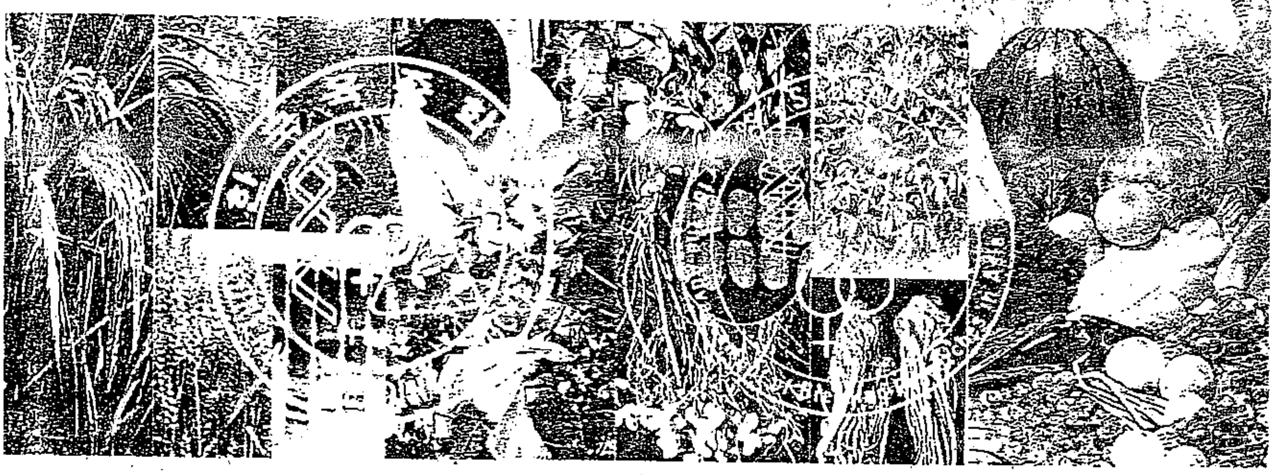
Harmonizing Agricultural Productivity and Conservation of Biodiversity: Breeding and Ecology

Proceedings of the 8th SABRAO General Congress and the Annual Meeting of the Korean Breeding Society

24-28 September, 1997, Seoul Olympic Parktel, Seoul, Korea



Published by

The Korean Breeding Society

and

The Society for Advancement of Breeding Researches in Asia and Oceania

December, 1997

The 8th SABRAO General Congress and the Annual Meeting of the Korean Breeding Society

"Harmonizing Agricultural Productivity and Conservation of Biodiversity: Breeding and Ecology"

24~28 September, 1997
Seoul Olympic Parktel, Seoul, Korea

SPONSORED BY

The Korean Breeding Society

CO-SPONSORED BY

The Society for Advancement of Breeding Researches in Asia and Oceania
Rural Development Administration

Address : c/o Dep. of Agronomy, Seoul National University

Suwon 441-744, Republic of Korea

FAX 82-331-292-0804

E-mail - heejkoh@plaza.snu.ac.kr

ISBN code : 89-950048-0-0 93520

Printed in Sangroksa Printing's Co., Suwon, Korea

BREEDING FOR ADAPTATION TO STRESS FACTORS AND FOR DIFFERENT CROPPING SYSTEMS IN LEGUMES

Nigam SN*, Saxena KB, Kumar J
International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India.

In spite of the significant role that legumes play in meeting the daily protein and fat (in the case of oil rich legumes) requirements of human diets, they have only a secondary place in Asian farming systems. They are generally grown in intercropped or mixed cropping systems, often in marginal lands with minimum inputs. Progress in legumes improvement has not been as spectacular as witnessed in many cereal crops due mainly to poor allocation of resources and personnel in their research and development. However, legumes have lately started receiving more attention from research administrators and policy planners because of declining availability of protein in daily human diets, and their significant role in sustainable agriculture. Because of their secondary place in farming systems, legumes have to adapt to available niches in space and time vis-à-vis the main crop, thus leaving them vulnerable to unfavorable growing conditions. In addition, legumes also attract a variety of diseases and insect pests which keep their productivity low. In this paper, we discuss the progress made in three legume crops mandated to ICRISAT: groundnut (*Arachis hypogaea*), pigeonpea (*Cajanus cajan*), and chickpea (*Cicer arietinum*) in (i) genetic amelioration of important abiotic and biotic stresses that affect their productivity in Asia, and (ii) genetic manipulation in their phenology to increase their productivity in cropping systems.

