Promoting the conservation and use of underutilized and neglected crops. 2.

Yam bean

Pachyrhizus DC.

Marten Sørensen

IPK
Institut für Pflanzengenetik und Kulturpflanzenforschung
GATERSLEBEN

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Foreword

Humanity relies on a diverse range of cultivated species; at least 6000 such species are used for a variety of purposes. It is often stated that only a few staple crops produce the majority of the food supply This might be correct but the important contribution of many minor species should not be underestimated. Agricultural research has traditionally focused on these staples, while relatively little attention has been given to minor (or underutilized or neglected) crops, particularly by scientists in developed countries. Such crops have, therefore, generally failed to attract significant research funding. Unlike most staples, many of these neglected species are adapted to various marginal growing conditions such as those of the Andean and Himalayan highlands, arid areas, salt-affected soils, etc. Furthermore, many crops considered neglected at a global level are staples at a national or regional level (e.g. tef, fonio, Andean roots and tubers etc.), contribute considerably to food supply in certain periods (e.g. indigenous fruit trees) or are important for a nutritionally well-balanced diet (e.g. indigenous vegetables). The limited information available on many important and frequently basic aspects of neglected and underutilized crops hinders their development and their sustainable conservation. One major factor hampering this development is that the information available on germplasm is scattered and not readily accessible,, i.e. only found in 'grey literature' or written in little-known languages. Moreover, existing knowledge on the genetic potential of neglected crops is limited. This has resulted, frequently, in uncoordinated research efforts for most neglected crops, as well as in inefficient approaches to the conservation of these genetic resources.

This series of monographs intends to draw attention to a number of species which have been neglected in a varying degree by researchers or have been underutilized economically. It is hoped that the information compiled will contribute to: (1) identifying constraints in and possible solutions to the use of the crops, (2) identifying possible untapped genetic diversity for breeding and crop improvement programmes and (3) detecting existing gaps in available conservation and use approaches. This series intends to contribute to improvement of the potential value of these crops through increased use of the available genetic diversity In addition, it is hoped that the monographs in the series will form a valuable reference source for all those scientists involved in conservation, research, improvement and promotion of these crops.

This series is the result of a joint project between the International Plant Genetic Resources Institute (IPGRI) and the Institute of Plant Genetics and Crop Plant Research (IPK). Financial support provided by the Federal Ministry of Economic Cooperation and Development (BMZ) of Germany through the German Agency for Technical Cooperation (GTZ) is duly acknowledged.

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Introduction

Among the Neotropical legume genera with edible tuberous roots, such as *Apios* Fabr., *Pachyrhizus* Rich. ex DC, *Pediomelum* Rydb. and *Vigna* Savi, the yam bean *(Pachyrhizus)* is the only one that is extensively cultivated, both as a garden crop, and, in the case of *P. erosus* (L.) Urban, also on a large scale for export. *P. erosus* originated in Mexico and Central America, and is cultivated in Mexico, Guatemala, El Salvador and to a limited extent in Honduras. It has been introduced to different pantropical regions, with notable success in Southeast Asia.

Of the five species within the genus, two other species, *P. ahipa* (Wedd.) Farodi and *P. tuberosus* are also cultivated. These species have a South American distribution. At present, *P. ahipa* is only recorded as being cultivated, and the crop is grown by small communities located in the subtropical east Andean valleys of Bolivia and northern Argentina.

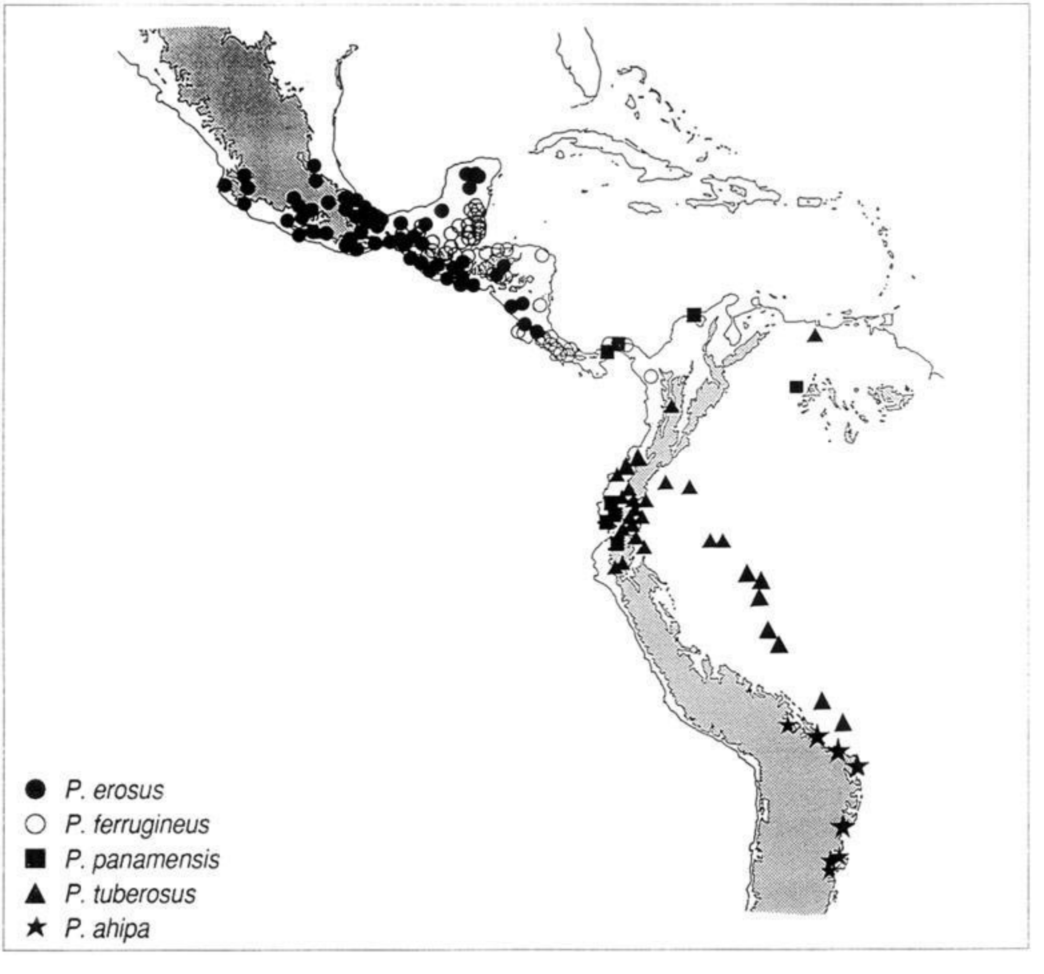

Fig. 1. Neotropical distribution of the genus *Pachyrhizus* (both wild and cultivated records).

P. tuberosus has been recorded as far south as the Río Paraná in eastern Paraguay and the departments of La Paz and Beni in Bolivia, and as far north as the Andean mountain ranges of Sierra de Perijá and Cordillera de Merida in Venezuela. (The distribution of the genus is shown in Figure 1.)

Generic variation is certainly considerable. Plants range from robust vines to small erect bushes; their growth seasons range from less than five months to more than a year. Landraces vary from those with multiple laterally produced tuberous roots to quite advanced cultivars with a single vertically produced tuberous root, and tuberous root qualities range from forms with a low dry matter content (less than 10%) consumed fresh to forms that are only consumed when cooked, because of their high dry matter content (25-30%).

Within each of the three cultivated species, a number of morphologically distinct landrace/primitive cultivar groups can be identified. The existence of these different groups is the result of geographically isolated agricultural selection processes, as in the case of the red-seeded, white-flowered landraces of *P. erosus* with varying degrees of lobed leaflets found in the Yucatan peninsula, or the various groups of *P. tuberosus* found along different river systems in the Amazon.

The information presented in this book has been generated within the context of the Yam Bean Project[1]. The aim of this multidisciplinary research project is to promote understanding of the biosystematics and the agronomic potential of the genus. To date, the project partners in Mexico, Costa Rica, Ecuador, Senegal, Benin, Thailand and Tonga have collected and evaluated a wide range of extant genotypes of both the wild and the cultivated species of *Pachyrhizus* (Table 1).

It is the author's hope that the great potential and attractiveness of this genus as an alternative tuber crop for tropical and subtropical regions will be clearly demonstrated.

Table 1. The Yam Bean Project Germplasm Collection (number of available accessions in each category)

Type of material	*P. erosus*	*P. ahipa*	*P. tuberosus*	*P. panamensis*	*P. ferrugineus*
wild/escaped	27	–	5	1	20
landraces	136	20	55	–	–
cultivars	5	–	–	–	–

1 Since its beginning in 1985, the Yam Bean Project has been funded by the European Union's Science and Technology Programmes (STD1, STD2 and STD3). The author gratefully acknowledges the generous support provided to the project by its various partners.

1 Taxonomy

1.1 General

For a long period, the nomenclature of the genus *Pachyrhizus* remained somewhat confused, owing to the early introduction of the species *P. erosus* to regions outside its original Mexican and Central American distribution area, e.g., the Far East. One of the first botanical references to the species presently known as *P. erosus* is made by Plukenet (1696), who described a plant from Mexico as *'Phaseolus nevisensis'*. It it worth noting, however, that Houttuyn (1779) suggested this was in fact a misnomer and that the correct spelling was probably *'nervisensis'*. Linnaeus (1753) used Plukenet's description as the basis for his *Dolichos erosus* and stated that this plant originated in the New World, i.e. the Neotropics. When Linnaeus published the second edition of his Species Plantarum in 1763, the origin of the species, now confusingly appearing under the name *'Dolichos bulbosus'*, was changed to India. The reason for this error appears to be a plant collected on the island of Amboina in the Moluccas archipelago (Indonesia), and described and depicted by Rumphius (1747) under the name *'Cacara bulbosa'*.

The first valid transfer of a species from the genus *Dolichos* L. to a new genus now considered congeneric with *Pachyrhizus* was made by Du Petit-Thouars (1806), who termed the new genus *'Cacara'*, in agreement with the name proposed by Rumphius (1747) for the species from Amboina. The generic name that is now the accepted one, *Pachyrhizus* (from the Greek words *pachys* = thick(ened), and *rhiza* = root), was originally used by L.C.M. Richard for a herbarium specimen in the illegitimate species name *Pachyrhizus angulatus.* De Candolle (1825) used the same spelling, i.e. with a single 'r', when he first published the name in 1825. Sprengel (1826) was the first to introduce the incorrect spelling of *'Pachyrrhizus'*. Later, when the generic name *Pachyrhizus* was favoured over the 'barbaric' name *'Cacara'* (Briquet 1906), the erroneous spelling *'Pachyrrhizus'* was retained. However, according to the present botanical code, the spelling used by L.C.M. Richard is correct, as it is the original one. Further details concerning the origin of the names of the genus and species are provided by Sørensen (1988).

1.2 Nomenclature

Genus: *Pachyrhizus* Richard ex DC. (1825: 402 nom. cons.); type species: *P. angulatus* L.C.M. Richard ex DC. (nom. illeg. = *P. erosus* (L.) Urban).

Generic synonyms:

Cacara Rumph. ex Du Petit-Thouars (1806: 35 nom. rej.); type species: *C. bulbosa* Rumph. ex Du Petit-Thouars
(= *P. erosus* (L.) Urban)

Taeniocarpum Desvaux (1826:421); type species: *T. articulatum* (Lam.) Desv. (= *P. erosus* (L.) Urban)

Robynsia Martens and Galeotti (1843:193); type species *R. macrophylla* Mart. et Gal. (= *P. erosus* (L.) Urban).

Vernacular names: yam bean (English), Jamsbohne or Knollenbohne (German) (most vernacular ‘generic’ names in languages other than these two do in fact refer to the species *P. erosus).*

1.3 The genus

According to Lackey (1977), the Neotropical genus *Pachyrhizus* Richard ex DC., i.e. the yam bean, is placed taxonomically in the subtribe Diocleinae, tribe Phaseoleae, within the legume family (Fabaceae). The genus currently comprises five species (Sørensen 1988). Three of these are cultivated for their edible tubers and the remaining two are only to be found in the wild.

The fact that, among the cultivated species, only the Mexican yam bean *(P. erosus)* has been introduced more or less pantropically, cannot be explained by the lack of agriculturally attractive characteristics in the remaining two cultivated species. *P. erosus* cultivars will generally have a higher yield in most situations. This is largely a coincidence, although it may be explained in part by the history of the Spanish and Portuguese conquest of Latin America.

The revision by Clausen (1945) rendered the taxonomy of the genus somewhat diffuse. This is especially true of the South American species, owing to the shortage of herbarium material caused by the Second World War. In addition, the narrow species concept held by Clausen has contributed to the considerable complexity of the present work, as is apparent from the great number of infraspecific taxa included. A new revision (Sørensen 1988) was justified by the new herbarium material available from European herbaria and the material that has been collected over the past 50 years.

The genus *Pachyrhizus* is morphologically delimited by the presence of the following characteristics: vines or semi-erect herbaceous to somewhat lignified perennial plants with one or more tuberous roots; trifoliolate leaves with stipules and pinnately arranged leaflets with caducous stipels. Inflorescence is a complex to simple raceme and the flowers have a tubular calyx and a papilionaceous corolla. The ovary has a basal crenate disc-formed nectarium, the recurving style is ciliated ventrally and the vertical surface of the stigma is subglobose. The straight legume is septate between the seeds,, which are a square, more or less flattened, or a rounded kidney, shape. Colours range from olive green and deep maroon to black, or from black and white to mottled cream.

Chemosystematic examinations of the phylogeny and interrelationships of *Pachyrhizus* at the generic as well as the subtribal level have so far been limited to the studies of (i) canavanine by Lackey (1977), who placed *Pachyrhizus* in the subtribe Diocleinae; and (ii) isoflavonoid phytoalexins by Ingham (1979, 1990), who suggests a close affinity between *Pachyrhizus* and the Palaeotropical genus *Neurautanenia* (subtribe Glycininae (Ingham (1979) and subtribe Phaseolinae (Ingham 1990)). According to Ingham (1979), this relationship could justify the transfer of *Pachyrhizus* to the subtribe Glycininae. Ingham (1990) suggests that the genera *Pachyrhizus* and *Calopogonium* (both Diocleinae) may bridge the gap between the genera *Neorautanenia* (Phaseolinae) and *Pueraria* (Glycininae).

Molecular analyses carried out by Bruneau *et al.* (1990) studied the significance of a chloroplast DNA inversion as a subtribal character in the Phaseoleae and demonstrated the presence of the inversion in 11 of its 23 genera. All six genera *(Calopogonium* Desv., *Canavalia* DC., *Cleobulia* Mart. ex Benth., *Dioclea* Kunth, *Galactia* P. Browne and *Pachyrhizus)* examined within the subtribe Diocleinae lacked the inversion These results thus corroborate the subtribal classification proposed by Lackey (1981). Partly because the chemosystematic studies carried out are not in complete concordance, but mainly due to a lack of information on infrageneric relationships, a new research project involving the study of isozymes, chloroplast DNA and ribosomal DNA has recently begun, involving R.J. Abbott, Department of Preclinical Medicine and Biology, University of St. Andrews, Scotland, and the Botanical Section, Department of Botany, Dendrology and Forest Genetics, Royal Veterinary and Agricultural University, Copenhagen, Denmark. The results of these studies,, which have yet to be published, have revealed considerable agreement between molecular systematic affinities and the numerical taxonomy based on morphological characters. Two main groups/branches have been identified, the first containing the species *P. tuberosus, P. ahipa* and *P. panamensis* (the species of South American origin) and the second one the Central American and Mexican species of *P. erosus* and *P. ferrugineus.* At the species level and below, these examinations indicate that molecular methods of analysis can serve to demonstrate variations not only between the species, but also between different genotypes within a single species, a subject of even greater interest (see discussion on the *P. tuberosus* complex in Section 6.1).

A palynological study of the genus (Sørensen 1989) revealed that interspecific variation was sufficient to allow unequivocal identification of the individual species. The greatest infraspecific variation was, unsurprisingly, observed in the pollen grains from the cultivated species, i.e. the pollen of wild species was quite uniform.

1.3.1 The cultivated species: *Pachyrhizus erosus* (L.) Urban

Pachyrhizus erosus (L.) Urban (1905: 311).
Basionym: *Dolichos erosus* L. (1753: 726).
Type: *Phaseolus Nevisensis* Plukenet (1694: Table 52, Figure.4) (holo).
Homotypic synonyms: *Dolichos bulbosus* L. (1763: 1021) *(nom. superfl.); Pachyrhizus angulatus* L.C.M. Richard ex DC[2]. (1825: 402) *(nom. illeg.); Stizolobium bulbosum* (L.) Sprengel (1826: *252) (nom. illeg.); Pachyrhizus bulbosus* (L.) Kurz (1876: 246) *(nom. illeg.); Cacara erosa* (L.) Kuntze (1891: 165) *(nom. rej.); Pachyrhizus erosus* (L.) Urban var. *typicus* Clausen (var. *superfl.).*

[2] DC = ex de Candolle.

Heterotypic synonyms: *Dolichos articulatus* Lam. (1786: 296).
Type: *Dolichos foliis ternatis, eroso-dentatis* Plumier (1759: Table 222) (holo);
Stizolubium domingense Sprengel (1826: *252) (nom. illeg.); Taeniocarpum articulatum* (Lam.) Desvaux (1826: 421); *Pachyrhizus articulatum* (Lam.) Duchassaing et Walpers (1853: 226).
Cacara bulbosa Rumph. ex Du Petit-Thouars (1806: 35).
Type: *Cacara bulbosa* Rumphius (1747: Table 132, Figure 3) (holo).
Dolichos palmatilobus Moçiño et Sessé ex DC. (1825: 399).
Type: Original illustration by Moçiño et Sessé from the Torner collection at the Hunt Institute for Botanical Documentation (lecto).
Pachyrhizus palmatilobus (Moç. et Sess. ex DC.) Bentham (1865: 540); *Cacara palmatiloba* (Moç. et Sess. ex DC.) Kuntze (1891: 165); *Pachyrhizus erosus* (L.) Urban var. *palmatilobus* (Moç. et Sess. ex DC.) Clausen (1945: 13).
Pachyrhizus jicamas Blanco (1837: 579).
Type: Lost
Robynsia lobata Martens et Galeotti (1843: 194).
Type: Galeotti, H. 3167, Mexico, Edo. Oaxaca, Juchatengo (BR, lecto; isolecto, BR, G).
Robynsia macrophylla Martens et Galeotti (1843: 193).
Type: Galeotti, H. 3278, Mexico, Edo. Vera Cruz, pres de la colonie allemande de Mirador (BR, holo).
Pachyrhizus strigosus Clausen (1945: 17).
Type: Clausen, R.T. et Cervantes G., R. 6098, Mexico, Edo. Chiapas, Hacienda Monserrate (BH, holo; iso, BH).
Vernacular names: jícama (Spanish); Mexican yam bean (English), mexikanische Jamsbohne or mexikanische Knollenbohne (German), pois batate or dolique tubéreux (French), sinkama (Philippines), bangkoewang (Indonesia) and man kaeo (Thai).

See Figures 2a and 2b.

1.3.2 The cultivated species: *Pachyrhizus ahipa* (Wedd.) Parodi

Pachyrhizus ahipa (Weddell) Parodi (1935: 137).
Basionym: *Dolichos ahipa* Weddell (1857: 113).
Type: Mandon, G. 747, Boliviense, prov. à Laracaja, Sorata ad rivum (P, holo).
Heterotypic synonyms: *Pachyrhizus ahipa* (Wedd.) Parodi var. *violacea* Parodi (1935: 138).
Type: Parodi, L.R. 12145, ex cult. in Hort. Bot. Fac. Agric. B. Aires (BAA, holo).
Pachyrhizus ahipa (Wedd.) Parodi var. *albiflora* Parodi (1935: 138).
Type: Parodi, L.R. 12l46, ex cult. in Hort. Bot. Fac. Agric. B. Aires (BAA, holo).
Vernacular names: ahipa (Spanish); Andean yam bean (English); andine Knollenbohne or andine Jamsbohne (German); l'ahipa or dolique tubereux d'Ande (French).

See Figure 3.

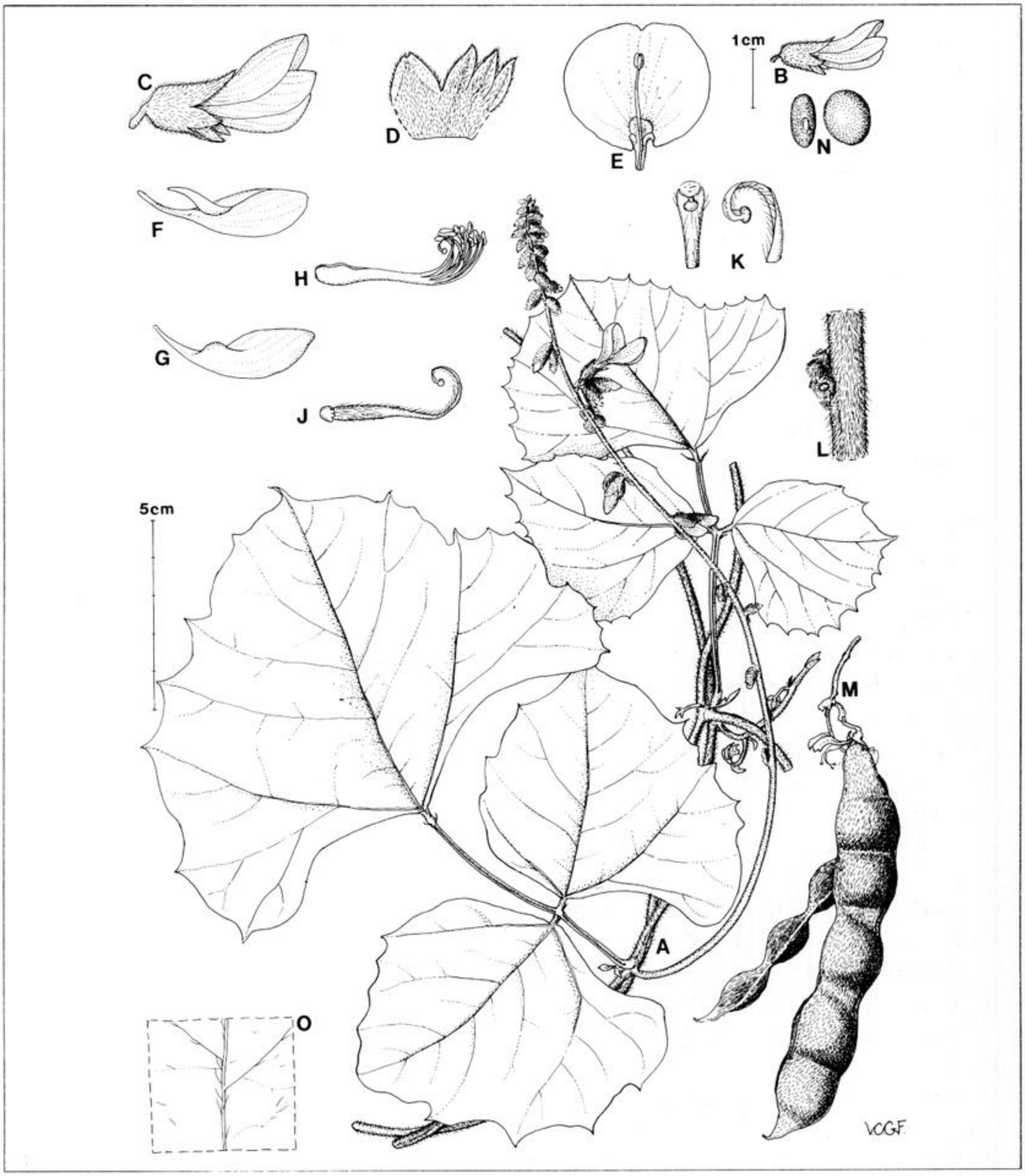

Fig. 2a. *Pachyrhizus erosus.* A. Habit, 2/3 of natural size. B. Flower, natural size*. C. Flower, side view. D. Calyx, opened. E. Standard with free median stamen. F. Wing. G. Keel. H. Stamens. J. Pistil with basal disc. K. Side and front view of style and subglobose stigma. L. Lateral axis of inflorescence. M. Mature legume. N. Side and top view of seed. O. Section of adaxial leaf surface. (All parts except legume from Abbott 404, GH; legume from grown from seeds from Oaxaca, Mexico). This figure, originally appearing in Sørensen (1988), is reproduced by kind permission of Nordic Journal of Botany.

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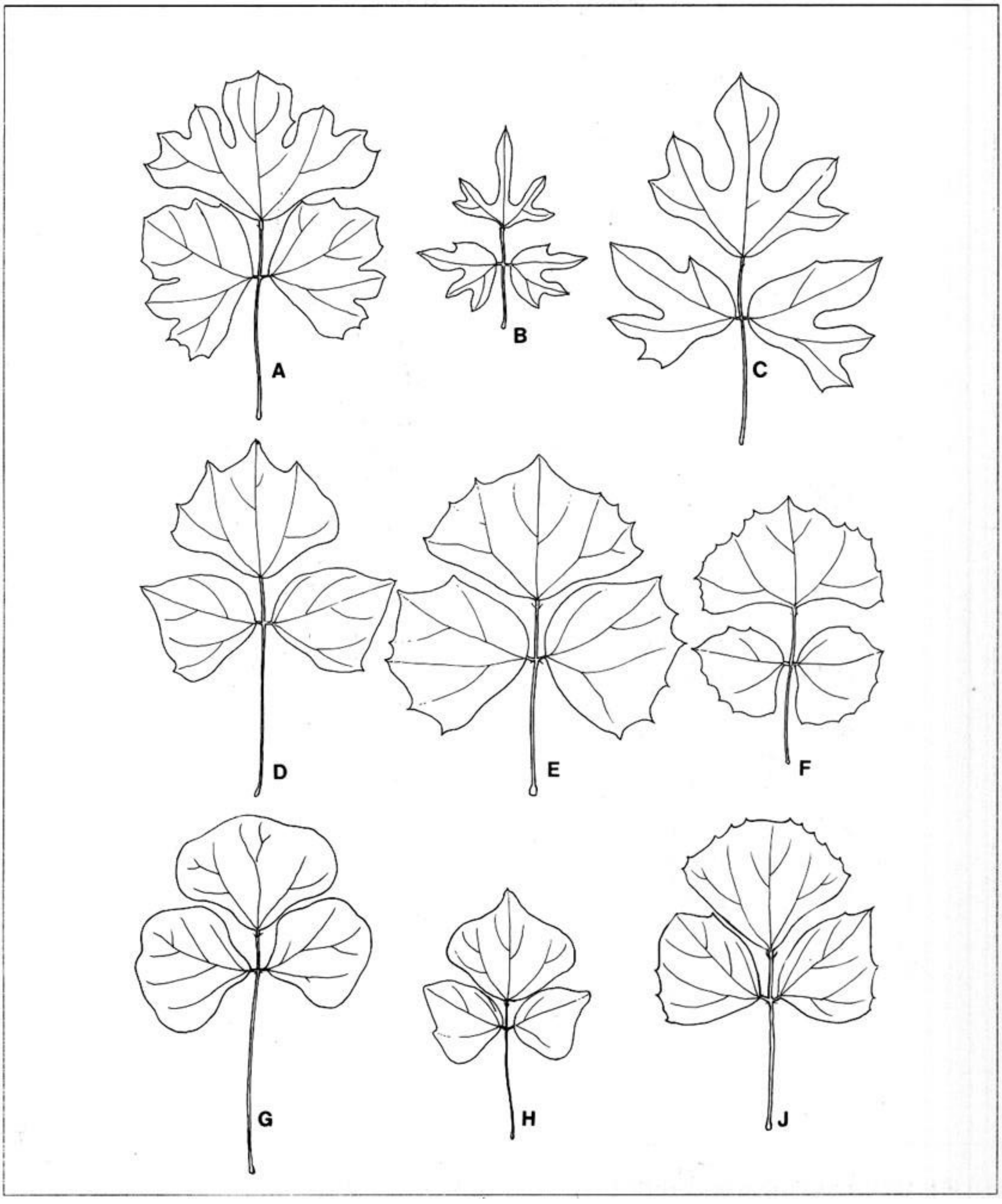

Fig. 2b. *Pachyrhizus erosus.* The variation in the outline of the leaflets. A. From Moyuta, Depto. Jutiapa, Guatemala. B. Prov. Guanacaste, Costa Rica. C. Prov. Guanacaste, Costa Rica. D. Prov. Cartago, Costa rica. E. Edo. Oaxaca, Mexico. F. Edo. Oaxaca, Mexico. G. Edo. Oaxaca, Mexico. H. Edo. Yucatan, Mexico. J. Edo. Nayarit, Mexico (all specimen collected by the author). This figure, originally appearing in Sørensen (1988), is reproduced by kind permission of Nordic Journal of Botany.

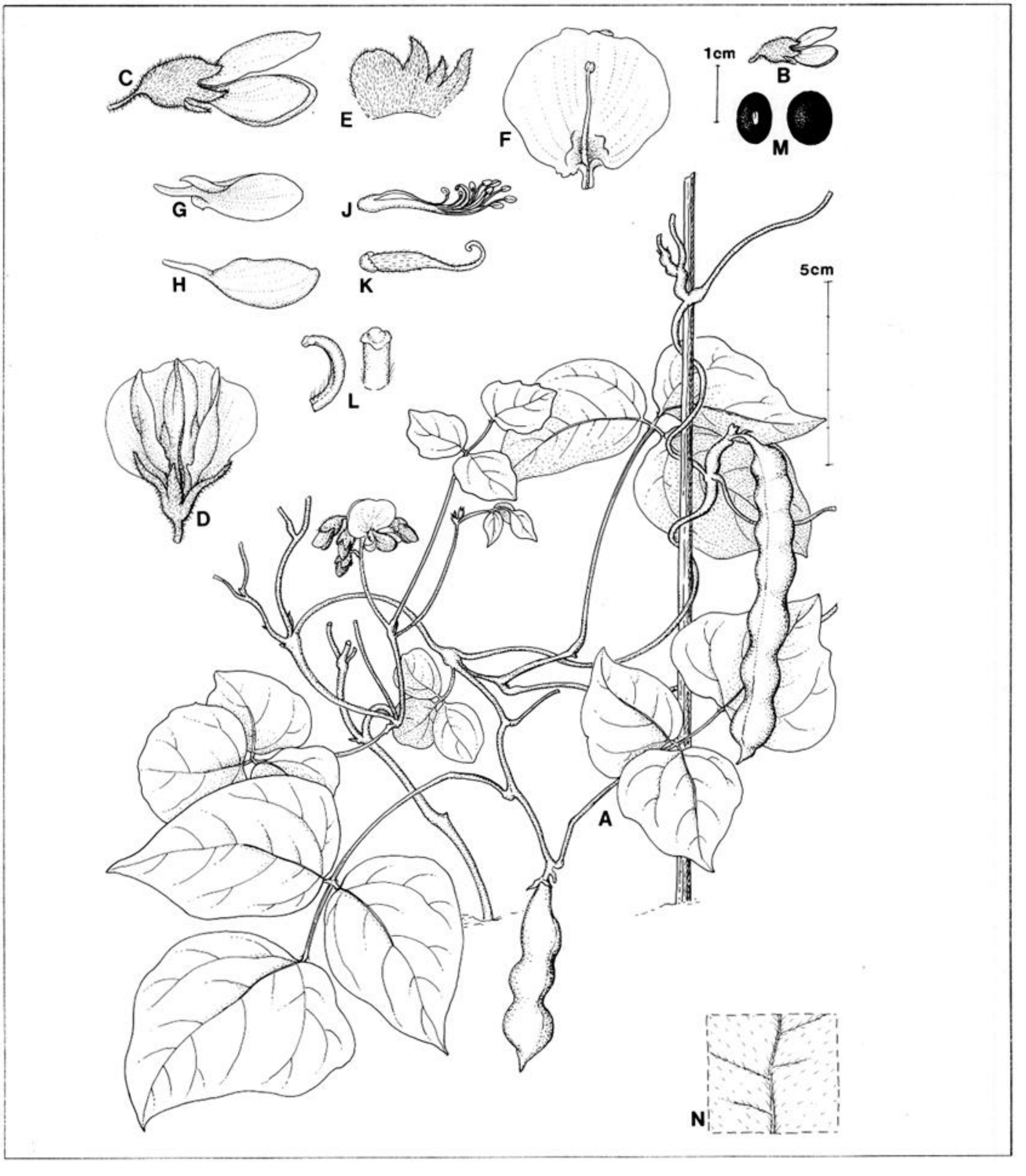

Fig. 3. *Pachyrhizus ahipa.* A. Habit, 2/3 of natural size. B. Flower, natural size*. C. Flower, side view. D. Flower seen from underneath. E. Calyx, opened. F. Standard with free median stamen. G. Wing. H. Keel. J. Stamens. K. Pistil with basal disc. L. Side and front view of style and subglobose stigma. M. Side and top view of seed. N. Section of adaxial leaf surface. (All parts from AC102, Prov. Tarija, Bolivia). This figure, originally appearing in Sørensen (1988), is reproduced by kind permission of Nordic Journal of Botany.

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1.3.3 The cultivated species: *Pachyrhizus tuberosus* (Lam.) Spreng.

Pachyrhizus tuberosus (Lam.) Sprengel (1827: 281).
Basionym: *Dolichos tuberosus* Lamarck (1786: 196).
Type: *Dolichos foliis integerrimis* Plumier (1759: Tab. 220) (lecto).
Homotypic synonyms: *Stizolobium tuberosum* (Lam.) Sprengel (1826: 252); *Cacara: tuberosa* (Lam.) Britton et Wilson (1924: 424) *(nom. rej.).*
Vernacular names: ashipa, chuin, jíquima (Spanish -different cultivar groups found in Ecuador, Peru and Bolivia); potato bean or Amazonian yam bean (English); amazonische Jamsbohne or amazonische Knollenbohne (German); pois cochon (French); jacatupé (Brazil); mbacucú (Guarani, Paraguay). NB: a linguistic survey of the different local South American names appears in Sørensen *et al*. (1996).

The interspecific hybridization experiments carried out so far have involved the three cultivated species and the wild species *P. panamensis.*

See Figs 4a and 4b.

