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Breeding for Promiscuous Soybeans at IITA

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1. Introduction

Soybean [*Glycine max* (L.) Merrill] is an annual legume that belongs to the legume family *Fabaceae*. It is a strictly self-pollinating legume with $2n = 40$ chromosomes. With 40% protein, 20% oil and 30% carbohydrate, soybean plays a very significant role in world agriculture. World demand for soybean has been able to absorb ever-increasing production at prices that are profitable to producers. Since 1970, world consumption of soybeans has grown at an annual rate of 4.8% on average and since the 1990s it showed an annual increase of 5.4% on the average (Flaskerud, 2003). The world's major supply of edible oil comes from soybean and it is likely that the trend will continue in the future. Soybean is also the major source of protein rich feed component for livestock, poultry, pig and fish farms.

According to three-year (2006-2008) average data of FAOSTAT, 94.1 million hectares were allocated to soybean production in the world and 222.9 million tons of grain were obtained (<http://faostat.fao.org/site/567/DesktopDefault.aspx?PageID=567#ancor>; Accessed 29 August 2010). For the same period, world average yield per ha was 2371 kg. Considering different continents of the world, Latin America had the highest area (41 million ha) and production (109.5 million tons) followed by North America with 30 million ha and 82 million tons. In the third place was Asia with 19.8 million ha and 26.8 million tons. The same data source showed that Africa's soybean area (1.3 million ha) and production (1.4 million tons) was the lowest in the world. In terms of productivity per unit area, the highest 2742 kg ha⁻¹ was from North America followed by South America (2673 kg ha⁻¹), Europe (1517 kg ha⁻¹), and Asia (1351 kg ha⁻¹). Africa's average productivity per unit area (1073 kg ha⁻¹) was the lowest among the continents and it was in fact, 45% of the world's average. Pertaining to individual countries, the main producer of soybean in the world is USA and in the second and third places are Brazil and Argentina. These countries are followed by China and India. Average data (2006-2008) of FAOSTAT showed that area harvested in USA, Brazil and Argentina was 28.8, 21.3 and 15.8 million ha, respectively. The corresponding production figures were 79, 56.7 and 44.7 million tons for USA, Brazil and Argentina, respectively.

Not less than 22 African countries produce soybean in varying quantities (Table 1). However, some soybean producing countries are not captured in FAOSTAT. A good example is Ghana where there is sizeable soybean production. The highest three-year (2006-2008) average production of 592,000 tons on an area of 625,667 ha was from Nigeria (Table 1). In the second place was South Africa with an average total production of 317,332 tons from 199,323 ha. Uganda was in the third place with 176,333 tons from 146,667 ha. Zimbabwe and Malawi were

in the fourth and fifth place by producing 96,008 and 50,000 tons from 60,679 and 71,333 ha, respectively. Other African countries with an average of more than 10,000 tons of production were Rwanda, Egypt, DR Congo, Zambia, and Benin. The total production of soybean in Africa, which was elevated to 1.4 million tons by 2008 was merely 0.2 million tons when IITA started to improve soybean in Africa and average yield was 660 kg ha⁻¹. By the year 2008, average yield for Africa increased by 67% to 1.1 tons ha⁻¹. The development of adapted promiscuously nodulating tropical germplasm and distribution to various African countries contributed to increase soybean production in Africa.

Country	Area (ha)	Production (tons)	Yield (kg ha ⁻¹)
Nigeria	625667	592000	946
South Africa	199323	317332	1578
Uganda	146667	176333	1202
Zimbabwe	60679	96008	1574
Malawi	71333	50000	700
Rwanda	42788	27046	632
Egypt	7981	25932	3242
DR Congo	33492	16177	483
Zambia	10000	12000	1200
Benin	18820	10711	625
Cameroon	12000	7000	583
Ethiopia	6826	6685	971
Burkina Faso	5177	5853	1130
Mali	3274	4131	1342
Liberia	7867	3183	404
Burundi	3700	3000	822
Gabon	2100	2200	1047
Kenya	2504	2092	835
Tanzania	5000	1900	380
Morocco	1000	1000	1000
Côte d'Ivoire	683	686	1015
Madagascar	50	50	1000

Table 1. Three-year (2006-2008) average area, production and yield of soybean in soybean producing countries of Africa (Source: <http://faostat.fao.org/site/567/DesktopDefault.aspx?PageID=567#anchor>; Accessed 29 August 2010)

2. Why soybean was considered by IITA?

The International Institute of Tropical Agriculture (IITA) started soybean improvement around 1974. The main reason to consider soybean was that there was little effort in improving this crop in Africa and as a result yield was extremely low (less than 0.5 ton per hectare). Other associated impediments were low seed viability, poor nodulation with native *Rhizobium* available in the soil and high shattering in the moist and dry savanna zones. Post harvest utilization of the crop was also limited as recipes suitable to small-scale farmers in Africa were not developed. These being the predicaments, IITA capitalized on

some of the opportunities soybean can provide to tropical agriculture. Preliminary yield trial carried out on soybean germplasm materials in 1974 revealed that yields were high as compared to other legumes. Of the genotypes included in the trial, TGM 249-3 gave the highest yield of 3615 kg ha⁻¹ (Dashieff et al., 1987). The excellent performance of soybean under tropical Africa condition was also a contributory factor to venture into soybean improvement. On top of being an excellent source of quality protein and vegetable oil, the existence of ample genetic diversity to solve some of the major constraints like poor seed longevity and efficient natural nodulation were reasons to invest in soybean. Moreover, in the 1970s some National Agricultural Research Systems (NARS) showed immense interest and commitment to expand soybean production and utilization. All these constraints and opportunities led IITA to engage in soybean improvement for over three decades.

