FURTHER EVIDENCE ON THE ORIGIN OF THE CULTIVATED WINGED BEAN, *PSOPHOCARPUS TETRAGONOLOBUS* (L.) DC. (FABACEAE): CHROMOSOME NUMBERS AND THE PRESENCE OF A HOST-SPECIFIC FUNGUS[1]

DANIEL K. HARDER AND JOSEPH SMARTT

Harder, Daniel K. *(Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299) and* **Joseph Smartt** *(Department of Biology, School of Biological Sciences, Medical and Biological Sciences Building, Bassett Crescent East, Southampton, SO9 5NH, United Kingdom).* FURTHER EVIDENCE ON THE ORIGIN OF THE CULTIVATED WINGED BEAN, *PSOPHOCARPUS TETRAGONOLOBUS* (L.) DC.: CHROMOSOME NUMBERS AND THE PRESENCE OF A HOST-SPECIFIC FUNGUS. *Economic Botany 46(2):187–191. 1992. Further evidence on the origin of the cultivated winged bean (*Psophocarpus tetragonolobus *(L.) DC.) is presented. Recent evidence concerning chromosome numbers of previously unavailable species in the genus and observational evidence of false rust (*Synchytrium psophocarpi *(Rac.) Gäumann) on* P. grandiflorus *Wilczek in Zaïre is discussed. Consideration includes previously published studies on morphology and cytology to support an African center of origin and points to* P. grandiflorus *as the progenitor species of the cultivated winged bean.*

Neue Daten bezüglich der Abstammung der kultivierten Goabohne, *Psophocarpus tetragonolobus* (L.) DC.: Chromosomenzahlen und Anwesenheit eines wirtspezifischen Rostpilzes. *Neue Daten bezüglich der Abstammung der kultivierten Goabohne (*P. tetragonolobus *(L.) DC.) werden vorgelegt. Chromosomenzahlen bislang unzugänglicher Arten der Gattung, sowie Beobachtungen am Falschen Rost (*Synchytrium psophocarpi *(Rac.) Gäumann) auf* P. grandiflorus *Wilczek werden im Zusammanhang mit bereits publizierten morphologischen und cytologischen Daten diskutiert. Die Ergebnisses unterstützen die Annahme eines Ursprungszentrums der Gattung in Afrika und deuten auf* P. grandiflorus *als die wilde Urform der Goabohne hin.*

Key Words: false rust; *Psophocarpus*; winged bean; origin.

The winged bean, *Psophocarpus tetragonolobus* (L.) DC., has long been an important vegetable crop throughout southeast Asia and Papua New Guinea. The exceptional nutritional quality of the edible portions of the plant and the fact that the plant provides a suitable human food source at all stages of its life cycle make it an excellent candidate for increased, widespread use in protein deficient, tropical areas of the world. Following the 1975 publication by the U.S. National Academy of Sciences of *The Winged Bean: A High Protein Crop for the Tropics* (NAS 1975), considerable effort has focused on the nutritional quality and climatic and ecological tolerances of the plant which has led to better management practices (Harder 1990; Khan 1982; Lubis 1978; Ruegg 1981; Stephenson 1978).

Wild species of *Psophocarpus* have also been shown to be suitable and even exceptional human food sources in their own right, and may be useful sources of disease resistance in the genetic improvement of the cultivated winged bean (Harder et al. 1990). The use of these genetic resources has not been explored to any extent due to the previous lack of viable seed material for these wild species.

Following a collection of seed and herbarium specimens of the wild species in the genus *Psophocarpus* in Zaïre in 1987 (Harder et al. 1990), new evidence has come to light elucidating the possible center of origin of the genus, and identifying the most probable progenitor species

---

[1] Received 1 March 1991; accepted 28 November 1991.

Economic Botany 46(2) pp. 187–191. 1992
© 1992, by The New York Botanical Garden, Bronx, NY 10458 U.S.A.

of the cultivated winged bean as *Psophocarpus grandiflorus* Wilczek. New information on chromosome numbers and pathology (due to *Synchytrium psophocarpi* (Rac.) Gäumann) are here presented and discussed with consideration of previously published work raising new questions regarding the systematic relationships within the genus and the process of domestication of the cultivated winged bean. Additionally we emphasize the need for further collections of species which are presently not available for taxonomic and genetic studies.

