INHERITANCE OF DWARFISM IN PIGEONPEA

(Cajanus cajan (L.) Millsp.)

MSc Thesis

By

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DECLARATION

I, Githiri Mwangi, hereby declare that the work presented in this thesis is my original research work and that it has not been submitted for a degree in this or any other university.

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Date 17-3-88

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TABLE OF CONTENTS.

LIST OF TABLES.

LIST OF FIGURES.

LIST OF PLATES

APPENDIX

ABSTRACT

Inheritance of dwarfism was studied in pigeonpea in F_1, F_2, F_3 and testcross generations involving three medium maturing dwarf mutants (D_6, PD_1, PBNA), that grow to a height of about a metre and four normal height genotypes: ICPL 1 (Early), BDN 1 (Medium), ICPL 366 and NP(WR) 15 (Late). Growth analyses of D_6 and BDN 1 were carried out by taking measurements on non-destructive parameters (plant height, internode numbers, and number of branches) every 12 days, and on destructive parameters (nodulation, and shoot and root dry weights) every 24 days. The results showed that the dwarf mutants had fewer and shorter internodes, and more secondary and tertiary branches than the normal tall plants. The D_6 dwarf had lower dry matter production. However, its growth pattern and nodulation was similar to the normal cultivar, BDN 1. The F_1 showed that the normal plant phenotype was completely dominant to the dwarf phenotype. Dwarfism was inherited as a monogenic recessive trait. The three dwarf cultivars were noted to be mutants at the same locus. D_6 and PD_1 dwarfs had similar alleles which were designated as t_3, while PBNA had different alleles which were designated as $t_{3'}$. In crosses among the dwarfs, the t_3 alleles were found to

be dominant to the t_3, alleles. A wide range in plant height was observed for the F_2 and F_3 generations thus suggesting that environmental conditions and modifiers were involved in the expression of height.

I

INTRODUCTION

Pigeonpea (Cajanus cajan (L.) millsp) is an important pulse crop of the semi-arid tropics (SAT). The SAT areas are generally characterised by poor soils and low and erratic rainfall. The deep root system and drought tolerance character of pigeonpea makes it a particularly useful crop for these areas. The crop is most important in India where more than 80% of the world's recorded production and consumption is found (ICRISAT, 1987). The crop is also important in East Africa, South-east Asia, parts of Central and South America, and the Caribbean. In Kenya, where the crop ranks as the second most important pulse crop, after field beans (Phaseolus vulgaris L.), pigeonpea is grown on an estimated area of 100,000 ha annually mainly in the marginal rainfall areas of Eastern and Central provinces where most other crops grow poorly (Onim, 1981).

Pigeonpea is sometimes cultivated as a sole crop, but most often it is grown in various intercropping mixtures with maize, sorghum, millet, cassava, cotton and a

range of other food crops. Yields realised by the farmers are generally low as a result of many factors which include low and erratic rainfall in SAT areas, use of unimproved seed, poor production systems, and lack of effective disease and pest control measures.

Pigeonpea suffers from damage caused by several species of insect pests, of which the podborer (Heliothis armigera) and the podfly (Melanogromyza spp.) are the two most important (ICRISAT, 1986). Bhatnager et al. (1982) reported that pigeonpea intercropped with sorghum suffers from greater pest damage than as a sole crop. They attributed this to a pest build-up in the earlier crop (sorghum), which was tranferred to the later crop (pigeonpea), and to the failure of the natural enemies of these pests to transfer from sorghum to pigeonpea. As identification and utilization of potential resistant lines to these pests continue at ICRISAT and elsewhere, one or two sprayings against these pests are required for growing a successful crop of pigeonpea. The tall stature (2.0 - 2.5 m) of the traditional pigeonpea types is a limitation to spraying, and effective insect control.

Jain (1976) reported that pigeonpea has the genetic potential for very high seed yields under favourable management, but lower yields of pigeonpea relative to

wheat are obtained because of their poor harvest index. Except for a few improved types, pigeonpeas are very tall (over two metres) and utilize a lot of photosynthates in the development of large woody stems at the expense of grain production.