3. Soybean growing agro-ecologies in Africa

IITA considered three major agro-ecological zones in Africa in the course of variety development. The main one was the moist savanna zone. Efforts were also made to develop soybean production technologies in the Sudan savanna and mid-altitude zones. The moist savanna zone covers an area of approximately 5.6 million km², representing 29% of the total crop land in sub-Saharan Africa (SSA). This zone is characterized by a growing period of 150 to 270 days (IITA, 2000). The moist savanna zone has high potential for crop and livestock production, and is widely viewed as the emerging bread-basket of sub-Saharan Africa. Favorable circumstances in this zone include: relatively good soils, high solar radiation, adequate rainfall, and relatively low disease and insect pressures. Soybean trials have been conducted at Zaria and Mokwa locations in Nigeria in this zone. These two locations represent different agro-ecological zones of the moist savanna (Table 2). Zaria lies in the northern Guinea savanna zone with a mean annual rainfall of about 900 mm per year concentrated almost entirely from June to September. Mokwa is situated in the southern Guinea savanna with a mean rainfall of about 1100 mm per year (Sanginga et al., 2000). Sudan savanna zone receives about 600 mm rainfall (IITA, 1999). Low moisture stress during growth and development of soybean is a constraint in this zone and the development of extra-early and drought tolerant varieties have been the major focus. In this zone, soybean trials are carried out at Minjibir Farm, Kano (Table 2). The mid-altitude zone covers about 40% of the land area in sub-Saharan Africa mainly in eastern and southern Africa (IITA, 2000). The mid-altitude ecologies also have conditions favorable for high yields, including cool temperatures that permit good crop growth, adequate rainfall in most areas, and some fertile volcanic soils. The main soybean breeding location for this zone is located at Chitedze Agricultural Research Station in Lilongwe, Malawi.

4. Why breeding for promiscuous nodulation?

Breeding for promiscuous nodulating genotypes was one of the approaches IITA followed to enhance biological nitrogen fixation of tropical soybeans. Soybeans that nodulate effectively with diverse indigenous rhizobia are considered as promiscuous, and the characteristic promiscuity (Kuneman et al., 1984). Hence, promiscuous genotypes of soybean form symbiotic association with available *Rhizobium* strains in the soil and thus fix atmospheric nitrogen whilst non-promiscuous genotypes need specific rhizobial strains to fix nitrogen from the air. In Africa cowpea-type rhizobia are indigenous and are abundant.

In the late 1970s, breeders at IITA observed that most high yielding soybean cultivars from USA have specific requirements for *Rhizobium japonicum* (Pulver et al., 1982) and inoculation of these varieties was found to be essential when growing them under tropical conditions of low soil nitrogen. In the early 1980s, it was assumed that most tropical countries did not have the facilities and personnel required for inoculum production, storage, and distribution and were dependent upon importation of the final product (Pulver et al., 1982). The non-abundance of commercial *R. japonicum* inoculants and nitrogenous fertilizers led to the option of breeding promiscuous cultivars in IITA since soybean genotypes that do form symbiotic association with indigenous cowpea-type rhizobia were identified. Generally, soybean varieties developed for promiscuous nodulation with the indigenous rhizobia were considered to increase production of soybean in tropical Africa with minimum cost affordable to small-scale farmers.

Location	Coordinates	Elevation (masl)	Rainfall (long-term average) (mm)	Vegetation
Mokwa, Nigeria	6°5'N, 9°48'E	308	900	Southern Guinea savanna
Zaria, Nigeria	11°11'N, 7°38'E	685	1100	Northern Guinea savanna
Kano, Nigeria	12°47'N, 9°2'E	700	600	Sudan savanna
Chitedze, Malawi	15° 55' S, 35° 04' E	1146	892	Plateau

Table 2. Some characteristics of soybean breeding locations in sub-Saharan Africa

5. Identification of promiscuously nodulating soybean germplasm

Observation on nodulation of some soybean cultivars in soils where soybean has not been cultivated previously and the non-nodulation of exotic varieties that were bred in the USA indicated the existence of genotypic variation in soybean for the ability to recognize and form symbiosis with diverse species of rhizobia. Pulver et al. (1982) reported genotypic variation in six soybean genotypes in their ability to form an effective symbiosis with local *Rhizobium spp.* These workers noted that local cultivars were more promiscuous as compared to improved cultivars from the USA. IITA screened 400 geographically diverse soybean germplasm accessions for their compatibility with indigenous rhizobia in a range of tropical environments and assessed the efficiency of symbiosis under greenhouse and field conditions (Pulver et al., 1985). Of the 400 genotypes screened for promiscuity, 10 germplasm accessions were found forming effective symbiotic relationships with the soil rhizobia at five locations in Nigeria. The source of these germplasm accessions were tropical Africa and south East Asia.

6. Breeding objectives and methodology

The main goal of soybean improvement at IITA has been to develop high yielding promiscuous and stable soybean varieties that are tolerant or resistant to biotic and abiotic constraints. Specific objectives set in their chronological order since the inception of soybean

improvement have been a) improving grain yield of promiscuous genotypes has been the main objective from the outset and still it is a top priority in soybean breeding and crop management at present as overall soybean yield in Africa is low in comparison to other continents; b) biological nitrogen fixation (BNF); c) pod shattering— this trait has been given top priority because it was found out that farmers lose their entire crop if they do not harvest as soon as the crop is mature; d) seed longevity and color; e) Diseases— the main ones are soybean rust, red leaf blotch, frog eye leaf spot, bacterial pustule, bacterial blight, and soybean viruses; f) insect pests that included pod sucking bugs and defoliating insects; g) resistance to lodging; h) tolerance to low Phosphorus; i) drought tolerance; j) *Striga* reduction ability through suicidal germination; and k) dual-purpose soybeans suitable for grain as well as fodder for livestock.