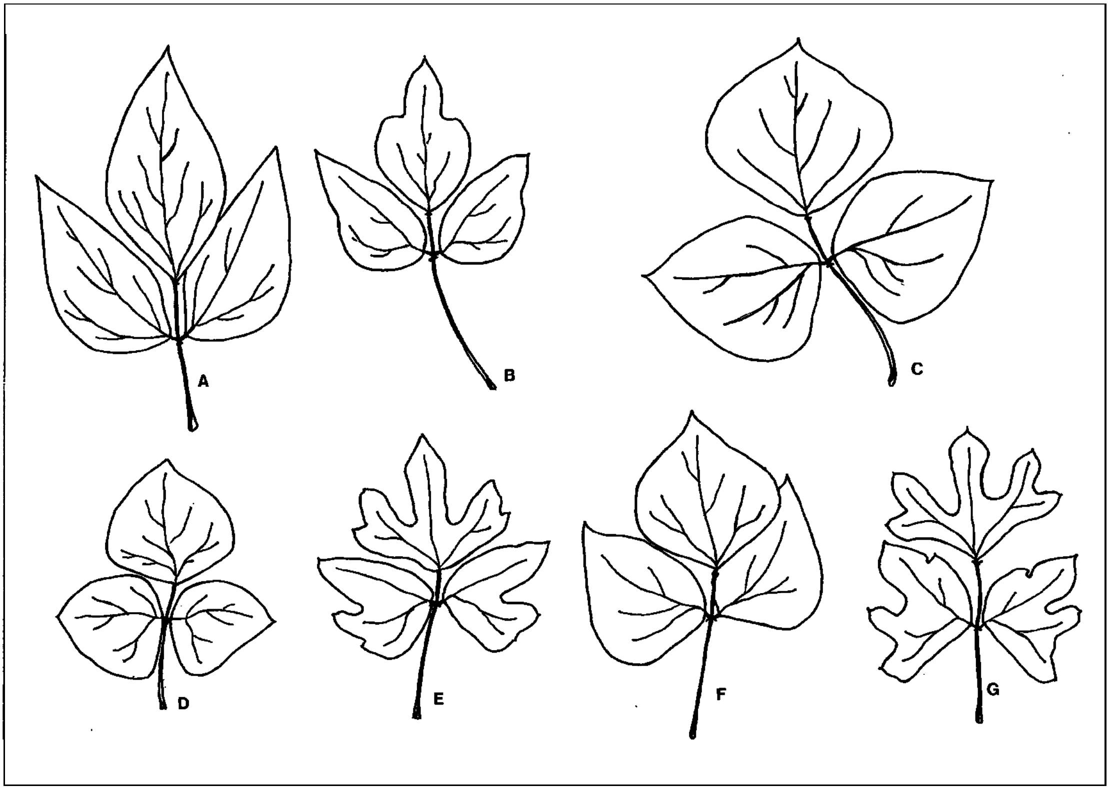

Fig. 4a. *Pachyrhizus tuberosus.* The variation in the outline of the leaflets. A. From Puerto, Amazonas, Peru, TC355, "Chuin" landrace. B. San Antonio, Amazonas, Peru, TC352, "Chuin" landrace. C. Depto. San Martin, Peru, Kvist *et al.* 1705, "Ashipa" landrace. D. Limoncocha, Ecuador, Conrad *s.n.*, "Ashipa" landrace. E. Depto. Cusco, Peru, TC538, "Ashipa" landrace. F. Prov. Los Rios, Ecuador, TW560, wild. G. Prov. Manabi, Ecuador, TC555, "Jiquima" landrace.

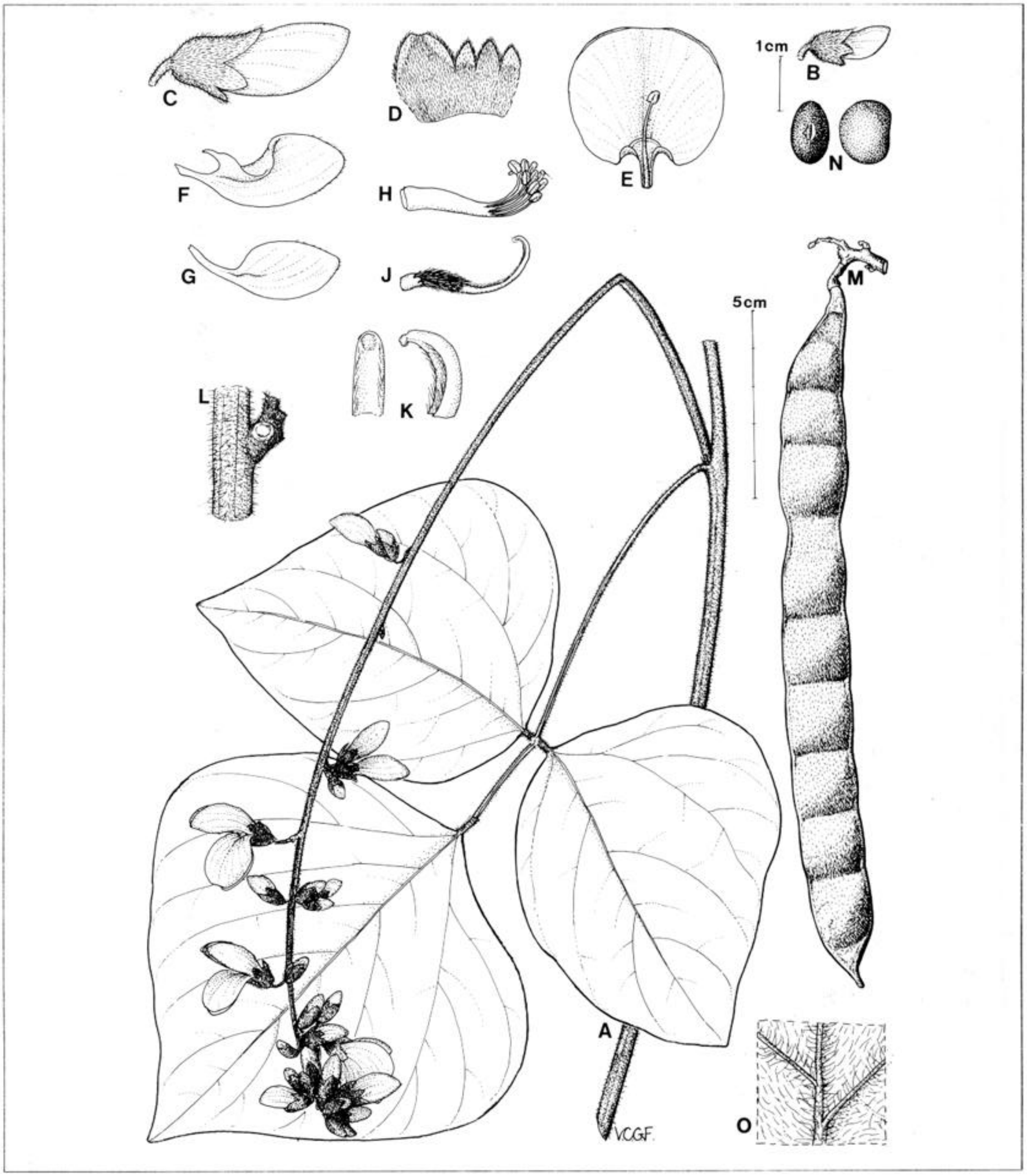

Fig. 4b. *Pachyrhizus tuberosus.* A. Habit, 2/3 of natural size. B. Flower, natural size*. C. Flower, side view. D. Calyx opened. E. Standard with free median stamen. F. Wing. G. Keel. H. Stamens. J. Pistil with basal disc. K. Side and front view of style and subglobose stigma. L. Lateral axis of inflorescence. M. Mature legume. N. Side and top view of seed. O. Section of adaxial leaf surface. (A-L and O from Asplund 15461, S; M from Lynch C43-25, BH; N from Clausen C43-25, BH). This figure, originally appearing in Sørensen (1988), is reproduced by kind permission of Nordic Journal of Botany.
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Table 2. Quantitative analysis of the specific variation (measured in mm) in 27 characters[1]

	P. erosus		*P. ferrugineus*		*P. panamensis*		*P. tuberosus*		*P. ahipa*	
Character[l]	(min)mean(max)	n	(min)mean(max)	n	(min)mean(max)	n	(min)mean(max)	n	(min)mean(max)	n
Stipels[l]	(1.3) 5.4 (16)	225	(1) 3 (7.6)	97	(0.8) 3.4 (6.3)	19	(1.9) 5.1 (8.6)	45	(1.5) 2.9 (4.4)	27
Petioles[l]	(3) 76.6 (162)	237	(24) 71.1 (233)	113	(36) 73.2 (109)	19	(34.2) 121.9 (277)	73	(45.4) 99.8 (166)	27
Stipules[l]	(1.2) 4.3 (11)	249	(1.3) 2.8 (5.9)	110	(1) 2.7 (4.1)	19	(1.0) 3.8 (6.5)	69	(0.9) 2.1 (4.1)	27
Terminal leaflet (l/w ratio)	(0.47) 0.86 (5.36)	246	(0.68) 1.19 (7.14)	116	(0.68) 0.86 (1.02)	19	(0.7) 0.99 (1.47)	76	(0.76) 0.88 (1.05)	27
Lateral leaflet (l/w ratio)	(0.82) 1.08 (3.61)	245	(0.75) 1.35 (4.7)	114	(0.86) 1.25 (1.67)	19	(0.92) 1.26 (1.76)	76	(0.93) 1.19 (1.56)	27
Raceme[l]	(13) 207 (635)	219	(14.) 222.6 (860)	104	(38.0) 90.7 (205)	18	(22.0) 163.8 (356)	54	(9.7) 27.5 (82.1)	25
Peduncle[l]	(12) 169.8 (415)	215	(5.2) 118.9 (323)	97	(50.1) 144.5 (227)	18	(32) 134.4 (289)	55	(1.9) 15.9 (58)	25
Flower[l]	(0.8) 1.81 (8)	159	(1) l.9 (13.1)	67	(1.3) 3.8 (8.2)	15	(1) 3.4 (22.9)	44	(1.7) 10.9 (15.8)	24
Prophyls[l]	(5.5) 20.16 (26.3)	185	(1.6) 13.6 (23.4)	72	(2.3) 15.4 (19.8)	13	(1.2) 20.9 (27.5)	47	(1.4) 5.5 (19.3)	24
Calyx[l]	(5.2) 9.6 (13)	188	(2.7) 8.3 (13.1)	74	(6.4) 8.6 (10.8)	15	(5.2) 10.4 (14.9)	50	(4.2) 7 (10.3)	24
Calyx large lobe[l]	(2.7) 5.4 (7.7)	188	(1.4) 4.1 (6.8)	75	(2.9) 4.7 (6.3)	14	(1.8) 5.3 (6.8)	50	(1.6) 3.5 (5.4)	24
Calyx tube[l]	(2.3) 4.8 (18.4)	188	(2.2) 4.2 (6.3)	74	(2.2) 4.2 (5.4)	14	(3.1) 6.14 (17.5)	49	(1.2) 3.5 (5.8)	24
Standard (l/w ratio)	(0.7) 1.21 (1.4)	171	(0.4) 1.16 (1.5)	70	(0.9) 1.15 (1.3)	11	(0.9) 1.24 (1.65)	45	(0.8) 1.03 (1.5)	24
Wing[l]	(4.3) 19.1 (23.9)	169	(7.1) 12.7 (21.6)	71	(8.4) 14.5 (18)	11	(4.2) 19.9 (27.3)	45	(12.4) 14.6 (17)	24
Wing claw[l]	(1.8) 5 (8.1)	171	(1.2) 3.7 (8.6)	71	(1.2) 3.9 (5.4)	11	(1.4) 5.3 (7.7)	45	(2.8) 3.8 (4.7)	24
Wing auricle	(1.3) 3.5 (19.4)	171	(0.4) 2.1 (13.1)	71	(1.6) 2.2 (2.7)	11	(1.6) 3.8 (16.4)	45	(1.6) 2.2 (3.6)	24
Keel[l]	(11.5) 19.8 (25.2)	167	(1.4) 13 (21.6)	69	(8.4) 15 (27)	11	(8.4) 20.8 (27)	45	(12.8) 15.1 (17.3)	24
Keel blade[l]	(6.7) 12.4 (16.2)	167	(4.9) 7.7 (13)	68	(3.) 9.1 (11.2)	11	(6.6) 12.9 (16.6)	45	(4.8) 9.7 (12.3)	24
Keel claw[l]	(2.2) 7.5 (18.4)	171	(2.2) 5.6 (10.8)	69	(4.3) 5.8 (7.2)	11	(4) 8.43 (16.8)	45	(1.8) 5.6 (8.8)	24
Stamen[l]	(7.2) 18.1 (23.9)	165	(4.8) 10.9 (18)	66	(6.4) 12.8 (16.4)	11	(8.5) 18.9 (25.2)	45	(12.4) 14.4 (17.6)	24
Pistil[l]	(19.6) 20.5 (21.4)	159	(7.0) 13.3 (18.5)	66	(8.2) 16 (20)	11	(10.4) 23 (29)	43	(14) 17.3 (20.3)	24
Legume[l]	(13) 72.2 (131)	100	(7.8) 86.0 (181)	59	(16.2) 76.2 (125)	10	(33) 132.8 (255)	41	(33.3) 91.7 (165)	23
Legume[w]	(0.1) 9.1 (27)	101	(2.3) 15.8 (107)	60	(2.7) 8.2 (11.7)	10	(3.1) 15.9 (27.2)	43	(8.5) 15.6 (21.2)	23
Legume segment[l]	(2.5) 8.9 (13.5)	70	(3.1) 14.4 (29)	45	(6.7) 8.3 (9.9)	7	(8.5) 17.4 (24.3)	32	(5.6) 13.7 (22.2)	23
Segment[#]	(5) 8.3 (11)	68	(3) 5.8 (16.3)	43	(6) 9 (11)	6	(4) 7.7 (12)	31	(2) 4.7 (8)	23
Seed[l]	(3.1) 7.5 (10.1)	85	(3.7) 9.4 (14.7)	33	(4.3) 5.8 (6.7)	5	(3.5) 8.6 (12.4)	30	(6.4) 8 (10)	21
Seed[w]	(3.8) 7.8 (11.3)	85	(4.4) 10 (15.3)	32	(4) 6.6 (8.)	5	(5) 10.3 (13.9)	30	(7.4) 8.9 (10.7)	21

[1] l = length, w = width, # = number (Døygaard, unpublished).

2 Description of the cultivated species

2.1 Botanical and morphological description of the genus/crop

The morphological characteristics delimitating the genus are the presence of a 'false beard' of short hairs along the dorsal (adaxial) side of the ovary, continuing almost to the base of the stigma along the incurved side of the style. The stigma itself is subglobular and is placed almost terminally. Also, all species have tuberized roots. Table 2 gives an overview of the morphological variation of 27 characters in the five species.

P. erosus

A herbaceous vine with great variation in the outline of the leaflets, from dentate to palmate. The species is defined by the lack of hairs on the petals, the number of flowers (4-11) per lateral inflorescence axis, i.e. by complex racemes, and an inflorescence length of 8-45 cm. Furthermore, morphological characters of the legumes (pods), qualitative as well as quantitative, are used to separate the species. Size (6-13 cm x 8-17 mm), reduction of the strigose hairs at maturity and colour (from pale brown to olive-green/brown) are characters specific to the legume of *P. erosus.* A number of seed characters are also specific: these include the colour, which ranges from olive-green to brown or reddish brown, and the shape, which is flat, and square to rounded, but never reniform (Sørensen 1988, 1990).

Clear taxonomic distinctions between wild and cultivated genotypes are difficult to make, owing to the vast number of ephemeral populations in Mexico and Central America originating from previous cultivation. However, wild material may be identified unequivocally by the generally smaller leaf size, the increased hairiness of leaves and legumes, the smaller and often elongated and irregular shape of the tuberous root, and the dark brown colour of the tuber surface. The legumes of both wild and cultivated genotypes are dehiscent, as the crop has never been selected for grain legume characteristics, i.e. seed producers harvest the legumes when not quite mature.

P. ahipa

P. ahipa is distinguished morphologically from the other species by being a herbaceous plant with entire leaflets (a few individual plants possessing dentate leaflets have been recorded), with short racemes (48-92 mm) and the general absence of lateral axes, i.e. simple racemes. The number of flowers per lateral raceme, if present, is as low as 2-6. The wing and keel petals are usually glabrous, but slightly ciliolated specimens have been seen. The wings curl outwards following anthesis, a feature seen only in *P. ahipa.* The legume is 13-17 cm long and 11-16 mm wide, and almost circular in cross-section when immature, i.e. only slightly dorsiventrally compressed. Seeds are black or black and white/cream mottled in colour, kidney-shaped, and measure 9 x 10 mm. The 100-seed weight is 29.2 (range 17.3-41.2 g).

This species is additionally unique in that both twining/trailing, semi-erect to short bushy erect growth habits are found: i.e. both determinate and indeterminate genotypes exist. Erect genotypes are 15-40 cm tall, semi-erect 30-60 cm, and twining types 60-200 cm long.

P. tuberosus

P. tuberosus is recognized by the following morphological characters. The largest species have stems of more than 7 m and terminal leaflets of 280 x 260 mm. The legumes are also larger than those of the other species, measuring 255 x 23 mm, and are conspicuously compressed between seeds. The seeds are black, black and white mottled or orange-red in colour, kidney-shaped and 12 x 14 mm in size.

In a manual (National Academy of Sciences 1979) an author speculated that *P. tuberosus* might only be a cultivar of *P. erosus*, selected because of its larger roots. Despite consulting such renowned taxonomists as Pittier, Steyermark and Ernst, Munos Otero (1945) had considerable difficulty in identifying the *Pachyrhizus* species of Venezuelan origin. He (erroneously) decided to use the illegitimate name *P. angulatus* (synonym. *P. erosus)* when publishing the first (and so far only) comprehensive agronomic study of *P. tuberosus.* However, all wild material and all landraces/cultivars have been morphologically quite distinct from *P. erosus* plants. Moreover, the molecular studies conducted by R.J. Abbott and colleagues (R.J. Abbott 1994, pers. comm.) have clearly demonstrated that even though both species contain considerable infraspecific variation, they can be distinguished easily on the basis of cpDNA analysis and isozymatic differences. Bentham's suggestion that the two species should be considered as being conspecific (Anonymous 1889b; Ernst 1888;. Bois 1927; Deshaprabhu 1966; National Academy of Sciences 1979) can be disregarded on the basis of examinations of both herbarium material and literature.

The specimen R. 4936 from Peru, collected by Spruce in Tarapoto, of which two duplicates exist at Kew, formed the basis for the illustration with the note from Kew (Anonymous 1889b). One sheet contains all the types of leaflets and the inflorescence shown in the illustration. On the other sheet, the specimen has a legume similar to the one in the illustration, but with deeply lobed leaflets which have not been illustrated. Live plant material representing both these leaflet types is now included in the germplasm collection originating from the regions west and southwest of Iquitos, Peru along the Río Ucayali, belonging to the ashipa cultivar group (Section 6.1). This clearly demonstrates that both leaf types occur within a single cultivar group (or a single population, as in *P. ferrugineus* and *P. erosus).* Both-multi- and monotuberous cultivars exist. Munos Otero (1945) states that the local black-seeded landrace from near Juan Largo in the Venezuelan state of Monagas generally produces five tuberous roots per plant.

2.2 Reproductive biology

All species have bisexual flowers which as a rule are self-pollinating. Some cross-breeding does occur (2-4%; highest incidence in *P. ahipa)* depending on the availability of pollinators, mainly different bumblebee species. Cross-breeding is limited when cultivation takes place during the dry season (material under irrigation), as is the case in Guanajuato, owing to the lack of pollinators. With the possible exception of *P. ferrugineus,* all species have been demonstrated to be compatible, resulting in fertile interspecific hybrids. However, no naturally occurring hybrids have been recorded in areas shared by two species, as the flowering period of the different species does not overlap under natural conditions. The cultivated species are propagated by seed, with the exception of the ashipa cultivar group.

P. erosus

The flowering season is within the natural distribution area. Flowering specimens have been seen from all months except January, with the majority (90%) from July to October. The latest flowering occurs in the southern parts of the distribution area, at the end of the rainy season. Mature legumes have been recorded from August to February, and were collected in mid-March in Costa Rica in 1985.

The floral biology of *P. erosus* was studied in some detail by Prasad and Prakash (1973). The flowering in the three cultivars examined commenced 58-68 days after sowing, and lasted 92-103 days. The stigma was found to become receptive at 12 hours before and to last for 18 hours after opening of the flower. The anthers generally dehisced 8-12 hours before opening of the flower. When the pollen grains were stored at room temperature, their germination percentage decreased after 4 hours. On average, they remained viable for 22 hours (Prasad and Prakash 1973).

P. ahipa

The crop is usually sown in August to October. Reproductive pruning (removal of flowers) starts in November to March, 4-7 months after sowing, with mature legumes in April to June. Two seed-multiplication strategies in this predominantly self-pollinating species were reported (Ørting *et al.* 1996). The more common strategy is to select the most vigorous plant for seed production within a field, and reproductively prune the remaining plants, in order to increase tuber growth. An alternative strategy involves leaving the legume produced first on each plant, for seed production, and the removal of all subsequently produced flowers. Whichever practice was followed, indirect selection on the basis of seed size and shape was performed through harvesting (Ørting *et al.* 1996).

P. tuberosus

Owing to the highly heterogeneous origin of both the wild and the cultivated material, and the uncertainty over its exact status, the precise time and length of the flowering season cannot be determined. Specimens in full bloom have been recorded throughout the year, except in the months of February and July, but most of the material flowered from October to June. Mature fruits have been seen from March to December. Locally, the flowering season can be well defined according to the cultivation period. This is the case with crops whose cultivation is linked to seasonal flooding, e.g the chuins and the jíquima. The former, which are exclusively cultivated on floodplains, and predominantly at the higher, irregularly or only briefly inundated levees, are sown in May to June and harvested in February to March. At the time of the tuber harvest, chuin also produces seeds, which are gathered, kept and sown after the inundation. As described below, the top of the tuber may also be replanted, and after 4 months will then produce many seeds but no tubers.

For the jiquima cultivar groups, the common planting months in Manabí are June to July, at the end of the rainy season. The short growth cycle of the jíquima allows harvest of both tubers and seed to take place after approximately 5 months. Seed availability is, however, limited, as seeds are only produced on-farm.

In Brazil, when studying *P. tuberosus* Menezes and Oliveira Nunes (1955) reported differences in pollen fertility of 0-53%, i.e. complete male sterility was observed. This observation corroborates analyses carried out on pollen originating from *P. tuberosus* and *P. ahipa* plants grown in greenhouse experiments at the Botanical Section, RVAU. When examining the specificity of the pollen morphology of the five species and interspecific hybrids, the author (Sørensen 1989) found a strong correlation between increased male sterility and infection with BCMV (bean common mosaic virus). Pollen observed by electron microscopy scanning from virus-infected plants was relatively distorted/collapsed, compared with pollen from healthy plants.

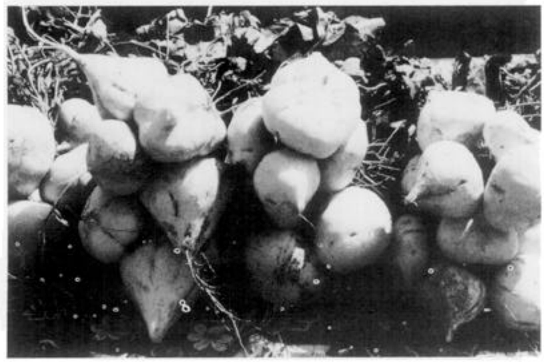
2.3 Cultivation practices

All cultivated species are usually grown as annual crops, although the plants have a perennial habit. In both *P. erosus* and *P. ahipa* reproductive pruning (the manual removal of fertile shoots) is generally practised to increase tuberous root growth. In *P. tuberosus,* only the cultivar group from the province of Manabí, Ecuador, is reproductively pruned. In this cultivar group, however, not only are the flowering shoots pruned, but up to a third of the vegetative shoots are also removed. In areas with high precipitation rates during the growth period (or in flood-irrigated fields), the crops are usually cultivated on ridges in order to increase drainage.

P. erosus

The present day Mexican cultivars (Figures 5a-h) are primarily used in the states of Guanajuato and Nayarit. The crop is traditionally intercropped with maize *(Zea mays* L.) and common bean *(Phaseolus vulgaris* L..*)* or monocropped when grown on a larger commercial scale, e.g. for exportation. The cultivars are morphologically very uniform, compared with the local landraces from such states as Oaxaca and Vera Cruz. Cultivars grown in the two major areas of commercial production, Nayarit and Guanajuato, do however possess several distinguishing morphological and physiological characteristics. Although these two regions are located vir-

a



b

c

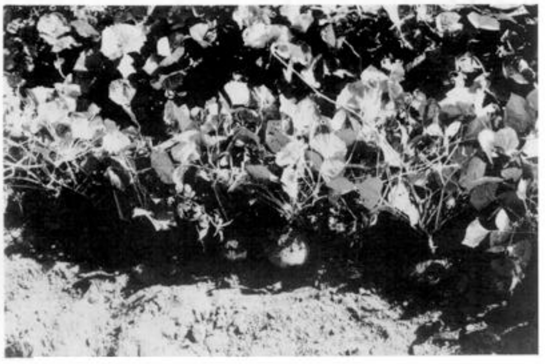
d

Fig. 5a. *Pachyrhizus erosus.* Fair sized tuber from Mexican landrace, INIFAP-CIR CENTRO, Campo Experimental Bajío, Celaya, Mexico (Photo, M. Grum).

Fig. 5b. *Pachyrhizus erosus.* Tuber for sale at roadside, State of Morelos, Mexico (Photo, M. Sørensen).

Fig. 5c. *Pachyrhizus erosus.* Commercial, flood irrigated field intercropped with Maize (harvested) near Celaya, Mexico (Photo, M. Sørensen).

Fig. 5d. *Pachyrhizus erosus.* Commercial, flood irrigated field intercropped with Maize (harvested) just prior to harvest of Yam Bean, near Celaya, Mexico. Notice the absence of legumes, i.e. reproductively pruned. (Photo, M. Sørensen).



e

f

g

h

Fig. 5e. *Pachyrhizus erosus.* Dryland, commercial field at 1 000 m a.s.l., State of Nayarit, Mexico. Notice the high planting density. (Photo, M. Sørensen).

Fig. 5f. *Pachyrhizus erosus.* Flood-irrigated field, commercial field (monocropped) at harvest, near Celaya, Mexico. (Photo, M. Sørensen).

Fig. 5g. *Pachyrhizus erosus.* Commercial harvest, NE of Bangkok, Thailand. Notice the small tuber size preferred. (Photo, M. Sørensen).

Fig. 5h. *Pachyrhizus erosus.* Tubers from field grown for seed production (not marketable size), NE of Bangkok, Thailand. (Photo, M. Sørensen).

tually at the same latitude, the major part of the cultivation in Nayarit takes place at sea level, and at 1700 m a.s.1. in Guanajuato. In both areas, the majority of the fields are flood-irrigated. Some smaller areas of dryland production are to be found at around 1000m a.s.1. in Nayarit. The main morphological differences are the colour and thickness of the skin/peel of the tuberous root, the Nayarit cultivars having thicker, dark brown skin and a rather milky sap, whereas the Guanajuato cultivars are thin skinned with a light brown to almost whitish colour and watery translucent sap. Physiologically, the two cultivar groups differ in their growth cycles (as a response to environmental factors), i.e. the Guanajuato cultivars need to be reproductively pruned two to three times during the growth period, in order to maximize tuberous root size. In the production of yam beans in Nayarit, on the other hand, reproductive pruning is never carried out at sea level. This is because flowering is not induced during the cultivation period there, i.e. planted at short days and harvested during increasing daylength.

Experiments involving accessions belonging to both cultivar groups, carried out in Tonga and Costa Rica, revealed that when planted at the end of the short-day period, the Nayarit cultivar group exhibits a considerable delay in flowering and seed production compared with the Guanajuato cultivar group. Also, recent experiments at CATIE, Costa Rica have indicated the likely importance of the origin of the accession/cultivar examined when estimating the photothermal sensitivity of the genotype, i.e. the greater the distance between the origin of the material and the equator, and the lower the altitude, the more pronounced is the photothermal sensitivity (Mora *et al.* 1996a). Three field experiments conducted over two consecutive seasons in Tonga did not confirm the correlation between origin and response to reproductive pruning. When examining genotypic and environmental responses to reproductive pruning in 32 accessions of *P. erosus,* it was revealed that reproductive pruning increased tuber yield uniformly across accessions. Furthermore, although the accessions differed in tuber shape, soluble sugar and dry matter tuber content, reproductive pruning did not have any influence on these quality traits (Grum *et al.* 1996).

Various authors give different figures for the yield increase obtained by reproductive pruning. Martinez (1936) states that increases of up to seven times the yield on non-reproductively pruned plants have been obtained in Mexico. Castellanos *et al.* (1996) report yield increases from 140 to 340% when testing the three highest yielding Mexican cultivars, whereas Grum *et al.* (1996) recorded yield increases of from 7 to 39% when testing 32 accessions in Tonga. This effect is most certainly environmental.

Owing to the difference in altitude of the two Mexican cultivation areas, their planting and harvesting periods are virtually opposite. The main harvesting period in Guanajuato is from mid-October to mid-November, i.e. when planting takes place at sea level in Nayarit. Usually, the harvest begins in late February/March in Nayarit, the time when planting takes place in Guanajuato. Planting may be delayed until May in Guanajuato and still result in good yields. In both areas, the crop is usually flood-irrigated, but small fields with dryland production have been observed in Nayarit at around 1000 m a.s.l., as mentioned above; where planting may take place from March to July with harvest following in September to December.

There is little difference in yield between the two areas when comparing large-scale production, i.e. 60-80 t/ha, and dryland production, which usually yields approximately 35-60 t/ha (see also Section 10.7). The traditional intercropping involving maize and bean will produce yields of approximately 0.5 t/ha of bean harvested at 60 days after sowing, 1.0 t/ha of maize harvested at 110-120 days and 35-45 t/ha of yam bean harvested at 140-150 days after planting. This cultivation method will produce sufficient beans and maize for tortillas to feed a family of 6-8 persons for a year, and the sale of the yam beans will constitute a major source of income.

One important aspect to be kept in mind when studying the different cultivation practices in Mexico and Central America is that the yam bean crop is never fertilized, and recent studies at the Estación Experimental de Bajío, Celaya, Mexico, carried out by J.Z. Castellanos R. and colleagues (Castellanos *et al.* 1996) have demonstrated *P. erosus* to be one of the most efficient crops in terms of biological nitrogen fixation, fixing 162-215 kg/ha. This may well be the reason why yam bean is an integral part of most traditional cropping systems in Mexico, especially in the 'milpa' agricultural systems found on the poor soils of the Yucatan peninsula (Teran and Rasmussen 1994).

The role of yam bean in crop rotation systems appears to be an important one, as the crop is grown in the same field for two consecutive seasons, producing a higher yield in the second than in the first. In the third season maize, common bean or onion *(Allium cepa* L. var. *cepa)* are grown, as, yam bean does not perform well, owing to the build-up of insect and nematode pests. The crop is next planted in the field again after a break of 3-4 years (A. Heredia Z. and E. Heredia G., pers. comm.). The average plant population used in the irrigated crops in Nayarit and Guanajuato is 110 000 plants/ha (Heredia Z. and Heredia G. 1994; Castellanos *et al.* 1996).

Today the Mexican yam bean *(P. erosus)* is known to be cultivated in large regions outside its original distribution area, e.g. in Southeast Asia, India and the Pacific (Sørensen 1990). *P. erosus* tubers are found on sale in vegetable markets in the Philippines, Indonesia, Malaysia, Vietnam, Laos, Thailand, Cambodia, Burma and in Taiwan and China. In China, in the provinces of Sichuan and Chengdu, *P. erosus* or soya bean *(Glycine max* (L.) Merr.) are usually planted on the ridges between rice paddy fields. This practice is unknown in Thailand, where these ridges are usually kept cleared as a precaution against rats. Several authors reporting from India give details on cultivation practices, e.g. in Orissa, according to Deshaprabhu (1966), the seeds are sown in June to July. Both the vegetative part of the plant and the reproductive shoots are pruned once or twice, with the first pruning taking place after about 2 months. A few flowers are left for seed production. In order to obtain optimal tuber quality, the crop is harvested before the seeds ripen, hence in December to March. Srivastava *et al.* (1973) give the following recommendation for the cultivation of *P. erosus,* locally known as 'sankalu', in Uttar Pradesh. The crop should be sown at the beginning of the rainy season, i.e. September to October. If grown for starch production, it should be left unpruned, but if the crop is for fresh consumption, the plants should be pruned when 1.5-2 months old, and then again after a further month. The crop will be ready to harvest in February to March, and the recommended seeding rate is 62-74 kg/ha.

Bhag Ma1 and Kawalkar (1982) give the following recommendation for cultivation in Maharastra, India: the plant population when grown on ridges should be 133 000 plants/ha, and the crop is best sown in June-July, with harvest following in December to January. The immature pods/legumes to be used as a vegetable can be picked continuously once they start to form. If the crop is to be used for fodder, it should be harvested when 50% of the plants are flowering, to ensure maximum yield and optimal nutrition.

The plant population used in Malaysia is approximately 95 500/ha (with three seeds sown at each planting station, 20-25 kg seed/ha). The crop is trellised and is sown at the beginning of the rainy season; the average yields are 7-10 t/ha, but may be as high as 95 t/ha (Sahadevan 1987) (see also Section 10.7).

P. ahipa

In Bolivia, Ørting *et al.* (1996) report that most Andean yam beans are grown as a monocrop (Fig. 6a), but that occasionally the crop may be found intercropped with maize. *P. ahipa* has been tested in field trials in Tonga, Mexico (Figs. 6b,c) and Portugal. These are the first reporting yield size under different climatic conditions (Table 3). In Tonga, the species has been tested over three growth seasons. The yield averaged between 3 and 22 t/ha depending on whether the flowers were removed or not, with plant populations ranging from 38 095 to 111 111 plants/ha. The first trials involving this species conducted in Mexico were flood-irrigated, with removal of fertile shoots and a plant population of 38 095. The yield was between 16 and 20 t/ha. Plant density was increased to 110 000 plants/ha in subsequent trials, resulting in a marked yield increase (see Section 10.7). The experiments in Tonga have shown *P. ahipa* to have one of the highest dry matter contents recorded among the cultivated species, >20%. This amount compares favourably with such traditional African tuber crops as cassava/manioc *(Manihot esculenta* Crantz), 32-36% DM and yams *(Dioscorea* L. spp.), 19-34% DM (Göhl 1981). The opportunity therefore exists for breeding new high-yielding yam bean cultivars more similar to those better-known tuber crops with a higher dry matter content.

P. tuberosus

The following general descriptions of the cultivation practices used in the three cultivar groups (Figs. 7a-e) are based on an agronomic study conducted in Venezuela (Munos Otero 1945; Sorensen et *al.* 1996).

P. tuberosus, belonging to the ashipa and chuin cultivar groups is generally grown in shifting cultivation by the Indians of the Amazon region (Brücher 1977; Duke 1981; Sørensen *et. al.* 1996).

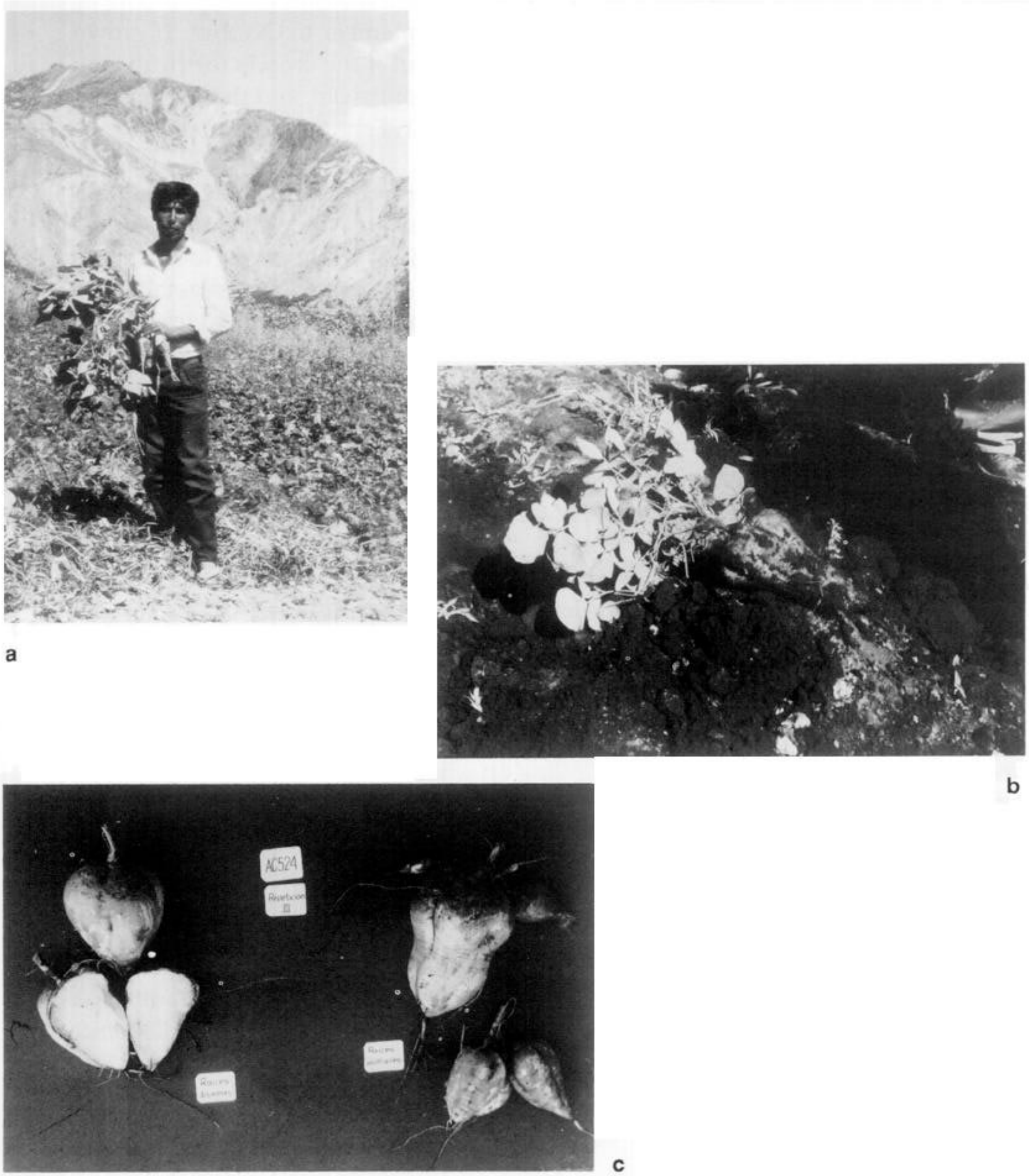


Fig. 6a. *Pachyrhizus ahipa.* Field in the Province of Loaiza, Bolivia. (Photo, B. P. Ørting).