A comprehensive revision of the genus was published by Verdcourt and Halliday (1978). More recently, Maxted (1989, 1990), using phenetic and principal components analysis, reevaluated the phylogenetic relationships between the nine described species of *Psophocarpus*. These studies resulted in slight modifications of the previous specific circumscriptions presented by Verdcourt and Halliday (1978).

Nine (eight of which are fully described; see Maxted 1990) of the species are endemic to Africa with a single extension of the cultivated species into southeast Asia and other tropical regions. Two of the wild species, *P. scandens* (Endl.) Verdc. and *P. palustris* Desv., are also found in natural and naturalized populations in Africa and their use as food and as a cover crop has been exploited in Asia and parts of the New World tropics (Harder et al. 1990; Hymowitz and Boyd 1977; Verdcourt and Halliday 1978).

Presumably, no known wild plants of *P. tetragonolobus* have ever been collected, although plants growing as garden escapes have been noted in Burma (Burkill 1906), the Philippines (Agcaoili 1929) and Hawaii. This has confounded the determination of the center of origin and the identification of the progenitor species of this economically important plant. The absence of *P. tetragonolobus* in the native flora in the center of its domesticated range and the difficulty in identifying a possible wild progenitor necessitated the need to employ indirect evidence.

The winged bean is most widely cultivated in Asia. Burma, Papua New Guinea, and Indonesia are the centers of germplasm diversity representing a long history of cultivation in these areas (Khan 1982; Pickersgill 1980). In the case of the winged bean, a complete transdomesticate (Smartt 1980a), the centers of origin, and apparent domestication are in different geographic locations, and this has caused considerable confusion in identifying these regions and a progenitor of the plant.

As reviewed by Zeven and deWet (1982), four widely separated areas have been proposed as the center of origin of the cultivated winged bean. Papua New Guinea is believed to be the center of origin based on the considerable genetic variation found there (Hymowitz and Boyd 1977). In an attempt to explain the absence of wild plants of *P. tetragonolobus* in Asia, another theory suggests the winged bean was domesticated from an unknown and now extinct endemic Asian progenitor (Verdcourt and Halliday 1978). Vavilov (1951) presumed the origin was in the Indo-Malayan center based on his knowledge of the cultivation of the plant in the Hill Tract of eastern Assam but an Indian origin for the winged bean has not attracted much support (Hymowitz and Boyd 1977). Burkill (1935) assumed the winged bean originated in Africa based on the African origin of what he assumed was the progenitor, *P. palustris*. Citing parallel African-Asian distribution patterns of other cultivated genera such as guar (*Cyamopsis tetragonoloba* (L.) Taub.) and *Sphenostylis stenocarpa* (Hochst. ex A. Rich.), Smartt (1980a) and Maxted (1984) supported the African origin theory.

LINES OF EVIDENCE

1. MORPHOLOGICAL CORRESPONDENCE

In general morphology, *P. grandiflorus* most closely resembles *P. tetragonolobus* (Smartt 1980a). Both of these species are indeterminate twining climbers (excluding the recently developed day-neutral and determinate varieties of the winged bean) with large flowers and seeds. Both are adapted to and reach their greatest development in high elevation areas (Smartt 1980a). Their resemblance is also verified by the taxonomic studies of Verdcourt and Halliday (1978) and of Maxted (1990) which consistently place them in the same subgenus *Psophocarpus*, section *Psophocarpus*. They also share the same basic stigma/style and stylar hair arrangements. Maxted (1990), however, considered *P. grandiflorus* to be a more remote member of this section. He showed that *P. grandiflorus* has a different stigma-style arrangement and exhibits discord in flower part size and shape with those found in other members of the section: *P. scandens*, *P. palustris*, and *P. tetragonolobus*. Maxted further placed *P. scandens* as the species most closely allied to *P. tetragonolobus.*

In addition to the characters differentiating *P. grandiflorus* from other species in the section mentioned above, *P. tetragonolobus* can be distinguished from *P. grandiflorus* by having larger, more succulent pods, glabrous stems, sometimes tending toward an annual growth habit, sometimes purplish stems and sepals, glabrous seeds with a small rim aril, and, in some varieties, by the presence of a tap-rooted tuber. These characters of the cultivated winged bean are the result of selection through domestication for the preferred edible products from the plant.

Palynological evidence reveals a similarity in ornamentation of the apocolpium and mesocolpium and the continuous nature of the foot layer in both *P. tetragonolobus* and *P. grandiflorus* suggesting common ancestral links (Poole 1980). Both of these species have distinctive pollen grains that express more advanced morphological characters within the genus, but *P. tetragonolobus* exhibits the greatest degree of specialization and advancement.