Groundnut

Groundnut, an annual legume, is a native of South America. It is grown in over 100 countries with a total estimated area of 22.2 million ha and production in shell of 29.2 million t. Asia (25 countries) with 61% of the area produces 69% of the world groundnut production. Important groundnut producing countries in Asia are China, India, and Indonesia.

Groundnut is grown under both subsistence and commercial systems. Under commercial cultivation, it is grown mainly as a sole crop with high levels of inputs whereas under subsistence conditions both sole crop and mixed or intercropping can be seen. About 70% of the world's groundnut is produced in the semi-arid tropics, the exclusive agroeco-system focus of ICRISAT. About two thirds of the total world production is crushed for cooking oil. The remaining one third is eaten directly as boiled or roasted nuts and as confectionery, an increasing trend over the years. Groundnut haulms are used as fodder and the cake remaining after the extraction of oil is used in animal feeds.

Average productivity of groundnut (pod in shell) in the world is about 1.31 t ha^{-1}. In USA, where most of the cultivation is commercial, an average yield of 2.63 t ha^{-1} is obtained and pod yields in excess of 4.0-5.0 t ha^{-1} are not uncommon. Average productivity at the subsistence system in Africa and Asia, however, remains very low.

The major abiotic factors affecting groundnut production include drought, high temperature, low soil pH, and iron chlorosis. Among the biotic factors, foliar diseases, virus diseases, bacterial wilt disease, aflatoxin contamination, and insect pests are important. Some of these stress factors operate globally whereas others are of regional importance.

The cultivated groundnut (*A. hypogaea*) is classified into two subspecies: *subspecies hypogaea* and *subspecies fastigiata*. The *subspecies hypogaea* is divided into two botanical varieties: variety *hypogaea* [Virginia (large seeded) and Runner (small seeded) market types] and variety *hirsuta* (*Peruvian* Runner market type). The *subspecies fastigiata* is divided into four botanical varieties: variety *fastigiata* (Valencia market type), variety *peruviana*, variety *aequatoriana*, and variety *vulgaris* (Spanish market type).

Abiotic Stress Factors

Drought

In the rainfed subsistence agriculture drought is the major cause for low and erratic pod yield in groundnut. Field techniques to screen genotypes for drought tolerance have been standardized. Genotypes with superior performance under mid- and end-of-season droughts have been developed and made available to national programs. Recent studies have indicated genotypic variation in transpiration, water use efficiency (WUE), partitioning of dry matter to pods (P), and rate of recovery from mid-season drought. It is also established that specific leaf area (SLA) can be used as a selection criterion to identify genotypes with high WUE (Wright *et al.*, 1994). However, negative relationship between WUE and P suggests that selection for high WUE might enhance dry matter production but not necessarily pod yield.

Acid soils

Many countries in Asia and Africa have acid soils, deficient in calcium, where groundnut yields are low and pod filling is poor (occurrence of pops or empty pods). Genotypes, tolerant of acid soils, have been identified in the Philippines (Samonte and Ocampo, 1989). These lines, however, failed to show tolerance when tested in acid soils in Indonesia. Breeding for tolerance of acid soils is complex since soil acidity may be associated with deficiency or toxicity of various nutrients depending on location.