The soybean breeding program at IITA from its inception has focused on combining the yield potential of cultivars bred in North America with the 'promiscuous' or 'naturally-nodulating' ability of landraces from Asia to form nodules and fix nitrogen without inoculation in African soils (Giller & Dashiell, 2006). Hybridization and selection have been the main methodology in developing varieties over the years. Excellent facility has been established at IITA-Ibadan to accomplish this task. Pedigree method of selection is followed to advance segregating populations by raising two generations per year - one during the main growing season and the second through off-season irrigation. Selection in the F₂ and F₃ generations are restricted to selecting good individual plants and discarding single plants and progeny rows susceptible to diseases such as bacterial pustule, frog-eye leaf spot and rust. In F₄ and F₅ generations, progeny rows (families) are discarded when they are found to be susceptible to frog-eye (*Cercospora*) leaf spot or bacterial pustule, or if they are of poor seed color or plant type. Single plant selections to establish homozygous lines are done at F₅ or F₆ generation during the main growing season. Seeds of selected individual plants are then multiplied during the off-season. At this stage lines are screened for pod shattering in the laboratory, seed size (10-13 g per 100 seeds), and uniform cream seed color. Progeny rows that passed the screening procedure are harvested in bulk grouped by maturity and were promoted to preliminary variety trials. The maturity groups in IITA trials are early (less than 100 days), medium (101 - 110 days) and late (more than 110 days).

Twenty-five to 30 superior lines are normally tested under preliminary variety trials at two to three locations in three replications for one year. Better performing lines for key traits are promoted to the advanced variety trial and the rest are discarded. In the advanced variety trial, lines are evaluated in at least three locations in four replications per country. The best lines from the advanced variety trial are distributed to collaborators mainly in Africa in the form of international trials. The purpose of the international trials are to test adaptation of elite soybean lines in different countries under diverse environmental conditions so that breeders from different national programs are able to compare their local varieties with the new lines and eventually release new varieties from IITA's lines. Moreover, it helps national breeders to access new germplasm from IITA for their breeding programs. Within Nigeria, these superior lines are promoted to the National Soybean Variety Trials, which are part of the Nationally Coordinated Research Projects on soybean. While evaluating lines, all the crop management practices are similar to farmer's condition. Starter fertilizer is incorporated into the soil before planting and the rate used is 100 kg ha⁻¹ NPK (15-15-15) and 50 kg ha⁻¹ single super phosphate. No fungicides, insecticides or *Rhizobium* inoculants are used and weeds are controlled using herbicides and hoe as needed.

7. Breeding lines developed for promiscuous nodulation

Over 2000 soybean crosses have been made since the late 1980s to select desirable segregants. Since late 1980s at least 66,220 segregating populations have been raised and more than 400 trials have been carried out. During the same period more than 20,000 soybean lines have been tested by IITA breeders in at least 20 locations in western and southern Africa. Large number of early, medium and late maturing promiscuous breeding lines has been developed over the past three decades. IITA's effort in breeding promiscuous early maturing soybeans has resulted in the development of 35 promising lines until 2006. These superior breeding lines are available for on-farm testing and release by national programs. In these materials maturity ranged from 91-107 days on the average (Table 3). Average grain yield ranged from 1257 kg ha⁻¹ for TGx 1826-5E in 1997 to 2959 kg ha⁻¹ for TGx 1895-4F in 2000. Percent increase of grain yield in these promising lines as compared to checks in the respective years ranged from 12-65%. Fodder yield ranged from 1548 kg ha⁻¹ for TGx 1805-8F to 3208 kg ha⁻¹ for TGx 1925-1F in 2004. It is to be noted that the average yield of 1257-1271 kg ha⁻¹ for grain yield in 1997 and 1998 were realized without any fertilizer or other input. However, in the years 1990 and 1999-2006 a basal fertilizer of 100 kg ha⁻¹ of 15:15:15 NPK plus 50 kg ha⁻¹ triple super phosphate were applied to attain those yields by the promiscuous lines.

Twenty five promising and medium maturing lines were developed from 1988-2006 for further utilization by the national programs. Average maturity date ranged from 100-120 days and grain yield ranged from 1275-2396 kg ha⁻¹ (Table 4). Similarly, average fodder yield ranged from 1194-2882 kg ha⁻¹ for these lines. Percent grain yield increase of these lines over their respective checks in different years ranged from 11-107%. As indicated for the early lines, trials in 1997 did not receive fertilizers and as a result yields were 1275-1424 kg ha⁻¹, which is much higher than farmer's yields. Breeding for late maturity has resulted in the development of 20 promising lines from 1989 - 2005 (Table 5). These lines exceeded the respective checks in grain yield in different years by 9-63%. Both grain and fodder yields were low in 1997 and 1998 since in those years breeders did not use starter fertilizer. These promising lines matured in 107-123 days on the average under West African condition. Grain and fodder yields were in the range of 1104-2500 kg ha⁻¹ and 1197-3000 kg ha⁻¹, respectively. Lower values were from the unfertilized years. These promiscuous lines are of significant value for agro-ecologies with long growth period and high rainfall. The breeding program also attempted to specifically develop desirable materials for drier Sudan savanna zone of Nigeria. That effort resulted in the development of 11 superior lines for environments similar to Kano. The lines matured in 86-101 days and their grain yields ranged from 1501-2365 kg ha⁻¹. Fodder yields also ranged from 1542-2333 kg ha⁻¹. Grain yield advantages over checks were 15-77%.