Pigeonpea has recently become important in various non-traditional pigeonpea growing areas within the SAT, such as in Australia, where mechanisation is necessary. Mechanised farming may, however, be limited because of the indeterminate nature and tall stature of most cultivated pigeonpea types (Wallis et al., 1981). Presently in Australia, mechanisation is practiced with induced dwarfs whose final height depends very much on the environmental conditions. Mohammed and Ariyanayagam (1983) suggested that since plant height fluctuates considerably from season to season, the use of dwarfing genes which reduce the amount of vegetative growth prior to flowering, would be more desirable for mechanical harvesting.

Research at ICRISAT centre has shown that improved short duration pigeonpea genotypes can be very high yielding when grown as close-spaced sole crops (ICRISAT, 1987). ICRISAT's pigeonpea breeding programme is emphasizing the identification and utilization of

genetic dwarfs for developing agronomically desirable cultivars with short plant stature and high yield potential. Seven sources of dwarfism available at ICRISAT have been described by Sharma et al., (In press) and a few more are being maintained. Relatively little work has been done to obtain information on the genetics of dwarfness in pigeonpea. Such information will be extremely useful in breeding programmes aimed at developing high yielding varieties with a desired plant height in different maturity groups. The main objectives of this study were, (i) to investigate the mode of inheritance of the dwarfing trait in three dwarf pigeonpea genotypes, ie., PD_1, PBNA, and D_6, (ii) study the allelic relationships among the dwarfing genes and (iii) understand the mechanism of dwarfism.

II

LITERATURE REVIEW

2.1. Introduction

The development of fertilizer-responsive short statured plants in wheat and rice that revolutionized the production of these crops received international acclaim in the 1960s. From then, dwarfism has been emphasized in most crops even though the purposes for shortening the plant height varies from crop to crop and with the crop management practices. For example, in wheat and rice, the dwarfism is used to prevent lodging under high input conditions; while in sorghum, dwarfism is necessary for convenience in mechanical harvesting. In plantation crops, such as citrus and coffee, dwarfism facilitates spraying and harvesting.

The concept of breeding short statured plants is not a recently formulated plant breeding objective. Wheat breeders in Japan and rice breeders in China used genetic sources of short straw to develop short statured plants in the nineteenth century (Hargrove et al., 1980; Reitz and Salmon, 1968). A measure of their success is

provided by the fact that most present day cultivars owe their semidwarf characteristics to two Japanese wheat genotypes, Akakomugi and Daruma, (Gale and Youssefian, 1985) and one Chinese rice genotype, Dee-gee-woo-gen (Hargrove et al., 1980). However, Vogel et al. (1956) reported that it was Vogel, while looking for sources of short straw specifically for use in the Pacific northwestern region of the USA in 1948, who suggested the usefulness of the dwarf growth habit with the increasing use of artificial nitrogen fertilizers in cereals. Less utilization of metabolites for straw production per unit of grain produced (ie. high harvest index) and the lodging resistance were the two reasons he gave for higher yields.

Jain (1986) reported that the recently released varieties in most crops are high yielding and shorter in height with a higher response to increased population and higher inputs. The higher yields have been achieved with no significant increase in the biological yield of the crops. He attributed the higher yields to a better redistribution of dry matter between vegetative and reproductive parts of the crops. This transformation has been accelerated in the last 20 years with the discovery of dwarfing genes which have a major effect on plant type (Gale and Youssefian, 1985).

2.2. The concept of dwarfness

Dwarfness generally results from the shortening of internodes. Some dwarfs have uniform shortening of internodes, while others have shortening in specific internodes. For example in pigeonpea, Sharma et al. (In press) described seven sources of dwarfness namely, D_0, D_1, D_2, D_3, D_4, D_5, and D_6. They reported that D_0 had uniform internode shortening, D_1 and D_2 had short basal internodes, while D_3 had short internodes in the top 25-30 cm of the main stem.

