenfassung

Die Genpools der Platterbse (*Lathyrus sativus* L.)

Berichtet wird über Artkreuzungen zwischen der Platterbse, *Lathyrus sativus* L., und 15 Wildarten der Sektion *Lathyrus*. Nur nach der Kreuzung mit den beiden Arten *L. amphicarpos* und *L. cicera* wurden lebensfähige F_1-Bastarde mit geringer Fertilität erhalten, wenn als männlicher Partner *L. sativus* verwendet wurde. Nach Kreuzungen von 6 weiteren Arten mit *L. sativus* als Bestäuber bildeten sich zwar Hülsen aus, aber entweder waren die Hülsen leer oder hatten nur völlig eingeschrumpfte Körner. Wenn Samen ausgebildet wurden, waren diese nicht keimfähig oder die Keimpflanzen nicht lebensfähig. Wurde *L. sativus* als mütterlicher Partner benutzt, konnten nur nach der Kreuzung mit *L. gorgoni* F_1-Samen erhalten werden; aber auch hier gingen die Keimlinge später zugrunde. Die Einordnung der genetischen Abstammung der Platterbse im Rahmen eines Genpool-Systems erfolgt in der Weise, daß *L. amphicarpos* und *L. cicera* dem 2. Genpool und alle anderen Arten dem 3. Genpool zugewiesen werden. Diese so aufgestellten Abstammungs- und Verwandtschaftsverhältnisse werden im Hinblick auf die Möglichkeit einer züchterischen Verbesserung der Platterbse diskutiert.

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References

ALLKIN, R., D. J. GOYDER, F. A. BISBY, and R. J. WHITE, 1986: Names and synonyms of species and subspecies in the Vicieae. Issue 3. Vicieae Database Project, Univ. of Southampton, U.K.

——, T. D. MACFARLANE, R. J. WHITE, F. A. BISBY, and M. E. ADEY, 1985: The geographical distribution of *Lathyrus*. Issue 1. Vicieae Database Project, Univ. of Southampton, U.K.

BALL, P. W., 1968: *Lathyrus* L. In: T. G. TUTIN, V. H. HEYWOOD, N. A. BURGERS, D. M. MOORE, D. H. VALENTINE, S. M. WALTERS, and D. A. WEBB (eds.), Flora Europaea **2**, 136—143.

BELL, E. A., 1964: Relevance of biochemical taxonomy to the problem of lathyrism. Nature **203**, 378—380.

——, and L. FOWDEN, 1964: Studies on amino acid distribution and their possible value in plant classification. In: C. A. LEONE (ed.), Taxonomic Biochemistry and Serology. The Ronald Press Company, New York.

CRUICKSHANK, M. DE LA P., 1984: Crossability relationships among some species of *Lathyrus* L. M. Sc. Dissertation, Univ. of Birmingham, U.K.

DAVIES, A. J. S., 1957: Successful crossing in the genus *Lathyrus* through stylar amputation. Nature **180**, 612.

——, 1958: A cytogenetic study in the genus *Lathyrus*. Ph.D. thesis, Univ. of Manchester, U.K.

DAVIS, P. H., 1970: *Lathyrus* L. In: P. H. DAVIS (ed.), Flora of Turkey and the East Aegean Islands **3**, 328—369.

GANAPATHY, K. Y., and M. P. DWIVEDI, 1961: Studies on clinical epidemiology of lathyrism. ICMR. Rewa.

HARLAN, J. R., and J. M. J. DE WET, 1971: Toward a rational classification of cultivated plants. Taxon **20**, 509—517.

HITCHCOCK, C. L., 1952: A revision of the North American species of *Lathyrus*. University of Washington Publications in Biology 5.

JACKSON, M. T., and A. G. YUNUS, 1984: Variation in the grass pea (*Lathyrus sativus* L.) and wild species. Euphytica **33**, 549—559.

KAUL, A. K., M. Q. ISLAM, and A. HAMID, 1986: Screening of *Lathyrus* germplasm of Bangladesh for BOAA content and some agronomic characters. In: A. K. KAUL and D. COOMBES (eds.), *Lathyrus* and Lathyrism. Third World Medical Research Foundation, New York.