Iron chlorosis

Iron chlorosis in groundnut grown on calcareous and/or alkaline soils can cause up to 30% loss in pod yield. Currently the problem is overcome by spraying ferrous sulphate solution on the plants. Screening of genotypes in calcareous soils has resulted in identification of several genotypes which are tolerant of iron chlorosis (Singh, 1994). Five loci are involved in determining the absorption efficiency of iron in groundnut. Among these one locus pertains to the basic gene and the remaining four loci are inhibitory complementary genes (Gowda *et al.*, 1993). Very little directed breeding is in progress for developing iron-efficient cultivars.

Biotic Stress Factors

Foliar diseases

Among all stress factors, foliar diseases, rust (*Puccinia arachidis*), early leaf spot (*Cercospora arachidicola*), late leaf spot (*Phaeoisariopsis personata*), have received most attention in resistance breeding in groundnut. These foliar diseases occur worldwide and can cause up to 70% loss in pod yield when they occur together. Following both, field and laboratory screening techniques, several stable sources of resistance to these foliar diseases have been identified in cultivated groundnut (Singh *et al.*, 1997). Both simple and complex inheritance of resistance to these diseases are reported in literature. Cultivars with high levels of resistance to rust and moderate levels of resistance to early- and late-leaf spots have been developed following pedigree and backcross methods of breeding and released to farmers in Asia and elsewhere.

Wild *Arachis* species are a reservoir of high levels of resistances to several stress factors including foliar diseases. Interspecific hybridization is being pursued in many programs to improve upon the level of resistance to foliar diseases in cultivated groundnut. However, high yield potential and high levels of resistance to foliar diseases do not generally go together. A balance needs to be struck between level of resistance and yield potential to achieve the maximum economic yield. Combining genetic resistance with minimum chemical control offers a better strategy to manage these foliar diseases (Nigam *et al.*, 1991).

Virus diseases

Groundnut is host to several virus diseases but only a few are economically important in Asia; peanut bud necrosis virus (PBNV) disease in South Asia and peanut stripe virus (PStV) disease in East and Southeast Asia. Genetic tolerance to PBNV and its vector, *Thrips palmi*, exists in cultivated groundnut. Several cultivars with consistently low PBNV disease in the field have been developed and released to farmers (Dwivedi *et al.*, 1995). Genetic resistance to PStV is available only in wild *Arachis* species which are incompatible with cultivated groundnut. Interspecific hybridization followed by embryo rescue and regeneration is yet to produce desired results. Genetic transformation of cultivated groundnut plant with coat protein genes of these virus diseases offers a more effective solution to manage them.

Bacterial wilt

Bacterial wilt (BW) of groundnut, caused by *Pseudomonas solanacearum*, occurs in many Asian countries. It causes significant yield losses (up to 30%) in China and Indonesia. Several sources of resistance to BW in cultivated groundnut have been reported (Singh *et al.*, 1997). They have long latent periods, less vascular browning, and lowest wilting rates than susceptible types. The information on the genetics of wilt resistance in groundnut is not conclusive and may differ with botanical types of the parents involved. Both partial dominance and recessiveness with a few major genes is reported for resistance in the literature (Mehan *et al.*, 1994). Schwarz 21, resistant to BW, was the first disease resistant cultivar, developed in 1925 in Indonesia. Since then, several high yielding, BW resistant cultivars have been released in China and Indonesia.

Aflatoxin contamination

Contamination of groundnut by aflatoxins, produced by *Aspergillus flavus* and *A. parasiticus*, is a serious health hazard in many Asian countries. Sources of resistance to preharvest infection, *in vitro* seed colonization, and aflatoxin production have been identified in cultivated groundnut. Through breeding, these resistances have been transferred in superior agronomic backgrounds. However, none of these resistances including cultural practices offers complete freedom from aflatoxin contamination (Upadhyaya *et al.*, 1997). New developments in molecular biology and genetic engineering are likely to provide long last succor against this problem.