8. Promiscuous varieties released

A total of 21 IITA bred tropical soybean varieties have been released in Africa (Table 6). Most of these varieties were released in Nigeria. Some were released by the national agricultural research systems (NARS) of Ghana, Benin, Togo, Democratic Republic Congo, Uganda and Ethiopia. In terms of maturity groups, seven varieties each were released from the early, medium and late, respectively. Grain yields ranged from 1 - 2.1 t ha⁻¹ in the early maturing varieties depending on locations. In medium maturing varieties grain yields ranged from 1 - 2.7 t ha⁻¹. In the case of late maturing varieties grain yields ranged from

Year	Line	Maturity date	Grain yield (kg ha ⁻¹)	Fodder yield (kg ha ⁻¹)
1990	TGx 1660-15F	96-99	1896-2250	1896
1997	TGx 1826-5E	97-103	1100-1670	2222
1998	TGx 1878-30E	94-113	1089-1714	1779-1958
1999	TGx 1805-8F	85-95	687-2280	1021-2444
1999	TGx 1830-20E	85-98	648-2365	1500-2500
1999	TGx 1831-32E	88-100	875-1569	979-1806
1999	TGx 1871-12E	91-97	1109-2204	1896-2444
1999	TGx 1835-10E	89-92	1550-2494	1562-3055
1999	TGx 1740-2F	92-96	1761-2232	1896-2278
1999	TGx 1876-4E	89-99	1023-1674	1146-1889
1999	TGx 1880-3E	98-119	963-1922	938-2167
1999	TGx 1842-1E	94-101	601-1501	1458-2194
1999	TGx 1834-1E	92-100	835-1842	1406-2194
2000	TGx 1895-4F	90-99	1068-4389	2375-3583
2000	TGx 1895-49F	93-104	1251-2639	1926-3417
2000	TGx 1895-33F	102-104	962-3117	1917-4037
2002	TGx 1903-3F	98-102	1423-2309	1667-1875
2002	TGx 1905-5F	96-101	1518-1935	1417-2125
2003	TGx 1903-8F	102-104	1534-1924	1000-2666
2003	TGx 1908-1F	103-110	1565-1847	1958-2353
2004	TGx 1925-1F	103-110	1468-2224	2958-3375
2004	TGx 1919-1F	101-108	1594-2148	2500-2833
2004	TGx 1904-2F	95-103	1540-1953	2437-2667
2004	TGx 1903-7F	96-104	1468-2021	1833-2396
2006	TGx 1954-1F	103-109	1771-2811	1893-3167
2006	TGx 1977-4F	102-106	1041-3374	1584-2751
2006	TGx 1951-4F	101-107	1503-2719	1338-3084
2006	TGx 1977-2F	97-102	904-3026	1479-2667
2006	TGx 1935-3F	79-105	1039-3052	1792-3042
2006	TGx 1971-1F	100-108	1576-2648	1625-2459
2006	TGx 1965-7F	100-102	1199-2913	1167-2375
2006	TGx 1972-1F	99-105	1437-2750	1417-2209
2006	TGx 1951-3F	100-105	1734-2460	1500-2726
2006	TGx 1945-1F	102-111	1209-2584	1959-3334
2006	TGx 1978-3F	100-105	1060-2666	1084-2125

Table 3. Ranges of maturity, grain and fodder yields of superior early maturing promiscuous soybean lines developed by IITA in the Guinea savanna of Nigeria from 1999 – 2006. Note: Lines identified in 1990 and from 1999-2005 received 100 kg ha⁻¹ of 15:15:15 NPK plus 50 kg ha⁻¹ triple super phosphate (TSP) whilst those identified from 1997-1998 did not receive fertilizer. In all cases no rhizobium inoculants were used.

Year	Line	Maturity date	Grain yield (kg ha ⁻¹)	Fodder yield (kg ha ⁻¹)
1990	TGx 1489-1D	101-113	2041-2718	-
1990	TGx 1440-1E	115-122	2247-2484	-
1990	TGx 1649-9F	110-120	1590-2382	-
1997	TGx 1837-2E	105-122	799-2004	1667-2000
1999	TGx 1805-31F	104-108	1257-2048	2062-2944
1999	TGx 1873-16E	104-115	1290-1938	1750-2833
2000	TGx 1894-3F	101-112	1192-3120	2396-3458
2000	TGx 1869-31E	96-106	1125-2955	1935-3292
2000	TGx 1888-15F	96-109	1252-3152	1833-3125
2003	TGx 1910-13F	103-116	1129-2001	2312-3124
2003	TGx 1904-3F	104-114	1324-2265	2312-2636
2003	TGx 1904-6F	104-114	1213-2248	1624-2457
2003	TGx 1905-2F	105-118	568-2137	1687-2353
2004	TGx 1908-3F	102-114	1295-2411	2625-3187
2004	TGx 1927-5F	103-114	1195-2269	2417-3125
2004	TGx 1926-4F	101-116	981-2139	2417-3021
2004	TGx 1908-8F	104-113	1010-2169	2333-3000
2004	TGx 1910-10F	105-115	937-2637	2458-3250
2006	TGx 1956-1F	103-110	1301-2878	1709-3042
2006	TGx 1963-3F	105-109	1452-2746	1917-2521
2006	TGx 1961-1F	102-105	1242-2877	1709-2709
2006	TGx 1965-5F	102-107	956-3124	1581-2626
2006	TGx 1937-1F	105-111	1364-2557	938-2876
2006	TGx 1955-4F	105-110	1373-2634	1584-2626
2006	TGx 1954-4F	106-113	1468-2493	1750-3042