Fig. 6b. *Pachyrhizus ahipa.* Landrace originally from the Province of Tarija, Bolivia, cultivated at INIFAP-CIR CENTRO, Campo Experimental Bajío, Celaya, Mexico. (Photo, M. Grum).

Fig. 6c. *Pachyrizus ahipa.* Tubers from landrace of unknown origin (probably Bolivian), cultivated at INI-FAP-CIR CENTRO, Campo Experimental Bajio, Celaya, Mexico. Notice purple colouring below epidermis in sliced tuber to the left. (Photo, E. Heredia G.).

Table 3. Results from *P. ahipa* field trials in Tonga, Mexico and Portugal.

Site	Access. No.	Plant density (plants/ha)	Pruned tuber				Unpruned tuber				
			Fresh weight (t/ ha)	Dry matter (t /ha (%))	Crude protein (kg/ha, (% of dry matter))	Accum. N (kg/ha)	Fresh weight (t/ ha)	Dry matter (t/ha (%))	Crude protein (kg/ha, % of dry matter).	Accum N (kg/ha)	Pods (t/ha)
Tonga[1]	AC102	38 095	11.8	1.7							
Tonga[2]	AC524	38 095	5.3-6.1	1.1	71 .0 (5.1%)						
Mexico	AC102	110 000	38.2	8.2		6.6	3.6	0.5		93.8	
Mexico	AC521	110 000	41 .0	7.8		3.2	2.5	0.3		80.5	
Portugal[a]	AC102	166 667	46.1	11.4 (24.7%)	991.8 (7%)		16.0	4.1 (25.9%)	496.1 (12.1%)		
Portugal[a]	AC521	166 667	39.2	13.8 (25.4%)	1324.8 (9.6%)		16.6	3.6 (21.5%)	442.8 (12.3%)		
Portugal[a]	AC524	166 667	54.3	14.6 (26.8%)	1620.6 (11.1%)		15.8	4.5 (28.3%)	598.5 (13.3%)		
Portugal[b]	AC102	166 667	8.2				7.5				
Portugal[b]	AC521	166 667	15.1				8.7				
Portugal[b]	AC524	166 667	10.1				8.9				
Portugal[c]	AC102	166 667	28.1				15.5				10.2
Portugal[c]	AC521	166 667	17.5				14.2				12.6
Portugal[c]	AC524	166 667	24.6				11.2				13.7

Tonga[1]- 1990 season; Tonga[2]- 1989 and 1990 seasons; Portugal[a]- 1992 season; Portugal[b]- 1993 season; Portugal[c]- 1994 season.
The growth period in in Tonga was 137 days for the 1989 season and 173 days for the 1990 season; in Mexico, 1994 season, the reproductively pruned plants were harvested 180-210 days after sowing (DAS) and the non-pruned plants after 220-246 DAS; in Portugal the 1992 season was 263 days, the 1993 season 245 days, and the 1994 season was also 245 days.
(Data from Mexico: Castellanos *et al.,* unpublished; data from Tonga: Grum *et al.* 1994; data from Portugal: Vieira da Silva 1995)

a

b

c

d

e

Fig. 7a. *Pachyrhizus tuberosus.* Local Ashipa landrace from the Province of Sur Yungas, Department of La Paz, Bolivia, 1 800 m a.s.l. (Photo, B. P. Ørting).

Fig. 7b. *Pachyrhizus tuberosus.* Local Ashipa landrace from the Province of Napo, Ecuador, 350 m a.s.l. (Photo, M. Sørensen).

Fig. 7c. *Pachyrhizus tuberosus.* Chuin landrace originally from the lquitos area, Peru. Cultivated for seed production at CATIE, Costa Rica. (Photo, M. Sørensen).

Fig. 7d. *Pachyrhizus tuberosus.* Chuin amarillo tubers from the lquitos area, Peru. (Photo, C. Thirup).

Fig. 7e. *Pachyrhizus tuberosus.* Jíquima tubers on sale at local market in Monte Cristi, Province of Manabi, Ecuador. (Photo, J. Estrella E.).

The ashipa cultivar groups are grown in areas with a permanently humid climate and mostly on land that is never inundated, i.e. largely infertile, acid and aluminium-loaded uplands (Salick 1989; Veléz and Veléz 1993a, 1993b; Sorensen *et al.* 1996). On such soil, it takes 8-12 months for tubers to develop; on more fertile land, e.g. on uneven flooded high levees along rivers, crops grow faster and produce larger tubers. Reproductive pruning is not practised in this cultivar group.

Ashipas appear to be always intercropped in slash-and-burn fields, and are typically mixed with crops such as plantain *(Musa* x *paradisiaca* L.), maniac and pineapple *(Ananas comosus* (L.) Merrill.), etc. Fields are rotated and left for fallowing after a few years' cultivation. It is common practice to sow a few ashipa seeds together at about 5 cm depth on hills 3 m apart. The plants are often trellised on 2-m poles or alternatively allowed to climb the intercropped manioc plants.

At harvest, which may occur at any time once harvestable tuberous root size is attained, some producers will harvest one or two of the laterally produced roots and leave the one closest to the vegetative top. This method allows subsequent production of new tuberous roots after about 8 months, and the production period may thus be changed from a strictly annual to an almost perennial one. Naturally, ashipas are seed-propagated.

The chuin cultivar group is also cultivated in a permanent humid climate, exclusively on floodplains, it seems, and predominantly at the higher, irregularly or only briefly inundated levees. These are known as high 'restingas' in Peru, where ashipa is sown in May-June and harvested in February-March. The crop is also grown on lower levees which are flooded for up to 6 months each year, and on river banks (locally known as 'playas') that have not yet been stabilized by vegetation. These are flooded for up to 8 months each year. Production of the crop is limited by the short growth period available here.

Chuins are intercropped with other floodplain crops. At the higher levees, these are typically plantain and maniac and at the lower levees, maize, beans and vegetables. As with ashipas, a number of seeds are sown in holes located about 3 m apart, and the plants are often supported by poles. They need a fertile, not-too-humid soil, and can be harvested after just 4 months. A longer growth period improves the size and quality of the tubers, however. When the tuberous roots are ready for harvesting, the chuins also produce seeds, which are gathered and kept for planting in the season following inundation. The vegetative top of the tuberous root may also be replanted. After an additional 4 months, this produces many seeds, but no tuberous root.

The jíquima cultivar group is grown in the seasonally dry coastal province of Manabí, Ecuador. In contrast to the Mexican jícama *(P. erosus),* which has become a very popular food in Central America, Mexico, Southeast Asia, and even in the United States, the jiquima must regrettably be considered a very minor crop in Ecuador (Sørensen *et al.* 1996).

According to local sources, monocropping was and still is a common practice, but intercropping with chilli *(Capsicum* spp.), sesame *(Sesamum indicum* L.), groundnut *(Arachis hypogaea* L.) and tomato *(Lycopersicon esculentum* Miller) is also practised. The jíquima is cultivated in small back gardens each containing between 60 and 100 plants in plots of 250-400 m2, i.e. a plant density of 1500-2400 plants/ha when intercropped. Approximately 70-90% of the plants from these plots are harvested when the tubers have reached a marketable size. The tubers are then sold locally, especially in the villages of Portoviejo, Montecristi and Jípijapa. The remaining 10-30% of the crop is left for seed production. A small number of the plants are used for home consumption and occasionally as presents for neighbours. The price per unit weight of jíquima is approximately three times that of manioc (Sørensen *et al.* 1996).

The difficulty in assessing the agronomic importance of *P. tuberosus* as a crop becomes apparent when considering traditional cultivation practices. In most areas of Amazonia where the species is cultivated, it forms an integral part of the shifting cultivation system. Usually, there is little or no trade in the tuberous roots, as they are consumed within the local community Other types of cultivation practices are to be found at lower altitudes in the East Andean valley in Bolivia and in the province of Manabí, Ecuador. In both these areas, monocropping is the rule, and the intensified landuse does not allow the practice of shifting cultivation.

2.4 Areas of major diversity

There is little doubt that the present distribution of all three cultivated species within the Neotropics (see also Sections 3.2 and 6.2) represents a mere fraction of the pre-Colombian distribution (Sørensen *et al.* 1996). It is likely that the many isolated landraces, cultivar groups and scattered wild populations were originally linked (with the possible exception of areas of introduction where there are no records of wild populations).

P. erosus

Only a few areas remain where the cultivars/landraces and the wild populations of *P. erosus* are to be found in close contact: the Mexican states of Veracruz, Tabasco, Oaxaca and Chiapas, and throughout Guatemala to northern Honduras. In these areas, local landraces/primitive cultivars may in theory become hybridized with the wild populations. However, there are no definite records of this having occurred, most probably owing to the limited outcrossing of l-3% and differences in flowering period due to local cultivation practices. The largest morphological variation among landraces/cultivars is also found in the Mexican states of Veracruz (Fig. 8), Oaxaca, Tabasco and Chiapas, and in Guatemala. Both entire and deeply lobed leaflets are recorded, of tuber shape and quality with smooth and lobed or cleft surfaces, watery-translucent or milky-cloudy juice, a bland or sweet flavour and both thin and thick skin.

Seed and flower colour varies from olive-brown to darkish maroon and from light-dark violet to white, respectively. Large differences in earliness exist: the landraces/cultivars with red or maroon-coloured seeds and white flowers often found

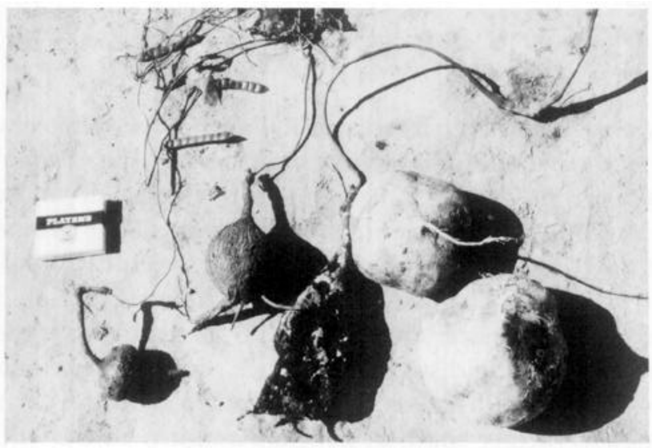


Fig. 8. *Pachyrhizus erosus.* Tubers from wild populations (left) near Veracruz, State of Veracruz, Mexico, and tubers from cultivars from near Celayo, State of Guanajuato Mexico (Photo, M. Sørensen).

in the Yucatan peninsula and southern Guatemala tend to be later than other genotypes (E. Heredia G., pers. comm.).

P. ahipa

Germplasm of Bolivian origin, representing 15 of the 20 available accessions at RVAU, has been found to have the greatest diversity recorded. Even within the 13 landraces/primitive cultivars from the two departments of La Paz and Cochabamba, a remarkable degree of genetic/morphological variation has been observed in earliness, growth rate of both vegetative and reproductive shoots, and in internodal lengths (Ørting) unpublished data). The single Argentinian landrace/cultivar seen from the northern province of Salta has several distinguishing traits: very short, erect bushy growth, reduced seed set and good tuber growth. The landrace/cultivar of known origin that most resembles the Salta cultivar was collected in the southern Bolivian department of Tarija. Hence, a thorough survey of the southern Bolivian/northern Argentinian germplasm may yet reveal additional diversity

P. tuberosus

By far the greatest diversity amongst landraces/cultivars has been recorded along the Río Ucayali, near Iquitos in Peru. The number of qualitatively (morphologically, agronomically and nutritionally) different cultivars within this limited area has yet to be matched elsewhere. It is quite likely, however, that the concentration of the diversity in this restricted area may have been exaggerated by the intensive surveys carried out by L.P. Kvist and colleagues, which have been partly recorded by Jensen and Thirup (Sørensen *et al.* 1996) and that other areas/regions may have as wide a diversity Several researchers, Drs Flores Paitan, C. Arbizu and L.P. Kvist (pers. comm.) have identified the upper reaches of the rivers Marañón, Mayo and Ucayali as the likely centres of origin of the different Amazonian cultivar groups and possibly areas where closely related wild populations may be located.

2.5 History

P. erosus

The pre-Columbian and early post-Columbian references to the cultivation history of the Mexican and Central American species *P. erosus* indicate that the 'jicama' (Aztec), 'mehen-chikam' (Maya) or 'guyati' (Zapotec) was cultivated by all major civilizations including the Toltec, Olmec, Aztec and Mayan (Hernandez 1790; Urbina 1906; Standley 1930; Martinez 1979). The uniformity found among the cultivars collected by the present author in geographically/climatically/edafically isolated localities outside the presumed original distribution area of the species, such as the Yucatan peninsula and central Mexico would suggest that these cultivars are remnants of ancient ones introduced from southern Mexico, the central/southern parts of Guatemala and/or from regions further south in Central America, where wild populations exist (Standley 1930).

The origin of the present Mexican, El Salvadorian and Guatemalan landraces has yet to be studied, but preliminary molecular analyses indicate that the Central American and Mexican landraces do not have the same origin (R.J. Abbott, pers. comm.).

The northernmost locality in the Neotropics where *P. erosus* is still to be found grown in shifting cultivation is the Guatemalan state of Petén. According to Bentham (1859), Pinto (1873) and Warming (1892), *P. erosus* was introduced and cultivated in Brazil. The history of the introduction of the species to the countries of Southeast Asia and southern China is somewhat unclear, but there is little doubt that it must have been first introduced from the Philippines to the coastal regions of China and Vietnam. From Vietnam, the crop spread into the neighbouring countries (which were formerly part of French Indochina). In many areas of production in Thailand, it is still considered a Vietnamese crop (N. Ratanadilok, pers. comm.).

P. ahipa

'Ahipa' or 'ajipa' is probably the species of the most obvious interest when breeding for improvement of the existing *P. erosus* cultivars: firstly, from a systematic viewpoint, because of the absence of known wild ancestral material (although Brücher (1989) suggests that the type known today was probably selected from wild material growing in Ceja de Montaña in Peru); secondly, from a morphological point of view, due to the species's erect, short growth habit; thirdly, from an agronomic aspect, because of *P. ahipa's* relative daylength neutrality, short growth season (5 months) and its considerable adaptability to climatic variation.

The distribution of *P. ahipa* is limited to the Andean valleys in Bolivia and possibly Peru, where the crop is virtually extinct today. The recorded history of *P. ahipa* in cultivation indicates that in contrast to the other two cultivated species, it has never been associated with shifting cultivation. The earliest indications of its use as a crop are remains of tuberous roots found among the plant residues in the 'mummy bundles' of the Paracas Necropolis on the southern coast of Peru, belonging to the

Nasca culture (Yacovleff 1933; Towle 1952; Ugent *et al.* 1986). Ceramics and embroideries from the Mochica (Brücher 1989) as well as the Nasca provide further evidence for the crop's cultivation by these cultures. At low altitudes, however, the crops grown may have belonged to the jíquima cultivar group, which has a very similar growth habit (Yacovleff 1933; Yacovleff and Muelle 1934; Herrera 1942a, 1942b; Mangelsdorf 1942; O'Neale and Whitaker 1947).

Considerable evidence therefore exists that *P. ahipa* was known and cultivated by at least one of the Indian cultures of pre-Columbian South America. Information contained in the manuscripts of Oviedo y Valdez (1535) also confirms pre-Columbian cultivation of the crop. Although some authors (Yacovleff 1933; Yacovleff and Muelle 1934; Hawkes 1986) have identified the crop as *P. tuberosus* from the archeological record, the typical growth habit and morphology of the inflorescences and the legumes allow a positive identification as *P. ahipa* (Ugent *et al.* 1986). Sauer (1950) mentions the crop as one of the common elements in the cropping systems of the terraced Andean fields of Peru. The cause of the prevalent uncertainty over the correct identification of these pre-Columbian materials lies in the extremely limited cultivation of *P. ahipa* in Peru and present knowledge of the crop. In turn, it appears probable that this situation is due in large part to selection on the basis of plants being monotuberous, as is also the case with *P. erosus.*

P. tuberosus

According to León (1987), the plant was already known in Peru for its edible tuberous root in the pre-agricultural period (12 200-8 500 BC). It is probable that the first domestication of this species took place somewhere along the eastern slopes of the Peruvian Andes, at the upper reaches of the Amazonian rivers (Flores Paitan, pers. comm.). However, owing to the lack of historical references covering the remainder of the distribution area, alternative centres of origin may yet become known (see Section 3.2 for further details).

3 Origin of the cultivated species and important centres of diversity

3.1 Other (wild) species in the genus

3.1.1 The species *Pachyrhizus ferrugineus* (Piper) Sørensen

Pachyrhizus ferrugineus (Piper) Sørensen (1988:181).
Basionym: *Calopogonium ferrugineum* Piper (1921:42).
Type: Tonduz, A. 12889 (US, holo(?) iso, BM).
Heterotypic synonyms: *Pachyrhizus vernalis* Clausen var. *typicus* (1945:27)
Type: Steyermark, J.A. 38553, Guatemala, depto. Izabal, Montana del Mico (F, holo).
Pachyrhizus angulatus (L.C.M. Richard *ex* DC.) var. *integrifuliulus* Donnell-Smith (1908:110).
Type: Tuerckheim, H. von 111671, Guatemala, depto. Alta Verapaz, Coban (US, holo).
Pachyrhizus vernalis Clausen var. *integrifoliolus* (Donnell-Smith) Clausen (1945:27).
Pachyrhizus vernalis Clausen var. *linearifoliolus* Clausen (1945:27).
Type: Bartlett, H.H. 11664, British Honduras (Belize), El Cayo Distr., Mountain Pine Ridge (MICH, neg. no. 3812, holo; iso, MICH, NY, US).

This wild species (Figs. 9a, b) is the only one in the genus which is evergreen (with the exception of wild accessions of *P. tuberosus)* and where the parts of the plant above ground are perennial (all species have perennial tuberous roots). Both the tuberous root(s) and stem(s) are woodier and more lignified than in the other species. The root is less tuberous, although plants grown in greenhouses have produced fair-sized tubers (± 0.5 kg). The outline of the leaflets (Fig. 9b) is as variable as in *P. erosus* (Fig. 2b). The leaflets are somewhat leathery (subcoriaceous), and they may occasionally be relatively\pubescent, with reddish-brown strigose hairs. Pubescence is often reduced when the leaflets are fully developed. The upper surface is dark green and the lower light green. The morphology of the inflorescence differs from the other species in the large number of flowers per lateral raceme (8-21) and the length of the main raceme axis (up to 860 mm). The wing and keel petals are prominently ciliolate. The length-width ratio of legumes (length 80-130 mm, width 12-23 mm) is markedly different. The prominent reddish-brown strigose hairs and the lack of constriction between the seeds are also distinguishing characters. The seeds are rounded (13 x 13 mm), laterally compressed, and thus are quite distinct from the seed shapes observed in the remaining species, with the exception of the wild populations of *P. tuberosus.*

The species is ecologically associated with evergreen to deciduous rain forest with soils low in available phosphorus (2-4 ppm in soil from the Cayo District, Belize), a remarkable characteristic in a tuberous plant (Sørensen 1990). The habitat of *P. ferrugineus* is often in the vicinity of rivers, along river banks, and its pods appear to possess considerable resistance to humidity, a useful character when considering *P. tuberosus* under Amazonian conditions (M. Grum, pers. comm.).

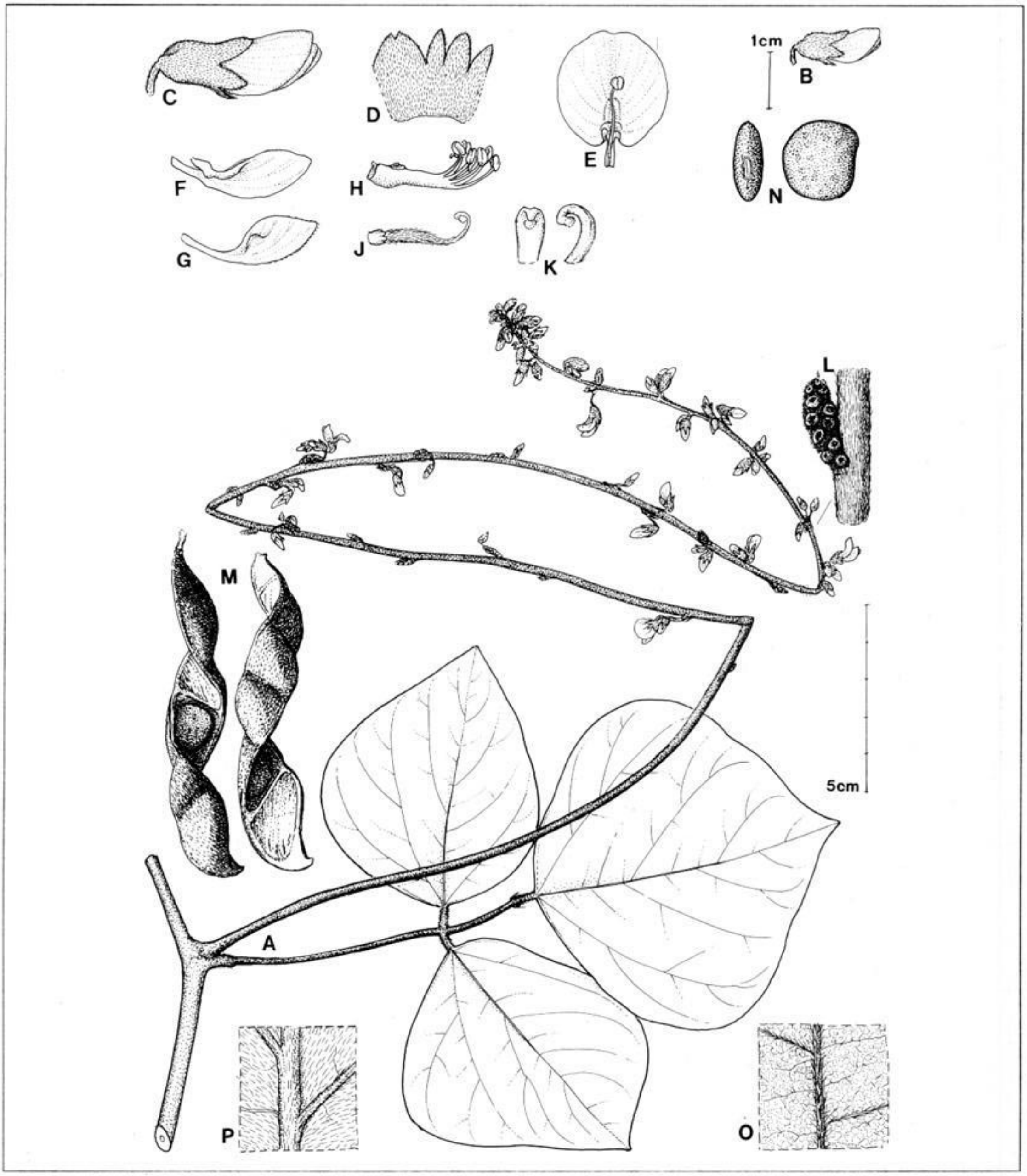


Fig. 9a. *Pachyrhizus ferrugineus.* A. Habit, 2/3 of natural size. B. Flower, natural size*. C. Flower, side view. D. Calyx opened. E. Standard with free median stamen. F. Wing. G. Keel. H. Stamens. J. Pistil with basal disc. K. Side and front view of style and subglobose stigma. L. Lateral axis of inflorescence. M. Mature legume. N. Side and top view of seed. O. Section of adaxial leaf surface. (All parts except legume from FW044, Depto. Izabal, Guatemala; legume from Breedlove 7441, F). This figure, originally appearing in Sørensen (1988), is reproduced by kind permission of Nordic Journal of Botany.
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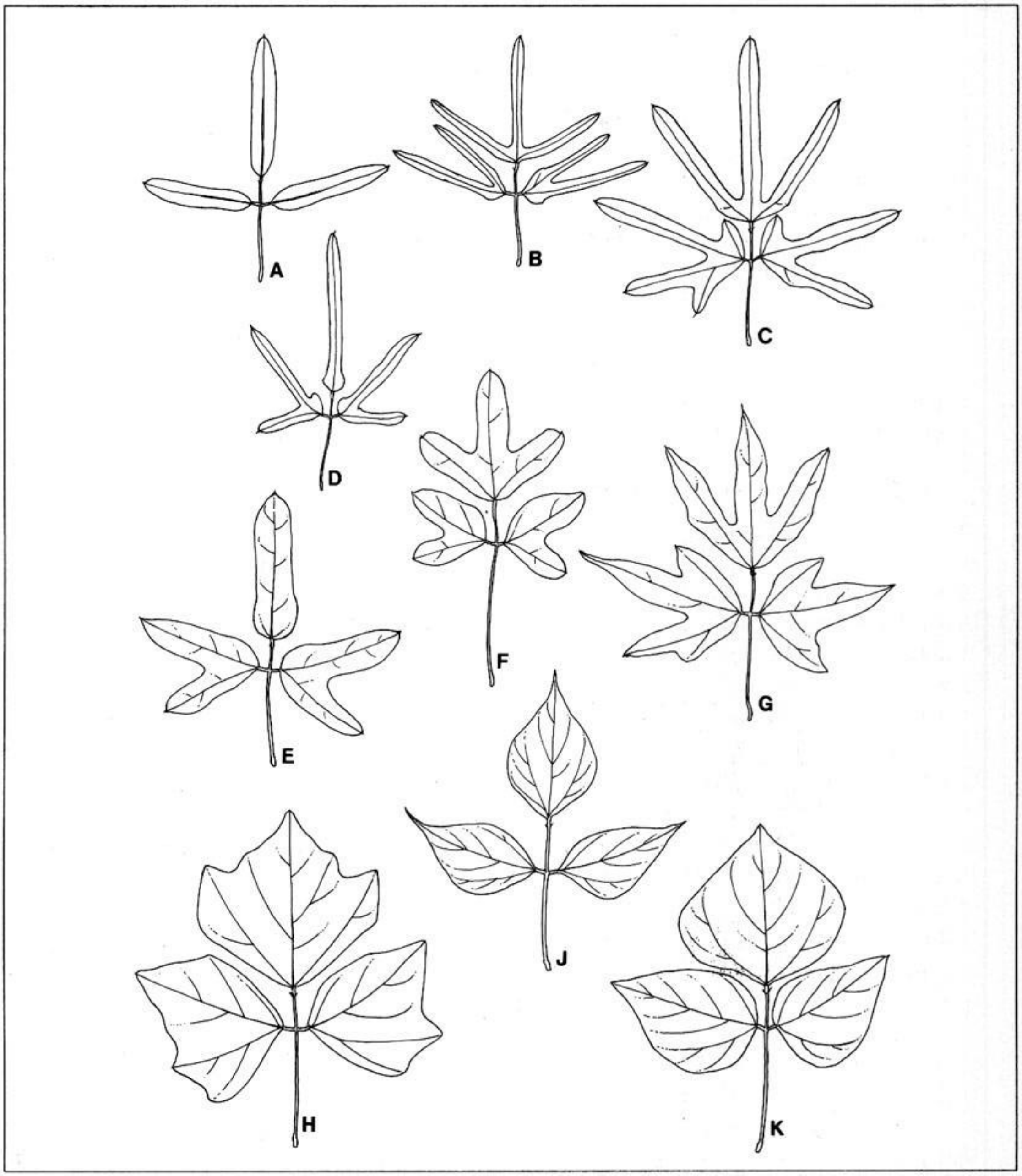

Fig. 9b. *Pachyrhizus ferrugineus.* The variation in the outline of the leaflets. A. From Belize Distr., Belize, Gentle 9469, S. B. Cayo Distr., Belize; Bartlett 11664, MICH. C. Maskall Pine Ridge, Belize, Gentle 1047, S. D. Cayo Distr., Belize, Bartlett 11664, US. E. Stann Creek Distr., Belize, Gentle 7854, S. F. Churchyard Pine Ridge, Belize, Gentle 1815, MICH. G. Depto. Zelaya, Nicaragua, Marshall and Neill 6479, F. H. Cayo Distr., Belize, Gentle 2279, K. Jr Depto. Alta Verapaz, Guatemala, von Tuerckheim II 1671, US. K. Depto. El Paraiso, Honduras, Molina 23291, F. This figure, originally appearing in Sørensen (1988), is reproduced by kind permission of Nordic Journal of Botany.

The distribution area is mainly along the Atlantic coast of Central America from the Mexican state of Vera Cruz to Panama, where it shifts to the Colombian department of Chocó on the Pacific coast. No records of any uses exist, but local farmers in Guatemala informed the author that the seeds are occasionally used as a vermifuge, probably because of their rotenone content (see Section 5). This species may constitute an attractive source of rotenone (an insecticide) and may eventually be involved in the breeding of new varieties in order to introduce the evergreen habit. Of even greater likely interest for breeding purposes is the adaptability of *P. ferrugineus* to soil with a low phosphorus content. It should be noted that this species has yet to be hybridized with any of the others, however.

3.1.2 The species *Pachyrhizus panamensis* Clausen

Pachyrhizus panamensis Clausen (1945:21).
Type: Killip, E.P. 12080, Panama Canal Zone, Ancon Hill (US no. 11677215, holo; iso, C, GH, NY).

On the basis of existing records, the second wild species exhibits a peculiar disjunct distribution. The best-documented area, with the largest number of records, covers the seasonally dry regions of central and Pacific Panama extending into the coastal deciduous forest in the Santa Marta department of Colombia. The remaining records are from the provinces of Guayas and El Oro in the western part of central Ecuador (Sørensen 1988) and (one) from the southernmost part of the Venezuelan state of Bolivar, 125 km north of Puerto Ayacucho, at the foot of the Guyana highlands (Steyermark, J.A., Holst, B. et Plamara, B. 131729 VEN). It is therefore likely that the species may have originally been distributed all the way from its northernmost present distribution area in Panama to the relatively dry coastal plains of the Ecuadorian province of Guayas.

Morphologically, the species is recognized by the white to light brown pilose hairs covering all parts of the plant including the wing and keel petals, and the low number of flowers per lateral raceme (4-7). The seeds are the smallest in the genus, rounded to slightly reniform in shape and measuring 6 x 7 mm (Fig. 10).

In Benin and Costa Rica, *P. panamensis* has produced fair-sized tubers in the greenhouse as well as in field trials (± 200 g). In 1991, field trials were initiated in Senegal to test the drought tolerance of this species. Together with the wild material of *P. erosus* from the province of Guanacaste in Costa Rica, *P. panamensis* is probably the best adapted to seasonal drought (D.J.A. Annerose, pers. comm.).

The species has recently been successfully hybridized (reciprocally) with *P. tuberosus, P. ahipa, P. erosus* and with an interspecific *P. ahipa x P. tuberosus* hybrid in both Tonga and Benin (DE Adjahassou 1993, pers. comm.; M. Grum,. pers. comm.; P.E. Nielsen, pers. comm.). Mr P.E. Nielsen reports from Tonga that several of the interspecific *P. panamensis* x *erosus* hybrids belonging to the F_2 generation have retained the prominent pubescence of the vegetative parts, and that provided the yield potential of *P. erosus* is maintained in the hybrid, this material will be attractive when looking for drought-tolerant genotypes.

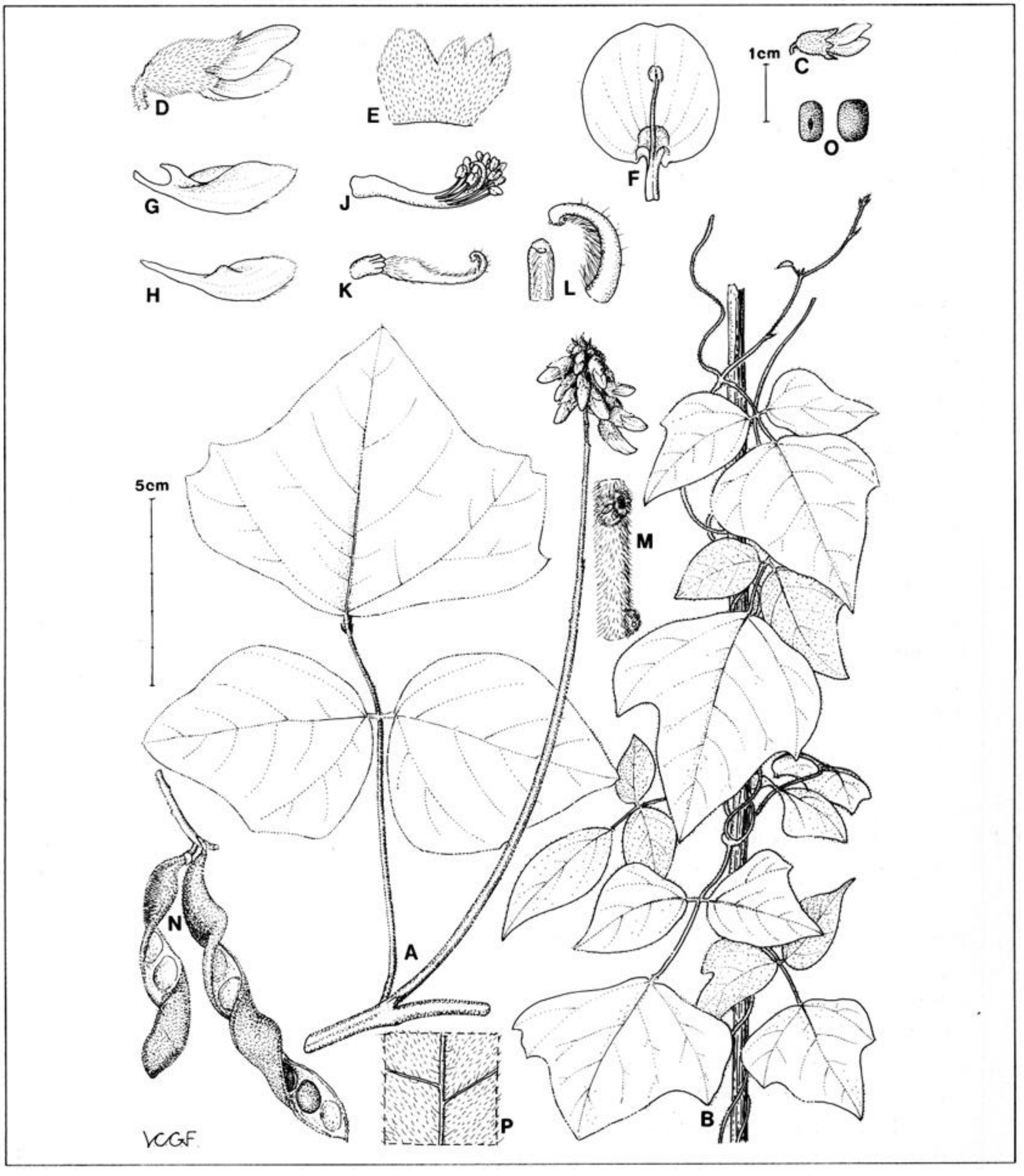

Fig. 10. *Pachyrhizus panamensis.* A-B. Habit, 2/3 of natural size. C. Flower, natural size*. D. Flower, side view. E. Calyx opened. F. Standard with free median stamen. G. Wing. H. Keel. J. Stamens. K. Pistil with basal disc. L. Side and front view of style and subglobose stigma. M. Lateral axis of inflorescence. N. Mature legume. O. Side and top view of seed. P. Section of adaxial leaf surface. (A, C-M and P from Allen 2027, US; B and 0 from PW055; N from Greenman 5053, MO). This figure, originally appearing in Sørensen (1988), is reproduced by kind permission of Nordic Journal of Botany.