Insect pests

Several insect pests attack groundnut but only a few are economically important to the crop either because they cause significant direct yield losses or because they are vectors of virus diseases. These includes aphids, thrips, jassids, leaf miner, *Spodoptera* and white grub in Asia. Except for the white grubs, the moderate levels of resistance have been identified for other insect pests in the cultivated groundnut. Moderate levels of resistance to thrips and jassids and tolerance of leaf miner and *Spodoptera* have been transferred into high yielding varieties following pedigree breeding method. However, wild *Arachis* species offer a much higher level of resistance to these insect pests and need to be exploited for resistance breeding (Nigam *et al.*, 1991).

Adaptation to Cropping Systems

Many cropping systems offer an opportunity to grow groundnut in the summer season with irrigation. However, high temperatures (>35 °C) prevailing in the summer season limit its productivity by interfering with different physiological processes. Recently a field screening of germplasm and breeding lines has been started jointly with Indian national program to identify plant characteristics associated with heat tolerance. Breeding for heat tolerance is yet to be initiated.

Groundnut is often intercropped with field and plantation crops which partially shade it. This partial shade results in etiolation of groundnut plants and a reduction in pod yield, Screening of groundnut genotypes for shade tolerance under an artificial shade structure using black nylon cloth, which provided 40-58% shading throughout the crop season, was carried out in the Philippines (Abilay *et al.*, 1991). Some lines were identified as tolerant of partial shade. This area of research has not received much attention elsewhere.

Availability of short-duration (<100 days) cultivars in groundnut has increased its versatility in different cropping systems (multiple cropping, rice follows, and residual moisture systems) and in areas with short growing seasons in Asia. Basing our selection on predetermined thermal time accumulation, several short-duration high yielding genotypes have been selected (Vasudeva Rao *et al.*, 1992). Incorporation of limited period of seed dormancy in spanish types has increased the crop utility in production systems where rains can occur unpredictably late in the season.

Pigeonpea

Pigeonpea is one of the major pulse crops of the tropics and subtropics. It originated in India and is presently cultivated on 3.5 million ha in Asia, Africa, and Americas. However, over 90% of its global cultivation is confined to Indian sub-continent. Endowed with several unique characteristics, it finds an important place in the farming systems adopted by small holder farmers in a number of developing countries. Pigeonpea is a perennial but is often cultivated as an annual crop. It is capable of producing over 3 t ha^{-1} but on average it yields only 0.7 t ha^{-1}. Drought, waterlogging, and salinity among abiotic stress factors, *Fusaruim* wilt, sterility mosaic and *Phytophthora* blight among diseases, and pod borers and pod fly among insect pests are responsible for low seed yields in the crop.

Pigeonpea is used in a wide variety of ways. Its main use in the India subcontinent is as human food. The dry seeds are dehulled and the split colytedons are cooked to make a thick soup primarily for mixing with rice. In Africa and Central America whole dry seeds are cooked. Its green seeds are cooked as vegetable peas. Green seeds are also processed for canning and freezing. The seed husks and pod walls are fed to cattle. Pigeonpea dry stems are an important household fuel wood in many countries.

Abiotic Stress Factors

Drought

Drought causes maximum yield loss throughout the semi-arid tropics, particularly if it occurs during reproductive stages. The genotypic differences for drought resistance in pigeonpea have been established under rainout shelters. These differences are associated with maintenance of dry mass production and its partitioning into leaves following drought period (Lopez *et al.*, 1996). A systematic breeding program for drought tolerance in pigeonpea has not been undertaken due to the complex nature of the stress.

Waterlogging

In the semi-arid tropics, heavy rainfall during the wet season can result in waterlogging especially in the poorly drained soils on which pigeonpea is often grown. In comparison to long-duration varieties, the losses due to waterlogging are high in the short-duration varieties due to their inability to recover from the damage. A greenhouse technique for screening for tolerance of water logged conditions has been developed and genotypes with tolerance have been identified at ICRISAT. Development of adventitious roots in waterlogged condition plays a major role in imparting the tolerance.

Salinity

Resistance to salinity has been found in wild *Cajanus* species. Resistance breeding has not yet been initiated.