Archeological evidence has yet to shed light on the origin or history of domestication of the winged bean. The detailed analysis of pollen morphology by Poole (1979) clearly showed that the differences are recognizable and could be used to differentiate the species in archeological deposits (Verdcourt and Halliday 1978).

2. CYTOTAXONOMIC EVIDENCE

A comprehensive cytological study of *P. tetragonolobus* and *P. scandens* was carried out by Pickersgill (1980). This work established conclusively that these two species have the same chromosome number of $2n = 18$. Prior to this study inconsistent counts had been reported. It is now clear that there had been confusion in the identification of *P. scandens* and *P. palustris* which further obscured the true situation (Haq and Smartt 1977). This has now been resolved by the studies of Verdcourt and Halliday (1978) and Maxted (1989). Though clearly closely allied, the two species can be distinguished reliably by differences in vegetative and reproductive morphology which are also maintained in greenhouse and garden culture (Harder pers. obs.). In addition, the two species are allopatric in Africa.

Harder has investigated the chromosome complements of four of the species which he and his co-workers have collected in Zaïre (see Harder et al. 1990). Accessions from each of the species were examined and it was found that the observed chromosome number was consistent ($2n = 18$) both within and between the species, *P. grandiflorus, P. palustris,* and *P. lancifolius* Harms. These counts were also the same as those reported by Pickersgill (1980) for *P. tetragonolobus* and *P. scandens.* Additionally, there was general agreement as to karyotype with three pairs of short and six pairs of long chromosomes in all five species of *Psophocarpus* studied. This chromosome complement and the karyotype described may well be characteristic of the whole genus (Harder, n.d.).

The above cytological information does not shed any new light on the origins or evolution of the winged bean. Both karyotype and chromosome number appear to be conservative characters in the evolution of this genus as far as is known at present. The critical test that Smartt (1980a) suggested would be "the ability of the two forms [*P. tetragonolobus* and *P. grandiflorus*] to cross and produce viable, fertile hybrids." Inferences as to chromosome homologies between species would have to wait the production of viable interspecific hybrids and the subsequent cytological studies of their meiosis. Alternatively, the development of suitable chromosome banding techniques, RFLP studies, and other advanced analyses might also be informative.

The difficulties experienced in obtaining living material of wild *Psophocarpus* species and, when collected, in inducing *P. grandiflorus* to flower freely have been an obstacle to the elucidation of genetic relatedness between it, *P. tetragonolobus,* and other species in the genus. It is possible that material collected elsewhere in Africa may prove more amenable to experimental study. An encouraging observation in the field concerning interspecific hybridization is that in attempts to hybridize *P. scandens* and *P. lancifolius,* ten of sixty-four attempted crosses produced seeds which were only slightly deformed. The viability of this seed and the behavior of the F_1 progeny are currently under investigation by the senior author.

3. SUSCEPTIBILITY TO THE PATHOGEN *SYNCHYTRIUM PSOPHOCARPI* (FALSE RUST)

Compelling evidence in elucidating the origin of the cultivated winged bean, uncovered during our collection in Zaïre, was the presence on

Psophocarpus grandiflorus of what appeared to be false rust caused by the fungus *Synchytrium psophocarpi* (Rac.) Gäumann. The presence of the pathogen on *P. grandiflorus* has been reported previously by Harder et al. (1990) and this has subsequently been confirmed on herbarium specimens of *P. grandiflorus* from Uganda (IMI 327691) (T. V. Price, pers. comm.).

False rust incites one of the major diseases of the cultivated winged bean in south east Asia. Some resistance to the disease has been identified in some Indonesian cultivars. Interestingly, however, no resistance has been identified in varieties from Papua New Guinea (Thompson and Haryono 1980) or anywhere else. The biology of the fungus, its dispersal, and the incidence and severity of the disease in Papua New Guinea have been described by Drinkall and Price (1979, 1983) and Price, Drinkall, and Munro (1982).