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3.2 Geographic distribution (traditional landraces, local and modern cultivars

The distribution area of the cultivated species extends from 20º N in Mexico to 20º S in Bolivia/northern Argentina (see Fig. 1, and Sections 2 and 6.2).

P. erosus

Wild material has been recorded in the following areas: the Mexican states of Jalisco, Guanajuato, San Louis Potosí, Michoacán, Morelos, Puebla, Guerrero, Oaxaca, Vera Cruz and Chiapas; Central and Western Guatemala; El Salvador; Western Honduras, Western Nicaragua and Northwestern Costa Rica. The species is cultivated in the Mexican states of Nayarit, Guanajuato, Morelos, Jalisco, Michoacán, Puebla, San Luis Potosí, Veracruz, Tamaulipas and Oaxaca, as well as in Yucatan and Quintana Roo, where pre-Columbian landraces of *P. erosus* have been introduced. It is often found escaped from cultivation. In the states where a wild distribution is recorded, different cultivars are often found as an escape. The plant is widely cultivated in most southern states of Mexico. This situation also applies to El Salvador and northwestern Honduras, where cultivation of the crop is widely practised (M. Grum, pers. comm.).

In Guatemala, only limited cultivation is practised today the main cultivation areas being the southern states of Santa Rosa, Jutiapa and Chiquimula. Furthermore, in the state of Petén, *P. erosus* can be found in shifting cultivation in the occasional field. The plant is often found as a relic from earlier cultivation, as well as from numerous locations of wild material. This general situation probably applies to central and western Honduras and Nicaragua as well, where little or no cultivation is currently practised. A number of *P. erosus* collections are recorded from Belize, but the plant was probably introduced for cultivation from the northern parts of the Yucatan peninsula (Fig. 1).

In Mexico, a distinction was formerly made between *P. erosus sensu stricto* and *P. palmatilobus*, now considered conspecific with *P. erosus*, based on the outline of the leaflets and the sap/juice quality of the tubers, i.e. *P. palmatilobus*, locally known as 'jícama de leche', has deeply lobed leaflets, a milky sap and less agreeable taste, whereas the leaflets of *P. erosus* 'jícama de agua' are dentate and the sap is watery translucent (Martínez 1936, 1956).

Bertoni (1910b) described the cultivation practices of *P. angulatus (= P. erosus)* used in French Guyana, but unfortunately did not provide an exact locality This information supports the observations of Perrottet (1821) and Guillemin *et al.* (1830) who state that *P. erosus* was introduced to the French colonies in the Indian Ocean and in Cayenne (French Guyana) from the Philippines(!)

A description of present-day yam bean cultivation in Thailand and the local cultivars used is given in Ratanadilok and Thanisawanyangkura (1994). Although the crop is widely grown in all countries in Southeast Asia, this is the only comprehensive source on the current cultivation of yam bean in the region. *P. erosus* was introduced to India during the period between 1880 and 1890 (Anonymous 1889a;

Tiwari *et al.* 1977). According to Deshaprabhu (1966) and Bhag Mal and Kawalkar (1982), the main cultivation of the species takes place in parts of West Bengal, Assam, Bihar, Orissa and Andhra Pradesh. Yam bean production in Hawaii is increasing, and detailed descriptions of the cultivation practices and post-harvest handling are provided in Paull and Chen (1988), Paull *et al.* (1988) and Fukuda and Paull (1994).

P. ahipa

The species is found in sporadic cultivation in Bolivia, and in the provinces of Jujuy and Salta in Argentina in subtropical Andean valleys along the eastern side of the range. The Argentinian genotypes probably originate from seeds introduced from the southern part of Bolivia. Bolivian farm labourers working in Argentina recall importing seed material from Bolivia when visiting relatives, and the genotypes are of the erect bushy type found in the Bolivian province of Tarija (Parodi 1935; Burkart 1952; Sørensen 1990; Ørting *et al.* 1996; R. Neuman, pers. comm.). It may be cultivated in Peru in the area surrounding Tarapoto, and is distributed in fertile subtropical valleys between altitudes of 1500 and 3000 m a.s.l.

The only herbarium specimens known to the author are from the provinces of Sorata and Tarija in Bolivia and Jujuy, Argentina. No herbarium specimen of Peruvian origin is known to exist. Today the cultivation of *P. ahipa* in Peru is either extinct or restricted to a few valleys in the area around Tarapoto (C. Arbizu, pers. comm.). Locating and conserving any remaining Peruvian germplasm is therefore an urgent priority.

No unmistakeably wild plants are recorded, and a wild progenitor of *P. ahipa* has yet to be identified. The geographical origin of the species is still obscure. Brücher (1977,1989) states that the likely location must have been in the 'ceja de montañas' Andean region, although J. Rea (pers. comm.) recently claimed to have found wild *P. ahipa* near Sorata, Bolivia, i.e. the locality where the type specimen was collected by G. Mandon (no. 747,1856). Until material of this genotype becomes available for morphological and molecular analyses, the phylogeny of the species cannot be conclusively determined, however. According to D. Debouck (pers. comm.), other possible locations where a wild progenitor may be found are the Peruvian valleys of Apurimac, Ene and Mantaro.

P. tuberosus

The species is distributed from the southern lowlands of Colombia and Venezuela (the Andean mountain ranges of Sierra de Perijá and Cordillera de Merida), where it is known as 'nupe' (Munos Otero 1945) through the Amazonian parts of Ecuador as far west as the province of Manabí, and in much of Brazil. In colonial Brazil, *P. tuberosus* was well known in cultivation. The main production areas were the states of Río, Minas Gerais, São Paulo and Espíritu Santo. According to Peckolt (1922), it was commonly used as food for slaves (its production and usage was equivalent to that of yam). The present distribution towards the east is somewhat unclear, due to the progressive agricultural intensification taking place in the Brazilian states of

Mato Grosso and Minas Gerais. However, there is little doubt that the species was originally to be found in large areas of the lower reaches of the Amazon, the departments of La Paz and Beni in Bolivia and the northeastern lowlands of Paraguay along the Río Paraná (L. Ramella 1988, pers. comm.). Brücher (1989) states that *P. tuberosus* appears to have disappeared from the latter country long ago.

Herbarium specimens have been seen from Colombia, Venezuela, British Guyana, Brazil, Bolivia, Peru and Ecuador. Herbarium specimens representing wild material have only been seen from Ecuador and Peru, and several wild populations have been (re)discovered by R. Castillo, J. Estrella E. and C. Tapia and associates from the plant genetic resources unit at INIAP in western Ecuador (Sørensen *et al.* 1996). Samples of these populations are now in cultivation at the Jardín Tropical, Esmeraldas, and have been successfully multiplied and found to produce sizeable tuberous roots.

P. tuberosus is presently known to be cultivated by numerous migrating indigenous peoples in the Amazonian region. It is also found occasionally in the vicinity of remote villages situated within the premontane rain forest, or 'selva alta' in Peru (Noda *et al.* 1991; Sørensen 1990; Sørensen *et al.* 1996).

Probably the earliest description of *P. tuberosus* and its uses is from the island of São Vicente (at the port of Santos, Brazil) by Padre José de Anchieta in his Chartas ineditas (1556) cited by Arruda (1921), Peckolt (1922) and Menezes and Oliveira Nunes (1955). Padre José de Anchieta recorded that the indigenous Indian people cultivated *P. tuberosus* because of the starchy and nourishing tuberous roots, and that the seeds were poisonous. Montenegro (1740) reported the plant as being cultivated by the Guarani Indians in Bolivia in what are now known as the departments of La Paz and Beni. Later descriptions such as those of Burmann (1768) and Peckolt (1922) confirm that cultivation of the plant was originally quite common in large areas of the humid tropics in South America. At the beginning of the century, Bertoni (1910a) found the plant cultivated in fields along the Parana river in Paraguay. Munos Otero (1945) used a landrace collected near Caripe in the state of Monagas, Venezuela in his thorough study of the potential of this species.

The jíquima cultivar group is at present only cropped in a few pockets of the Manabíta valleys in the province of Manabí, Ecuador, where it was previously commonly grown in most parts of the province. The rapid progress of current genetic erosion is most definitely endangering the extant landraces within this cultivar group. The process may be due to a number of factors: (i) low rainfall - the precipitation rate is decreasing rapidly as a consequence of serious deforestation; (ii) seed availability - only seeds from individual on-farm seed production are available (originally specialized seed producers would have ensured seed availability), and (iii) high labour input - three to four bud and flower prunings in areas where labour is scarce and expensive.

P. tuberosus is the only other species which was introduced to areas outside the continent in pre-Columbian times, as it is highly probable that the Arawak/Arvak Indian communities of Venezuela, Guyana, Surinam and French Guyana cultivated the crop in pre-Columbian times and introduced it into the Caribbean together with the other tuberous crops of South American origin. Introductions have been recorded from the Caribbean islands of Trinidad (Grisebach 1860), Hispanola (Liogier 1985), Puerto Rico (Liogier and Matorell 1982; Urban 1905), Jamaica (MacFadyen 1887) and Cuba (Sauvalle 1869).

There are no substantiated records of any introductions in Central America or tropical areas outside the Neotropics until the recent ones carried out by the Yam Bean Project. According to notes from Kew (Anonymous 1889a), seeds of *P. tuberusus* from Trinidad were distributed to the botanic gardens of Calcutta, Ceylon, Brisbane, Melbourne, Sydney and Adelaide. However, it has not been possible to confirm this information, as no herbarium specimen of the species has been found outside the Neotropics. An obvious explanation could be the misidentification of the material distributed, if the seeds mentioned above (Anonymous 1889a) were in fact *P. erosus* and not *P. tuberosus.* As the taxonomic confusion between these two species has a long history, care should be taken not to accept the information from 1889 without proof *(vide* National Academy of Sciences 1979; Purseglove 1968; Sørensen 1990). Within the last five years, *P. tuberosus* has been introduced to Costa Rica, Benin, Thailand and Tonga in the South Pacific, in Benin with excellent results. Further introductions have been made to Zaïre, Ghana and Papua New Guinea.

4 Properties of the species

The developmental stages of the genus according to Grum (1990) and Sørensen *et al.* (1993) are presented in Table 4. The duration of the various stages varies according to species and genotype, and the cultivation practices, i.e. timing of the reproductive prunings, are adjusted accordingly.

Table 4. The developmental stages of *Pachyrhizus,* based on morphology and physiological changes according to Grum (1990) and Sørensen *et al.* (1993)

Reference	Stage	Description
V0	Germination	Appearance of the primary root
V1	Emergence	Primary leaves and epicotyl emerge
V2	Primary leaves totally opened	Primary leaves fully unfolded
V3	First trifoliate leaf opens	Second trifoliate leaf appears
V4	Third trifoliate leaf opens	Buds at lower nodes produce branches
R5	Preflowering	First flower bud or reproductive shoot appears
R6	Flowering	First flower opens
R7	Pod formation and filling	At the end of this stage the pods feel hard
R8	Post-pod growth	Pods filled and are hard
R9	Physiological maturity	Leaves senesce and defoliation starts

4.1 Biological nitrogen fixation

Like other members of the legume family, the genus has an efficient symbiosis with nitrogen-fixing *Rhizobium* and *Bradyrhizobium* bacteria. These bacteria provide the plants with a source of nitrogen and, as a result, there is no need for an additional supply of nitrogen fertilizer. In contrast with many of the grain legumes, a substantial amount of the fixed nitrogen is returned to the soil if the vegetative aboveground parts are left in the field. The crop therefore forms an integral part of a sustainable land-use system, from both an ecological and a socioeconomic standpoint. Recent studies (Kjaer 1992; Halafihi 1994; Halafihi *et al.* 1994) have been conducted under both greenhouse and field conditions to examine the efficiency of the biological nitrogen fixation.

Field collections of indigenous strains of *Rhizobium* and *Bradyvhizobium* were carried out in 1993 in Central and South America, and subsequent isolation of the collected material and evaluation under greenhouse conditions have been completed to select *Pachyrhizus* genotypes and bacteria strains with high potential for nitrogen fixation. The emphasis of this research is on the improvement of the host plant range, to provide simple technology that can be used by farmers in the developing countries.

Castellanos *et al.* (1996) conducted the first field test quantifying the actual amount of nitrogen fixed by two accessions of *P. ahipa* (58-80 kg N/ha) and three cultivars of *P. erosus* (162-215 kg N/ha). Approximately 50% of the N harvested, i.e. ±130 kg/ha, or close to 800 kg protein/ha (N x 6.25), was accumulated in the tuberous root in *P. erosus.* This is a value which equals or outyields the amount of protein harvested in grain legumes. The amount of N recorded in the residue (hay) of *P. erosus* was 120-150 kg/ha, twice the amount recorded in the *P. ahipa* residue and is higher than the quantity recorded in practically all grain legumes. (The plant population of both species in the trials were 110 000 plants/ha and the plants were reproductively pruned.)

4.2 Chemical composition of the used parts

Another common generic characteristic is the presence of an insecticidal compound called rotenone ($C_{23}H_{22}O_6$). This ingredient is to be found in the mature seeds but not in toxic amounts in the tuber itself or in any other part of the plant. Many scientists have participated in the quest for new efficient chemical compounds, which began in the last century. The insecticidal or fungicidal properties present in the seeds, pods, stems and leaves have been extensively studied (Peckolt 1880; Greshof 1890,1893,1900; Sillevoldt 1899a, 1899b; Boorsma 1910; Peckolt 1920; Nag *et al.* 1936; Hwang 1941;.Liu and Hsu 1941; Hansberry and Lee 1943; Norton 1943; Plank 1944; Norton and Hansberry 1945; Lepage *et al.* 1946; Meijer 19%; Hansberry *et al.* 1947; Jakobs 1949; Simonitsch *et al.* 1957; Holz and Hong 1964; Ollis 1964; Krishnamurti and Seshadri 1966; Krishnamurti *et al.* 1970; Sahu and Hameed 1983; Bortolato *et al.* 1985; Magalhães *et al.* 1987; Magalhães *et al.* 1988; Jimenez B. 1994).

Mature seeds contain a high amount of good-quality vegetable oil (approximately 30% in *P. erosus* (Jimenez B. 1994), 11-15% yellow-green oil (Bouillenne *et al.* 1935), but also too much rotenone to be edible (approximately 0.5% pure rotenone and 0.5% rotenoids and saponins). Studies of the composition and quality of the *P. erosus* seed oil are presented in Greshof (1890), Cruz (1950), Broadbent and Shone (1963) and Jimenez B. (1994). These studies agree that if the insecticidal/anti-nutritional compounds are removed, the oil then has a composition comparable to that of groundnut and cottonseed oil: palmitic acid 26.7%, stearic acid 5.7%, oleic acid 33.4% and linoleic acid 34.2% (Broadbent and Shone 1963). This attractive possibility was identified by Brazilian scientists working on the Amazonian yam bean and has been confirmed more recently by studies of the rotenone content of different plants and species carried out at the University of Costa Rica (Jimenez B. 1994).

As is clearly demonstrated in Sørensen (1990, Table 2), practically all studies of the insecticidal compounds and their properties have been conducted on one species, i.e. *P. erosus* only (until the recent examinations by Lackhan (1994) and Scramin (1994)). One exception known to the author (and the list of studies appearing in Sørensen (1990) represents the majority of analyses published) is the study published by Hansberry *et al.* (1947). This included the species *P. strigosus* (now considered conspecific with *P. erosus), P. ahipa* and *P. tuberosus.* Knowledge of the properties of the genus has been increased by this extension of the material by Hansberry and his associates (the differences they found between the species are remarkably few). The analyses conducted by Lackhan (1994) and Scramin (1994) will, however, be of further value and will possibly lead to renewed commercial interest in the exploitation of the insecticidal properties of yam bean seed.

The identification and quantification of rotenone and pachyrhizin in *P. tuberosus* have been recently carried out in Brazil. Scramin (1994) and Villar and Válio (1994) suggest that the presence of these rotenoids in the seeds and leaves may lead to ecological advantages for the species, as the compounds are likely to have a protective effect against insect predators. Lackhan (1994) studied the potential of *in vitro* techniques to produce rotenone and rotenoid from callus cultures.

P. erosus

Many of the considerable number of the rotenone content analyses also include evaluations of the insecticidal potential of this species: Hwang (1941), Cheu and Li (1942), Hansberry and Lee (1943), Norton (1943, 1944), Ippisch (1944), Norton and Hansberry (1945), Hansberry *et al.* (1947), Helson (1949), Holz and Hong (1964), Duke (1981), Adjahossou and Sogbenon (1994) and Halafihi (1994). If the rotenone is present at extractable levels in the mature legumes/pods and in the seeds, again the possibility of utilizing the insecticidal compounds on a commercial basis or alternatively on a rural scale exists (Duke 1981). Both rotenone and the rotenoids may also be used as a piscicide according to Greshof (1893,1900) and Sillevoldt (1899a, 1899b).

Field experiments evaluating the utilization of *P. erosus* seed extract as a low-cost plant protective agent are reported by Adjahossou and Sogbenon (1994) in a crop of cowpea *(Vigna unguiculata* (L.) Walp. subsp. *unguiculata)* and Halafihi (1994) in garden cabbage *(Brassica oleracea* L. var. *capitata* K-cross). Both studies demonstrated that good control of leaf-eating insects using an aqueous solution of ground seeds can be obtained, but with little or no control of leaf-piercing insects. Sahu and Hameed (1989) studied the controlling effect of *P. erosus* seed extract on the tobacco caterpillar *(Spodoptera litura* F.) and Walker and Anderson (1943) examined the control of aphids and diamond-back moth larvae on collards *(Brassica oleracea* var. *viridis* L.) and kale *(Brassica oleracea* var. *sabellica* L.) with rotenone-nicotine dusts.

In laboratory experiments, using a *P. erosus* seed oil emulsion, Cheu and Li (1942) reported excellent control of the sugar cane woolly aphid *(Oregma lanigera* Zehntner) and declared yam bean seed to be a promising source of insecticides.

P. ahipa

P. ahipa has been subjected to few chemical analyses of the compounds with insecticidal or fungicidal properties in the seeds, pods, stems and leaves. As mentioned above, Hansberry *et al.* (1947) included the species *P. erosus, 'P. strigosus'* (considered conspecific with *P. erosus* according to Sorensen 1988), *P. ahipa* and *P. tuberosus* in their study. The recent analyses carried out in Brazil (Scramin 1994) and in Trinidad (Lackhan 1994) include *P. ahipa.* A summary of the analyses conducted by Lackhan (1994) is given in Table 5.

Table 5. Composition (%) of rotenone, rotenoids and non-rotenoids, chloroform extract fractions in *Pachyrizus* seeds (Lackhan 1994)

Accession no.	Rotenone	Pachyrhizin & 12a-hydroxyrotenone	Other rotenoids	Non-rotenoids
EC041[a]	0.06	0.15	0.53	0.25
EC104[a]	0.16	0.22	0.40	0.22
EC033A[a]	0.03	0.15	0.48	0.34
EC550[a]	0.11	0.14	0.54	0.20
mean[a]	0.09	0.17	0.49	0.25
PW055[b]	0.14	0.11	0.65	0.11
TC239[c]	0.03	0.29	0.38	0.29
AC102[d]	0.16	0.32	0.43	0.08

a - *P. erosus;* b - *P. panamensis; c - P. tuberosus;* d - *P. ahipa*

P. tuberosus

Analyses of dry matter constituents in material from field trials carried out in Tonga have revealed that *P. tuberosus* has a starch content approaching that of *P. ahipa).* The yields recorded to date in field trials of this species have not been impressive (see Table 6), but the climatic conditions prevailing in the test sites may not have been optimal and cultivation practices will also have to be modified. In Ecuador, the plants are pruned two to three times: this includes not only strict reproductive pruning, but the also the cutting back of the vegetative parts by two-thirds once during the growing season to increase tuber growth (M. Grum, pers. comm.; Sørensen *et al.* 1996). However, photothermal neutrality has also been recorded in some genotypes belonging to the jíquima cultivar group of this species, and it has also been shown to tolerate the higher precipitation rates of the more humid tropics better than the other species, where cracking or splitting of the tuber is frequently a problem. *P. tuberosus* has been successfully hybridized with *P. erosus* (reciprocally), *P. ahipa* (one way only, *P. ahipa* as female) and *P. panamensis* (reciprocally).

Table 6. **Tuber and top yields in *P. tuberosus,* from yield and multiplication field experiments, Tonga**

Access. no./ cultivar group	Origin, country	Tuber yield (g/plant) Min.	Max.	Mean	Soluble solids (%)	Dry matter (%)	Mean yield, top (g/plant)	Dry matter top (%)
Ashipa								
TC118[a+d]	Haïti	145.4[1]	398.6[2]	260.9	7.5	22.4	199.5	26.4
TC300[c]	Ecuador	-	-	5080.9	5.8	10.4	517.1	28.0
TC303[c]	Ecuador	-	-	1067.9	6.0	11.3	224.8	25.5
TC306[c]	Ecuador	-	-	4090.9	6.3	9.3	227.3	24.6
TC307[c]	Ecuador	-	-	2532.1	6.8	9.4	308.8	33.6
TC308[c]	Ecuador	-	-	494.1	6.7	9.5	49.4	42.4
TC309[c]	Ecuador	-	-	513.9	6.5	8.9	128.5	26.5
TC310[c]	Ecuador	-	-	2754.0	7.0	9.5	168.6	28.3
TC525[a+d]	Brazil	25.8[2]	686.81	355.5	6.6	20.7	106.0	28.4
TC526[c]	Brazil	-	-	1901.5	7.5	17.9	496.0	46.3
TC530[a+d]	Brazil	72.3[1]	772.22	440.4	6.6	18.8	69.4	27.8
TC532[c]	Bolivia	-	-	1618.7	7.0	13.2	899.3	23.2
TC533[a+d]	Bolivia	343.4[2]	809.52	427.5	7.0	19.0	91.6	29.8
TC534[c]	Peru	-	-	1095.6	6.5	16.5	249.0	21.0
TC535[c]	Brazil	-	-	2038.0	7.2	19.3	494.1	19.8
TC536[c]	Brazil	-	-	2173.9	6.2	13.8	543.5	43.6
TC538[c]	Peru	-	-	3057.6	6.0	12.0	472.1	26.1
TC556[c]	Ecuador	-	-	2545.5	7.0	14.8	136.4	31.7
TC557[c]	Ecuador	-	-	5136.4	6.2	8.8	409.1	28.0
Means		146.7	666.9	371.1	6.7	14.0	116.6	29.5
		±140.1	±186.1	±82.4[x1]	±0.5	±4.6	±57.3[x2]	±7.3
Chuin								
TC350[c]	Peru	-	-	2318.2	6.3	12.2	863.6	25.1
TC353[c]	Peru	-	-	1235.2	9.8	28.9	329.4	49.4
TC354[c]	Peru	-	-	1275.5	10.3	24.5	425.2	33.8
Means		-	-	1609.6	8.8	21.9	539.4	36.1
				±614.0	±2.2	±8.7	±284.8	±12.3

Continued on p.50

Table 6. Continued. Tuber and top yields in *P. tuberosus,* from yield and multiplication field experiments, Tonga

Access. no./ cultivar group	Origin, country	Tuber yield (g/plant) Min	Max.	Mean	Soluble solids (%)	Dry matter (%)	Mean yield, top (g /plant)	Dry matter top (%)
Jíquima								
TC238[a+d]	Ecuador	6.9[1]	1099.1[2]	34.9	6.6	24.5	199.2	23.0
TC239[a+d]	Ecuador	3.6[2]	363.6[2]	73.9	6.7	24.0	107.2	26.2
TC311[c]	Ecuador	-	-	49.8	8.5	14.0	448.2	27.7
TC550[b]	Ecuador	-	-	68.3	7.8	24.5	795.5	24.1
TC551[b]	Ecuador	-	-	56.8	7.9	23.1	930.4	27.0
TC552[b]	Ecuador	-	-	63.9	8.7	-	752.8	23.6
TC553[b]	Ecuador	-	-	121.8	8.4	-	933.4	23.1
TC554[b]	Ecuador	-	-	189.4	7.7	-	669.2	31.0
TC555[c]	Ecuador	-	-	99.2	8.2	16.3	496.0	31.7
Means		5.3 ±2.3	731.4 ±520.1	54.4 ±27.6[y1]	7.8 ±0.7	21.1 ±4.7	153.2 ±65.1[y2]	26.4 ±3.2

1 - non-pruned
2 - reproductively pruned
a - experiment 41, yield trial, 1994, plant density 81 632 plants/ha
b - experiment 42, multiplication, 1994, plant density 10 000 plants/ha, all plants non-pruned
c - experiment 54, multiplication, 1994, plant density 10 000 plants/ha, all plants non-pruned
d - experiment 61, yield trial, 1994, plant density 81 632 plants/ha
Ashipa: x1 - mean tuber yield (g/plant) in yield trials only, total mean yield 1978.2±1544.6 g/plant; mean yield multiplication only 2407.9±1460.4; x2 - mean top yield (g/plant) in yield trials only, total mean yield 304.8±220.7 g/plant; mean yield multiplication only 354.9±221.6
Jíquima: y1 - mean tuber yield (g/plant) in yield trials only, total mean yield 84.2±47.2 g/plant; mean yield multiplication only 92.7±49.7; y2 - mean top yield (g/plant) in yield trials only, total mean yield 592.4±300.7 g/plant; mean yield multiplication only 717.9±192.9.
The yields are based on a common standard of a 250 days growth period.
(Nielsen, unpublished)

A Brazilian study (Menezes and Oliveira Nunes 1955) reported the following composition from analysis of a local genotype belonging to the ashipa cultivar group, based on 100 g fresh weight of tuberous root: water 90.4 g, nitrogenous compounds/proteins 1.0 g, lipids 0.09 g, non-nitrogenous compounds/starches/sugars 7.6 g, fibres 0.61 g and minerals 0.28 g. The same analysis yielded the following results based on 100 g dry matter: nitrogenous compounds/proteins 10.43 g, lipids 0.92 g, non-nitrogenous compounds/starches/sugars 79.4 g, fibres 6.4 g and minerals 2.9 g.

As part of the same study, Menezes and Olivera Nunes (1955) included an analysis of a shoot (both stem and leaves) taken prior to flowering, based on 100 g fresh weight: water 87 g, nitrogenous compounds/proteins 3.5 g, lipids 0.6 g, non-nitrogenous compounds/starches/sugars 4.5 g, fibres 3.2 g and minerals 1.3 g. The same analysis, but based on 100 g dry matter, produced the following constituents: nitrogenous compounds/proteins 2.2 g, lipids 3.6 g, non-nitrogenous compounds/starches/sugars 34.3 g, fibres 24.6 g and minerals 10.3 g. Peckolt (1880) and Peckolt (1922) presented one of the very first analyses of the chemical composition of the seeds, the green pod/legume (without seeds), the fresh (peeled) tuberous root and the ash, the peel of the tuberous roots and lastly the dried starches/sugars resulting from the evaporation of an aqueous extract. These results do not differ significantly from the data obtained by Menezes and Oliveira Nunes (1955). As in *P. erosus,* pods/seeds belonging to this species contain rotenone and pachyrhizin (Villar and Válio 1994).

Hansberry *et al.* (1947) demonstrated the toxic effect of the seed extract of this species on larvae of the Mexican bean weevil. Lepage *et al.* (1946) evaluated the toxic effect of the constituents of the *P. tuberosus* seeds on aphids *(Aphis brevicoryne* var. *brassicae* (L.)). The analysis involved two methods of extraction of the insecticidal compounds: ether and oil pressure.

4.3 Nutritional aspects

P. erosus

Aguilar (1958) presents figures for the nutritive value of tubers from four different species: *P. angulatus,P. palmatilobus, P. tuberosus* and *P. erosus;* however, later studies indicate that these 'species' were in fact different cultivars of *P. erosus* and probably material collected from the wild. Schmar *et al.* (1987) studied the structural changes in yam bean tubers as a result of microwaving. The treated tuber pieces were subsequently fed to rats and were found to have increased digestibility, compared with fresh tubers. Several studies of the nutritional composition of *P. erosus* tubers, immature legumes and seeds have been published. A summary of older and more recent analyses is presented in Table 7.

P. ahipa

Recent analyses of the sugar and protein contents of tuberous roots harvested at the experimental station at Tras-os-Montes, Portugal, carried out at the Fraunhofer Institute, Germany, have demonstrated that sugars constitute 50% of the dry matter and the protein content accounts for 10%. Of the protein content, 80% is water soluble but not readily extractable within a pH range of 2-10. The lipid content is below 1%, i.e. *P. ahipa* tubers have a nutritionally ideal composition (A. Borcherding 1995, pers. comm.). The results from field trials in Tonga, Mexico and Portugal are presented in Table 3.

An analysis of the tubers from 20 different non-reproductively pruned accessions grown in a trial under greenhouse conditions yielded a range of 8.7% (minimum), 10.8% (average), 14.2% (maximum) protein content in the dry matter. The

Table 7. Nutritional composition of tuber, immature legumes and seed of P. erosus, per 100 g fresh weight, compiled from various authors

Constituent	Tubers														Immature legumes			Seeds
Reference	i	ii	iii	iv	v	vi	vi	viii	ix	x	xi	xii	xiii	mean	iii	ix	xiii	v
Moisture (%)	82.4	78.0	85.0	88.0	90.0	87.1	-	87.0	89.0	87.0	94.0	87.0	88.9	87.0	86.0	-	88.9	6.7
Proteins (g)	1.5	2.2	1.6	1.2	1.1	1.2	1.1	1.4	1.4	0.8	1.0	1.0	1.4	1.3	2.6	1.9	3.6	26.2
Lipids (g)	0.1	0.8	0.1	0.1	0.2	0.1	0.1	0.1	0.0	-	-	0.2	-	0.2	0.3	0.3	7.5	27.3
Carbhydrs(g)	14.9	14.0	-	10.6	8.9	10.6	8.4	11.0	8.7	6.5	4.6	11.0	-	9.9	10.0	7.4	7.8	20.0
Starch(g)	9.7	-	10.7	-	-	-	-	-	-	2.1	-	-	-	7.5	-	-	5.5	-
Red.sugars(g)	2.2	-	1.7	-	-	-	-	-	-	3.4	-	-	-	2.4	-	-	3.0	-
-red.sug. (g)	3.0	-	-	-	-	-	-	-	-	1.0	-	-	-	2.0	-	-	3.1	-
Fibres(g)	0.6	1.4	0.7	0.7	0.5	0.7	0.9	0.6	-	-	-	0.6	-	0.7	2.9	2.1	0.2	7.0
Ash (g)	0.5	0.8	0.6	0.3	0.3	0.3	0.4	0.6	-	-	-	0.6	-	0.5	0.7	0.5	-	3.6
Minerals (g)																		
Ca (mg)	16.0	-	-	18.0	14.0	-	-	-	15.0	-	4.0	-	27.0	15.7	-	-	-	high
P(mg)	-	-	-	16.0	15.0	-	-	-	-	-	19.0	-	17.0	16.8	121.0	-	-	high
Fe (mg)	1.1	-	-	0.8	0.4	-	-	-	-	-	0.2	-	-	0.63	1.3	-	-	-
Cu (mg)	0.43	-	-	-	-	-	-	-	-	-	-	-	-	0.43	-	-	-	-
Na(mg)	-	-	-	-	-	-	-	-	6.0	-	-	-	-	6.0	-	-	-	-
K(mg)	-	-	-	-	-	-	-	-	175.0	-	-	-	-	175.0	-	-	-	-
Vitamins	-																	
Retinol (A)	-	-	-	traces	traces	-	-	-	-	-	-	-	-	traces	575iu	-	-	-
Thiamine(B1)	0.05	-	-	0.03	0.05	-	-	-	-	-	0.1	-	-	0.06	0.11	-	-	-
Riboflavin (B2)	0.02	-	-	0.03	0.02	-	-	-	-	-	0.1	-	-	0.02	0.09	-	-	-
Asc. acid (C)	14.0	-	-	21.0	14.0	-	-	-	22.0	-	17.2	18.0	-	17.7	1056	-	-	-
Niacin	0.2	-	-	0.3	0.2	-	-	-	-	-	-	-	-	0.2	0.8	-	-	-
Energy(cal)	-	-	58.0	45.0	39.0	-	36.0	47.0	22.0	45.0	22.0	-	-	39.3	45.0	-	-	-

i - Nag *et al.* (1936) [identical figures appear in Rattan and Sen (1941)]; ii - Porterfield (1951); iii - Martínez (1956); iv - Wu and Flores (1961); v - Manila Food and Nutritional Research Center (1964); vi - Purseglove (1968); vii - National Academy of Sciences (1979); viii Duke (1981); ix - USDA (1984); x - Tadera *et al.* (1984): xi - Sahadevan (1987); xii - Hoof and Sørensen (1989); xiii - Ratanadilok and Thanisawanyangkura (1994).

dry matter content ranged from a minimum of 15.3% and an average of 20.5% to a maximum of 30.7% (Ørting, unpublished data).

P. tuberosus
Duke (1981) reports the presence of adenine and choline in the tuberous roots and the content of adenine, choline and the anti-nutritional compounds rotenone and saponin in the mature seeds. Sales *et al.* (1990) published the complete characterization and quantification of the amino acid composition of *P. tuberosus* seed compared with soyabean seeds. Their results indicate that the protein quality of *P. tuberssus* compares favourably with that of soyabean, i.e. the amount of sulphuric amino acids is limited, as is the amount of valine. Although the seeds are rich in both proteins and lipids/oils, the presence of high levels of isoflavonoids (rotenoids and pachyrrizide) make them unsuitable for human consumption (Alvarenga and Válio 1989; Scramin 1994).

P.E. Nielsen (1995, pers. comm.) reports the following findings from field experiments in Tonga on total soluble sugars and total dry matter in the tubers for (i) two accessions belonging to the chuin cultivar group: TC353 (9.8% soluble sugars, 28.9% D.M., 9.5% protein on D.M. basis; six plants in the experiment) and TC354 (10.3% soluble sugars, 24.5% D.M., 10.0% protein on D.M. basis; based on seven plants); (ii) one accession belonging to the ashipa group: TC307 (6.8% soluble sugars, 9.4% D.M.; no analysis of protein content; based on eight plants); (iii) accessions belonging to the jíquima group (see Table 6). The results of the analysis of protein content have been made available by W.J. Grüneberg.

4.4 Industrial and other aspects

P. erosus
Provided that an optimal method of preserving the crisp texture of the processed tubers can be developed, yam bean tubers may well be marketed as an attractive product to be used in various dishes, and also as a snack (Mudahar and Jen 1991). According to Kundu (1969), *P. erosus* tubers are used in the production of a high-grade flour in India.