Biotic Stress Factors

Fusarium wilt and sterility mosaic

Wilt, caused by *Fusarium udum*, is the most important disease with annual losses estimated to be around US $ 41 million (Kannaiyan *et al.*, 1984). The genetics of wilt resistance is complex and has not been fully understood. Sterility mosaic disease causes severe losses and an early infection to the plants causes up to 100% yield loss (Kannaiyan *et al.*, 1984). Resistance to sterility mosaic in pigeonpea was reported to be controlled by four independent non-allelic genes (Singh *et al.*, 1983) and by four alleles at two loci (Sharma *et al.*, 1984). In most pigeonpea growing areas both wilt and sterility mosaic diseases are problems, therefore, high yielding genotypes with combined resistance to both the diseases have been developed using field screening techniques at ICRISAT. These lines have yield potential similar to that of control but the level of disease resistance is very high.

Phytophthora blight

Blight, caused by *Phytophthora drechsleri*, is a problem when pigeonpea crop is subjected to waterlogging at early growth stage. Due to variation in pathogen, stable sources of resistance to this disease are not available.

Alternaria blight

Blight, caused by *Alternaria tenuissima*, is of importance only in the post-rainy season crop. The resistance to *Alternaria* blight is controlled by a single recession gene (Sharma *et al.*, 1987). Several high yielding resistant lines have been developed by breeders.

Insect pests

Pigeonpeas are fed upon by insects with over 200 species. It, however, being a perennial plant, rapidly recovers the damage caused to its vegetative parts. However, recovery of the reproductive parts is low, uncertain, and dependent on plant type, soil moisture, and climatic conditions. The losses due to flower, pod and seed damaging insects range between 50-100 %. Podfly (*Melanagromyza obtusa*) and pod borers (*Helicoverpa armigera* and *Maruca testulalis*) are major insect pests. Using field screening methodology, sources of resistance to all the three major insect pests have been identified from pigeonpea germplasm including its wild relatives. The resistance level in these sources is low. Breeders have used these sources to combine insect pest resistance with other economic traits. Success in breeding for host-plant resistance for these insect pests has been limited. Under unsprayed conditions, these selections yield 0.86 t ha^{-1} with about 50% pod damage compared with 0.11 t ha^{-1} with 90% pod damage in the control.

At ICRISAT, the partial natural out-crossing of pigeonpea has been exploited to develop high yielding hybrids. These hybrids have shown over 30% yield advantage and high stability in performance over environments and years (Saxena *et al.*, 1989). Because of their higher growth rate and more vigorous root system as compared to pure line varieties, they produce high yield under severe moisture stress conditions (Saxena *et al.*, 1996). Under disease pressure also the hybrids show yield advantage over pure line varieties.

Adaptation to Cropping Systems

Pigeonpea is unique in that its duration is a continuum from extra-short-duration (<90 days) to perennial types. This nature of the species allows it to adapt to a wide range of cropping systems and soil and climatic variations in semi-arid tropics. Perennial pigeonpea is widely grown as backyard crop while long (>250 days)- and medium (160-180 days)- duration types are invariably grown as an intercrop with cereals under rainfed low input conditions. Short-duration pigeonpeas are of recent origin and are cultivated as a sole crop under high density production system and in rotation with wheat and paddy. ICRISAT has also developed lines which can mature in <90 days and are relatively less sensitivity to photoperiod permitting their adoption in diverse production systems up to 40-45^{0} latitude. Most perennial as well as long-duration cultivars are landraces or selections from landraces. Due to natural out-crossing the cultivars/land races are heterogeneous for various agronomic traits, and breeders have successfully isolated high yielding pure lines from this material. Although these are cultivated under intercrop, the selections have been exercised under pure culture. Studies conducted at ICRISAT have shown that such selections perform well both under pure as well as intercrop situations.