Table 4. Ranges of maturity, grain and fodder yields of medium maturing promiscuous soybean lines developed by IITA in the Guinea savanna of Nigeria. Lines identified from 1988-1989 received 100 kg ha⁻¹ of 15:15:15 NPK plus 200 kg ha⁻¹ triple super phosphate (TSP); Lines identified from 1990-1991 and from 1999-2005 received 100 kg ha⁻¹ of 15:15:15 NPK plus 50 kg ha⁻¹ TSP whilst those identified from 1997 did not receive fertilizer. In all cases no rhizobium inoculants were used.

1.3 - 2.3 t ha⁻¹. These yields were achieved through natural nodulation and only starter fertilizers were applied. In addition to grain yield and promiscuous nodulation, several other traits were incorporated into these varieties. Some of them are fodder yield, seed longevity, resistance to shattering and lodging, suitability for processed products such as soymilk, resistance to major foliar diseases such as bacterial blight and pustule, frog-eye leaf spot and tolerance to rust in recently released varieties.

Year	Line	Maturity date	Grain yield (kg ha ⁻¹)	Fodder yield (kg ha ⁻¹)
1989	TGx 1410-1D	120-121	2468-2834	-
1989	TGx 1483-3D	113-115	1981-2692	-
1989	TGx 1440-1E	116-125	666-4365	-
1989	TGx 1448-1E	115-125	1074-3768	-
1990	TGx 1448-2E	115-117	2403-2458	-
1990	TGx 1489-1D	101-113	2041-2718	-
1997	TGx 1843-35E	119-131	688-1540	1792-1875
1998	TGx 1828-4E	106-125	1191-1236	1019-1375
1999	TGx 1844-4E	120-125	1800-2500	2200-3000
1999	TGx 1844-18E	113-115	803-1718	1542-2639
2002	TGx 1905-5F	116-116	1629-3048	2313-2792
2003	TGx 1910-2F	117-123	2289-2521	2166-2374
2003	TGx 1910-8F	104-119	1848-2870	2624-3374
2003	TGx 1910-3F	119-127	2157-2452	2416-3249
2003	TGx 1910-6F	116-127	2080-2416	2541-2832
2003	TGx 1910-14F	112-123	2035-2433	2353-2916
2004	TGx 1927-1F	115-118	1847-2127	2453-2500
2004	TGx 1910-11F	110-115	1285-1825	1542-2625
2004	TGx 1924-2F	114-117	1757-1802	2042-2875
2005	TGx 1949-7F	113-121	1417-2257	2042-2250

Table 5. Ranges of maturity, grain and fodder yields of late maturing promiscuous soybean lines developed by IITA in the Guinea savanna of West Africa.

9. Promiscuous soybeans in cropping systems of the savanna

The role of promiscuous soybeans for soil health and effect on productivity of subsequent cereal crops after soybean has been investigated in a greater detail by IITA scientists in the past two decades. The study carried out by Carsky et al. (1997) estimated the value of residual soybean nitrogen on subsequent maize grain yield under the prevailed situation of soybean residue removal at 10 sites in the Guinea savanna of Nigeria using one early (TGx 1456-2E) and one medium maturing (TGx 1660-19F) varieties of soybean. These researchers reported that the yield increase following the medium duration soybean variety was similar to that from 40 kg ha⁻¹ nitrogen applied four weeks after planting to maize preceded by maize. Their study also revealed that the total nitrogen in the 0-10 cm depth of the previous TGx 1660-19F plots (0.063%) was significantly greater ($p < 0.05$) than in the previous maize plots (0.058%) considering all sites of the study. Carsky et al. (1997) concluded that the effect of previous soybean crop on maize grain yield was due to residual nitrogen availability either from the roots, fallen plant parts of soybean or nitrate-sparing effect. Nitrogen fixation and nitrogen contribution by different promiscuous nodulating soybean lines were further studied in the southern Guinea savanna of Nigeria by Sanginga et al. (1997). These workers reported that nitrogen derived from the atmosphere and nitrogen derived from the soil were the major sources of nitrogen accounting for 84 and 75 kg N ha⁻¹ or 46% and 43%, respectively, of the plant total nitrogen. They observed a great variation among soybean genotypes in that a late maturing genotype, TGx 1660-19F, derived on the average 126 kg N

ha⁻¹ (52% of plant total nitrogen) from N₂ fixation as compared to the early maturing line IAC 100 with 37 kg N ha⁻¹ (38%). Sanginga et al. (1997) estimated a net contribution of 18 kg N ha⁻¹ to soil on the average after grain removal and it ranged from -8 to 43 kg N ha⁻¹ depending on the soybean line grown.