The reported figures for the total amount of extractable rotenone contained in the mature seeds vary considerably. A recent analysis of four different *P. erosus* accessions recorded a range of 0.03-0.11% rotenone (Lackhan 1994), although Deshaprabhu (1966) advises that some Chinese landraces may contain as much as 0.5-1.0% (see Table 5). The possibilities of utilizing the rotenone content of the seeds as a pesticide and the tubers as a source of starch or alternatively as a fodder appear attractive. However, at present the world market for rotenone as an insecticide is limited: it is mainly used in flea powders, and further studies are needed to identify new applications of this chemical, e.g. as a plant protective agent and in the cleaning of eutrophied lakes. As a cheap crop protective agent, it would clearly be an attractive option for producers in the developing world.

P. ahipa

In addition to recent advances in the evaluation of this species as a new vegetable crop in Europe, it has been demonstrated that the *P. ahipa* tuber has a dry matter content of 25-50% starch (95-99% amylopectin) with 47% sugar and N-free extracts and 10% protein. The latest analysis of the variation in the protein content on a dry matter basis yielded a range from 8 to 18% in 20 accessions (W.J. Grüneberg 1995, pers. comm.). *P. ahipa* may thus be cultivated as both a food crop and a renewable resource. By comparison, sugar beet, a crop of considerable industrial importance in Europe, contains only 20% sugar. Also, the total protein yield per hectare exceeds that of soybean *(Glycine max* (L.) Merr.), even though the protein content of the tuber at present is lower than that of the grain legume beans. The protein market is of high economic interest to the European Union, as Europe has to import several million tonnes of soybean protein each year. The possibility of utilizing the virtually pure source of amylopectin in non-food products is currently being investigated. Thus, the development of new *P. ahipa* cultivars in concordance with the industrial requirements for non-food crops may become a reality.

P. tuberosus

According to several older references reporting on uses in Jamaica (Anonymous 1889a, 1893, 1904; Buttenshaw, 1905; Harris 1913), and also more recently Deshaprabhu (1966), Duke (1981) and Sørensen (1990), once the large tuberous roots are dried and ground, they produce a high-quality flour which may be used in cakes and deserts. The properties of this flour are comparable to those of manioc flour, according to Peckolt (1922), who also examined the starch grains microscopically and reported them to be distinctly different from those of manioc starch. Vidal and Pimentel (1985) published a biochemical, topochemical and structural characterization of the protein bodies of this species.

Peckolt (1922) also studied the quality of the seed oil of *P. tuberosus* and found it to be quite thick, with a distinct though not disagreeable taste/flavour. It may be used as a substitute for almond oil or similar oils used for technical purposes by the industry.

5 Uses

5.1 Domestic, industrial and environmental uses

P. erosus

The tubers are used in Mexico in a number of different ways: (i) as a fruit - fresh tubers are cut into sticks and sprinkled with lime juice and chilli (these are often sold by street vendors); (ii) as a vegetable - fresh tuber slices are used in various salad dishes; (iii) cooked tubers are used to prepare a soup, on their own or with other vegetables; (iv) tuber slices may be stirfried, or (v) sliced or diced tubers may be preserved in vinegar with onion and chilli and used as a snack with drinks. Martínez (1936) also reports that the sliced pieces may be preserved in vinegar together with the immature legumes.

In Thailand, not only the tuber of the yam bean is used as food: the young pods are eaten as a substitute for French beans and are said to have a pleasant taste (Ratanadilok and Thanisawanyangkura 1994). Nutritionally, these pods may be compared with soyabean legumes/pods (Nag *et al.* 1936; Cruz 1950; Broadbent and Shone 1963).

Shag Mal and Kawalkar (1982) also report from India that once they are cooked, the young pods may be used as a vegetable in the same way as French beans. They further recommend the use of tubers in the preparation of pickles and chutney, and in the preparation of a tasty drink called ‘kheer’, containing tuber gratings boiled in milk. In Malaysia, the fresh young tubers are sliced and eaten with other young fruits in a pungent sauce. This traditional dish is known as ‘rujak’ (Sahadevan 1987; Hoof and Sørensen 1989).

In Mexico, in addition to the use of tubers and their young pods or beans for human or animal consumption, the dried hay which remains after harvest provides a source of animal fodder. It should be noted that as the cultivated yam bean is reproductively pruned, the rotenone content of the hay does not reach anti-nutritional levels, and the yam bean hay is commonly mixed with lucerne and maize hay before use. At higher concentrations, this compound is toxic to humans. The highly efficient natural way in which the plant absorbs nitrogen makes it an attractive alternative for cultivation on poorer soils (see also Castellanos *et al.* 1996).

Provided that the rotenone can be extracted in economic quantities from the mature seeds, the remaining seed oil is fit for consumption and can be marketed as an alternative to groundnut or cotton seed oil (Cruz 1950; Broadbent and Shone 1963; Jimenez B. 1994; see also Section 4.2). The rotenone itself may also be put to good use. It can be sold as a high-value naturally derived chemical or, using simpler extraction methods, be employed locally as a plant protective agent (Adjahossou and Sogbenon 1994; Halafihi 1994). Once both rotenone and oil have been removed, the remaining seed cake has a protein content comparable to that of soybean cakes (Cruz 1950). In spite of the numerous reports on the insecticidal and piscicidal (fish-killing) effect of the rotenone and rotenoids isolated from the seeds (see Section 4.2), yam bean has yet to be grown on a commercial scale for the production of rotenone-based crop protective agents. The frequent accounts of the seed having been utilized as a piscicide in Indonesia, e.g. Meijer (1946), are at variance with the first reports from Southeast Asia on the poisonous effects of the seeds, i.e. Greshof (1890, 1893,1900) and Sillevoldt (1899a, 1899b). Both authors state that the local population did not use the seeds as a piscicide, although they considered the seed poisonous.

P. ahipa

The tuber is locally considered as a fruit rather than a vegetable, and is therefore sold on the street or at the market by fruit rather than vegetable vendors (Ørting *et al*. 1996). It is generally consumed raw, as an apple-like snack, sliced and served mixed with vegetables in various local dishes, or prepared as juice.

P. tuberosus

The tuberous roots of the jíquima cultivar group, with their white-cream coloured flesh, and also the ashipa cultivar groups are usually eaten raw, as a vegetable. The extremely succulent, crispy and tasty tubers can also be used to make a refreshing ‘fruit’ juice. In the case of jíquima tubers, this may be mixed with milk (see also the previous section on the uses of *P. ahipa).* Chuin tubers are cooked and eaten in much the same way as the common staple manioc. Like manioc, they may be grated, squeezed and dried and prepared for farina (although tubers from the chuin cultivar group do not contain any anti-nutritional constituents (see Section 6.1)). According to Alvarenga and Válio (1989), the tubers of the ashipa group contain 6.5-9.0% protein and 20% starch/sugars, which makes them an attractive food source. The higher starch content of the chuin cultivar group is being studied by W.J. Grüneberg and associates at the Institut für Pflanzenbau und Pflanzenzüchtung at the University of Göttingen, Germany The nutritional quality is comparable to that of the tubers of *P. erosus* (Purseglove 1968).

The legumes/pods are rarely used as **a** vegetable, as most cultivars have hairy (strigose) legumes (Anonymous 1889b; Duke 1981; Purseglove 1968). However, some cultivars have legumes which, not being strigose, can be quite delicious as a vegetable when immature, e.g. the jíquima cultivar from Manabí, Ecuador (Sørensen 1990; Sørensen et al. 1996). Porterfield (1939) reports that in Sri Lanka, the legumes of *P. tuberosus* are consumed, but not those of *P. erosus,* as the former have less pubescence and are said to be of the same quality as ‘haricots verts’. This information may be incorrect, however, as there are no substantiated records of *P. tuberosus* ever having been introduced to Sri Lanka. It is therefore probable that the plants in question were cultivars of the only species with a recorded history of introduction to this region, i.e. *P. erosus.* Furthermore, several genotypes of *P. tuberosus* have young legumes with greatly reduced pubescence.

The tubers, which pigs tend to find very palatable, are also used as pig feed. The foliage may be used either as green hay or as silage, but if it is to be used for the latter purpose, the vegetative parts are harvested at the beginning of the flowering stage (Menezes and Oliveira Nunes 1955). In Brazil, the foliage has been used as a forage since colonial times (Peckolt 1922)

5.2 Ethnobotanical, anecdotal and economic data

P. erosus

Escobar (1943) reports that in the state of Veracruz, the seeds are commonly used in the treatment of skin diseases. In the pre-Columbian period, the tuber was used to cure fevers, peeling skin and flux, and crushed tubers to cure itching or mange. The old Mexican pharmacopoeia mentions a tincture made from the seeds, used to treat pruritis and mange, as well as head lice *(Capitis pediculus* L.), that was also effective in the control of cattle louse (Huart 1902). A l/10 concentration of ground seed to wettable sulphur was applied to treat three species of cattle louse with the following results: 100% control in *Bovicola bovis* L. and *Linignathus vituli* L., and 90% control in *Solenopotes capillatus* Enderlein (Matthysse and Schwardt 1943). Yang and Tang (1988) describe the controlling effect of insecticides derived from yam bean seed on the rice leafhoppers *Heliothis assulta* and *Aulacuphura femoralis-chinensis.*

Martínez (1936) advises that the seed oil can be used as a purgative when administered in doses of 40 g. In Cuba, the tubers are considered to have an analeptic effect when consumed; and the use of the flour obtained from them is recommended in the treatment of dysentery and haemorrhoids (Roig y Mesa 1988). In China, 250-500 g of peeled fresh tubers are consumed each morning and evening to treat fever with thirst; 500 g of the juice of fresh crushed and squeezed tuber is sipped slowly three times daily to treat inflammation of the throat or tonsils; 250 g of fresh peeled tuber is eaten three times a day as a laxative, and fresh tuber juice mixed with sugar is considered. a remedy for hangovers (Yin-fang and Cheng-jun 1987). Pételot (1952) reports that pulverized seeds are used in an ointment to cure skin diseases and boils in Java, and that the ingestion of half a seed is thought to have a laxative effect. Citing Balansa, Pételot (1952) further reports that the seeds are consumed as a vermifuge in North Vietnam. *P. erosus* is fairly common in Taiwan, where it is valued as a refreshing food. As the tubers keep fresh for an extended period, even without refridgeration, it is especially popular with the local fishermen, who have traditionally taken yam bean roots with them on long trips. If yam bean has played an important historical role as a food supply on sea voyages, the wide geographical distribution of the crop can be easily understood (M. Hermann, pers. comm.).

One early reference to the little-known uses of the species is made by Houttuyn (1779), who reports that in China, the tubers of *P. erosus* (presumably diced) are preserved in syrup and consumed as sweets. Hernandez (1790) describes a similar process from Mexico, in which the tubers are preserved in syrup or dices covered in pastry and exported to Spain.

Economic data for this species exist for various production areas. The following gross income figures are available for Thailand: US$1440-1680/ha in Prabath and Saraburi; US$1800-2400/ha in Kuelom and Lampang with yields of 18-24 t/ha, but a figure of only US$700-1200/ha in the Makasarakam area. The highest gross income of US$2700-6000/ha (yields of 60-90 t/ha) was recorded in the Nakorn Prathom area, i.e. an average price per kg is US$0.03-0.10. According to Sahadevan (1987), the gross income in Malaysia is US$5400 (based on a calculated yield of 9 t/ha). Singh *et al.* (1981) estimate the gross income (based on an average yield of 14 t/ha) at US$890 in the province of Bihar, India. In Mexico, the gross income from irrigated fields in Guanajuato (with a marketable yield of 40 t/ha) is US$5250, and the net profit, US$2500 (A. Heredia Z., pers. comm.).

There are few data available on seed costs. In Thailand, with average seed yields of 720-840 kg/ha, the gross income is US$800=1000/ha (Ratanadilok and Thanisawanyangkura 1994). In Guanajuato, Mexico (1995), the amount needed per hectare was 30 kg for an irrigated crop, and the cost was US$246, or US$8.20/kg (A. Heredia Z. 1995, pers. comm.).

P. ahipa

No records on the use of the insecticidal properties or ethnobotanical uses of the plant have been recorded, but during the interviews conducted in Bolivia by Ørting *et al.* (1996), it was repeatedly stated that the consumption of *P. ahipa* tubers has a cleansing effect upon the body, is beneficial to the lungs and cures infections of the air passages, i.e. coughs, etc. A recent field report from Bolivia did not confirm the report by Cárdenas (1969) that *P. ahipa* tubers are considered to be a cure for gout (Ørting *et al.* 1996).

The economy of *P. ahipa* production in Bolivia has also been studied by Ørting *et al.* (1996). At the central markets in the major cities, the price of *P. ahipa* per kg is comparable to that of groundnuts and potatoes (*Solanum tuberosum* L.), i.e. US$0.5-1.0 (at 1994 prices). The price at the local markets is somewhat lower (US$0.25), and the price obtained when selling to wholesalers varies between US$0.15 and US$0.40 per kg. The highest price is obtained from May to June, and the lowest, from August to September, when the competition for fruits produced in Las Yungas is at its peak. Wholesalers reportedly make a gross profit of 50-100% when reselling to retailers. The latter will then also increase the price by 50-100%. Even though the price of *P. ahipa* tubers was higher than that of potatoes or yuca (manioc) per kg, the profit margin per unit area may exceed that of *P. ahipa.* More importantly, however, these other crops provide a continuous cash flow through the year, unlike such short-season crops as *P. ahipa.* The market share of *P. ahipa* in both urban and rural areas is small and is steadily declining, possibly as a result of the labour-intensive practice of reproductive pruning, which is especially marked in *P. ahipa,* due to the short simple racemes and the low number of flowers per raceme, combined with an increased demand for industrially produced soft drinks.

P. tuberosus

Bertoni (1913) reported that the Indians at the Parana river (Paraguay) used an extract of *P. tuberosus* leaves as an insecticide. A. Ernst (quoted by Anonymous 1889b) reported that the seeds are used as a decoction or powder to control vermin. Fresh pods/legumes ground or chewed and mixed with lard may be used as an ointment to cure itching and mange (Perry and Metzger 1980).

In Brazil, the cooling effect produced by consumption of the tubers is believed to check various kinds of fever. The starch content is commonly used in the preparation of lemonades to treat infections of the bladder and various ailments of the urinary system. In doses of 3-4 teaspoons per day, mixed with water, sugar and lime, it is also used to treat haemorrhoids. The juice obtained from the tubers is considered an effective diuretic and is commonly used in the treatment of nephritis. An aqueous-alcoholic extract of fresh tubers administered in doses of 0.05-0.25 g is also used as a diuretic (Peckolt 1922).

In an interview with the shaman Bolívar Santi, at Río Chico in the province of Pastaza, Ecuador, the following beneficial effects of ashipa consumption were recorded: improved lactation in breastfeeding mothers and a curative effect on digestive ailments in children. The latter corroborates the findings of the digestibility studies of *P. erosus* conducted by Tadera *et al.* (1984), who found that yam bean starch is highly digestible and is therefore suitable for use in diets to treat a range of disorders.

Among the three cultivar groups, only the tubers belonging to the jíquima cultivar group are marketed in the Manabí province in Ecuador. According to Sørensen *et al.* (1996) the average price of tubers was US$0.20/kg. No economic data are available on seed production.

6 Genetic resources

In 1985, when the Yam Bean Project began, few seed samples and very little information about the species were available from the world's various genebanks. Some 20 samples of the Mexican yam bean and two samples of the Andean species were obtained through different contacts. Virtually no details concerning the exact origin of this material, the cultivation practices involved, or other relevant data exist, however. Thus, in order to make a comprehensive examination of the crop's potential, a thorough recording of the natural and cultivated distribution of the genus, based on information available from herbarium specimens had to be undertaken (Grum *et al.* 1991b; Sørensen *et al.* 1993). Subsequently, a number of field collections were carried out, and today approximately 200 accessions covering both wild and cultivated material are available from the Yam Bean Project germplasm collection (see Table 1) for the hybridization and evaluation experiments currently in progress.

6.1 Genetic variation

P. erosus

The major characteristics of potential breeding value observed in *P. erosus* may be divided into (i) the morphological - multituberous *versus* monotuberous genotypes, genotypes with prominent strigose hairs on all vegetative parts, and deeply lobed *versus* dentate leaflets, and (ii) the physiological - tuber growth/yield potential, tuber quality (dry matter content, soluble sugar and protein contents), earliness (short production period), climatic and edaphic adaptability, seed production/abscission rate, difference in response to reproductive pruning, pest and disease resistance, drought tolerance, efficiency of biological nitrogen fixation and the rotenone/rotenoid content of the mature seeds.

P. erosus is the only species in which a number of consistently high-yielding cultivars developed by pure line selection exist. Hence, when evaluating landraces or primitive cultivars of Mexican, Central American or Far Eastern origin, the possibility of comparing these genotypes with material of proven quality assists the identification of agronomically attractive traits not present in the existing high-performance cultivar.

Successions of both wild as well as ephemeral material also possess characteristics of potential interest when breeding for new cultivars. Several accessions representing wild material have been found to have a high resistance to insect pests, owing to the hairiness of the foliage. As individual wild populations are associated with climatically different areas, i.e. wet forests in Veracruz (Mexico); deciduous forests in Baja Verapaz (Guatemala) and dry savannahs in Huehuetenango (Guatemala) and Guanacaste (Costa Rica), it is possible to breed for cultivars with increased climatic tolerance. The tubers of all wild, and most ephemeral, material have been found to have a significantly higher dry matter content than those of cultivated material.

Preliminary molecular studies (Philips *et al.*, unpublished data) have demonstrated that the *P. erosus* complex may be separated into two major subdivisions which partly correspond to the old distinction between *P. erosus* of Mexican origin, and *'P. palmatilobus'* (= *'P. erosus* var. *palmatilobus')* of Central American origin. The latter 'species' was principally distinguished from *P. erosus* on account of its deeply lobed leaflets *(P. erosus sensu stricto* having dentate leaflets). However, this characteristic has also been found to occur within material of Mexican origin, particularly among the landraces found in the Yucatan peninsula. It therefore follows that morphological characters cannot form a valid basis for the separation of these two groups. *'P. palmatilobus'* is currently considered conspecific with *P. erosus*, but further molecular analyses which include wild *P. erosus* material of both Mexican and Central American origin are needed to clarify the phylogeny of the species.

The apparent association of the white flowered, red/maroon seeded landraces from the Yucatan peninsula (both the Mexican and Guatemalan parts) with an increased tolerance of high temperature but also with a longer production period, should be examined in detail. Within a number of the Yucatan landraces, the genotypes of both the white flowered, red seeded and the violet-blue flowered, olive-green seeded kind are found. Little is known of why these two morphologically different genotypes have been maintained within a single landrace, save that they have both been found to perform well according to seasonal variations.

P. ahipa

In this species, the recent analysis of infraspecific variation conducted by B. Ørting (unpublished data) under greenhouse conditions has clearly succeeded in demonstrating that what was previously regarded as a fairly homogeneous taxon does in fact possess a wide range of morphological and physiological diversity. Both twining vines and genotypes with very short internodes and an erect bushy growth habit exist. Furthermore, both multituberous and monotuberous lines have been identified (though the monotuberous form appears to be dominant). Strikingly different abscission rates occur, and the number of flowers produced by the individual plant, as well as the actual number of seeds produced per plant, differs considerably. The yield potential of the 20 accessions so far analyzed also differs.

Field evaluations currently in progress in Tonga will serve to further confirm the diversity available within the species, as will the physiological drought tolerance studies conducted by J. Vieira da Silva (University of Paris VII) and D.J.M. Annerose (CERAAS, Senegal). Moreover, the recent examination of photothermal sensitivity and of the rotenone/rotenoid contents of *P. ahipa*, conducted by I.F.M. Válio and associates, will certainly serve to increase the available information on its diversity.

P. tuberosus

Until recently, little was known about the diversity of this species (Sørensen *et al.* 1996). Furthermore, it is difficult to assess the agronomic importance of the crop, because of (i) the absence of economic data and (ii) its main area of cultivation, i.e. lowland Amazonia, where it is principally consumed within the rural communities. However, the obvious breeding potential of both wild material and the different cultivar groups, as well as the apparent nutritional qualities of several of the cultivar groups, calls for a comprehensive presentation of this species.

When examining the available herbarium specimens for taxonomic revision, the morphological variation of the landraces/primitive cultivars of *P. tuberosus* became apparent, as did the fact that a considerable number of local cultivars exist within this species. Furthermore, the few introductions to areas outside the original distribution area and the low level of interest in cultivating the species in these areas were attributed to the lack of more uniform, 'sophisticated' and high-yielding cultivars. Live material was only then known from Haïti, where the tubers are gathered and consumed by the local population. Cultivation of the plant is minimal; it has been allowed to escape, and the tubers are collected from 'wild' populations, according to T.A. Zanoni (1986, pers. comm.). This may mean that *P. tuberosus* has been subjected to very little selection: the jíquima and chuin cultivar groups described below had yet to become known, even in areas of introduction, and cultivars were therefore almost indistinguishable from known wild forms.

Of the three cultivated species, *P. erosus, P. ahipa* and *P. tuberosus*, the first two must be regarded as crops primarily selected for cultivation at higher altitudes or at least in drier areas with different cropping systems involving maize and common bean. This fact is mainly due to the uniform appearance of these species' tubers, and the non-twining habit of *P. ahipa.* Furthermore, *P. erosus* and *P. ahipa* have the longest recorded history of cultivation. The lack of historical records on the agronomic status of *P. tuberosus* is attributable to the physical conditions of the Amazon, and also to cultural traditions in this region. The species was selected for a different agricultural system, where the monotuberous plant has no evolutionary advantage. Physical conditions in the Amazon include shade, humidity and rapid weed growth, and most of the cultivar groups in the *P. tuberosus* complex, i.e. ashipa and chuin, are perfectly suited to these conditions. The exception is the fairly uniform monotuberous jíquima, which is selected for the dry, lowland conditions of coastal Ecuador (and possibly Peru).

The cultivars present in the germplasm collection were initially divided into two distinct groups based on internodal length and leaf morphology: (i) cultivars with long internodes, entire leaflets and long racemes (up to 360 mm), i.e. the *P. tuberosus* genotypes of Amazonian and Caribbean origin, and (ii) cultivars with short internodes, deeply lobed leaflets and racemes interrupted by leaflets with abruptly alternating left-and right-turning growth (Sørensen 1990). The genotypes belonging to this second group, the 'jíquima' cultivars, are described below. These are only known in western Ecuador. Germplasm collection carried out since 1990, however, has revealed that the actual variation is significantly more complex.

The typical cultivar forms of *P. tuberosus,* a newly discovered distinct group of cultivars from the Ucayali river in Peru, and the morphologically distinct form grown in western Ecuador, will be discussed separately below. Henceforth, they will be referred to as the ashipa, chuin and jíquima groups, respectively, although they are often known locally by other names. The majority of the observations from Peru which follow concerning the chuin group, and most concerning the ashipa group, are from an unpublished report by L. Jensen and C. Thirup (Sørensen *et al.* 1996.).

As has been mentioned above, a morphologically distinct landrace is still to be found in cultivation, quite frequently in western Ecuador, in the province of Manabí, but also occasionally in the province of Los Rios. This cultivar group, locally known as jíquima, has been exhaustively collected. Furthermore, the evaluation trials conducted by the various partners in the Yam Bean Project have clearly demonstrated the high level of uniformity between material/lines collected from different localities. The only variations which have been seen are slight differences in leaf outline and flower colour; the material of Manabí origin all has white flowers, while the Los Rios material has white and violet- flowered forms. The growth habit and tuber shape/quality do not vary. The phylogeny of this morphologically very distinct material is rather intriguing, as there are no other genotypes (wild or cultivated) with a similar growth habit recorded in the vicinity. The nearest material is the wild population belonging to *P. tuberosus* at the biological station of Río Palenque in the province of Los Ríos, and the wild material of *P. panamensis* previously recorded from the province of Guayas. Both these groups are robust vines with inflorescences and legumes of quite dissimilar morphology.

The distribution of the species to the east of the Andes is somewhat obscure, owing to the progress of intensified agricultural cropping systems in the Brazilian states of Mato Grosso and Minas Gerais. There is little doubt, however, that *P. tuberosus* was originally to be found in large areas of the lower reaches of the Amazon. As mentioned above, the species is recorded from several of the greater Antilles, and one accession from Haïti has been used in the hybridization programme.

The ashipa cultivar group can be further subdivided into two groups: (i) the multituberous (with two subgroups, 'Ashipa 1' and 'Ashipa 2') and (i) the monotuberous (containing one subgroup only, 'Ashipa 3'). Thus local growers distinguish between these three separate forms within the ashipa cultivar group. 'Ashipa 1' and 'Ashipa 2' produce several large oblong tubers per plant, with the tubers spreading out laterally. The difference between 'Ashipa 1' and 'Ashipa 2' is the colour and sweetness of the tuber flesh: 'Ashipa 1' has white flesh with little sweetness, whereas 'Ashipa 2' has yellow-coloured flesh with a much sweeter taste. The third cultivar form, 'Ashipa 3', produces a single large turnip-shaped vertical tuber with whitish flesh and little sweetness. All forms have kidney-shaped seeds of an orange-red/brown-red to dull-black colour. Both white and violet flowered forms exist. In addition to the cultivation of the ashipa group taking place in Colombia, Venezuela, Ecuador and Bolivia, it is also grown in Peru by the same ethnic group as the chuin cultivars. The ashipa cultivar group is found further downstream, near Iquitos, and possibly also much further upstream (near Pucalpa), where it is grown by the Shipibo Amerindians.

Chuin (as it is known locally) forms a very distinct cultivar group. It is presently only known from a small area along the Río Ucayali, both upstream and downstream from the town of Requena. It is predominantly the Cocama ethnic group and/or their descendants who grow chuin. This cultivar group differs from the majority of the ashipas in the following ways: (i) it is invariably monotuberous; (ii) its vertically produced tuber, which resembles a radish or a somewhat thickened carrot; (iii) its high dry matter content, which is comparable to that of manioc roots[3]; (iv) its leaf morphology - the lateral leaflets have a completely different length/width ratio from those of both the ashipa and jíquima groups, and (v) the morphology of the legume and seeds.

To date, the phylogeny of this group remains obscure. Like the ashipa group,, the chuins may be further subdivided according to the skin/peel colour of the tuberous root and colour of the tuber flesh. 'Chuin l', locally known as 'chuin blanco', has white skin and white flesh; 'Chuin 2', known as 'chuin amarillo', has yellow skin and flesh, and 'Chuin 3', known as 'chuin morada' has dark purple to violet skin and white flesh.

The accessions representing the wild material collected so far all originate on the western slopes of the Andes, and no cultivated material has been identified in the immediate vicinity. The altitudinal range is 300-800 m a.s.1. and the habitat is at the edges of rainforests and often along rivers. Morphologically the wild material resembles some of the genotypes seen within the ashipa cultivar group and the wild species *P. ferrugineus*, and the foliage is evergreen. The plants seen were all of the monotuberous type, with a very elongated shape and high dry matter content (40-50%). Tubers from the different cultivar groups and the wild material are shown in Figure 4b.

In summary, the *P. tuberosus* complex possesses a wider variation of agronomic traits than either of the two other cultivated species. Of obvious interest when contemplating breeding initiatives are the tolerance of *P. tuberosus* to high precipitation rates, and the differences in tuber quality.

[3] According to L. Jensen and C. Thirup (Sørensen *et al.* 1996, Chapter 4.3).

6.2 Geographic distribution of important traits in the entire genepool

P. erosus

As stated above, the highest-yielding cultivars have been developed in the Bajío region, in the state of Guanajuato, Mexico. The five most well-known cultivars: 'agua dulce', 'cristalina', 'San Miguelito, 'San Juan' and 'vega de San Juan' have all been selected by A. Heredia Z. (Heredia Z. and Heredia G. 1994). These cultivars, which have been selected from various so-called 'criollo' material, i.e. local Mexican landraces, have successfully demonstrated the impressive yield potential of this species; 81-125 t/ha yield results have been repeatedly confirmed in field trials, as well as in commercial production. Moreover, A. Heredia Z. has succeeded in combining high yield with earliness: i.e. San Miguelito, yielding 114 t/ha needs a production period of 210 days to harvest, while vega de San Juan, yielding 125 t/ha is ready for harvest in only 150 days.

The red-seeded, white-flowered landraces occurring in the Yucatan peninsula (both the Mexican and the Guatemalan parts) have been shown to be persistently lower yielding when evaluated in field trials at Celaya, in the state of Guanajuato (E. Heredia G., pers. comm.). They also appear to be more susceptible to insect damage (Grum *et al.* 1994; J.A. Morera, pers. comm.). The landraces from the department of Jutiapa in southern Guatemala, morphologically distinguished by their deeply lobed leaves, produced high yields in field trials in Tonga (Grum *et al.* 1994).

The best disease and pest resistance has been recorded in the material from wild populations collected in the department of Huehuetenango, Guatemala and in the province of Guanacaste, Costa Rica (J.A. Morera and P.E. Nielsen, pers. comm., Sørensen, pers. observ.). This material is distinguished by the smaller size of the leaflets (Huehuetenango) and the deeply lobed leaflets (Guanacaste). The material from both localities has subcoriaceous leaves and the Huehuetenango material in particular is recognized by the prominent brown strigose hairs covering all vegetative parts (Sørensen 1988, pers. observ.).

Practically all the material from wild populations, with the exception of the material collected in the state of Veracruz, Mexico, has been multituberous. However, the wild material from Veracruz was all monotuberous, with a much thicker dark-brown tuber peel. As mentioned above, the wild material evaluated in field experiments has been observed to possess a high level of pest and disease resistance, mainly due to the hairiness of the leaves, but probably also due to a higher rotenone content in the foliage (J.A. Morera and P.E. Nielsen, pers. comm.; Sørensen, pers. observ.).

Among the Far Eastern accessions, a number of the Thai landraces were found to have quite a short production period when they were evaluated at Celaya. These results corroborate the findings of Ratanadilok and Thanisawanyangkura (1994).

P. ahipa

Initial analysis of genetic variation within the 20 accessions available demonstrated that both indeterminate landraces (quite robust vines) and determinate landraces (from those with dwarf-like bushy growth to semi-erect plants with near vine-like appearance) exist. When accessions were grown under greenhouse conditions in Denmark, the general geographical distribution of the growth habit of P. ahipa became apparent: the strongest vine-like genotypes are located in the north, near La Paz in Bolivia, and the smallest bushy landraces are found in the south, in the state of Salta, Argentina. Short semi-erect, determinate genotypes have nonetheless been observed near La Paz (M. Grum, pers. comm.). The considerable variation in flower/seed production recorded among the different accessions may well be the result of differences in the agronomic selection pressure. The short bushy landraces produced less than 100 flowers and less than 20 seeds per plant, and had pollen fertility percentages of less than 45%, whereas several accessions from the La Paz area produced more than 800 flowers and more than 100 seeds per plant, and had practically 100% fertile pollen. Obviously, depending on the aim of a breeding scheme, the variation that still exists is considerable.

P. tuberosus

The distribution of *P. tuberosus*, as described above, is evidently the widest of any one species within the genus. Hence, when contemplating breeding for new and improved cultivars, a comprehensive assessment of the infraspecific variation and identification of the various agronomically attractive traits is needed. Because of its long history of cultivation over a considerable part of the South American continent, there is some difficulty in determining the extent of the natural distribution of *P. tuberosus*. Additional field surveys are urgently needed. It may, however, be deduced that in isolated areas, where the species show little or no variation, the existence of such morphologically uniform cultivars may be the result of a single introduction from neighbouring communities.

Initially, when the first field collections were conducted in 1985, only three accessions were available for taxonomic analysis and agronomic evaluation[4]. Although these three accessions did possess a few distinctive morphological characteristics, e.g. flower colour, inflorescence and legume size, and seed colour, they all had tuberous roots of similar quality, i.e. with relatively low dry matter content. However, 10 years later, the efforts made to increase the information available on the diversity of this species have revealed that the *P. tuberosus* genepool includes an astonishing variety of almost all agronomically important traits, i.e. tuber shape and quality, multi-/monotuberosity, determinate/indeterminate growth habit, drought resistance, and pest and disease resistance/tolerance. The difficulty arises when trying to identify a well-defined geographical area where several of these traits may be found. Again, this is due to the vast area of sporadic cultivation and the lack of information on the location of wild populations.

[4] TC1 18 from Haïti, and TC525 and TC526 from Goiâna, Edo. Minas Gerais, Brazil.

To summarize, the greatest known variation in tuber shape and quality is found in the region along the central part of the Río Ucayali in the Peruvian Amazon. However, as described above, several isolated cultivar groups have been identified (in Ecuador, Peru and Bolivia), and according to the information available from herbarium specimens, several additional populations may possess agronomic characteristics of potential interest, notably in Colombia, Venezuela and Paraguay. The collected wild material still has to be multiplied in sufficient quantity to allow field evaluations for pest and disease resistance/tolerance.

6.3 Importance of wild relatives as a source of diversity

If the high disease and pest resistance observed in *P. ferrugineus* and recorded in multiplication plots in Tonga, Ecuador and Costa Rica can be successfully transferred to the cultivars, this would be of obvious agronomic interest. However, although interspecific hybridization experiments have been repeatedly performed in both Costa Rica and Tonga, combinations involving this species have yet to be developed. The ecological association of *P. ferrugineus* with soil types low in available phosphorus might also be of potential breeding interest, as could be the evergreen habit.

As mentioned above (Section 3.1.2), interspecific hybridization experiments have hybridized *P. panamensis* with *P. erosus, P. ahipa* and *P. tuberosus.* The objective of such experiments is the transfer of the strigose pubescence of the vegetative parts and subcoriaceous leaf type to high-yielding genotypes that are susceptible to insect damage and/or which may need improved drought tolerance in order to increase climatic adaptability. The strigose pubescence has been successfully transferred, and among the resulting hybrids, genotypes with high yield potential have been identified (P.E. Nielsen, pers. comm.).

Pubescence as a means of increasing pest resistance may also be transferred to the cultivars by infraspecific hybridization with genotypes identified within the wild populations belonging to *P. erosus* from either the department of Huehuetenango, Guatemala or from the province of Guanacaste, Costa Rica.

Until actual analyses of the variability in the rotenone content of the two wild species as well as the wild populations of the cultivated species have been undertaken, it can only be speculated whether some genotypes among these groups may possess sufficiently high levels of rotenone to make commercial extraction economic.

6.4 Institutions holding germplasm collections

A comprehensive list of the institutions holding *Pachyrhizus* germplasm is given in Appendix 2. Seed samples have been made available from a large number of institutions to the partners within the Yam Bean Project. The recorded viability of the received germplasm varied from 0 to 100%. Regrettably, most of the samples representing the wild species *P. ferrugineus* received from Central Farm, Belize, have not been viable. This problem is due to the storage facilities available to institutions located in humid tropical conditions. A high humidity content has been found to be especially critical when storing *P. ferrugineus* seeds. *Pachyrhizus* seeds generally lose viability within one year if insufficiently dried; moisture content must be below 10% (preferably 5%) if the seeds are to be stored for prolonged periods, i.e. they are orthodox. The temperature is critical, although to a lesser extent, i.e. temperatures below 5°C are recommended.

Of the *Pachyrhizus* material registered with institutions holding germplasm collections (IBPGR 1981), 98% represents one species only: *P. erosus.* Some accessions may have been registered as belonging to other species, and misidentifications are common.

Very few of the institutions involved have the financial means, interest and knowledge needed to implement an efficient regeneration programme. Furthermore, a number of the recorded accessions stored with institutions which do not form part of the Yam Bean Project are no longer viable. Complete passport data are also lacking for many accessions. Therefore, it is highly recommended that further collecting missions be mounted and new germplasm of this valuable genetic resource be collected.