Chickpea

Chickpea is grown globally on about 10 million ha with a mean annual production of 7.5 million t. It's average productivity is 0.7 t ha^{-1}. It is predominantly consumed as a pulse; dry chickpea is also used in preparing a variety of snack foods, sweets, and condiments. Green fresh chickpeas are commonly consumed as a vegetable for short period before the crop is mature. Chickpea straw has a forage value comparable to other straws commonly used for livestock feed. The crop is mainly grown rainfed and is relegated to marginal lands because of its low mean and unstable productivity. Its major production areas are the Indian sub continent, West Asia, North and Eastern Africa, Southern Europe and Latin America. In recent years Australia and to some extent North America have shown increased interest in growing this crop.

Two types of chickpea are distinguished, the more common (85-90%) brown (or other colors) seeded, usually small in size and with wrinkled seed coat; and white seeded, usually large with smooth owl's head shape. Although research station yields of over 6 t ha^{-1} and farmer field yields of around 5 t ha^{-1} have been reported, these are rarely realized (Kumar *et al.*, 1996). A number of abiotic and biotic stresses result in low and unstable productivity of this crop. These include; foliar and root diseases, pod borer, drought, extreme temperatures, soil salinity and unseasonal rain and hailstorms (Table 1). Their importance as major yield reducers varies from region to region if the production zones which may broadly be distinguished by differing latitudes are considered.

Abiotic Stress Factors

Drought

End-of-season drought is the major abiotic stress limiting chickpea yields. Breeding for drought resistance has not yet been fruitful. Large root volume appears to confer drought resistance but its effects on yield has not yet been positively correlated. Much success has been achieved in breeding for drought escape by development of short-duration varieties (85 days to mature compared to 110 days for the traditional varieties). Now we have lines maturing in 70 days (Kumar and Rao, 1996).

Biotic Stress Factors

Fusarium wilt

Wilt, caused by *F. oxysporum*, is wide spread and reported from all the chickpea growing areas of the world. Three loci are known to confer late wilting in chickpea. Any two of these together confer complete resistance. Much success has been achieved in developing Fusarium wilt resistant varieties.

Ascochyta blight

Blight, caused by *A. rabiei*, is most serious between the latitudes 30° and 45°, where relatively low temperatures (15°-25°) prevail during the crop season. A few genes for resistance to *Ascochyta* blight are known. These do not confer a high level of resistance and are known to break down. However, a number of *Ascochyta* blight resistant varieties have been bred through breeding.

The genetics of resistance to other diseases has not been studied and breeding efforts are at best only empirical.

Insect pests

Little progress has been made in enhancing resistance to *Helicoverpa* pod borer, a major pest of chickpea. However, tolerant lines have been bred.

Adaptation to Cropping Systems

In recent years reduction of crop duration from about 110 days to 85 days in peninsular India where temperatures are warm, has increased mean chickpea productivity from about 0.4 t ha^{-1} to 0.8 t ha^{-1}. Shorter duration cultivars also make it more suitable for inclusion in newer cropping systems e.g. in rice follows of the Indo-Gangetic plain. Yield gains are possible in sub-tropical conditions also, if the crop duration is reduced from 170 days to about 120 days (Kumar *et al.*, 1996). Such varieties are not yet available. This intervention may raise the mean global productivity to more than 1 t ha^{-1} and increase the total production by nearly 50%.

Table 1. Important stress factors affecting chickpea productivity in different zones (A-D based on latitudes) of the world.

	Zones			
Stress factors	A (0-20°)	B (20-25°)	C (25-35°)	D (35-50°)
Biotic				
Fusarium wilt	1[a]	1	2	3
Ascochyta blight	*	*	3	1
Botrytis gray mold	*	2	3	5
Root rots	1	3	2	4
Stunt	3	2	2	4
Helicoverpa pod borer	1	1	2	5
Leaf miner	5	5	?	2
Nematodes	4	?	4	4
Abiotic				
Drought	1	1	1	1
High temperature	1	2	4	3
Low temperature	*	5	3	1
Salinity	2	2	2	?
Excessive moisture	*	4	3	3

[a] where 1 = most important; 5 = least important; ? = little or no information; * = is not known to occur