Further study by Sanginga et al. (2002) substantiated the beneficial effect of soybean to maize in that 1.2 – 2.3-fold increase in maize yield was obtained when grown after soybean as compared to maize after maize. On-farm study in southern Guinea savanna using TGx 1456-2E and TGx 1660-19F indicated that these lines fixed 39-54% of their total nitrogen requirement that amounted to 56-70 kg N ha⁻¹ in TGx 1456-2E and 51-78 kg N ha⁻¹ in TGx 1660-19F (Osunde et al., 2003). A maize grain yield of 3 t ha⁻¹ was reported by these workers indicating the tremendous contribution from a 2-year soybean rotation. They recommended growing of promiscuous soybeans in rotation with maize even without the residues of soybean being returned to the farm land. Overall, studies indicated that under the Guinea savanna condition of Nigeria, promiscuous lines of soybean derive 46% of their plant total N (85 kg N ha⁻¹) from the atmosphere and the balance 43% (75 kg N ha⁻¹) from the soil. Thus, Sanginga (2003) suggested that breeding for higher nitrogen derived from the atmosphere lines should continue along with the development of efficient *Bradyrhizobium* strains as inoculants.

10. Dual-purpose soybean lines

Most of the IITA promiscuous soybean varieties and lines have been bred for dual-purpose to fit into the mixed farming system of the savanna. For some of the varieties specific studies were carried out to identify their feed value. From all maturity groups of soybean, lines were identified with high grain and stover yields and good stover quality assessed based on crude protein, neutral detergent fiber and dry matter digestibility (IITA, 2000). Lines that possess these qualities from the early maturity group are TGx 1878-30E, TGx 1880-3E, TGx 1019-2EB, and TGx 1871-12E and from medium maturity group they are TGx 1873-6E, TGx 1869-14E, TGx 1880-15E, and Samsoy-1. From the late maturity group TGx 1869-13E, TGx 1440-1E, TGx 1871-6E, and TGx 1872-23E are identified as the best lines.

11. Breeding promiscuous soybeans for low phosphorus tolerance

Phosphorus is a limiting factor to soybean growth as the process of nitrogen fixation needs phosphorus. Ogoke et al. (2001) studied the role of phosphorus in enhancing soybean residue contribution to soil fertility. They reported that litter residue increased by 42-46% with phosphorus application as compared to no phosphorus treatment. Further work of Ogoke et al. (2003) demonstrated that application of fertilizer phosphorus was justified and necessary in soils where phosphorus levels were below 7 mg kg⁻¹ in the savanna since soybean nitrogen content increased as a result of phosphorus application. They reported that total nitrogen content in soybean was increased by 40-47% when phosphorus was applied. A study was carried out for two cropping seasons (2002 and 2003) at Mokwa and Zaria in Nigeria to see the response of four soybean varieties to different levels of phosphorus. Two levels of phosphorus (0 kg ha⁻¹ and 30 kg ha⁻¹) and four varieties (M 351, TGx 1485-1D, TGx 1844-18E, and TGx 1871-12E) were evaluated in a split plot design with three replications (IITA, 2003). Data on grain yield, fodder, number of nodules, and plant height were recorded. The results showed that grain yield, fodder yield, number of nodules,

and plant height were higher for the new varieties (TGx 1844-18E and TGx 1871-12E) than the old ones (M 351 and TGx 1485-1D) both at 0 and 30 kg ha⁻¹ of phosphorus application. The average grain yield of the new varieties was 58% higher than the old varieties at 0 kg ha⁻¹ and 65% higher at 30 kg ha⁻¹ of phosphorus. Increases in grain, fodder, number of nodules and plant height were obtained due to P application.

Year	Variety	Maturity class and date ¹	Grain yield (t/ha)	Releasing Country
1989	TGx 297-10F	108-118 (M)	2.0-2.1	Ghana
1989	TGx 297-192C	105-112 (M)	1.4-1.8	Ghana
1989	TGx 306-036C	118-125 (L)	1.5-2.0	Ghana, Nigeria
1989	TGx 888-49C	121-125 (L)	1.4	Ghana
1989	TGx 923-2E	118-122 (L)	1.5-2.0	Nigeria
1989	TGx 536-02D	100-110 (M)	1.0-1.5	Ghana, Nigeria
1989	TGx 813-6D	105-110 (M)	1.5-2.0	Ghana
1989	TGx 814-76D	110-117 (L)	1.3-1.8	DR Congo
1989	TGx 849-294D	97-103 (E)	1.2-1.8	DR Congo
1991	TGx 849-313D	109-115 (M)	1.4-1.8	Nigeria
1991	TGx 1019-2EN	98-106 (E)	1.5-1.8	Nigeria
1991	TGx 1019-2EB	105-110 (M)	1.5-2.0	Nigeria
1992	TGx 1440-1E	115-120 (L)	1.7-2.2	Nigeria (1992); Benin and Togo (1998)
1992	TGx 1448-2E	115-120 (L)	1.7-2.3	Nigeria (1992); Benin, Ghana and Togo (1998)
1998	TGx 1485-1D	85-95 (E)	1.0-1.5	Nigeria (1992); Benin and Togo (1998)
1998	TGx 1740-2F	95-100 (E)	1.0-1.5	Nigeria (1992); Benin and Togo (1998)
2005	TGx 1830-20E	90-93 (E)	2.1	Ghana (2005)
2005	TGx 1904-5F	92-97 (E)	-	Ghana (2005)
2004, 2009	TGx 1835-10E	90-95 (E)	2.0	Uganda (2004), Nigeria (2009)
2007	TGx 1892-10E	121 (L)	1.5	Ethiopia
2009	TGx 1904-6F	101-108 (M)	2.5-2.7	Nigeria

Table 6. Promiscuous soybean varieties developed by IITA and officially released by different national programs in Africa. ¹Maturity class: E=Early, M=Medium, L=Late