The principal germplasm collections are located with the individual partners involved in the Yam Bean Project. A complete collection is kept at the Research Division, the Ministry of Agriculture and Forestry, Tonga (South Pacific), where all accessions are being regenerated at regular intervals, and a core collection is kept at the Botanical Section, the Royal Veterinary and Agricultural University, Copenhagen, Denmark. All available passport data are included in the germplasm list available from the author. The completion of a comprehensive catalogue, which will include experimental data on each accession from the pan-tropically conducted field trials, will be a valuable tool when selecting genotypes for introduction to new regions. The largest collection kept by any institution not associated with the Yam Bean Project is kept at the Southern Regional Plant Introduction Station, USDA-ARS in Georgia, USA.

6.4.1 Available data on individual accessions

The available data on individual accessions are generally limited to their origin (although a number of accessions kept at different institutions are of unknown origin) with little or no information on geographic, climatic, edaphic, ecological and agronomic data. This has been one of the major constraints when evaluating accessions obtained from existing germplasm collections, as it is difficult to assess the influence of the selection method used (if any) when comparing the performance of different landraces. Ørting *et al.* (1996) found that Bolivian farmers use very different criteria when selecting plants for seed production.

The partners in the Yam Bean Project have nonetheless endeavoured to collect as much information as possible on the cultivation practices associated with accessions originating from the field collections they have conducted (Ørting *et al.* 1996; Sorensen *et al.* 1996).

6.4.2 Gaps in existing collections

P. erosus

Wild material from the Mexican states of Veracruz, Chiapas and Oaxaca is virtually only known from herbarium specimens. As most of the remaining wild populations are threatened by the deforestation associated with increased land use, initiatives should be taken to conserve these potentially interesting genotypes.

A comprehensive survey of the existing landraces within El Salvador and the neighbouring regions in Honduras is needed. Likewise, surveys of the present status of landraces in India, Vietnam, Laos, Cambodia, Burma, Indonesia and the Philippines have not been undertaken to date.

P. ahipa

Among the gaps in the existing germplasm collections, the lack of any wild *P. ahipa* material is probably the most generally acknowledged. If the report by J. Rea (pers. comm.) from Bolivia on the recent collection of such material can be further substantiated and the material be made available for taxonomic and agronomic research, this would add valuable information on the phylogeny of this species. Moreover, the material is likely to be of considerable interest for present and future breeding programmes.

From what little is known of the extant landraces of the Tarija Province, Bolivia, as well as those from the Argentinian provinces of Salta and Jujuy (to date, only two accessions known to originate in this southernmost part of *P. ahipa's* distribution area have been included in the germplasm collection), it appears that these landraces are morphologically distinguishable by their short bushy growth habit ‘and earliness. Moreover, they have been identified as being highly efficient plants with regard to the three most important quantitative traits: (i) tuberous root growth (high); (ii) growth of the aboveground vegetative parts (determinate and erect/bushy), and (iii) reproductive shoot formation (limited). Clearly, therefore, a survey of these landraces is a high priority.

P. tuberosus

During the last 5 years, the number of new accessions belonging to this species available from the Yam Bean Project germplasm collection has increased dramatically In 1988/89, only three accessions were available: one from Haiti and two from Brazil. As a result of the many field collecting missions conducted during the last few years, the Yam Bean Project germplasm collection now includes some 60 accessions. However, the increased knowledge of the considerable diversity present within the species, combined with the additional information on localities recorded from little-known herbarium specimens, has served to identify a number of localities from which material has yet to be collected. These include northwestern Venezuela/northeastern Colombia, the Colombian Amazon, and the Acre region of Brazil and Paraguay Cultivation is known to be practised in all these areas, but the local landraces are only known from bibliographical references or from herbarium specimens. As the recent 'discovery' of the chuin cultivar group has shown, new genotypes possessing agronomically attractive traits may well exist.

Only seven of the 60 available accessions represent wild material, and it will obviously be of importance to carry out additional field and molecular studies in order to clarify the phylogeny of the different cultivar groups. Furthermore, special attention must be given to the identification of certain genotypes, e.g. those with good resistance/ tolerance to nematodes.

P. ferrugineus

This species has been found to have a very slow multiplication rate. The period from germination to maturity of the seeds is the longest found within the genus, i.e. more than 10 months. Also, seed production is low, generally less than 100 seeds per plant. Hence, even though some 20 accessions have been collected, the quantity of seed available for experiments is limited. One of the main problems when collecting this species is its late seed production; in Central America, mature seeds are available from December to March, while *P. erosus* has mature seeds from August to October. This means that most *P. ferrugineus* accessions have been collected as live plants which have then been transferred to multiplication plots, with a considerable loss of plants as a result.

The morphological variation in leaf outline recorded from field observations is considerable, even within populations. Care should be taken to conserve this variation when collecting. There have been very few studies of tuber quality and the rotenone content of the seeds in this species. Moreover, as preliminary observation in multiplication trials has demonstrated, *P. ferrugineus* is extremely resistant to pest damage and viruses. Full-scale field evaluations would therefore most certainly contribute valuable information on the species.

The available germplasm is limited to material of Costa Rican and Guatemalan origin, and efforts should therefore be made to collect and multiply samples from Mexico, Belize, Honduras, Nicaragua, Panama and Colombia.

P. panamensis

Only one accession of this species is available, and further accessions are urgently required. Although this accession has been included in several field trials, and lately, also in interspecific hybridization experiments, additional germplasm would allow thorough description/evaluation of the infraspecific variation available.

The accession available was collected in Panama in 1985, and additional collections should be conducted in this country. However, as the species has a remarkably disjunct distribution, particular effort should be made to collect and conserve the highly endangered populations in the Sierra Nevada de Santa Marta (Colombia), the Ecuadorian province of Guayas, and also the recently recorded populations in southwestern Venezuela.

6.5 Conservation of the species: *ex situ, in situ* and on-farm techniques and methods

At present, only standard *ex situ* conservation techniques are being used to preserve the germplasm collected. There is some indirect *in situ* conservation of wild populations of *P. ferrugineus, P. panamensis* and *P. tuberosus,* as populations belonging to these three species are located in national parks and forestry reserves, e.g. Mountain Pine Ridge Forest Reserve (Belize), the Canal Zone (Panama) and La Perla (Ecuador). The species are thus in no imminent danger of extinction.

Wild *P. erosus* populations in Central America are generally located along secondary forest edges, and in a few cases, in deciduous forests. None of the populations has been seen within nature reserves, however, and this material may therefore be considered endangered.

From surveys of the status of the present landraces that exist, knowledge of alternative *in situ* methods of conserving rare and endangered cultivar groups is rapidly increasing. A survey of the Bolivian *P. ahipa* was conducted from April to June 1994, in order to record its present status in cultivation, to examine the infraspecific variation and to conserve as many extant local landraces as possible (Ørting *et al.* 1996). During the nine weeks the survey lasted, some 16 localities were visited, 24 farmers were interviewed and 17 new accessions (15 of *P. ahipa* and 2 of *P. tuberosus)* were collected. These collections prove that landraces are still to be found. Nonetheless, only 65% of farmers interviewed intended to continue to cultivate this crop, a situation which calls for urgent action.

In the case of *P. tuberosus,* a similar situation applies to the jíquima cultivar group in the province of Manabí, Ecuador, where a substantial proportion of the farmers interviewed did not intend to continue cultivating the crop. The ashipa and chuin cultivar groups are also in jeopardy, seriously threatened by the ever-increasing speed with which traditional cultivation systems are being replaced by monocropping of a limited number of cash crops. The situation is practically identical for the rare *P. erosus* landraces grown in shifting cultivation, or for other traditional cropping systems in the Yucatan peninsula.

On-farm seed storage in both *P. ahipa* and jíquima involves the use of insecticides (rarely fungicides) and sealed containers. Usually the seeds are dried prior to storage, either in the sun or close to the fire. In the Amazon, seeds are only kept for 4-5 months, i.e. the period from harvest to replanting, as the viability of the seeds is rapidly reduced by longer storage. *In situ*/on-farm methods could well be used successfully in the conservation of both the *P. ahipa* and the jíquima cultivar groups. And given the clearly exiguous current knowledge of and interest in these crops, their promotion by agricultural policy-makers would further contribute to their survival.

6.6 Use of germplasm in research, breeding and crop improvement programmes

In principle, all accessions included in the Yam Bean Project germplasm collection have been or will be morphologically described and evaluated for agronomic potential. The feasibility of this process obviously depends on the quantity of seed available, but results from field trials involving some 50 accessions have been published (Grum *et al.* 1991b, 1994,1996).

At present, the only intensified breeding for new cultivars involving traditional methods is conducted at the INIFAP, CIR-Centro, Estación Experimental de Bajío (Mexico). Over the last 30 years here, A. Heredia Z. has produced the high-yielding Mexican *P. erosus* cultivars, using local landraces and an intensive selection method based on initial evaluation at commercial spacing, including reproductive pruning. The best-performing individual plants are then selected according to tuber quality (shape and taste), habit and earliness at harvest, and replanted to produce seed during the following season. (The inflorescences are isolated in order to ensure self-pollination.) This cycle is then repeated on the individual lines until the desired plant type is obtained.

The use of advanced radiation techniques in the breeding of new *P. erosus* cultivars has been attempted at the Department of Botany, University of Kerala, Trivandrum, India. Because of the lack of infraspecific variation in *P. erosus*, the aim of these experiments was to obtain an increase in phenotypic variation through induced mutation. Determinate, erect, bushy *P. ahipa*-like plants resulted from the experiments (Nair 1989; Nair and Abraham 1985,1989,1990).

Initial hybridization experiments were conducted to examine the interspecific compatibility of the three cultivated species, *P. erosus, P. ahipa* and *P. tuberosus* (Grum 1994a; Heredia G. 1994; Sørensen 1989, 1991; Sørensen *et al.* 1993). Fertile interspecific hybrids from all combinations (including reciprocal crosses) were obtained, with the exception of the cross between *P. ahipa* (female) x *P. tuberosus* (male), where seeds were produced but were not capable of germinating. The pollen fertility of the hybrids was generally reduced by 10-20%, compared with the parental species.

Hybridization experiments involving the wild species *P. panamensis* conducted in Benin and Tonga have demonstrated that this species is fully compatible with the three cultivated species (Grum 1994a; D.F. Adjahossou and P.E. Nielsen, pers. comm.). Hybrid combinations involving the fifth species *P. ferrugineus* have not yet been successful. Although they have been repeatedly attempted, only one such combination (*P. ferrugineus* x *P. erosus*) has produced seeds (P.E. Nielsen, pers. comm.).

Field trials evaluating the initial interspecific hybrids have been in progress since 1989. As a result of these experiments, hybrid lines selected in Mexico are now approaching non-segregating generations (+F_6) According to information from A. Heredia Z. (pers. comm.), this material may be released to producers in l-2 years. The new 'cultivars' of *P. erosus* x *ahipa* origin will possess traits inherited from one species or the other, e.g. the tuber quality of *P. erosus* combined with the erect, determinate growth habit and earliness of *P. ahipa*.

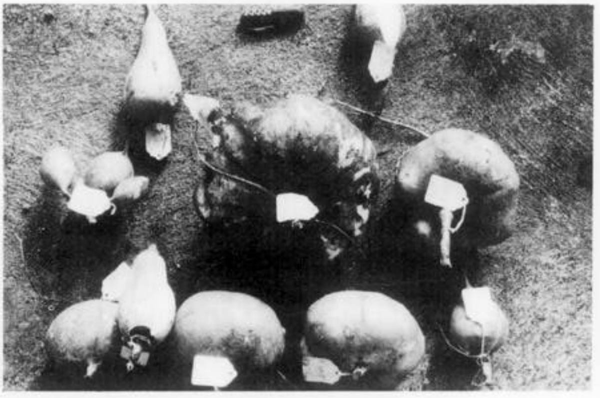
Similar field experiments involving both the *P. erosus* x *ahipa* combinations tested in Mexico, as well as *P. erosus* x *tuberosus* and triple hybrid combinations involving *P. tuberosus* x (*P. erosus* x *ahipa*), have been conducted in Tonga. These trials are being performed according to the pedigree method (5%), with tuber shape/size, determinate growth habit, pest resistance and seed yield as the selection criteria. Seed yield is included as a selection criterion in the breeding of new cultivars from interspecific hybrids, as an inbreeding depression has been found to reduce seed set below a critical level in later generations (pers. observ.). Reduced germination rates have also been recorded in interspecific hybrids, but when testing the frequency in multi-location trials, the results were inconclusive (Grum 1994a).

7 Breeding: brief description of the common-breeding selection procedures

Although there are only five species of yam bean, the genetic and morphological variation is considerable, and quite sufficient to provide the basis for substantial improvements through breeding. The potential of the genus as a sustainable crop with a wide range of uses, producing high yields under different climatic and edafic conditions, has been clearly demonstrated. Furthermore, it has been shown to be readily accepted in Africa by consumers unfamiliar with the crop. The exported crop has also been accepted by farmers and consumers in the Pacific, albeit at a slower rate.

The breeding programme within the Yam Bean project involves hybridization experiments focusing on the development of new, high-yielding cultivars (Figs. 11a, b). All known varieties (Mexican, Indian or Far Eastern) are the result of selection without previous hybridization. In India, some experimental genotypes have resulted from radiation experiments (Tiwari *et al.* 1977; Nair 1989; Nair and Abraham 1985, 1989,1990).

a



b

Fig. 11a. (left) *Pachyrhizus erosus.* Isolation of inflorescences to ensure selfing, from multiplication of new accessions, INIFAP-CIR CENTRO, Campo Experimental Bajío, Celaya, Mexico (Photo, M. Sørensen).

Fig. 11b. (right) *Pachyrhizus erosus.* Tubers from *P. erosus* x *ahipa* hybrids (F_3) from a single cross, grown at Vaini Research Station, Tonga. (Photo, M. Sørensen).

Hybrids combining the growth characteristics and reduced photothermal sensitivity (daylength and temperature neutrality) of the Andean yam bean, the vigour of the Amazonian species and the high yield capacity of the Mexican yam bean, will theoretically result in the breeding of cultivars with considerably increased climatic/edaphic adaptability. To date, four of the five species have been successfully hybridized. Selections based on yield and adaptability experiments began in 1989, and the evaluation of third to sixth generation hybrids is currently underway. At present, some 600 hybrids are being tested at the experimental stations in Mexico, Costa Rica and Tonga cooperating within the project (Sørensen *et al.* 1993; Grum 1994; Hartmann 1994; Heredia G. 1994).

7.1 Challenges for the traditional and more advanced production areas

The major challenge for the main large-scale *P. erosus* production areas in Mexico is the development of new early maturing cultivars that will allow continuous production within the country alternating between the lowland regions, i.e. the State of Nayarit, and the areas at higher altitudes in the states of Guanajuato and Michoacán. Breeding of new cultivars with a thicker skin in order to decrease susceptibility to bruising during transport and prolong shelf-life is a trait also given high priority by local producers. These characteristics are present in wild material and some cultivars from the state of Nayarit.

The development and introduction of improved *P. erosus* cultivars to be used by most smallholders in the traditional intercropping systems of Mexico and Central America should also be given high priority. Given the high heritability of selecting for diameter and its high correlation with yield, participatory breeding methods may be appropiate here (Sørensen *et al.* 1993).

In India and Southeast Asia, extensive evaluation of the advanced Mexican cultivars as well as new cultivars of hybrid origin will have to be carried out under field conditions.

The remarkable success of the recent introductions of both *P. erosus* and *P. tuberosus* in a number of West African countries should be followed up by trials evaluating a wide range of the available genotypes and interspecific hybrids. Furthermore, the potential of the chuin cultivar group (*P. tuberosus*), with its high dry matter content similar to the traditional root crops cultivated in this region, should be evaluated in multilocational trials. It ‘seems probable that new cultivars developed from the chuins would have immediate consumer appeal. Furthermore, being legumes, they would obviously be highly sustainable and nutritious, and their higher starch content increases their potential role as a stable food.

As mentioned above, in order for these crops to remain attractive to local farmers, the development of improved cultivars of both *P. ahipa* and *P. tuberosus* (the jíquima group) is urgently needed.

7.2 Major constraints and possible solutions

The yam bean rather uniquely combines the yield reliability of a root/tuber crop, with the high sustainability of a legume with efficient biological nitrogen fixation and an ideal nutritional composition of proteins and carbohydrates. When its high climatic and edaphic adaptability and good disease and pest tolerance/resistance is added, the potential of the genus cannot be ignored Yet, despite its obvious agronomic advantages, the yam bean remains a little-known and underutilized crop.

If the crop (either fresh or processed) was produced in sufficient quantities to become registered as a commodity with world trade potential, the scientific and developmental interest in yam beans, which until recently has been negligible, would most certainly increase. There is little doubt that if the genus were to receive more attention from researchers in both basic and applied sciences, knowledge and consequently Production of yam bean would increase dramatically. That this has not happened to date is attributable to a number of unfortunate coincidences.

The ‘fruity’ tuberous root quality found in the majority of the yam beans is a major constaint to their introduction to areas unfamiliar with tuber/root crops of this type. (As mentioned above, the crop is also threatened locally in traditional areas of cultivation by the promotion of ‘new' cash crops.) A solution to the problem of fruitiness has fortunately been found in Peru with the identification of the chuin cultivar group. This will allow the introduction of a high-yielding tuberous legume with a tuber quality similar to that of the traditional root crops. Once the chuin has been successfully introduced, it will be easier to widen the range of yam bean cultivars to include those having the fruity or vegetable-like tuber quality

Alternatively, new sweet-flavoured, fruity cultivars maybe selected or bred from the ashipa landraces. However, the promising *P. tuberosus* landraces identified so far are all multituberous, and the tubers are produced at considerable depth. Further evaluations and screening for these traits must therefore be conducted prior to actual breeding.

Lastly considering the crop’s growing status in the United States, there is every reason to suppose that the untapped European market could also offer valuable export opportunities for yam bean growers.

Although a seed-multiplied tuber /root crop has some obvious advantages over the vegetatively propagated ones, seed production may be a major constraint to spread of the crop. There are few results available on optimization of seed production, and in some production areas, the storage and control of seed-damaging insects, e.g. bean weevils (bruchids), are major limitations. To resolve these problems, further studies are needed on seed set, seed size (there is a strong positive correlation between seed size and yield in *P. erosus,* according to M. Grum, pers. comm.), rotenone content of mature seeds (in order to reduce insect damage), and analyses of the germination/storage capabilities of different genotypes.

Because of the obvious competitive source-sink relationship between tuber growth and seed production, there is a need for field studies of the correlation in different cultivars/landraces between the response to reproductive pruning with regard to tuber yield and the seed yield of unpruned plants (Grum *et al.* 1996). In order to ensure seed availability, it will be important to breed for new cultivars which will produce high tuber yields when reproductively pruned, but which will also retain a high seed yield when grown for seed production (the possibility of using chemical treatment to effectively control pollination has so far only been examined in India by Srivastava *et al.* (1973) using 2,4-D).

In *P. ahipa,* the simple racemes and the low number of flowers per raceme make inflorescence pruning extremely difficult. Bolivian farmers report that their fingers bleed after 2 days of removing flowers individually. The introgression of a *P. erosus*-style inflorescence would alleviate this vital problem by making inflorescence pruning considerably easier.

7.3 Opportunities for modern biotechnology

The use of *in vitro* techniques is an attractive possibility when contemplating the rapid multiplication of genotypes of limited availability for conservation purposes, or of hybrids or new material from field collections possessing agronomically attractive traits identified in field trials. If such genotypes were instantly to become available in sufficient quantities, they could be subjected to field evaluations almost immediately after their identification/selection.

Several institutions, in Costa Rica, Denmark, Ecuador and Trinidad, have initiated studies in this field (Forbes and Duncan 1994). The experiments conducted so far have involved regeneration and multiplication from adventitious and axillary shoots (explants), and callus formation with subsequent organogenesis, i.e. the development of a protocol for somatic embryogenic systems. To date, these experiments have succeeded in generating callus, shoot and root formation in selected accessions of *P. erosus* (Muñoz E. and Krogstrup 1996).

Molecular taxonomy, the relationship between the different species, is currently being studied at the Plant Sciences Laboratory, School of Biological and Medical Sciences, University of St. Andrews (Philips *et al.*, unpublished). Molecular analysis appears to be an obvious new approach in the improvement of agricultural production of yam bean. Ultimately however, the use of this technique depends on the availability of appropriate germplasm for developing drought-tolerant, photothermally neutral, and pest- and pathogen-resistant cultivars that are capable of producing high yields over a wide range of climatic and edaphic conditions. In view of the situation concerning *Pachyrhizus* germplasm in South America, which is widely recognized as critical by national and international agencies, a genetic resources assessment programme is a top priority

The molecular research in progress involves cross-breeding and examination of the stability of various genetic characters, utilizing isozyme variation over 20 enzyme systems. It also uses polymerase chain reaction (PCR) to resolve randomly amplified polymorphic DNA sequences (RAPDs) analysis and assess and resolve the level and distribution of genetic diversity within and between *Pachyrhizus* species. The analyses are carried out on a representative sample of the existing germplasm collection of *Pachyrhizus* that includes all species and a wide range of cultivars, landraces and wild material.

A survey of molecular-genetic diversity in the germplasm collections of *Pachyrhizus* will allow the following:

(i) estimation of the level and distribution of genetic diversity within and among species
(ii) location of natural centres of genetic diversity for collection and conservation
(iii) analysis of phylogenetic relationships within the genus *Pachyrhizus*, with particular emphasis on the origin of the cultivated species, *P. ahipa*, *P. erosus* and *P. tuberosus*
(iv) fingerprinting specimens exhibiting genetic traits associated with valuable constituents, e.g. production of the insecticide rotenone.

7.4 Alternative approaches for crop improvement

P. erosus

The diversity of the available *P. erosus* germplasm that is sufficient to breed a wide range of new cultivars depends on the climatic/edaphic conditions prevalent in new production areas, as well as on local consumer preferences regarding tuber quality. Once multilocational field evaluations include all available lines, it will be possible to identify the best-performing genotypes to be used when breeding new cultivars.

As almost all traditional cropping systems involving *P. erosus* are of the multiple or intercropping type, there seems to be a clear need to include field trials examining the performance of different genotypes in association with a variety of traditional neotropical crops. Crops of African or Asian origin should also be tested, however.

P. ahipa

Recent molecular studies of the phylogeny of the different species indicate that *P. ahipa* must be considered a monophyletic group, with *P. tuberosus* as its closest relative.

Interspecific hybridization experiments involving the three cultivated species have demonstrated that it is possible to breed new cultivars possessing agronomically desirable characters, e.g. short cultivation season (4 months from sowing to harvest of marketable tubers in Celaya, Guanajuato and Mexico (Sørensen, pers. observ.)) and erect to semi-erect growth habit.

As wild material of *P. ahipa* is at present unknown, additional field collecting would be of considerable value in substantiating current notions of the-phylogeny of this species. Furthermore, wild forms of *P. ahipa* may have been of the multi-tuberous type, and this hypothesis cannot be confirmed until a wild progenitor of this species has been localized.

P. tuberosus

The three different cultivar groups, i.e. the chuin, jíquima and ashipa, have each been developed according to different criteria. The chuins, with their high dry matter and soluble sugar content, are unique in being the only yam beans which may be considered a true source of stable food; all other cultivars and landraces are of the fruity or vegetable type. Thorough investigations examining the various cultivation aspects of this group must be completed prior to any large-scale promotion of new cultivars developed from this material. However, the theoretical attractiveness of a leguminous alternative to the traditional root/tuber crops cannot be ignored. Any study of the fascinating potential of inter- and infraspecific hybrids involving the chuins will require the collaboration of a number of scientists over an extended period, however. If a new cultivar possessing the tuberous root quality of the chuins and the erect, bushy habit and earliness of *P. ahipa* were to be bred, its cultivation potential in most developing countries would be inestimable.

Results from field trials examining the potential of the jíquima group are still limited. Although several accessions belonging to this group have been repeatedly tested at both CATIE, Costa Rica and in Tonga, their recorded yield performances have so far been disappointing, i.e. 0.5-5.0 t/ha. Although there was a remarkable response to reproductive pruning, the cultivation practice involving pruning of the vegetative part did not significantly improve yield (Nielsen *et al.*, unpublished). The more humid climatic conditions and the very different soil types at the trial sites in Costa Rica and Tonga may be the main reason for the poor results to date. Also, the low planting densities used in Manabí could well account for the lower yields obtained when the crop is grown at a much higher density in the trials. The drought tolerance of the jíquima group has yet to be examined, but it seems reasonable to assume that genotypes selected for a prolonged period under the dry climatic conditions and short production period in Manabí would have developed adaptational advantages that are not present in the other two cultivar groups.

In the ashipa cultivar group, several landraces with a remarkably sweet and refreshing tuber quality (soluble sugar content 6-7%) have been identified. However, as the genotypes belonging to this group are very large vines and in general have a long production period, breeding for smaller and earlier plants may result in new cultivars with a rather different fruity tuber quality The most promising genotypes identified have yet to become available in sufficient quantities to allow large-scale field evaluations.

8 Ecology

8.1 Photothermal neutrality (daylength/temperature sensitivity)

It is a generally held view that yam beans are short-day plants, i.e. that flowering and tuber production will only take place under decreasing daylength. However, both field studies/observations and experiments conducted under greenhouse conditions have demonstrated the existence of genotypes with reduced or almost absent photothermal sensitivity.

P. erosus

Daylength sensitivity in *P. erosus* has been studied by several scientists. Paull *et al.* (1988) reporting from experiments conducted under field conditions in Hawaii using local cultivars observed a significant overlap between flowering and tuberization during short days. Also, the field examinations conducted at the INRA experimental station in Guadeloupe FWI have increased knowledge on the response to different planting dates and tuber growth (Robin *et al.* 1990: long-day; Sørensen *et al.* 1993; Vaillant and Desfontaines 1995: shortday; Zinsou *et al.* 1987, 1987b, 1987c, 1988; Zinsou and Venthou-Dumaine 1990). The results from Guadeloupe confirm the findings by Paull *et al.* (1988) thus demonstrating the strong competition between shoot growth, flowering, pod formation and tuber growth. Conversely, during long days, tuber growth was seen to begin after 4-6 weeks, but the vigorous shoot growth had a limiting effect on tuberization. Flowering was first initiated when the daylength approached 12.5 hours. Cotter and Gomez (1979) studied the behaviour of two Mexican cultivars under both short-day (9 hours natural light) and long-day greenhouse conditions (9 hours natural light + 4 hours artificial light). They also observed increased tuberization during short days.

Although it is highly probable that temperature, especially the difference between day and night temperature, influences tuber growth and flower initiation, no reports on the significance of this factor have been seen for this species.

P. ahipa

The species has been grown continuously in the greenhouses at RVAU, Denmark. Seeds have been planted in almost all months of the year. *P. ahipa* accessions have been observed to have the most rapid flower initiation, i.e. from 87 days after sowing (in plants with determinate growth habit) to 140 days (in indeterminate plants), regardless of the season (Ørting, unpublished). Furthermore, the tuber growth does not appear to be influenced by variations in daylength, hence this species may for all intents and purposes be regarded as daylength neutral, and neutral lines may be bred from interspecific hybrids involving the species.

According to I.F.M. Válio (1995, pers. comm.) M. de Fatima Ferrine has studied daylength sensitivity in 4-5 accessions under different light and temperature regimes at UNICAMP, Brazil. However, the results from these experiments have yet to be published.

P. tuberosus

Alvarenga and Válio (1989) evaluated the effect of different temperature and photoperiodic regimes on the initiation of flowering and tuberous root formation in genotypes belonging to the ashipa cultivar group. They observed that flowering was only induced in this species at intermediate daylengths, i.e. 9-16 hours. The crop may be considered a short-day plant with respect to tuberization, as this process only occurs at photoperiods of less than 16 hours. The day/night temperatures of 30/25°C delays and reduces flowering, and completely inhibits the formation of the tubers, processes which are both increased at day/night temperature regimes of 25/20°C and 20/15°C (Alvarenga and Válio 1989).

8.2 Climatic and edaphic requirements

Physiological studies of the response to drought in *Pachyrhizus* have been carried out under field conditions in Senegal (Annerose and Diouf 1994) and under greenhouse conditions in France (Vieira da Silva 1994, pers. comm.).

The studies in Senegal demonstrated *P. erosus* to be good drought avoider and *P. ahipa* to be a drought-tolerant species. The latest trials, designed as pot trials, are aimed at studying developmental competition between the reproductive organs (flower, legume and seed) and the storage organ (tuberous root) under the influence of drought. The experiments using *P. ahipa* include four different treatments: (i) reproductive pruning and water stress; (ii) reproductive pruning without water stress; (iii) no reproductive pruning with water stress, and (iv) no reproductive pruning, without water stress. The results indicate that reproductive pruning has no influence on the physiological response to drought.

The experiments studying the drought tolerance of the accessions of *P. ahipa* based on the correlation of leaf polar lipids and fatty acid composition on the cell membrane resistance to osmotic stress demonstrated the considerable variation in response to drought between these three accessions (AC102, AC521 and AC524) and the comparative high drought tolerance in comparison with other tropical leguminous crops (Vieira da Silva 1995).

As a general rule *P. erosus* will thrive best in light, rich, sandy-loam or alluvial soils in zones with a moderate precipitation rate, i.e. approximately 1500 mm m.a.p.r. (mean annual precipitation rate). Depending on the genotype, both lower and higher precipitation rates will allow successful cultivation. Srivastava *et al.* (1973), however, recommend a heavier clayey soil. For example, *P. erosus* will produce economic yields in the Ecuadorian province of Esmeraldas at precipitation rates of +6000 mm m.a.p.r. (A. Arévalo T. 1993, pers. comm.). At Dakar, Senegal, with 240 mm m.a.p.r., yields of between 15 and 34 t/ha were obtained for the species (Annerose and Diouf 1995a, 1995b).

P. erosus

In areas with an annual dry season, the habitat is along deciduous forest edges and in scrub vegetation, on soil types ranging from deep clay to sandy loam. The species is recorded from 0 to 1750 m a.s.l., with the majority of records from 500 to 900 m a.s.1. The rainfall range varies from 250-500 mm to over 1500 mm (m.a.p.r.). The optimal day/night temperature range is between 30 and 20°C.

In cultivation, well-drained, sandy, alluvial soils are preferred, especially when the crop is irrigated. Experiments in Tonga indicate that soils low in available phosphorus may limit the efficiency of the biological nitrogen fixation (P.E. Nielsen, pers. comm.).

P. ahipa

The habitat of this species, which (as has been described above) is only known in cultivation, is cool tropical/subtropical valleys. It appears to be well adapted to an altitudinal range of 1800-2600 m a.s.l., though the crop has been recorded at +3000 m a.s.1. in sloping north-facing fields fully exposed to the sun. The region of cultivation is located along the border between the warm (‘terra templada’) and cold tropics (‘terra fria’). The average temperature within the region, where climatic conditions are extremely dependent on the time of day, is 16-18°C. The temperature oscillates between a minimum of 0-5°C and a maximum of 30-35°C. As the average annual precipitation rate is between 400 and 700 mm, occurring within 4-6 months of the year, the remaining months forming the dry season, the climate is semi-arid. Farmers reported that the cultivation period lasts 5-10 months, depending on the length and intensity of the rainy season. The *P. ahipa* plant will tolerate long dry spells, but in order to increase tuber yield, an additional water supply is essential. Cultivation is predominantly carried out along loamy river banks, although in some cases, sloping hillsides with loamy soil may also be used. A well-drained soil type with a pH value of 6-8 will meet the edaphic requirements of the crop (Ørting *et al.* 1996).

P. tuberosus

This species prefers (and performs optimally) in somewhat sandy or light, well-drained but fertile soils. Cultivated in forest clearings or along rivers in the tropical regions of South America. The optimal altitude is 1200 m a.s.l., but cultivation is. possible within an altitudinal range of from 550 to 2000 m a.s.1. according to Munos Otero (1945). The precipitation range is 640-5000 mm m.a.p.r., with temperatures varying between 21.3 and 27.4°C and a soil pH range of 4.3-6.8 (Munos Otero 1945; Duke 1981; Sørensen 1990; Sørensen *et al.* 1996).

Jíquima is found at 30-350 m a.s.1.; precipitation 450-500 mm m.a.p.r.; maximum temperature 31.l-31.6°C, and relative humidity 90% during the rainy season.

Ashipa is found at 300-2000 m a.s.1.; precipitation 1500-5700 mm a.p.r.; average temperature 20.7-25.5°C; minimum temperature 11.0-13.2°C; maximum temperature 29.7-35.4°C, and relative humidity 84-92% (figures from Ecuadorian Amazonia).

Chuins are found at 100-300 m a.s.1. The limited altitudinal range is due to the restricted area in which landraces belonging to this cultivar group have been so far identified. The annual precipitation along the Ucayali is ±3000 mm.

8.3 Impact on the environment

The beneficial effects on the environment, mainly as a result of biological nitrogen fixation, must be considered to outweigh the harmful ones. The positive environmental effects of *Pachyrhizus* spp. include: (i) highly efficient nitrogen fixation and increased vigour among the neighbouring plants (especially on poorer soils); (ii) good drought tolerance and provision of high protein forage for livestock and other herbivores; (iii) effective control of soil erosion, although not as vigorously as *Pueraria* spp.

Negative effects include: (i) seed propagation, i.e. the crop may easily be spread into the wild vegetation bordering fields cultivated for seed production; (ii) rotenone/rotenoid content – the poisonous seeds may cause problems in livestock foraging on escaped plants among the wild vegetation; (iii) possible damage to ecosystems caused by unauthorized piscicidal use of seeds; (iii) vigorous growth – a few of the *P. tuberosus* genotypes are very large, strong vines that may upset fragile indigenous flora; (iv) risk of infection of escaped plants of the species by different viruses and their serving as hosts for such diseases - in areas suffering from heavy infestation by nematodes, escaped plants may serve to maintain a high level of infestation, and some insect pests, e.g. *Diabrotica* spp., may also find refuge on escaped plants.

Obviously, rigorous quarantine measures should be implemented when introducing the crop to new regions, in order to minimise the risk of introducing diseases (especially possible seed-borne viruses). More importantly, the bean weevils (bruchids) specific to *Pachyrhizus* do not occur in any of the areas outside the neotropics.

9 Major and minor production areas

As described in Section 3, the major production areas of *P. erosus* in the neotropics are Mexico, Guatemala and El Salvador. In the palaeotropics, they are Southeast Asia including the Philippines, China and India. Production takes place on a minor scale in the other Central American countries of the Caribbean, in French Guyana and Brazil, in some West African countries, and also on several Pacific islands.

There are no major production areas of *P. tuberosus* and *P. ahipa,* although the tubers of both species may occasionally be found on sale at the markets of the major cities in Ecuador, Peru and Bolivia.

9.1 For home consumption

All three species are localized, grown by smallholders for home consumption throughout their respective distribution areas. In the case of *P. erosus,* minor home garden production may be found scattered throughout the Mexican states south of latitude 20°N. In Central America, cultivation takes place in isolated areas of practically all countries. In Southeast Asia, with the exception of the recent survey of the status of the crop in Thailand (Ratanadilok and Thanisawanyangkura 1994), little information on the present cultivation area and localities is available. In Vietnam and Cambodia, the crop is of considerable importance, according to M. Hermann and J. Engels (pers. comm.). Hence, although *P. erosus* is known to be generally cultivated within the region, Indonesia and the Philippines included, no governmental agricultural research institution has undertaken a national survey to date.

Both *P. ahipa* and *P. tuberosus* are mostly cultivated for home consumption only. Indeed, the local chuin and ashipa landraces of *P. tuberosus* cultivated in Amazonia are exclusively grown for use by the individual families themselves, or within a small community.

9.2 For local markets

Tubers of *P. erosus* landraces grown in Mexico, El Salvador, Guatemala, Belize, Honduras and Nicaragua are occasionally sold at the nearest local village market. This is also the case in the Philippines, Malaysia, Cambodia, Burma, Laos, Vietnam, Thailand, Indonesia, China and India. The majority of the *P. erosus* tubers produced in Hawaii are sold locally, but a part of the produce is marketed in California:

In Bolivia, the *P. ahipa* tubers for commercial use are principally sold at the nearest village vegetable market. For this reason, only a fraction of production reaches the markets in the larger cities.