KHAWAJA, H. I. T., 1988: A new interspecific *Lathyrus* hybrid to introduce the yellow flower colour into sweet pea. Euphytica **37**, 69—75.

KISLEV, M. E., 1989: Origins of the cultivation of *Lathyrus sativus* and *L. cicera* (Fabaceae). Econ. Bot. **43**, 262—270.

KUPICHA, F. K., 1983: The intrageneric structure of *Lathyrus*. Notes Roy. Bot. Gard. Edinb. **41**, 287—326.

LAL, M. S., I. AGRAWAL, and M. W. CHITALE, 1986: Genetic improvement of chickling vetch (*Lathyrus sativus* L.) in Madhya Pradesh, India. In: A. K. KAUL and D. COOMBES (eds.), *Lathyrus* and Lathyrism. Third World Medical Research Foundation, New York.

MARSDEN-JONES, E. M., 1919: Report to the Scientific Committee. J. Roy. Hort. Soc. **45**, xcii.

MARSHALL, D. R., 1990: Crop genetic resources: Current and emerging issues. In: A. H. D. BROWN, M. T. CLEGG, A. L. KAHLER, and B. S. WEIR (eds.), Plant Population Genetics, Breeding, and Genetic Resources. Sinauer Associates Inc., Publishers, Sunderland, Massachusetts.

MARTIN, F. W., 1959: Staining and observing pollen tubes in the style by means of fluorescence. Stain Technol. **34**, 125—128.

MAXTED, N., and D. J. GOYDER, 1988: A new species of *Lathyrus* (Leguminosae — Papilionoideae) from Turkey. Kew Bull. **43**, 711—714.

MURTI, V. V. S., T. R. SESHADRI, and T. A. VENKITASUBRAMANIAN, 1964: Neurotoxic compounds of the seeds of *Lathyrus sativus*. Phytochemistry **3**, 877—891.

RUTTER, J., and S. PERCY, 1984: The pulse that maims. New Scientist **23**, 22—23.

SAW LWIN, 1956: Studies in the genus *Lathyrus*. M.Sc. Thesis, Univ. of Manchester, U.K.

SENN, H. A., 1938: Experimental data for the revision of genus *Lathyrus*. Amer. J. Bot. **25**, 67—78.

SIMOLA, L. K., 1966: Chemical and morphological characteristics of some endemic species of *Lathyrus*. Suomen Kemistilehti **B 39**, 148—150.

——, 1967: The effect of some non-protein amino acids on pollen germination and pollen tube growth in five species of the Vicieae. Planta **77**, 287—297.

SMARTT, J., 1979: Interspecific hybridization in the grain legumes — a review. Econ. Bot. **33**, 329—337.

——, 1980: Evolution and evolutionary problems in food legumes. Econ. Bot. **34**, 219—235.

——, 1984a: Evolution of grain legumes. I. Mediterranean pulses. Expl. Agric. **20**, 275—296.

——, 1984b: Gene pools in grain legumes. Econ. Bot. **38**, 24—35.

——, 1986: Evolution of grain legumes. VI. The future — the exploitation of evolutionary knowledge. Expl. Agric. **22**, 39—58.

——, 1990: Grain Legumes. Cambridge University Press, Cambridge.

TOWNSEND, C. C., and E. GUEST, 1974: Flora of Iraq, Vol. 3, Leguminales. Ministry of Agriculture and Agrarian Reform, Baghdad.

VAVILOV, N. I., 1951: Phytogeographic basis of plant breeding. In: F. VERDOORN (ed.), The Origin, Variation, Immunity and Breeding of Cultivated Plants. Chronica Bot. **13**, 13—54. The Ronald Press Company, New York.

YAMAMOTO, K., T. FUJIWARA, and I. D. BLUMENREICH, 1986: Karyotypes and morphological characteristics of some species in the genus *Lathyrus* L. Jap. J. Breed. **34**, 273—284.

YUNUS, A. G., 1990: Biosystematics of *Lathyrus* Section *Lathyrus* with special reference to the grass pea, *L. sativus* L. Ph.D. Thesis, Univ. of Birmingham, U.K.

——, M. T. JACKSON, and J. P. CATTY, 1990: Phenotypic polymorphism of six enzymes in the grasspea (*Lathyrus sativus* L.). Submitted for publication.

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