12. Breeding promiscuous soybeans for shattering resistance

Pod shattering resistance is another trait considered for improving promiscuous soybeans at IITA. Pod shattering is the opening of pods along both dorsal and ventral sutures of the soybean pod (Tukamuhabwa et al., 2000). A seed loss of 50-100% can occur in susceptible varieties as a result of delayed harvesting after physiological maturity (IITA, 1986). Genetic studies revealed that pod shattering in soybean is under control of two pairs of genes and is partially dominant over resistance (Tukamuhabwa et al., 2000). This trait is highly heritable

with narrow sense heritability values of 0.70-0.79 (Tukamuhabwa et al., 2000; 2002). These findings indicated that pod shattering resistance can be improved with simple breeding procedures. Therefore when line evaluation trials are being conducted in the field, observation is made for shattering by visual rating of border rows of plots two weeks after harvesting. Laboratory method of screening for shattering resistance has also been followed since 1984. In this method 25 light brown pods are collected from each plot in paper bags and are put on a shelf and stored at room temperature for 10-20 days (Dashieil et al., 1987). Samples are then put in an oven set at room temperature, and each day the temperature in the oven is increased by 5°C and the number of shattered pods is counted. The assumption with this method is that samples that remained in the oven for a longer period of time without shattering had a good resistance (IITA, 1985). All IITA developed varieties and lines have some degree of pod shattering resistance.

13. Promiscuous soybean lines that reduce *Striga hermonthica* seed bank

Trials in 1996 and 1997 showed less number of *Striga* emergence on maize plot previously used for growing soybean, and grain and stover yields of maize were higher following soybean as compared to following sorghum (IITA, 1997). This observation prompted further work on the role of soybean in *Striga* control. Study was carried out on the screening of soybean lines for their efficiency in suicidal germination of *Striga hermonthica* seeds. Germination of *Striga* seeds stimulated *in vitro* by 159 lines of soybean varied with both the populations of the parasite and the soybean lines (IITA, 2003). Percentages varied from 0.0 to 31.2 (Gezawa population), from 0.1 to 36.0 (Mokwa population), and from 0.2 to 13.1 (Zaria population). The highest germination percentage among the Zaria population (13.1) was only 36% and 42% of those among the Mokwa and Gezawa populations. The germination percentage induced by the top 20 lines ranged from 6.6 (TGx 1805-8F) to 31.2 (TGx 1844-18E) for the Gezawa population, from 5.1 (TGx 1912-7F) to 13.1 (TGx 1924-4F) for the Zaria population, and from 12.5 (TGx 1908-1F) to 36.0 (TGx 1910-16F) for the Mokwa population. Further work involved testing the effect of a soybean crop as compared to sorghum as control on *S. hermonthica* parasitism in a subsequent maize crop and this study also assessed the effects of increasing soybean plant density and phosphorus fertilizer application on *Striga* reduction (Carsky et al., 2000). Application of phosphorus to soybean at higher soybean densities resulted in higher root length density, lower emerged *S. hermonthica* on maize and significantly higher maize yield (Carsky et al., 2000). These investigators reported that soybean rotation increased maize yield by 90% and suggested that the use of an efficacious soybean cultivar reduces *Striga* parasitism on a succeeding maize crop and that the effect is increased by application of phosphorus to the soybean.

14. Genetic gains in breeding for promiscuous soybeans

Knowledge on the genetics of promiscuity is essential to develop a naturally nodulating soybean varieties. From preliminary work at IITA, Kueneman *et al.* (1984) suggested that promiscuity in soybean is a heritable trait as they observed a large number of well nodulating plants in early generation from a cross of promiscuous and specific types of soybean genotypes. Gwata *et al.* (2004) carried out a study on the genetics of promiscuous nodulation using nodule dry weight and leaf color score as a measure of nitrogen fixation effectiveness in six basic generations produced from two contrasting parents (promiscuous

and non-promiscuous). For nodule dry weight trait, non-promiscuity was reported to be partially dominant controlled by four loci and for leaf color score non-promiscuity was reported to be completely dominant and it was controlled by two loci (Gwata *et al.*, 2004). These authors suggested that leaf color (deep greenness) score as a reliable trait to assess nitrogen fixation in soybean as it represented the total effectiveness of nodulation to provide nitrogen to the plant. Further study on the inheritance of promiscuous nodulation in F_2 segregation pattern revealed that two alleles at each of two independent loci with a dominant gene action and function controlled promiscuous nodulation (Gwata *et al.*, 2005). These authors identified that green (N_2 fixing) genotypes were double recessive and any individual possessing at least one dominant allele at either locus would be non-promiscuous. Gwata *et al.* (2005) proposed *gene 1* and *gene 2* for the two alleles that control promiscuous nodulation. These authors also suggested that the leaf color (green) method was a rapid and least expensive procedure as compared to other methods like acetylene reduction or xylem ureide assay. They argued that the leaf score method is adequate in plant breeding programs concerned with rapid screening methods for promiscuous nodulation under nitrogen-depleted growth conditions.