Experiments have been conducted to examine how changes in cell number and/or cell size are associated with reduced plant height. In barley, Blomstein and Gale (1984) attributed reduced plant height to reduced cell number. In wheat, Allan et al. (1962) found that some dwarfing genes caused fewer cell numbers while others affected cell size. However, there is no clear evidence that the dwarfing genes operate exclusively to reduce either cell division or cell extension (Gale and Youssefian, 1985).

The application of the knowledge of the growth stimulatory effects of gibberellic acid (GA) on growth has contributed greatly in the studies on dwarfness. Gale and Youssefian (1985) reported that the GA-

insensitive character of Norin 10 and Tom Thumb semi-dwarfing genes in wheat was first noted by Allan et al. in 1959. These workers observed that the GA-insensitive varieties differed from most other tall and dwarf genotypes in that applied GA did not elongate their stems, and they responded by producing more tillers. In pigeonpea, N.P. Saxena (1987, personal communication) observed that GA did not elongate the stems in three dwarf genotypes. He suggested that these pigeonpea dwarfs did not produce the enzymes required to metabolize GA within the plants. A similar explanation was given for some genetic dwarfs in wheat by Gale and Youseffian (1985).

For the expression of GA-insensitive dwarf phenotypes, Gale and Youssefian (1985) suggested that other plant hormones particularly auxins (IAA) may also be involved since an application of GA results in an increase in extractable IAA in tall wheat varieties but not in GA-insensitive dwarfs. However, the authors reported that the exact way in which the dwarfing genes affect GA levels and IAA responses is not yet clear.

2.3. Sources of dwarfness

2.3.1. Induced sources

Dwarfness can be induced in most crops by applying growth retardants. Gupta (1978) reported that 2-chloroethyltrimethyl ammonium chloride (CCC) is the most commonly used growth retardant in crop plants. In pigeonpea, Mishra and Mohanty (1966) observed that plant growth was retarded by soaking the seeds in 0.125, 0.25, or 0.5 percent solution of B-nine (N-dimethyl amino succinamic acid) before planting. The resultant plants were short in height. In quantitatively short-day plants like pigeonpea, dwarfness can also be induced by planting the crop in shorter daylenghts. Spence and Williams (1972) recognised the importance of this form of restricting vegetative growth in the pigeonpea for mechanical harvesting. They suggested that in order to achieve high yields, sowings in inductive photoperiods should be at higher densities to compensate for the reduced vegetative growth.

2.3.2. Genetic sources

Dwarfness can also be genetic and hence heritable. These types of dwarfs are valuable because of their stability over diverse environmental conditions. Gupta

(1978) reported that although it is possible to reduce plant height and achieve the benefits of higher inputs and mechanisation with induced dwarfs of cereals, genetic dwarfs have other attributes like better architecture, photosynthetic efficiency, efficient translocation of metabolites etc. that cannot be achieved with induced dwarfs.

Gale and Youssefian (1985) reported that breeding and exploitation of semi-dwarf varieties has been going on for many years in many crops, but unfortunately, relatively few genes have been genetically characterised. They attributed this to the quantitative nature of the height character and suggested that demonstrable variation will be observed only in the cases of recessive mutants at the concerned loci. Even then, they cautioned that these allelic differences need to be large or associated with other easily identifiable traits before they give rise to discrete segregations necessary for conventional Mendelian analyses.

2.4.Genetics of dwarfing genes

2.4.1. Dwarf genes in crops other than pigeonpea

In wheat (Triticum aestivum), which ranks among the best studied crops, dwarfness is conditioned by about a

dozen genes (Gale and Youssefian, 1985; Konzac et al., 1984). However, from all the reported sources of dwarfism, only four or five have made an appreciable impact on varietal production (Gale and Youssefian, 1985). The dwarfing genes that are utilized commercially have been shown to have developmental effects on the vegetative and reproductive parts of the crop (Gale et al., 1982; McClung et al., 1986; Vogel et al., 1956) which subsequently improve productivity and lodging resistance. According to Gale and Youssefian (1985), some of the dwarfing genes have deleterious effects on yield and are subsequently not utilized commercially.