In the Manabí province of Ecuador, the tubers of the jíquima (*P. tuberosus* complex) are only marketed locally. There are no reports of the tubers of the chuin and ashipa being sold, even at local markets. This situation is probably attributable to a lack of access to local markets, due the geographical isolation of Amazonian communities.

9.3 For international export

Only *P. erosus* is cultivated for exportation. The only large-scale export production takes place in the Mexican states of Nayarit, Michoacán and Guanajuato. All the tubers of export quality are transported and sold on the US market, the only one for which estimates are available on total export: circa 11 500 t per year are sold through wholesalers at an approximate market value of US$1.00/kg. In Thailand, a small fraction of the production is exported and sold through the oriental speciality stores in the major cities of Europe. China and Malaysia export a minor part of their produce to Japan.

10 Agronomy

10.1 Propagation of the crop

All three species are as a rule seed-propagated. The seeds are campylotropous and the seedling development is hypogeal.

P. erosus

In large-scale tuber production, the yam bean grower will generally buy the necessary seeds from a seed producer. In Mexico, the production of seed on a large scale is carried out in separate fields/plots as the crop is trellised in order to facilitate the harvest of mature legumes/pods (Sørensen 1991, pers. observ.). In Thailand, the method used is similar although trellising is not used (1994, pers. observ.). The production period is from 8 to 10 months, the crop is harvested manually and the shelling can be mechanized.

Smallholders will not have separate plots for seed production, but will either buy the seeds from neighbouring producers or alternatively leave sufficient plants in their field for seed production when harvesting the tubers.

The seed rate used varies according to the cultivation system and desired tuber size, and seeding rates of 60-240 kg/ha have been recorded in Mexico and Thailand (A. Heredia Z. 1990, pers. comm.; Ratanadilok and Thanisawanyangkura 1994). Deshaprabhu (1966) incorrectly states that *P. erosus* may be propagated by tubers as well as by seed.

P. ahipa

Ørting *et al.* (1996) report that two different methods are used when selecting plants for seed production: the grower will either (i) select the healthiest and most vigorous-looking plants and leave these without reproductive pruning to produce seeds or (ii) leave the first-developed legume/pods on all plants and remove all those produced subsequently

Seeding rates of 21-105 kg/ha have been recorded, but general rates are 40-65 kg/ha. Again, factors such as preferred tuber size, soil fertility and obviously seed weight play a major role in determining the rates (Ørting *et al.* 1996).

P. tuberosus

Munos Otero (1945) reports either 15 kg/ha when planting at 0.60 m between rows and 0.30 m between plants, or 35-40 kg/ha when broadcast, depending on the cultivation system used. When planted by hand, three seeds are usually sown at each planting station (Munos Otero 1945). Germination is somewhat slow, usually occurring 10-12 days after planting (Munos Otero 1945; P.E. Nielsen, pers. comm.). The seed will remain viable for one year at the most under humid conditions (A. Arévalo T., pers. comm.) and for 2.5-3 years when kept dry (Munos Otero 1945), but significantly longer when stored under optimal conditions in seed banks (P.E. Nielsen, pers. comm.).

In the case of the jíquima cultivar from Manabí, the seed rate used is 45-50 kg/ha Sørensen *et al.* 1996). The ashipa and chuin cultivar groups are planted at significantly lower plant densities. As has been mentioned, some of the tubers produced by the multituberous cultivars may occasionally be harvested individually, leaving the plant with one remaining tuberous root in place to produce additional tubers. A single report from Brazil states that small tuberous roots may occasionally be used as propagation material (Peckolt 1880). This observation has yet to be reconfirmed, however.

10.2 Crop husbandry

P. erosus

The traditional cropping system involving common bean, maize and *P. erosus* is described in Section 2.3. When cultivating the crop as a monocrop on a larger scale, the preferred soil types are light (alluvial) and well drained, as these remain loose after rain or irrigation. Heavy soils are not desirable because of their poor drainage and as they also may cause deformation of the tubers.

Field preparation must be thorough to ensure an even germination and to avoid fungal attacks. Fields should be ploughed to a depth of 0.25 m and harrowed to smooth the seedbed. Time of planting depends on the area.

In Mexico, the recommended plant density/distance for irrigated fields is in double rows on ridges with 0.75 cm between furrows, 0.25 m between rows and 0.15-0.20 m between plants. The seeds should be planted at a depth of ±30 mm when dry planting and ±60 mm when irrigated. A seed rate of approximately 35-40 kg/ha is required at this density depending on the cultivar/seed size. In general no fertilizer application is needed,, although adding phosphorus may be recommended to obtain the optimal biological nitrogen fixation. It is likewise recommended to harrow (or weed manually) at least twice during the first couple of months, to eliminate weeds, and, the second time, to earth up the ridges to cover the growing tubers. These may otherwise be attacked by rodents and insect pests.

In Mexico the crop is never fertilized (A. Heredia Z, pers. comm.; Sørensen, pers. observ.). If the crop is dry planted, the first irrigation is crucial for even germination. Once the crop is well established, a suitable soil moisture content must be maintained and care must be taken not to overwater or stress the plants. The number of irrigations will depend on soil type and evaporation.

Reproductive pruning is necessary to obtain maximum yields. As has been demonstrated in numerous field trials, the effect of the operation depends on the cultivar, the season used (whether long or short day) and the climate. In some areas, not only are the reproductive shoots removed, but the top half of the vegetative part is also pruned. In most Mexican *P. erosus* cultivars, two reproductive prunings will suffice to ensure a good yield.

In general no insecticides are used in disease and pest control. Plants infected by viruses are removed and destroyed (A. Heredia Z, pers. comm.; Sørensen, pers. observ.).

Depending on the species and cultivar/landrace grown, harvest may commence from 4 to 10 months after sowing. In Mexico, the tubers may be lifted immediately or left in the field for 3-4 months until the best market price can be obtained.

P. ahipa

P. ahipa is generally grown as a monocrop, but may in some instances be intercropped with maize. Crop rotation is always practised and *P. ahipa* is cultivated prior to maize/potato, maize/tomato, maize/oca *(Oxalis tuberosa* Molina), groundnut or manioc. Planting distances vary from 20 to 60 cm between rows and 6 to 25 cm between plants within rows, i.e. 8-35 plants/m^2. The crop is planted on ridges when flood irrigated, which in general is necessary in this region. As part of the land preparation, the soil was loosened to a depth of 15-25 cm using a hoe, and thoroughly cleaned of weeds and stones. There were no reports of later weeding, but the practice of reproductive pruning was regarded as being of considerable importance. This manual operation was reported to be conducted twice to obtain the optimal tuber size.

There are no records of disease problems in this species (Ørting *et al.* 1996). Some damage to the foliage is caused by leaf-eating insects, but as the plots are generally small, larvae are removed by hand. The most serious problem is caused by tuber-damaging nematodes, and the only means of control practised is crop rotation and avoiding the use of known ‘problem fields’.

P. tuberosus

P. tuberosus is a crop that makes few demands when grown (i) by various indigenous peoples of the Amazon region and occasionally in ‘chacras’, i.e. fields, surrounding remote villages located in the premontane rain forests of Peru; (ii) in the seasonal flood bank cultivation found along rivers like the Río Ucayali, or (iii) in shifting cultivation in the Amazon proper. The initial preparation of the field is of some importance to ensure uniform germination. Some weeding is needed to achieve good plant cover, but otherwise only pruning of the vegetative and fertile shoots is practised, as in the case of the jíquima cultivar group (Duke 1981; Sørensen *et al.* 1995; A.M. Sørensen pers. comm.; see also Section 10.3).

Plants are easily propagated by seed and, except for the bud and flower prunings to increase tuber growth, they require little agronomic attention. The most common time for planting jíquima in Manabí is at the end of the rainy season, i.e. June-July. Once the main crop (maize, etc.) has been harvested, the jíquima will be planted some days later. It is, however, interesting to compare this with the practices used in some of the other small communities, where the time of planting has been shifted to November-December. The explanation of these differing planting times may be that farmers in the first area depend almost exclusively on income from agricultural production. They will therefore plant the most profitable crops during the optimal (rainy) season. In contrast, farmers in other areas usually have additional sources of income from part-time employment with small factories, etc.

and many have sufficiently large fields to allow simultaneous planting of both major and minor crops (Sørensen *et al.* 1996).

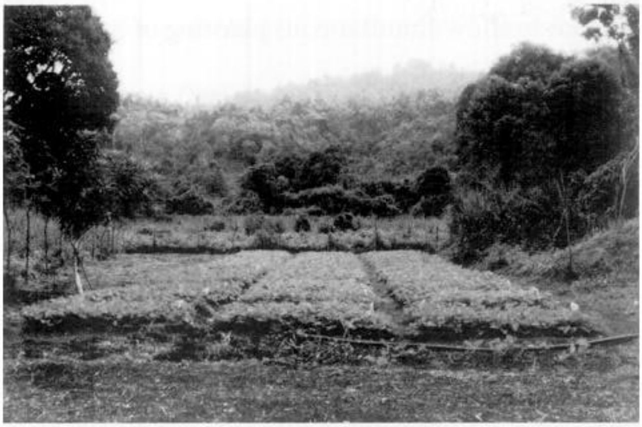
Farmers usually carry out two bud prunings (called 'deshijar') and one apex pruning (called 'despuntar') manually. The different methods and sequence of prunings are: (i) bud and floral pruning (removal of reproductive shoots) at an early stage; (ii) apical stem pruning, and (iii) floral stem and secondary sprouts and bud pruning. Sometimes a fourth pruning, a repetition of the third pruning, may be done if considered necessary, depending upon plant growth and rainfall. If the prunings are carried out using tools, it is believed that the tuber becomes fibrous ('paluda'), lignified and not succulent. The pruning work, called 'deshijado' or 'desmamantado' as a general term, is carried out on each waning of the moon. This practice is believed to reduce insect damage and has an empirical basis. Nowadays, fertilization with urea is occasionally used, whereby the urea is applied directly to the soil and covered. This procedure appears to be a modern technique adapted to jíquima from other crops (Sørensen *et al.* 1996).

No special irrigation is applied to the crop. In general the farmers use the water remaining in the soil from the previous rainy season. During the rainy season the crops usually grown are maize or rice (*Oryza sativa* L.), as they constitute better agricultural alternatives for the market (Sørensen *et al.* 1996). Harvesting can take place after approximately 5 months, owing to the short growth cycle of the jíquima (Sørensen *et al.*, l996). Fertilization with an N, P, K, fertilizer (10-30-10) may be used in some communities. Furthermore, an insecticide application (Ambush) following recommendations for other crops is often used.

10.3 Field trials

Numerous field trials have been carried out by different partners within the Yam Bean Project in Mexico, Costa Rica, Ecuador, Senegal, Benin, Thailand and Tonga, to examine the potential of existing genotypes (Fig. 12a-c). Two different types of the Mexican yam bean have yielded between 80 and 160 t/ha in trials carried out in Benin, Costa Rica, Mexico and Tonga, for example. One Haitian cultivar of the Amazonian *P. tuberosus* has produced a yield of 70-80 t/ha in Benin. Lately, six comparative field evaluations of 60 *P. erosus* accessions have been concluded in Tonga (Nielsen *et al.* 1996), and the first three trials examining the effect of different cultivation practices on the yield of *P. tuberosus* have been completed (Nielsen *et al.*, unpublished). All field experiments were carried out using dryland farming techniques, with the exception of the trials in Guanajuato, Mexico (where the record yield of 160 t/ha was obtained) and in Senegal (where yields of *P. erosus* of 40 t/ha and 100 t/ha were recorded at Bambey and at Tiago respectively.

The various experiments conducted have clearly demonstrated the considerable potential of *P. ahipa* for immediate utilization in subtropical regions as a high-yielding tuber/root crop with high sugar and protein contents, as well as for its use in interspecific hybrid combinations with the other two cultivated species, in the development of early photothermally neutral and bushy type cultivars. In trials



a

b

c

Fig. 12a. *Pachyrhizus erosus.* Accession trial at the northernmost archipelago of Vava'u, Tonga. (Photo, P.E. Nielsen).

Fig. 12b. *Pachyrhizus erosus.* Tubers from plants grown for seed production. Notice legumes on the plants in the field. Tongatapu, Tonga. (Photo, P.E. Nielsen).

Fig. 12c. *Pachyrhizus erosus.* Field experiment with Yam Bean/Manioc intercropping, CATIE, Costa Rica. (Photo, A. Mora Q.).

carried out in Portugal by the French partner in the project, the Andean yam bean (*P. ahipa*) was demonstrated to have astonishing potential under Mediterranean conditions: yields of 54 t/ha with up to 24% dry matter were achieved, with crude protein percentages of 9.6-11.1 (DM).

Material from Ecuadorian landraces belonging to the ashipa cultivar group of the Amazonian yam bean (*P. tuberosus*) that has recently been collected suggests a similarly encouraging yield potential in this species. Various trials are being carried out at different altitudes and cover a wide range of soil and climatic conditions. Both high rainfall and semi-arid regions are included. When the crop was first introduced into Tonga, local consumers were reluctant to accept the new type of tuber presented to them. Although the traditional Tongan diet is based in large part on tuber and root crops, the crisp, juicy quality of yam bean appeared to be too ‘exotic’ for local tastes. It was also regarded as strange that it could be eaten fresh. However, with increased demand for yam bean among the local Asian and European communities, and its easy cultivation, the Tongans are now growing, marketing and consuming the crop in increasing quantities.

The news from Benin is similar, if not more encouraging. Thanks to local media coverage, a peculiar situation has arisen, with several of the field trials subjected to ‘unauthorized testing and sampling’ at night, by local farmers! There, the biggest current problem is the availability of seeds for local cultivation.

Additional information concerning the design of and results from the field trials are reported in Grum *et al.* (1994), Heredia G. (1994) and Morera (1994a, 1994b).

10.4 Diseases and pests

Although diseases and pests are listed below according to observations made in the three cultivated species, there is little doubt that regardless of the disease-inflicting organism, the majority of both the diseases and insect pests will in fact be common to all three species. The differences recorded between the species are thus due to geographic, climatic, ecological and edaphic conditions. This has been confirmed in field trials in Tonga, Costa Rica, Ecuador and Thailand. When all five species are cultivated in one location, bean common mosaic virus (BCMV) will infect all three cultivated species and will also infect the wild species *P. panamensis*, although with some delay, due to the prominent hairiness of all vegetative parts, which has a repelling effect on the aphid vectors. Only the other wild species, *P. ferrugineus*, appears to possess any resistance to this virus.

P. erosus

In all species, the most serious pests endangering cultivation are without doubt the various bruchids, which may destroy as much as 80% of the locally stored seeds. In *P. erosus*, the two bruchids *Acanthoscelides sanfordi* Johnson and *A. taboga* Johnson were isolated from two seed samples collected in Yucatan in 1985. The sincama mosaic virus (SMV) is probably identical to the bean common mosaic virus (BCMV), although when originally describing the disease, Fajardo and Marañon (1932) claimed that this virus was not transmitted to the common bean.

Another disease spread by insect vectors is the witch's broom disease, first diagnosed by Thung and Hadiwidjaja (1957) and probably caused by mycoplasma-like organisms. The most likely vectors of these diseases are a number of species of leaf-piercing insect pests. These are aphids (*Aphis rumicis* L., *Brevicoryne brassicae* L., *Oregma lanigera* Zenthner), mealy bug (*Ferrisia virgata* Cokerell) and white flies (*Orusius argentatus*). The BCMV or SMV may become a serious problem locally, particularly in fields bordering on wild vegetation with frequent *P. erosus* escapes. The typical symptoms are irregular chlorosis of the leaves, young shoots becoming brittle and the seed set being reduced as a result of atrophied pollen (the pollen fertility of infected plants is reduced from 95-100% to less than 10%). Tuber growth is also affected and yield will decrease by 20-40%. Whether the virus may also be seed-borne is uncertain, although during the 6 years of introducing new accessions through the quarantine screenhouse in Tonga, neither BCMV nor SMV has been identified. Although it has occasionally been recorded in Tonga, witch's broom disease has never been observed to affect more than a few plants in any one field. As the disease leads to complete deformation of the reproductive shoots, seed contamination is not a problem. The disease must 'survive' in wild vegetation.

In Mexico, the bacterial disease called bean halo blight, caused by *Pseudomonas syringae* (Burkh.) Dowson pv. *phaseolicola* has been observed on several occasions in *P. erosus* (Diaz A. 1979). The same disease was reported in Hawaii by Birch *et al.* (1981). However, the disease does not appear to reduce yields significantly (Diaz A. 1979).

Several fungi have been reported to cause severe damage in *P. erosus.* D.J.M. Annerose (1995, pers. comm.) recorded a high mortality rate in young plants as a result of 'root attacks' by *Pythium* spp., *Corticium* spp. and *Macrophomina* spp. in multilocational field trials in Senegal. In China, *Pythium aphanidermatum* (Edson) Fitz. is the cause of root rot in *P. erosus* (Yu *et al.* 1945). Mohanty and Behera (1961) reported a severe leaf spot disease observed in Bhubaneswar, India and succeeded in identifying the fungus as *Cercospora canescens* Ellis *et* Martin.

A number of insect pests are reported to cause leaf, tuber and seed damage in *P. erosus.* Species belonging to the genus *Diabrotica* are serious pests in many humid areas, and the leaf damage is often quite extensive, although differences in susceptibility between accessions have been recorded, i.e. more hairy genotypes tend to suffer less from attacks. In Tonga the rosebeetle (*Adoretus versutus* Harold) has been identified as the maincause of leaf damage (Grum *et al.* 1991b). In Mexico and Central America, flower buds and the young pod may be damaged by Thecla jebus. If localized, *Phyllophaga* Harris (n.v. 'gallina ciega') may cause severe tuber damage (Heredia Z. (1985). The bruchids *Acanthoscelides sanfordi* Johnson and *A. taboga* Johnson have been isolated from seeds from landraces collected in the Mexican state of Yucatan.

Plants in a recent field trial (1994) at Maracay, Venezuela were heavily attacked by insect pests previously not considered to cause serious problems in *P. erosus.*

Termites (Termitidae) hollowed the stems of young plants, destroying 15-20% of the plants. *Andrector* spp. (Gelerucidae) and *Nezara viridula* (Pentatomidae) caused severe leaf damage, and an as yet unidentified larvae also attacked a considerable number of the tubers (F. Espinoza 1995, pers. comm.).

The nematode *Meloidogyne marioni* (Cornu) Chitwood et Oteifa (syn. *Heterodera marioni* (Cornu) Marcinowski) is cited by Duke (1981) as the cause of tuber damage.

P. ahipa

In Bolivia, local producers did not identify any insect pests as being of importance when cultivating the crop (Ørting *et al.* 1996). When it is introduced to other areas for evaluation, most insect pests normally associated with the other species will attack *P. ahipa*, however. In Tonga, seed damage caused by the coffee bean weevil (*Araecerus fasciculatus* De Geer) has been recorded in seed belonging to all species during storage (J. Kingsolver, 1996, pers. comm.).

Even though the mature seeds have the highest amount of endogenous rotenone of any part of the plant, it is the seed which suffers the most serious attack by an insect pest, e.g. the bean weevil (Bruchideae). The bruchid *Caryedes icamae* Guerin-Meneville was identified in five seed samples from different localities in Bolivia in 1994. Bruchids are known to damage the seeds of several legume genera containing toxic constituents.

Nematodes may be a problem locally, and when evaluating a Bolivian accession in Esmeraldas, Ecuador, the nematode *Meloidogyne* sp. completely destroyed all tubers in the test plants (Bertelsen and Stagegaard, unpublished). In Bolivia, the most severe tuber damage observed was rot, due to lack of irrigation management and/or nematodes. No other serious damage caused by pests or diseases during the vegetative period was recorded. This may be due to the presence of rotenone in the leaves and stems of the plants.

P. tuberosus

This species is reported to be infected by the following fungi: *Colletotrichum pachyrrhizi* (although only the species *C. truncatum* (Schwein.) Andrus et Moore has been confirmed to attack *Pachyrhizus;* E. de Neergaard, 1994, pers. comm.); *Phakopsora pachyrrhizi* and *Pythium aphanidermatum.* The species is also reported to be infected by the nematodes *Meloidogyne arenaria* (Neal) Chitwood and *Pratylenchus* sp., a cause of dramatic local yield reduction, especially on sandy soils (Noda 1979; Duke 1981; Arévalo T., unpublished; Bertelsen and Stagegaard, unpublished). The two latter reports have been confirmed, by personal observations in the field trials at Jardín Tropical, Esmeraldas, Ecuador. Farmers also cite nematodes as one of the most important problems affecting tuber quality in the jíquima cultivar group. The symptoms, which they describe as ‘warts’ (locally known as ‘verruga’ or ‘peste’) give the affected tubers a bitter taste.

The author has previously reported that plantlets belonging to this species (seeds originating from Brazil) grown under greenhouse conditions at the Botanical

Section, RVAU, were gravely infected by and appeared to be highly susceptible to BCMV (Sørensen 1990). Over a 5-year experimental period, the plantlets were found to be infected during the initial fortnight following germination. In infected *P. tuberosus* plants, growth of the tuberous root did not take place, and as mentioned, pollen fertility was greatly reduced.

Locally, and especially in very humid conditions such as those in the province of Esmeraldas, Ecuador, leaf-eating insects such as the species belonging to the genus *Diabrotica* and *Disonycha glabrata* F. may cause extensive damage (Bertelsen and Stagegaard, unpublished). Several nematodes have been reported as being the cause of significant yield reductions in *P. tuberosus*, in Brazil. Noda *et al.* (1991) observed serious damage caused by attacks by *Meloidogyne* Goeldi and *Pratylenchus* Filipjev. This observation was confirmed by the first field trial conducted during the rainy season in Esmeraldas, Ecuador, where one accession belonging to the jíquima cultivar group (*P. tuberosus*) did not produce any marketable tubers, owing to nematode (*Meloidogyne*) damage (Bertelsen and Stagegaard, unpublished). Duke (1981) mentions the species *Meloidogyne arenaria* (Neal) Chitwood as an important cause of tuber damage.

When cultivating accessions belonging to the jíquima cultivar group outside Manabí, very serious problems have been observed to be caused by leaf-eating insects as well as by nematodes. Of the farms monitored by INIAP, 57% reported the presence of the nematode *Meloigyne* spp. in their soils. Although nematodes may cause tuber damage in Manabí, only crop rotation and the use of non-infested fields are used as control measures, i.e. nematicides are not used. The insect damage observed elsewhere also seems to be a problem in Manabí, where 'the white fly complex' (*Aleutotrachelus* sp., *Bemisia* sp. *Alerothrixus* sp. Homoptera, fam. Aleyrodidae) has been observed in jíquima plants (T. Estrella E., pers. comm.).

As mentioned above, the most serious threat to the cultivation of *P. tuberosus* in small local communities is the seed damage caused by bruchids. The following species have been isolated from collected seeds: *Caryedes icamae* Guerin-Meneville in the department of Loreto, Peru; *Acanthoscelides obtectus* Say in the department of La Paz, Bolivia, and *Caryedes icamae* in the province of Esmeraldas, Ecuador.

10.5 Harvesting

Harvest takes place once the tuberous roots have attained marketable size, i.e. depending on whether small, medium sized or large tubers are preferred by the consumers. In *P. erosus* this means that the Mexican cultivars are harvested from 5 to 7 months after planting, as there are both early and late-maturing cultivars available. The preferred tuber size is around 0.7 kg. In Thailand, harvesting of the same species follows at 4.5-6 months after planting, as the local consumers like small 'onion'-sized tubers. Again, both early- and late-maturing cultivars exist. *P. ahipa* tubers are generally harvested after 7-9 months in Bolivia (as confirmed in field trials in Portugal), but the species has been found to be the earliest of all genotypes tested in the field trials in Mexico, i.e. marketable tubers were produced after only 4 months.

Lastly, *P. tuberosus* needs the longest growth period of all: 8-11 months, and as described above, this species may even be cultivated in a 'perennial' production system.

In *P. erosus,* the ridges in which the tubers are produced are loosened mechanically with a so-called 'subsoiler' mounted on a tractor and equipped with a cross-bar. Once the soil has been loosened, the tubers are lifted by hand, the vegetative top is removed with a pair of shears and left to dry in the field (to be used later as forage hay) and the tubers are collected and stacked in sacks. Alternatively they are loaded straight into the lorries which transport the crop directly to a local market, to the central market in Mexico City, or to the US border for cleaning and repackaging, ready to be sold in the American supermarkets. Once the vegetative top has been removed, crops grown by smallholders for domestic consumption or small-scale marketing locally may be left in the ground for several weeks until they are eaten or sold (A. Heredia Z., pers. comm.; Sørensen, pers. observ.).

Bolivian growers of *P. ahipa* are reported to harvest the tubers by hand, using a hoe. The vegetative top is left to be incorporated in the soil, and occasionally the lifted tubers are left to dry in the sun for 1-2 weeks (this procedure increases the sugar content by conversion of the starch) before being sold at local or more distant markets (Ørting *et al.* 1996).

10.6 Post-harvest handling

As discussed above, *P. erosus* is the only species which is marketed at considerable distances from the production areas. The Mexican crop is sold in the US market, for example, and the Thai crop produced to the north of Bangkok, in various oriental stores in the major European cities. Hence, this is the only species in which post-harvest and storage handling has been studied in some detail. The chilling sensitivity of the tuberous roots has been demonstrated (Bruton 1983; Barile and Esguerra 1984; Paull and Jung Chen 1988; Cantwell *et al.* 1992). Low-temperature storage has been found to reduce storage life considerably, and the optimal storage temperatures are between 12.5 and 17.5°C. The only post-harvest treatment reported is washing, trimming (removal of the non-tuberous part of the root and the basal part of the stem) and dipping in a high-concentration chlorine solution to obtain sterilizing and bleaching effects (Cantwell *et al.* 1992).

Prolonged storage will serve to alter the starch/sugar ratio. Paull and Jung Chen (1988) found that after 3 months of storage at 12.5°C, the sucrose content tripled and only one-sixth of the starch remained. As many consumers prefer a sweeter tuber, this may also explain the post-harvest treatment of *P. ahipa* observed in Bolivia, where some producers leave the tubers in a sunny place for up to 2 weeks prior to marketing (Ørting *et al.* 1996).

If the entire plot containing the crop is to be harvested in one operation, the tubers of the jíquima cultivar group *(P. tuberosus* complex) may be stored for 22-30 days during the post-harvest stage, provided well-ventilated indoor conditions are available. One apparent advantage to the farmers is that the jíquima may be handled like the manioc grown in the tropical lowlands, i.e. it can be ‘stored’ in the field and harvested when needed, and it is almost unaffected by poor management. A popular post-harvest treatment is to dry the tubers in the sun for 2-3 days before consumption. This may serve to increase the sugar content, as in the similar treatment of the *P. ahipa* tubers practised in Bolivia (Sørensen *et al.* 1996).

10.7 Yield

P. erosus

The average market size for the US market is 600-1200 g, but larger tubers will be marketable in Mexico. In contrast, tubers weighing as little as 350 g will be sold in Thailand, where the maximum marketable size is 1100 g. In Mexico, the average yields obtained in flood-irrigated fields in the Bajío region of the state of Guanajuato are 60-80 t/ha, and similar yields are produced in the lowland area of the state of Nayarit. The yield sizes produced on dryland range from 35-60 t/ha (fresh tubers). In field trials in Mexico (flood irrigated), Costa Rica (dryland) and Tonga (dryland), record yields of 100-145 t/ha (fresh tubers) have been repeatedly obtained (Heredia G. 1994; Heredia Z. and Heredia G. 1995; Morera 1994; Nielsen 1995). The difference in yield performance between 13 landraces and 4 wild accessions was observed in field trials conducted in Tonga during two consecutive years. For the landraces, these gave results in the range of 33.1-72.0 t/ha (fresh tubers) and 2.72-7.46 t/ha dry matter. For the wild accessions, results were 24.8-51.5 t/ha (fresh tubers) and 3.47-5.73 t/ha dry matter.

The fresh tuber yield recorded in the field evaluation of 60 accessions ranged between 125.9 and 77.0 t/ha (99.9-40.4 t/ha marketable tubers) for the 20 highest-yielding accessions. From these experiments, the consistently high yields of the Mexican cultivars were confirmed. Of the 20 best-yielding accessions, 9 were of Mexican, 4 of Brazilian, 3 of Guatemalan, 1 of Costa Rican, 1 of Thai, 1 of Malayan and 1 of Nigerian origin (from IITA) (Nielsen *et al.* 1996a) (see Table 8).

Several comparative studies have been conducted in India. Ramaswamy *et al.* (1980) reported the following high yields in the two best-performing Mexican lines: 140.0-186.6 t/ha. The growth season was approximately 220-245 days (April to December) and the plant density used was 66 650 plants/ha. In the state of Bihar, India, the yields of the so-called ‘Desi’ (or ‘Dasi’) cultivars and 32 introduced Mexican lines were tested (Singh *et al.* 1981). The average yields of the local cultivars were reported to be between 6.7 and 9.4 t/ha, with a production period of 225-250 days. The selected Mexican lines were reported to yield 10.2-12.3 t/ha on average, with 180-200 days to harvest. Similar results were achieved when testing 32 Mexican lines (probably the same ones) at the Plant Introduction Station, Amravati, Maharashtra in 1972-74 (Bhag Mal and Kawalkar 1982).

Table 8. Fresh weight tuber yields for the top scoring accessions of *P. erosus.*

Access. no	Origin country	Origin position	Test site	Years / seasons	tuber yield (FW t/ha)
EC523	Nigeria	IITA	Alajuela[1]	1992	125.8
EC114	Brazil	3.23S; 51.51W	Turrialba[1]	1992	62.7
EC523	Nigeria	IITA	Turrialba[1]	1993	57.3
EC543	El Salvador	13.28N; 88.10W	Alajuela[1]	1991	50.5
EC509	Costa Rica	9.56N; 83.4W	Guácimo[1]	1991	49.4
EC510	Mexico	19.51N; 90.31W	Turrialba[1]	1991	47.9
EC509	Costa Rica	9.56N; 83.4W	Turrialba[1]	1991	38.7
EC032	Mexico	20.48N; 89.01W	Río Claro[1]	1992	23.5
EC120	Guatemala	14.18N; 89.52W	Turrialba[1]	1991	22.9
EC509	Costa Rica	9.56N; 83.4W	Turrialba[1]	1992	15.8
EC511	Mexico	14.54N; 92.15W	Turrialba[1]	1990	10.1
EC548	Brazil	3.06S; 60.00W	Vaini[2]	1994	125.9
EC201	Mexico	20.31N; 100.49W	Vaini[2]	1992-94	109.9
EC558	Mexico	19.33N; 103.22W	Vaini[2]	1994	109.7
EC114	Brazil	3.23S; 51.51W	Vaini[2]	1992-94	108.0
EC526	Mexico	19.32N; 98.52W	Vaini[2]	1992-94	104.3
EC509	Costa Rica	9.56N; 83.40W	Vaini[2]	1992-94	98.3
EC551	Brazil	3.07S; 60.00W	Vaini[2]	1994	97.3
EC504	Mexico	20.23N; 89.28W	Vaini[2]	1994	96.8
EC555	Brazil	3.07S; 60.00W	Vaini[2]	1994	95.0
EC531	Mexico	17.03N; 96.42W	Vaini[2]	1992-94	90.5
EC236	Mexico	19.25N; 99.07W	Vaini[2]	1992-94	89.2
EC523	Nigeria	IITA	Vaini[2]	1992-94	88.9
EC004	Mexico	21.02N 104.21W	Vaini[2]	1992,1994	88.9
EC120	Guatemala	14.18N; 89.52W	Vaini[2]	1992-94	88.3
EC116	Guatemala	14.39N; 90.49W	Vaini[2]	1994	86.4
EC006	Mexico	17.03N; 96.42W	Vaini[2]	1992-94	83.5
EC536	Mexico	20.31N; 100.53W	Vaini[2]	1994	83.3
EC234	Thailand	Pud Tabaht	Vaini[2]	1992-94	78.2
EC043	Guatemala	14.02N; 90.04W	Vaini[2]	1992-94	77.1
EC109	Malaysia	Kuala Lumpur	Vaini[2]	1994	77.0
EC503	Mexico	20.31N; 100.53W	Abomey[3]	1993-94	74.6
EC040	Guatemala	14.12N; 90.01W	Abomey[3]	1993-94	72.4
EC201	Mexico	20.31N; 100.49W	Abomey[3]	1993-94	58.5
EC557	Mexico	20.31N; 100.53W	Abomey[3]	1994	47.9
EC114	Brazil	3.23S; 51.51W	Thies[4]	1993	43.2
EC117	Thailand	Kasetsart Univ.	Thies[4+1]	1994	92.9
EC114	Brazil	3.23S; 51.51W	Thiago[4]	1993-94	17.4

Continued on page 98.

Table 8. Continued. Fresh weight tuber yields for the top scoring accessions of *P. erosus.*

Access. no	Origin country	Origin position	Test site	Years / seasons	tuber yield (FW t/ha)
EC114	Brazil	3.23S; 51.51W	Dakar[4].	1993-94	32.1
EC033	Mexico	20.42N; 88.49W	Bambey[4]	1994	40.2
EC033	Mexico	20.42N; 88.49W	Djibélor[4]	1994	20.8
EC114	Brazil	3.23S; 51.51W	Tamba[4 + i v]	1994	12.9

Yields were recorded in field trials conducted at different test sites in Costa Rica, Tonga and Senegal. (1 - Costa Rica; 2 - Tonga; 3 - Benin; 4 - Senegal; +i - irrigated; +iv - 4 months growth, all other experiments are based on 6-8 months growth). The data have been compiled from Morera (1994a, 1994b), Morera et al. (1993), Nielsen et al. (unpublished), Adjahossou (1995) and Annerose and Diouf (1995a, 1995b); S. Døygaard has provided the positions).

P. ahipa

In Bolivia, according to Ørting *et al.* (1996), tuber sizes of 1000-1500 g are preferred, and the yield varies between 12 and 30 t/ha. During the past 4 years, field trials conducted at both the DRATOM experimental Station, Tras-os-Montes, Portugal and the INIFAP/CIFAP-CEBAJ experimental station, Celaya, Guanajuato, Mexico, have tested the three accessions initially available. With a growth season of 7 months (in Portugal) and 4 months (Mexico), yields of fresh tuberous roots ranging between 29-50 t/ha have been recorded with dry matter percentages of 19-25% (Vieira da Silva 1995; Castellanos *et al.* 1996.). Ørting studied seed yields of 20 accessions under greenhouse conditions and reported considerable variance, from 4.8±3.2 to 130.3±51.8 seeds/plant (Table 9).

Table 9. Seed yield in P. ahipa, based on an experiment conducted under greenhouse conditions (Ørting, unpublished)

Accession	No. of seeds/plant	No. of plants in test (n)	Accession	No. of seeds/plant	No. of plants in test (n)
AC102	7.7±7.4	7	AC209	23.3±19.8	6
AC201	83.6±33.3	9	AC213	39.4±22.5	8
AC202	98.8±24.2	6	AC214	29.1±18.8	7
AC203	80.0±25.9	7	AC215	18.8±21.1	4
AC204	86.0±33.7	8	AC216	49.0±9.0	3
AC205	91.3±38.5	6	AC217	78.0±0.0	1
AC206	86.9±26.2	7	AC521	6.2±9.1	5
AC207L	130.3±51.8	6	AC524	15.6±10.1	5
AC207S	106.3±26.9	4	AC525	74.0±46.2	6
AC208	101.7±31.7	3	AC526	4.8±3.2	4

P. tuberosus

According to Duke (1981), the yield performance (tuberous roots) of *P. tuberosus* ranges between 7 and 10 t/ha, the latter figure is in agreement with Munos Otero (1945), but Menezes and Oliveira Nunes (1955) indicate that in a fertile soil, yields of 30 t/ha-are quite possible during the first year of cultivation. The truth is that there are very few results available from field trials evaluating the yield performance of this species.