Synchytrium psophocarpi is an obligate biotroph which is host specific and, through manual inoculations, has been shown not to infect *Arachis hypogaea* L. (peanut), *Glycine max* (L.) Merr. (soybean), *Phaseolus coccineus* L. (scarlet runner bean), *P. vulgaris* L. (common bean), *Pisum sativum* L. (pea), *Vigna radiata* (L.) Wilczek (green gram), *Vicia faba* L. (faba bean), *Vigna unguiculata* subsp. *sesquipedalis* (L.) Verdc. (yardlong bean), *V. unguiculata* (L.) Walp. (cowpea) and *Psophocarpus scandens* (Drinkall and Price 1986). Based on field observations in Zaïre, the disease was not apparent on *Psophocarpus scandens, P. lancifolius,* or *P. lecomtei* Tisserant nor indicated on herbarium specimens of these species held at Kew (K) or Missouri Botanical Garden (MO). These resistant species, possibly constituting a tertiary or quaternary gene pool (Smartt 1980b), may be a future source of genetic resistance for the cultivated winged bean (Harder et al. 1990). The fact that *P. scandens* is not susceptible to infection by false rust also reinforces the conclusion reached by Pickersgill (1980), Verdcourt and Halliday (1978) and Poole (1979) that this species is unlikely to be the immediate wild relative of *P. tetragonolobus*.

The taxonomic significance of the susceptibility of *P. grandiflorus* to false rust must be interpreted with caution, however. The use of the presence of a host specific disease as a taxonomic tool and in identifying the centers of origin of a crop plant has some precedents in work with *Crambe* (Leppik and White 1975) and peanut (Subrahmanyam et al. 1989). It is obvious that more work is necessary to test the susceptibility of the other species of *Psophocarpus* to the disease before firmer conclusions can be drawn. Further collections of herbarium specimens and seeds of the presently unavailable species, *P. lukafuensis, P. monophyllus,* and *P. obovalis,* or others (sp. A; Maxted 1990), are needed to verify the biosystematic relationships within the genus.

Smartt (1980a) postulated that the present distribution of *P. grandiflorus* in East Africa, in the highlands of Burundi, Ethiopia, Kenya, and Uganda above 1750 m, was sufficiently close to the previously used and extant trade routes to Asia that the movement of the plant could have been easily possible. The present multipurpose utilization of *P. grandiflorus* in Zaïre and the exceptional nutritional quality of the edible portions of the plant also substantiate this possibility (Harder et al. 1990).

CONCLUSIONS

Although the similar chromosome numbers of *Psophocarpus grandiflorus, P. lancifolius, P. lecomtei* and *P. palustris* neither support nor negate the possibility of *P. grandiflorus* being the progenitor of the winged bean, the morphological and plant pathological evidence does strongly support this claim. If *P. grandiflorus* is the closest wild relative of the cultivated winged bean, and no other described species has as much compelling evidence in its favor, other questions need attention. How did domestication select for the tuber-producing ability in the cultivated winged bean from a non-tuber forming progenitor, *P. grandiflorus*? Through what specific changes after domestication did *P. grandiflorus* become the cultivated winged bean, *P. tetragonolobus*? How did *P. grandiflorus,* an African endemic, get to be distributed so widely in southeast Asia through transdomestication as suggested by Smartt (1980a)? Finally, did preliminary domestication of *P. grandiflorus* or an intermediate occur in Africa or Asia?

ACKNOWLEDGMENTS

We would like to thank H. G. Baker, W. H. Lewis, J. P. Talbot, J. Zarucchi, and anonymous reviewers for their comments on an earlier version of the manuscript. We thank T. V. Price for indicating the presence of false rust on Ugandan material of *P. grandiflorus* and S. Liede for the German translation.

LITERATURE CITED

Agcaoili, F. 1929. Sequidilla bean. Philippine Journal of Science 40(4):513–514.

Burkill, I. H. 1906. *Psophocarpus tetragonolobus* (goa bean)—Goa bean in India. The Agric. Ledger 4(96): 51–64.

———. 1935. A dictionary of the economic products of the Malay Peninsula. Crown Agents, London.

Drinkall, M. J., and T. V. Price. 1979. Studies of *Synchytrium psophocarpi* on winged bean in Papua New Guinea. Trans. Brit. Mycol. Soc. 72:91–98.

———, **and** ———. 1983. Dispersal of *Synchytrium psophocarpi* in Papua New Guinea. Plant Path. 32: 229–237.

———, **and** ———. 1986. Studies of the infection of the winged bean by *Synchytrium psophocarpi* in Papua New Guinea. Ann. Appl. Biol. (Great Britain) 109:87–94.

Haq, N., and J. Smartt. 1977. Chromosome complements in *Psophocarpus* spp. Trop. Grain Legume Bull. 10:16–19.