Since promiscuous nodulation is a heritable trait, IITA breeders have been able to recover lines with good agronomic characteristics and the ability to nodulate well with indigenous rhizobia by crossing promiscuous germplasm with varieties from the USA that have got superior agronomic traits (Kuneman *et al.*, 1984). IITA breeders have assessed the genetic gain made in breeding early, medium and late maturing promiscuous soybeans in tropical Africa. The average rate of increase per year per release period of 1980 to 1996 for grain yield was 24.2 kg ha^{-1} , which amounted to a genetic gain of 2.2% (Tefera *et al.*, 2009). In the same study fodder yield also showed an annual increase of $22.8 \text{ kg ha}^{-1} \text{ year}^{-1}$. Gain in improving natural nodulation was 1.72% per year (Tefera *et al.*, 2009). Similarly in medium maturing varieties of soybean the annual rate of progress against year of release was found to be 23.6 kg ha^{-1} or 1.99% (Tefera *et al.*, 2010). For late maturing varieties, the annual rate of breeding progress during 16 years of improvement period was 22.2 kg ha^{-1} or 1.42% (Tefera *et al.*, 2010).

15. Future direction of breeding for promiscuity

Promiscuous varieties and lines were developed at IITA to enhance biological nitrogen fixation (BNF) of soybeans so that small-scale farmers do not need to apply nitrogen fertilizer. In the past three decades this approach of breeding soybeans has been implemented vigorously and almost all varieties and lines at IITA have promiscuity character. The breeding program needs to select for enhanced promiscuity trait while developing varieties resistant to biotic and abiotic stresses. It is essential to select plants with high biological nitrogen fixation capacity in early segregating generations preferably on soils with low nitrogen. Selection at early stage will help to maximize gains in breeding for promiscuity trait. While handling large number of segregating populations easy to measure traits as indicator of biological nitrogen fixation should be used as suggested by Gwata *et al.* (2005).

In addition to breeding for promiscuous nodulation, effort should be made to develop adapted high yielding specific varieties with specific strains of *Bradyrhizobium*. The use of effective inoculant strains could enhance the biological nitrogen fixation capacity of promiscuous genotypes. Generally, the identification of soybean cultivars with a high

capacity for biological nitrogen fixation is important when recommending cultivars to farmers, as well as determining cultivars for use as parental genotypes in breeding programs (Hungria and Bohrer, 2000). Several investigators have demonstrated that breeding soybean for enhanced N₂ fixation can be successful (Hungria and Bohrer, 2000; Alves et al., 2003). For profitable and sustainable soybean production a continuous and coordinated selection of the most effective host genotype and rhizobial strain is essential. There is a great potential to enhance N₂ fixation in soybean through breeding genotypes with enhanced capacity to interact with *Rhizobium* bacteria. Improved N₂ fixing in soybean may result from manipulating both the host genotype and rhizobia. Hence, the breeding program will employ selection of soybean lines under inoculation for enhanced BNF.

16. Conclusion

Soybean is emerging as an important feed, food as well as raw material for producing high-quality protein products in Africa. In the past five years, soybean area has been increasing at an average of 5% per year whilst total production has been increasing at a rate of 7% per year in Africa. Such an increase has not been sufficient to satisfy the demand for soybean in the continent. Hence, the development of adapted and high yielding soybean varieties is necessary. IITA has been leading this effort in the past several decades by way of developing promiscuous varieties and through the promotion of soybean processing and utilization in the continent. A total of 21 IITA bred promiscuous tropical soybean varieties have been released in different countries of Africa. These varieties are easily grown by farmers without requiring specific inoculants or nitrogen fertilizers and thus an appropriate technology for small-scale farmers. These varieties give up to 2.7 tons/ha grain yield, much higher than the 1 ton/ha average yield for Africa, in addition to the high fodder yield for livestock feed. Breeding for promiscuity character has been a success at IITA. Genetic gain in breeding early, medium and late maturing varieties has been 2.2%, 1.9% and 1.4%, respectively. Efforts will be made to avail these superior promiscuous genotypes to different countries in Africa to test their adaptation and use them as variety per se or consider them as parental materials in their soybean improvement work. In IITA the breeding program will pursue to further enhance the biological nitrogen fixation capacity of new breeding lines through the promiscuity approach as well as matching genotypes with effective inoculant strains.

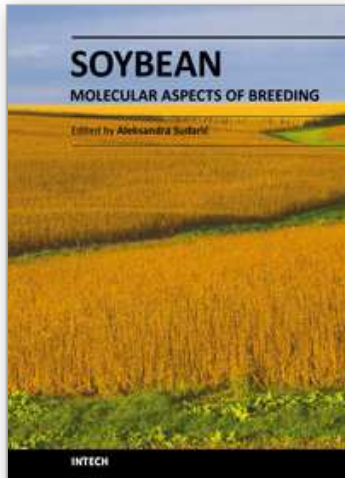
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Soybean - Molecular Aspects of Breeding

Edited by Dr. Aleksandra Sudaric

ISBN 978-953-307-240-1

Hard cover, 514 pages

Publisher InTech

Published online 11, April, 2011

Published in print edition April, 2011

The book Soybean: Molecular Aspects of Breeding focuses on recent progress in our understanding of the genetics and molecular biology of soybean and provides a broad review of the subject, from genome diversity to transformation and integration of desired genes using current technologies. This book is divided into four parts (Molecular Biology and Biotechnology, Breeding for Abiotic Stress, Breeding for Biotic Stress, Recent Technology) and contains 22 chapters.

How to reference

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Hailu Tefera (2011). Breeding for Promiscuous Soybeans at IITA, Soybean - Molecular Aspects of Breeding, Dr. Aleksandra Sudaric (Ed.), ISBN: 978-953-307-240-1, InTech, Available from:
<http://www.intechopen.com/books/soybean-molecular-aspects-of-breeding/breeding-for-promiscuous-soybeans-at-iita>

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