The fleshy, tuberous roots of the jíquima can weigh up to 3-4 kg, but the average weight is 2-3 kg. The initial trial (Grum *et al.* 1991b) only included a single accession, which yielded 8.7 t/ha in comparison with the yields of more than 60 t/ha recorded in five of the 16 *P. erosus* accessions evaluated. Six accessions (4 ashipa and 2 jíquima) have been tested in three trials over three seasons, examining yield performance as a result of three different cultivation practices: (i) reproductive pruning (weekly); (ii) vegetative pruning of stems longer than 0.5 m (50 mm behind the growth point), and (iii) both reproductive and vegetative pruning. Treatments (i) and (iii) yielded 27.2 and 27.3 t/ha (average fresh tuber yield at 81 600 plants/ha), whereas treatment (ii) and the control treatment (no pruning) yielded 16.3 and 15.4 t/ha respectively (Nielsen *et al.* 1996). The highest yields so far recorded (70.3±3.4 t/ha in the 1993 season and 52.9±3.2 t/ha over several consecutive seasons) were obtained in Benin by D.F. Adjahossou and his colleagues using the same ashipa accession from Haïti as used in the trials in Tonga (Adjahossou 1995). In Tonga, the three highest yielding accessions gave 103.5 t/ha (an ashipa landrace of Brazilian origin) and 80.4 and 43.4 t/ha (two jíquima landraces from Ecuador). The trials currently in progress at the Vaini Experimental Station on the island of Tongatapu in Tonga are the first to carry out comparative studies of some 20-25 different accessions of *P. tuberosus* originating from Haïti, Ecuador, Peru, Bolivia and Brazil.

Under experimental conditions in Brazil, a seed yield of 0.6 t/ha was reported (Menezes and Oliveira Nunes 1955; Duke 1981). Munos Otero (1945) estimates the seed yield at some 2 t/ha. The foliage yield recorded by Menezes and Oliveira Nunes (1955), again in a fertile soil, was 25-30 t/ha.

11 Limitations of the crop

One of the main constraints in the cultivation of yam bean is the rapid decrease in germination when the seeds are stored under humid conditions. This has been observed repeatedly by the Yam Bean Project partners in Ecuador, Costa Rica and Tonga. There is an apparent correlation between seed weight, robustness/thickness of the testa, and tolerance towards high levels of humidity. Thus the small and durable seeds of the wild species *P. panamensis* have been found to retain a high germination percentage for a considerably longer period under adverse storage conditions. In a comparative germination test between winged bean (*Psophocarpus tetragonolobus* (L.) DC.) and *P. erosus* seeds, conducted by Araújo *et al.* (1991), the first species had 99.42% germination and the second, 87.67%. (The yam bean species included in the test was identified as *P. erosus*, but as the source and seed shape/colour/weight were not mentioned, the identity of the species is uncertain. Araújo and associates use the vernacular name for *P. tuberosus,* jacatupé in their paper.) When examining the possibility of utilizing *P. erosus* as an indicator for plants for rare earths and/or thallium-containing soils usually associated with the cadang-cadang disease of coconut palms (*Cocos nucifera* L.), Velasco *et al.* (1979) found that tuber formation did not take place in these soil types.

The most serious pest problem, namely the various species of bean weevils (bruchids) is also related to the yam bean seeds. As differences in susceptibility to attack by this pest group vary between species, as well as between accessions belonging to the same species, it may be feasible to breed for increased resistance.

Among the leaf-damaging insects, the genus *Diabrotica* is by far the most serious pest recorded in the humid parts of the Latin American tropics. Again, considerable resistance to attacks has been recorded in the different accessions, as well as clearly reduced susceptibility in all genotypes possessing various degrees of pubescence of strigose hairs. Also, the subcoriaceous leaves of the wild species *P. ferrugineus* have been found to be virtually undamaged.

The bean common mosaic virus (BCMV) is without doubt the most serious viral disease in yam beans. Although the disease is not fatal, the yields of infected plants are reduced by 20-40%. As this disease may be seed- transmitted at a low rate, if infected plants are seen in plots for seed production, they should be removed.

As described above, because of the laboriousness of the process of reproductive pruning, it is considered a major constraint in current yam bean cultivation practices. This is particularly true of *P. ahipa*, because of the location and morphology of the inflorescences: simple short racemes often placed close to ground level in both determinate and indeterminate genotypes. In Bolivia, the laboriousness of reproductive pruning is the major reason for farmers' reluctance to continue growing this crop (Ørting *et al.* 1996). The problem may be overcome by the introduction of genotypes with reduced flower/pod set, or with a growth habit approaching the habit of *P. erosus*, where the erect inflorescences are produced above the vegetative part of the plant, thus facilitating easy removal.

Splitting or cracking of the tubers prior to harvest may be a serious problem under certain climatic/edaphic conditions (Ramaswamy *et al.* 1980). If the crop is irrigated, care should be taken not to irrigate for some weeks before harvest (A. Heredia Z., pers. comm.).

Tubers- that are physically damaged during harvest are susceptible to attack by common fungi and increased dehydration when stored (Cantwell *et al.* 1992). Wounded yam bean tubers suffer greatly from textural changes, decay and internal browning caused by the fungi *Rhizopus stolonifer* (Ehrenb. ex Link) Lind., *Cladosporium* sp. and *Penicillium* sp. when stored at low temperatures and high relative humidity (+80%) (Bruton 1983).

Avila *et al.* (1986) tested five treatments involving different concentrations of NaCl, citric acid and sugar; 2 g of $CaCl_2$ were added to all treatments, to preserve the crunchy texture of the tuberous roots. Both firmness and crispiness were retained in all treatments. However, when evaluated on the basis of flavour and taste, the treated tubers all scored poorly The white colour was least affected by the treatment containing 0.5 g citric acid. The best scoring treatment contained 100 g sugar and 1.04 g citric acid in 200 ml distilled water. Mudahar and Jen (1991) examined the texture of raw and canned yam bean (the species examined was definitely P. erosus, the Mexican yam bean, and not *P. tuberosus*, as erroneously stated in their paper) and Chinese water chestnut (*Eleocharis dulcis* (Burm. F.) Trinius ex Henschel). Conventional boiling in water for 32 minutes will reduce the retained fracturability/crispness of *P. erosus* tubers by 65%, but only by 20% in Chinese water chestnut. However, the decrease in crispness may be considerably reduced, to 31%, by infusing the yam bean tuber dices/cubes with 0.1% polygalactic acid by vacuum infiltration, blanching for 40 minutes at 71°C and canning in a 0.2% CaCl solution (Mudahar and Jen 1991). The inferior ability of yam bean (*P. erosus*) tubers to retain their crispy texture when processed, compared with the Chinese water chestnut is probably attributable to the structure and composition of the cell wall polysaccharides, as has been shown by Klockman *et al.* (1991). Further studies involving different genotypes/species may well reveal differences in the processing characteristics within the genus.

Hernandez (1790) and subsequently Urbina (1906) report that if the tubers are consumed in excessive amounts, they may cause flatulence. Martinez (1936,1956) and Anonymous (1976) state that consumption of the fresh tubers was considered by some to cause indigestion, especially in young children, and it was recommended that nursing mothers should avoid eating the tubers. This information is obviously contradictory to the recommended use of *P. tuberosus* tubers mentioned in Section 5.1. Martínez (1936) also states that consumption of yam bean tubers may cause diarrhea in some people. Fine (1991) reported a case of hypersensitive reaction to the ingestion of *P. erosus:* a 40-year-old man developed an allergic itch of the scalp and upper body upon eating raw sliced yam bean, and also to a minor degree when eating cooked yam bean.

P. erosus

Although *P. erosus* has repeatedly been introduced into Africa (both Tanzania in the east and Senegal, Sierra Leone, Cameroon and Zaïre in the west, according to Sorensen (1990)), it has never succeeded in becoming an established crop. Several different explanations of this situation may be put forward: (i) *P. erosus* tubers do not have as high a dry matter content as conventional African tuber crops such as cassava, sweet potato (*Ipomoea batatas* (L.) Poir.) and yams; (ii) *P. erosus* tubers are cooked differently from the traditional tuber crops (again owing to the lower dry matter content), or are consumed fresh like carrots (*Daucus carota* L.), and lastly (iii) *P. erosus* is propagated by seed and needs to have the fertile shoots pruned repeatedly during the growing season in order to produce a higher tuber yield (Noda and Kerr 1983; Heredia Z. 1985). This cultivation practice differs from the cultivation practices of the conventional tuber crops. However, *P. erosus* has recently been (re)introduced into Senegal and Benin (Sørensen *et al.* 1996) to be tested in comprehensive field trials. J.H. Seyani (pers. comm.), who has tested *P. erosus* in preliminary trials at the National Herbarium at Zomba in Malawi, is convinced that the crop has great potential in this part of Africa. In another observation from Malawi, M. Grum (pers. comm.) has reported the common practice of consuming uncooked cassava roots. This practice would certainly be made healthier by changing to *P. erosus* tubers, which do not contain toxic (e.g. cyanogenic) compounds.

The photothermal sensitivity recorded in the majority of accessions tested may be a constraint to the crop's successful introduction into new areas. As the highest yields in these photothermally sensitive plants are obtained by cultivating the crop when daylength is decreasing, it will be crucial to identify locations where the precipitation will be sufficiently high during the 'winter' season to allow cultivation. In an alternative approach, *P. erosus* genotypes with determinate growth (i.e. those less influenced by variations in daylength) and photothermally neutral lines selected from interspecific *P. erosus* x *ahipa* hybrids have also been identified.

P. ahipa

According to Ørting *et al.* (1996), the most serious threats to the crop's continued cultivation (and its successful introduction to other suitable regions) are linked to (i) the need for reproductive pruning in order to obtain economic yields and (ii) the number of flowers produced per plant - some landraces may produce more that 800 flowers/plant while others have less than 50 flowers/ plant. Ørting (unpublished) also reports that the abscission rate varies significantly, as do the pollen fertility percentages. The initial screening for infraspecific variation has demonstrated that selection/breeding for new cultivars with little or no need for reproductive pruning will be feasible.

P. tuberosus

The three cultivar groups within *P. tuberosus* have different limitations which depend on their different ecological preferences and uses. For instance, the jíquima group is poorly adapted to high precipitation rates, as was seen when evaluating an accession from the Manabí province, Ecuador during the rainy season in the neighbouring province of Esmeraldas. This particular accession suffered greatly from fungal and nematode attacks (Bertelsen and Stagegaard, unpublished). With the completion of the survey of extant genetic resources in Manabí, the uniformity of this cultivar group has become apparent. It does not therefore seem likely that without infra- or interspecific hybridization it will be possible to breed new cultivars which are superior to the present landraces. The earliness and drought tolerance of the jíquima group may thus be a disadvantage in humid conditions. Another serious threat to the continued cultivation of the jíquima landraces is their high susceptibility to bean weevils, which may be partly due to their low rotenone/rotenoid content (Table 5). Screening for variation in rotenone/rotenoid content may reveal genotypes with a higher content and increased resistance. In the ashipa cultivar group, the major limitations are the long growth cycle, the depth at which the tubers are produced and the lack of tuber uniformity. However, genetic variation is considerable, and the number of highly local landraces appears to be inestimable. A combination of selection and breeding is likely to produce new cultivars with several attractive traits, which is of obvious potential when looking for possible ways to achieve diversification in, for example, African agriculture.

Current knowledge of the chuins is poor, and the specific limitations of this cultivar group can only be identified when results from the first field evaluations become available.

12 Prospects

12.1 Advantageous features of the cultivated species

P. erosus, P. ahipa and P. tuberosus all share a unique combination of the general qualities present in most cultivated legumes, which makes them attractive to the producer, the consumer, the processor and the environment, respectively:

- good adaptability to a wide climatic and edaphic range
- yield reliability of the root/tuber
- well-balanced and nutritious composition of their protein/starch contents
- agreeable taste
- good post-harvest/storage characteristics
- biological nitrogen fixation (sustainability)
- low fuelwood demand (most cultivars produce tubers that are consumed fresh).

12.2 Quality aspects

The quality aspects of each of the utilized parts (tuberous root, forage hay and mature seed) for the extraction of rotenone and rotenoids differ among species.

P. erosus

The tubers of *P. erosus* have been subjected to a number of nutritional analyses. Quality criteria among consumers differ according to cultural traditions, e.g. in Mexico (and in the US market) a crunchy juicy tuber should weigh 0.35-0.9 kg, the sap should preferably be watery and not milky, and the taste should not be too sweet. In Southeast Asia, the optimal tuber size is smaller, 0.25-0.6 kg, although consumers in this region also prefer the flavour not to be too sweet. Three field trials were conducted in Tonga, involving 32 different and reproductively pruned accessions including Mexican, Central American and Southeast Asian cultivars and landraces. The average dry matter percentage recorded in the tubers was 9.9-13.7% (the overall range was 8.5-14.0%), and the average percentage of soluble sugars ranged from 7.03 to 8.24%. Crude protein and total nitrogen tuber yields have been studied in Tonga and Mexico. Three Mexican cultivars (EC201, EC550 and EC557) yielded 97.6-127.4 kg N/ha in reproductively pruned plants and 44.0-80.0 kg N/ha in unpruned plants (Castellanos *et al.* 1996). Twelve reproductively pruned accessions (including both wild material, landraces and cultivars of Mexican and Central American origin) tested in Tonga yielded 291-540 kg crude protein/ha with a crude protein percentage of the dry matter of 6.6-9.8% (Grum *et al.* 1994). This demonstrates that significant variation exists among accessions, which will allow breeding for different objectives.

As seeds in most major production areas are comparatively expensive, cultivars with a high seed yield are preferred (see discussion in Section 6.3). The average seed yield recorded in a high-yielding Mexican cultivar (EC201) ranges between 0.6 and 1.0 t/ha in Mexico and 1.0 t/ha in Tonga (A. Heredia Z. and P.E. Nielsen, pers. comm.). In Thailand, the average seed yield obtained in local landraces is 0.72-0.84 t/ha.

The rotenone and rotenoid content appears to vary among different accessions. To date, however, there has not been a comprehensive study of the possible linkage between climatic, ecological, geographic or genotypic factors and rotenone/rotenoid levels. Rotenone/rotenoid content also depends on the breeding objectives, i.e. whether the seeds are to be used for commercial extraction or for increased pest resistance (which require increased levels), or if the mature seeds are to be used as food/feed (in which case rotenone/rotenoid levels should be decreased to reduce their anti-nutritional effect).

The legume hay may be used either as a forage or as a green manure (Ratanadilok and Thanisawanyangkura 1994; A. Heredia Z., pers. comm.; Sørensen, pers. observ.). In Vietnam, the flowers, young leaves and pods are used as a vegetable (Gilbert 1917). Castellanos *et al.* (1996) report the following dry matter yield of the aboveground parts for three Mexican cultivars (EC201, EC550 and EC557): 3.4-4.8 t/ha (= 119.5-151.2 kg N/ha) in reproductively pruned plants and 9.1-12.1 t/ha (= 197.8-289.5 kg N/ha) in unpruned plants. Sorensen (1990) gave the following mineral composition of P. erosus leaves (dry matter basis average of nine accessions): Ca 22.9±3.4, Mg 3.9±0.6, K 24.9±4.2, N 44.4±2.8 and P 3.5±1.0 g/kg. Unfortunately, no comprehensive analysis of the nutritional value of the foliage is available. Similar studies of different accessions would provide the needed information to breed for true multiple-purpose cultivars.

P. ahipa

At present, the limited germplasm available has been included in a number of field trials evaluating yield performance and tuber quality In general, the *P. ahipa* tubers are not favoured by the Mexican consumer, due to their excessive dry matter content and sweetness. This tuber quality is preferred by Bolivian and Northern Argentinian consumers.

Field trials conducted in Mexico, Tonga and Portugal have yielded quite different results (see Table 3). Tuber quality varies according to climatic conditions, i.e. faster growth and lower dry matter in warm climates and short growth seasons. The very high dry matter content recorded in the trials in Portugal demonstrates the possibility of utilizing *P. ahipa* tubers in processed and non-food products (see also Section 4.1).

There are very few studies available on the quality aspects of the forage hay of *P. ahipa*. The recent field experiments conducted in Mexico by Castellanos *et al.* (1996) report the following yields and nitrogen contents of *P. ahipa*'s aboveground parts.

- Accession number AC102: 1.7 t/ha dry matter with 55.1 kg N/ha in reproductively pruned plants, and 5.8 t/ha with 147.7 kg N/ha in unpruned plants.
- Accession number AC521: 1.8 t/ha dry matter with 62.8 kg N/ha in reproductively pruned plants and 5.9 t/ha dry matter with 129.8 kg N/ha in unpruned plants.

These results. demonstrate that nitrogen concentration as a percentage of the aboveground parts increases as a result of reproductive pruning, although forage yield decreases, from 3.24-3.49% in pruned plants to 2.20-2.54% in unpruned. Also, the total amount of nitrogen fixed (kg/ha, tuber + aboveground parts) did not differ significantly between the pruned and unpruned plants; in *P. ahipa* 68.7-74.3 kg N/ha for pruned plants and 58.4-79.7 kg N/ha for unpruned.

The only results available on seed yield in *P. ahipa* are based on greenhouse experiments involving 20 different accessions. The number of mature seeds harvested per plant are given in Table 9.

Both the yield results, but especially the seed yield results, indicate that in this species, sufficient variation may be available to implement a pre-breeding programme aimed at the development of new high-yielding cultivars with acceptable seed production.

P. tuberosus

In this species with its three distinctly different cultivar groups the quality aspects vary, not only between groups, but in the case of the ashipa cultivar group, also within the group, i.e. both multi- and monotuberous landraces exist and both sweet and less sweet landraces are cultivated. As proper surveys of producer and consumer preferences are lacking, the information given below is based on interviews with local villagers throughout the production area.

A preliminary study of tuber yields, contents of soluble solids, dry matter and yields of aboveground parts has been conducted in Tonga. These data are presented in Table 6. The tuber yield and vegetative aboveground parts of the chuins have been examined in Tonga; total fresh weight yield per plant was 2-3 kg with 20-50% dry matter. The total number of pods produced per plant ranged from 113-178.

There are no comparative studies of the nutritional value of the three cultivar groups, and no data are available on the feeding value of *P. tuberosus* hay However, the largest tubers and the greatest production of aboveground vegetative parts are found in *P. tuberosus*. Further details must await the results of the field trials currently in progress.

Within the chuin group, the various landraces all have high dry matter content and different coloured tuber flesh, and also differ slightly in taste. This variety is not unlike that known in sweet potato (*Ipomoea batatas* L.). As the landraces are cultivated on seasonal flooded levees, growth must be adjusted to the cultivation season available. The seeds should maintain an acceptable germination rate under quite unfavourable conditions, a quality which has been found to be absolutely vital to the continued cropping along the Ucayali river in Peru. Here, the occasional out-of-season flooding of the levees may eradicate the crop completely, and few villagers store extra seed as a precaution against such events. Many small villages lose the crop for several years, until seeds become available from neighbouring villages, following renewed multiplication. Most villagers have stated that they prefer flour and cooked tuber from the chuins to similar products from manioc (Sørensen *et al.* 1996).

Ashipa landraces are always consumed fresh or made into fruit juice; therefore sweetness and juiciness are qualities much appreciated by consumers. When harvesting a multiplication plot in Tonga in 1995, the local field labourers immediately decided that one accession was the sweetest they had ever tasted. It originally came from the small village of Tzapino in the centre of, Ecuadorian Amazonia. The importance of this observation must be appreciated, as until 1989, the crop was unknown. Project staff have nonetheless tested some 200 different accessions to date (P.E. Nielsen 1995, pers. comm.). New cultivars with unique tuber qualities may well be developed from this material.

As for the chuins, seed quality and availability are important to maintain the crop. Furthermore, none of the villagers interviewed stated that they practice any kind of selection in their material, i.e. all plants producing seed are harvested regardless of tuber quality or individual plant growth. The only separation practized is based on the different tuber qualities, in that yellow-fleshed, multituberous, sweet-tasting landraces are grown separately from monotuberous, white-fleshed landraces with little sweetness. The ashipa outyields all other cultivated landraces in forage production, but only the old Brazilian and Venezuelan references mention the ashipa hay being used as cattle forage (Peckolt 1880; Peckolt 1922; Munos Otero 1945).

In the province of Manabí, Ecuador, the quality of the tubers from the jíquima cultivar group is rated in much the same way as the ashipas, i.e. according to juiciness and taste, because they too are only consumed fresh. There are no records of any systematic use of the jíquima hay, but as sources of forage are limited to maize hay and field grasses, a high-protein hay from any leguminous crop is obviously used when available. Also, as reproductive pruning is practized in the cultivar group, the hay does not contain any anti-nutritional compounds. The climatic problems of significant importance in the chuins and the ashipas are as important in the storage of the jíquima seeds. The most serious problem, however, is insect damage by bean weevils (bruchids). The jíquima seed has been identified as having the lowest rotenone content of the four *Pachyrhizus* species studied (Lackhan 1994), and this may in part explain its susceptibility to insect damage.

12.3 Future conservation and utilization of the species

It is of major importance to conserve, both *in situ* and *ex situ,* the widest possible range of the endangered landraces within all three cultivated species. Surveys of wild populations, whether belonging to the cultivated or the exclusively wild species, should also be completed. All genotypes yet to be studied cytologically (including molecular analyses) and evaluated for agronomic/breeding potential should be included in projects as quickly as possible. The information thus obtained will enable a comprehensive manual to be published that will describe the available variation and identify those wild populations and 'rare' landraces most urgently in need of conservation measures.,

As has been indicated above, the yam bean is currently constrained as an attractive alternative to traditional root/tuber crops by a number of factors. A worldwide breakthrough for the genus could be achieved either by using interspecific hybridization combined with intensive breeding methods, or by comprehensive screening and selection within existing landraces.

The possibilities of utilizing the unique starch quality of the high dry matter genotypes (*P. ahipa* and *P. tuberosus*) for industrial purposes should be examined.

13 Further research needs: recommended plan of action

The results of the experiments concluded to date indicate a number of specific courses of action:

- collecting, conservation and evaluation of germplasm:
  (i) *P. tuberosus* (both wild material and rare landraces) in Bolivia, Brazil, Colombia, Paraguay, Peru and Venezuela
  (ii) *P. ahipa* (both wild material and rare landraces) in northern Argentina, Bolivia and Peru
  (iii) *P. panamensis* (wild material only) in Colombia, Ecuador, Panama and Venezuela
  (iv) *P. ferrugineus* (wild material only) in Central America and Colombia
- taxonomic and phylogenetic studies using both molecular and numerical systematic methods of analysis in order to clarify the ontogeny of the cultivated species
- physiological analysis of the source/sink relationship in species other than *P. erosus,* with specific reference to the competition between tuberous root growth and legume formation
- physiological studies of drought tolerance in *P. panamensis* and interspecific hybrids involving this species
- physiological studies of biological nitrogen fixation in *P. tuberosus, P. ferrugineus, P. panamensis* and interspecific hybrids
- biochemical analysis of the nutritional composition of the recently identified *P. tuberosus* landraces (i.e. the chuin cultivar group) with high dry matter and soluble sugar contents
- biochemical analysis of the nutritional composition of the most promising interspecific hybrids, i.e. lines that are approaching release as new cultivars
- biochemical analysis and evaluation of *P. ahipa* and landraces belonging to the chuin cultivar group (*P. tuberosus)* as potential non-food crops
- biochemical analysis and evaluation of all species as sources of rotenone/rotenoids with technical and/or agronomic potential
- breeding of new interspecific hybrids involving the recently identified *P. tuberosus* landraces with high dry matter and soluble sugar contents, high-yielding *P. erosus,* and early bushy *P. ahipa* accessions
- initiation of a breeding programme to improve the existing landraces of *P. ahipa* and the jíquima cultivar group (*P. tuberosus*) to ensure continued cultivation of these endangered crops in Argentina, Bolivia and Ecuador
- promotion and marketing initiatives for new cultivars, e.g. the high dry matter chuins and the sweet multituberous ashipas, locally as well as in the existing export markets
- development of new export markets, e.g. Europe, Australia and New Zealand.

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Appendix 1. *Pachyrhizus* research (scientists, institutes and research field)

Benin

D.F. Adjahossou, Laboratoire de Biologie Végétale Appliquée, Jardin d'Acclimatation et de Propagation des Espèces Végétales Utilitaires; Faculté des Sciences Agronomiques; Université Nationale du Bénin; B.P. 2417 Cotonou; Fax: +229 300047.	Agronomy

Bolivia

J. Rea, Casilla de Correo 13-357, La Paz.	*In situ* /on-farm conservation
G. Espindola, IBTA, E.E. Patacamaya, Cajon Postal 5783, La Paz. Fax: +591 2370883.	Germplasm acquisition

Brazil

I.F.M. Válio, (rotenone) Departamento de Fisiologia Vegetal; Instituto de Biologia; Universidade Estadual de Campinas; C. Postal 6109; 13081 Campinas; SP; Fax: +55 192 393124.	Physiology/biochemistry

Burundi

S. Ndani, IRAZ de la CEPGL, B.P. 91, Gitega.	Agronomy

Costa Rica

J.A. Morera, Unidad de Recursos Fitogeneticos; Centro Agronomico Tropical de Investigación y Enseñanza (CATIE); CATIE 7170; Apdo. Correo 25; Turrialba; Fax: +506 561533; e-mail: "jmorera@catie.ac.cr".	Agronomy, *in vitro* propagation, *ex situ* conservation

Costa Rica
V. Vasquez,
Escuela de Ingeniería Química,
Faciltad de Ingeniería,
Universidad de Costa Rica,
San Pedro de Montes de Oca.
Fax: +506 2255622;
e-mail: "vvasquez@perry.eiq.ucr.ac.cr".

Biochemistry (rotenone)

Cuba
L. Fernández Granda,
Unidad de Recursos Geneticos;
INIFAT;
Calle 2, Esq. 1;
Santiago de las Vegas;
Ciudad de la Habana;
Fax: +53 7336409.

Agronomy

Denmark
M. Sørensen,
Botanical Section;
Department of Botany,
Dendrology and Forest Genetics;
Royal Agricultural and Veterinary University;
Rolighedsvej 23;
DK-1958 Frederiksberg C;
Fax: +45 35282821;
e-mail: "marten.soerensen@botge.kvl.dk".

Biosystematics,
experimental taxonomy

Ecuador
R. Castillo T.,
Departamento Nacional
de Recursos Fitogeneticos;
Instituto Nacional Autonomo
de Investigaciones Agropecuarias (INIAP);
Estación Experimental "Santa Catalina";
Casilla Postal 340;
Quito;
Fax: +593 2 504240;
e-mail: "castillo@fitogen.sc.iniap.gov.ec".

Germplasm acquisition,
ex situ conservation,
in vitro propagation,
molecular systematics

A. Arévalo T.,
Jardín Tropical;
Universidad Técnica "Luis Vargas Torres";
Casilla 08-01-0173;
Esmeraldas,
Fax: +593 2 714033.

Agronomy, *ex situ* conservation

France	
J. Vieira da Silva, Centre de Recherche de Botanique, Laboratoire de Biochimie et Physiologie de 1'Adaptation Végétale; Université VII Denis Diderot; 2 Place Jussieu; 75251 Paris Cédex 05; Fax: +33 1 40517108; e-mail: "jsilva@ccr.jussieu.fr".	Physiology (drought tolerance)
Germany	
W.J. Grüneberg, Institut für Pflanzenbau und Pflanzenzüchtung; Universität Göttingen; Von Siebold Strasse 8; D-37075 Göttingen; Fax: +49 551 394601; e-mail: "wgruene1@gwdg.de".	Biometrics, pre-breeding, biochemistry (starches)
Guadeloupe	
V. Vaillant, Laboratoire de Physiologie et Biochimie Végétales, INRA; Centre des Antilles et de la Guyane; B.P. 1232, 97185 Pointe-à-Pitre CEDEX; Guadeloupe F.W.I. Fax: +590 255924; e-mail: "vaillant@antilles.inra.fr".	Physiology) (assimilate partitioning
Guatemala	
J.J. Castillo M., Facultad de Agronomia; Universidad de San Carlos de Guatemala; Apartado Postal 1545 Ciudad de Guatemala; Fax: +502 2 954519.	Agronomy, inventory of national germplasm
Mexico	
A. Heredia Z., Campo Experimental Bajío, INIFAP/CIR-CENTRO; Apdo. Postal 112, 38000 Celaya; Guanajuato; Fax: +52 461 15431.	Breeding, agronomy

Peru
C. Arbizu,
Departamento de Recursos Geneticos;
Centro International de la Papa (CIP);
Apartado 1558;
Lima;
Fax: +51 14 351570;
e-mail: “c.arbizu@cgnet.com”.

Germplasm acquisition/ taxonomy

Portugal
F. Gusmão,
Direcção Regional de Agricultura
de Trás-os-Montes (DRATOM);
Rua da Republica 197;
5379 Mirandela;
Fax: +351 78 23328.

Agronomy.

Senegal
D.J.M. Annerose,
Laboratoire de Physiologie
de I’Adaptation à la Sécheresse;
C.E.R.A.A.S.;
ISRA/CNRA;
B.P. 59 Bambey;
Fax: +221 736197;
e-mail: “annerose@ceraas.orstom.sn”.

Agronomy, physiology (drought tolerance)

Spain
E.O. Leidi,
Instituto de Recursos Naturales
y Agrobiología de Sevilla;
CSIC; Reina Mercedes Campus;
Apartado 1052;
E-41080 Sevilla;
Fax: +34 5 4624002;
e-mail: “leidi@cica.es”.

Biological nitrogen fixation

Thailand
N. Ratanadilok,
Agronomy Department,
Faculty of Agronomy,
Kasetsart University;
Kamphaengsaen Campus;
Nakorn Pathom 73140;
Fax: +66 34 351406.

Agronomy

Tonga

P.E. Nielsen,
Research Division MAF;
Vaini Experimental Station;
P.O. Box 14 Nuku'alofa;
Fax: +676 24271.

Agronomy, *ex situ* conservation, breeding, biological nitrogen fixation

Trinidad

G. Sirju-Charran,
Department of Plant Science;
Faculty of Agriculture;
University of the West Indies;
St. Augustine;
Trinidad and Tobago.
Fax: +1 809 6621182;
e-mail: "gcharran@centre1.centre.uwi.11".

Physiology, plant anatomy, biochemistry (rotenone), *in vitro* propagation

United Kingdom

R. J. Abbott,
Plant Sciences Laboratory;
School of Biological and Medical Sciences;
University of St Andrews;
Sir Harold Mitchell Building;
St Andrews;
Fife KY16 9TH;
Scotland, U.K.
Fax: +44 334 463366;
e-mail: "rja@st-andrews.ac.uk".

Molecular taxonomy

Venezuela

F. Espinoza,
Instituto de Investigaciones Zootecnicas (IIZ);
Centro Nacional de Investigaciones Agropecuarias (CENIAP);
FONAIAP;
Apartado 4653;
Maracay 2101;
Aragua;
Fax: +58 43 831655.

Agronomy

Appendix 2. Centres of crop research, breeding and genetic resources

Centres of crop research
Benin, Denmark, Costa Rica, Ecuador, France, Germany, Portugal, Senegal, Thailand, Tonga, Venezuela: same addresses as in Appendix 1.
India-Central Tuber Crops Research Institute, Sreekariyam, Trivandrum 694 017, Kerala.

Centres of breeding
Benin, Denmark/ Costa Rica, Ecuador, Germany, India, Mexico, Senegal, Thailand,, Tonga and UK: same addresses as in Appendix 1.

Genetic resources
The figures in brackets list the accessions (not including breeding lines or hybrids) recorded in the germplasm collections at the various institutions; A: = P. *ahipa,* E: = P. *erosus,* F: = P. *ferrugineus,* P: = P. *panamensis,* T: = P. *tuberosus.*

Belgium
Laboratory of Plant Genetics; (A: 0, E: 1, F: 0, P: 0, T: 1)
Free University of Brussels;
Rhode St Genese Paardenstraat 65-67;
Brussels.

Jardin Botanique Nátional de Belgique; (A: 1, E: 1, F: 0, P: 0, T: 0)
Meise Domaine de Bouchout.

Benin
same address as in Appendix 1. (A: 0, E: 5, F: 0, P: 1, T: 4)

Brazil
same address as in Appendix 1. (A: 5, E: ?, F: ?, P: 1, T: ?)

Empresa Brasileira de Pesquisa (A: 0, E: 0, F: 0, P: 0, T: 2)
Agropecuária (EMBRAPA) /
Centro Nacional de Pesquisa de Recursos
Genéticos e Biotecnologia (CENARGEN);
S.A.I.N. - Parque Rural;
C.P. 0.2372; CEP 70.770;
Brasilia, D.F.

Instituto Nacional de Pesquisas da Amazonia (INPA); (A: 0, E: 7, F: 0, P: 0, T: 2)
Estrada do Aleixo 1756;
CR 478;
69011-970 Manaus, AM.

Colombia
Centro Internacional de Agricultura Tropical (CIAT); (A: 0, E: 13, F: 0, P: 0, T: 0)
Apdo. Aéreo 6713
Cali.

Costa Rica
same address as in Appendix 1. (A:3, E:83, F:2, P:1, T:21)

Asociación de Nuevos Alquimistas; (A:0, E:1, F:0; P:0, T:0)
Sabanilla;
Apdo. 170
Montes de Oca.

Cuba
Instituto Nacional de Viandas Tropicales; (A:0, E:1, F:0, P:0, T:0)
Santo Domingo;
Apdo. 6 Villa Clara.

Denmark
same address as in Appendix 1. (A:20, E:170, F:20, P:l, T:62)

Ecuador
(both institutions) (A:16, E:23, F:1, P:1, T:30)
- same address as in Appendix 1.

Ethiopia
International Livestock Research Institute (ILRI); (A:1, E:2, F:0, P:0, T:0)
P.O. Box 5689,
Addis Abeba.

France
same address as in Appendix 1. (A:6, E:2, F:0, P:l, T:2)

Germany
same address as in Appendix 1. (A:18, E:2, F:0, P:1, T:4)

Guatemala
Proyecto de Recursos Fitogeneticos; (A:0, E:10, F:0, P:0, T:0)
Instituto de Ciencia y Tecnologia Agricolas;
Barcena;
Villa Nueva km 21.5,
Carretera a Amatitlan.

India
National Bureau of Plant Genetic Resources; (A:0, E:40, F:0, P:0, T:0)
Pusa Campus;
New Delhi 110012.

Central Tuber Crops Research Institute; (A:0, E:20, F:0, P:0, T:0)
Sreekari yam;
Trivandrum 695017, Kerala.

Mexico
same address as in Appendix 1. (A:7, E:20, F:1, P:1, T:1)

Biblioteca Central; (A:0, E:2, F:0, P:0, T:0)
Universidad Autonoma Chapingo;
Apdo. 56230
Chapingo.

Philippines

Institute of Plant Breeding; (A:0, E:9, F:0, P:0, T:0)
College of Agriculture;
University of the Philippines at
Los Baños, College;
Laguna 4031.

Philippine Root Crops Research (A:0, E:24, F:0, P:0, T:0)
and Training Center (VISCA);
Baybay, Leyte.

Thailand

same address as in Appendix 1. (A:3, E:41, F:0, P:0, T:4)

Tonga

same address as in Appendix 1. (A:10, E:130, F:3, P:1, T:58)

USA

Southern Regional Plant Introduction Station; (A:0, E:8, F:0, P:0, T:0)
USDA-ARS; 1109 Experiment Street;
Griffin,
Georgia 30223-1797.

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