Harder, D. K. 1990. Developmental physiology of the cultivated winged bean (*Psophocarpus tetragonolobus* (L.) DC.): Growth attributes and mineral contents. Ph.D. dissertation, University of California, Berkeley.

———, **P. M. L. Onyembe, and T. Musasa.** 1990. The uses, nutritional composition and ecogeography of four species in the genus *Psophocarpus* (Fabaceae, Phaseoleae) in Zaire. Econ. Bot. 44(3):391–409.

———. n.d. Chromosome counts in *Psophocarpus* (Fabaceae). Kew Bull. 47(3):in press.

Hymowitz, T., and J. Boyd. 1977. Origin, ethnobotany and agricultural potential of the winged bean—*Psophocarpus tetragonolobus*. Econ. Bot. 31(2):180–188.

Khan, T. N. 1982. Winged bean production in the tropics. Food and Agriculture Organization Plant Production and Protection Paper 38. Rome.

Leppik, E. E., and G. A. White. 1975. Preliminary assessment of *Crambe* germplasm resources. Euphytica 24(3):681–689.

Lubis, S. H. A. 1978. Flowering behavior of the winged bean. Pages 121–123 *in* The winged bean. Papers presented at the First International Symposium of the Winged Bean, January, 1978, Philippine Council for Agriculture and Resources Research. Los Baños, Philippines.

Maxted, N. 1984. The inter- and intra-generic relationships between *Psophocarpus* spp. and their allies. M. Phil. thesis, The University, Southampton, UK.

———. 1989. A phenetic investigation of the *Psophocarpus palustris-P. scandens* complex (Leguminosae, Phaseoleae, Phaseolinae). Kew Bull. 44(4):731–742.

———. 1990. A phenetic investigation of *Psophocarpus* Neck. ex DC. (Leguminosae-Phaseoleae). Bot. J. Linn. Soc. 102(2):103–122.

National Academy of Sciences. 1975. The winged bean: A high-protein crop for the tropics. Washington, D.C., USA.

Pickersgill, B. 1980. Cytology of two species of winged bean, *Psophocarpus tetragonolobus* (L.) DC. and *P. scandens* (Endl.) Verdc. (Leguminosae). Bot. J. Linn. Soc. 80(4):279–291.

Poole, M. M. 1980. Pollen morphology of *Psophocarpus* (Leguminosae) in relation to its taxonomy. Kew Bull. 34(2):211–224.

Price, T. V., Drinkall, M. J., and P. E. Munro. 1982. Studies of the incidence, severity and distribution of false rust (*Synchytrium psophocarpi*), leaf spot (*Pseudocercospora psophocarpi*) and powdery mildew (*Oidium* sp.) on winged bean (*Psophocarpus tetragonolobus*) in Papua New Guinea. Ann. Appl. Biol. (Great Britain) 101:473–482.

Ruegg, J. 1981. Effect of temperature and water stress on the growth of winged bean (*Psophocarpus tetragonolobus* (L.) DC.). J. Hort. Sci. 56:331–338.

Smartt, J. 1980a. Some observations on the origin and evolution of the winged bean. Euphytica 29(1): 121–123.

———. 1980b. Evolution and evolutionary problems in food legumes. Econ. Bot. 34(3):219–235.

Stephenson, R. A. 1978. Field studies on winged bean growth and yield. Pages 191–196 *in* The winged bean. Papers presented at the First International Symposium of the Winged Bean, January, 1978. Philippine Council for Agriculture and Resources Research. Los Baños, Philippines.

Subrahmanyam, P., V. Ramanatha Rao, D. McDonald, J. P. Moss, and R. W. Gibbons. 1989. Origins of resistance to rust and late leaf spot in peanut (*Arachis hypogaea,* Fabaceae). Econ. Bot. 43(4):444–455.

Thompson, A. E., and S. K. Haryono. 1980. Winged bean: Underexploited tropical food crop. HortSci. 15(3):233–238.

Vavilov, N. I. 1951. The origin, variation, immunity and breeding of cultivated plants (trans. by K. Starr Chester). Chronica Botanica, vol. 13. The Ronald Press Co., New York.

Verdcourt, B., and P. Halliday. 1978. A revision of *Psophocarpus* (Leguminosae: Papilionoideae: Phaseoleae). Kew Bull. 33(2):191–227.

Zeven, A. C., and J. M. J. de Wet. 1982. Dictionary of cultivated plants and their regions of diversity: Excluding most ornamentals, forest trees and lower plants. Centre for Agricultural Publishing and Documentation. Wageningen, p. 138.