Literature Cited

Abilay RM, Magpantay MH, and Lantican LA 1991 Page 437 *in* Groundnut - a global perspective: proceedings of an international workshop, 25-29 Nov 1991, ICRISAT Center, India (Nigam SN ed.) Patancheru, Andhra Pradesh 502 324, India: International Crops Research Institute for the Semi-Arid Tropics

Dwivedi SL, Nigam SN, Reddy DVR, Reddy AS, and Ranga Rao GV 1995 Pages 35-40 *in* Recent studies on peanut bud necrosis disease: proceedings of Meeting, 20 March 1995, ICRISAT Asia Center, India (Buiel AAM, Parlevliet JE, and Lenne JM eds.) Patancheru 502 324, Andhra Pradesh, India: International Crops Research Institute for the Semi-Arid Tropics; and P O Box 386, 6700 AJ Wageningen, The Netherlands: Department of Plant Breeding, Agricultural University of Wageningen

Gowda MVC, Kulkarni VN, Nadaf HL, Habib AF, and Nadaf SK 1993 Crop Improvement 20:197-200

Kannaiyan J, Nene YL, Reddy MV, Ryan JG, and Raju TN 1984 Tropical pest management 30:62-71

Kumar J, Rao BV 1996 International Chickpea and Pigeonpea Newsletter 3:17-18

Kumar J, Sethi SC, Johansen C, Kelley TG, Rahman MM, and van Rheenen HA 1996 Indian J. Dryland Agrl. Res. & Dev. 11:28-32

Lopez PB, Johansen, C, and Chauhan YS 1996 Journal Agronomy and Crop Science 177:311-320

Mehan VK, Liao BS, Tan YJ, Robinson-Smith A, Mc Donald D, and Hayward AC 1994 Information

Bulletin no. 35 Patancheru, Andhra Pradesh 502 324, India: International Crops Research Institute for the Semi-Arid Tropics

Nigam SN, Dwivedi SL, and Gibbons RW 1991 Plant Breeding Abstracts 61:1127-1136

Samonte HP, Ocampo AM 1989 The Philippine Agriculturist 72:137-146

Saxena KB, Chauhan YS, Singh L, Kumar RV, and Johansen C 1996 Research Bulletin no. 19 Patancheru, Andhra Pradesh 502 324, India: International Crops Research Institute for the Semi-Arid Tropics

Saxena KB, Gupta SC, Kumar RV, Reddy LJ, Singh L, and Faris DG 1989 International Pigeonpea Newsletter 9:8-10

Sharma D, Gupta SC, Rai GS, and Reddy MV 1984 Indian Journal of Genetics and Plant Breeding 49:84-90

Sharma D, Kannaiyan, and Saxena KB 1987 SABRAO Journal 19:109-114

Singh AK, Mehan VK, and Nigam SN 1997 Information Bulletin no. 50 Patancheru 502 324, Andhra Pradesh, India: International Crops Research Institute for the Semi-Arid Tropics

Singh AL 1994 Pages 289-294 *in* Plant productivity under environmental stress (Singh K and Purohit SS eds.) Agro Botanical Publishers, Bikaner, India

Singh BV, Pandya BP, Gautam PL, Beniwal SPS, and Pandey MP 1983 Indian Journal of Genetics and Plant Breeding 43:487-493

Upadhyaya HD, Nigam SN, Mehan VK, and Lenne JM 1997 Pages 81-85 *in* Aflatoxin contamination problems in Asia: proceedings of the First Asia Working Group Meeting, 27-29 May 1996, Ministry of Agriculture and Rural Development, Hanoi, Vietnam (Mehan VK and Gowda CLL eds) Patancheru 502 324, Andhra Pradesh, India: International Crops Research Institute for the Semi-Arid Tropics

Vasudev Rao MJ, Nigam SN, and Huda AKS 1992 Peanut Science 19:7-10

Wright GC, Nageshwar RC, and Farquhar GD 1994 Crop Science 34:92-97