The performance of a dwarfing gene may be affected by the environmental conditions and/or the genetic background in which measurements are made. Allan (1980), studied the effects of dwarfing genes on coleoptile length in wheat and concluded that the effects of the same dwarfing gene were modified by the background genotype in which the measurements were made.

Gale and Youssefian (1985) reported that under water stress, the dwarf varieties performed poorly relative to their tall counterparts. Reviewing the results on this aspect, they concluded that since rooting could be modified by selection during breeding,

the poor performance of the dwarfs under water stress conditions was not caused by poor root development, but resulted from other developmental effects in the plant which affect water relations. At high levels of irrigation and fertilizers, however, the dwarf varieties exploit their high yield potential and outyield the tall varieties.

In rice (Oryza sativa), three non-allelic semi-dwarfing genes have been described (Singh et al., 1979; Mackill and Rutger, 1979). A new potential locus has recently been reported by McKenzie and Rutger (1986). In the majority of cases, rice breeders have relied on the Dee-gee-woo-gen and IR-8 germplasm, both of which have the sd_1 gene, as a source of semi-dwarfness (Hargrove et al., 1980). The semidwarf genes have pleiotropic effects on seed size, tillering ability, and panicle size (Mackill and Rutger, 1979; Siddiq et al., 1984) and leaf angle (Siddiq et al., 1984). The pleiotropic effects have enabled the dwarf rice varieties to be high yielding and to possess stems that do not lodge even on very fertile soils (Siddiq et al., 1984).

In pearl millet (Pennisetum typhoides), four dwarf genes have been reported (Burton and Fortson, 1966; Rao et al., 1986). At present, only one dwarfing source (d2)

is extensively used in breeding (Rao et al., 1986). Dwarfness is used to reduce plant height of the millet in order to allow combine harvesting.

In barley (Hordeum vulgare), four sources of reduced plant height have so far been described (Sears et al., 1981), but only two of these have been extensively exploited in commercial barley production (Blomstein and Gale, 1984). In many instances the phenotype of the dwarf plant displays modified vegetative characters in thick upright stems, modified ear morphology, and tillering ability (Blomstein and Gale, 1984). The modifications in plant morphology resulted in reduced lodging and higher yield potentials.

Quinby and Karper (1954) proposed that genes at four loci and a modifying complex are important in the control of plant height in sorghum (Sorghum bicolor). Tallness was reported to be partially dominant over dwarfness. The dwarfing effect of the recessive genes at any of the four loci was observed to reduce internode length, but the peduncle length, head size, leaf number and maturity remained unchanged. The reduction in height has enabled easy combine harvesting.

Jain (1986) reported that an important objective of maize research today is to make the plant shorter in

height, which is associated with lodging resistance and high harvest index. He reported that Sprague (1982) in a personal communication, had noted that no suitable dwarfing genes of the Norin-10 kind in wheat have so far been found in maize.

Werner et al. (1987) reported that five dwarf strains have previously been reported in soybean (Glycine max), although, only four are in existence. All the genes in these strains were reported to be completely recessive and independently inherited with respect to each other.

Although dwarfness is inherited as a recessive trait in most crops, cases of dominant dwarfness have also been observed. Singh and Gutierrez (1984) reported two complementary dominant genes that occur at very low frequencies to cause dwarfness in beans (Phaseolus vulgaris). They observed that dwarfness was associated with lethality in the seedlings or very poor seed production in F_1 hybrid of the crosses involving small-seeded and medium or large-seeded genotypes. They suggested that lethality acted as an isolation mechanism to limit free genetic recombination between any two germplasm groups with different seed size.

in coffee (Coffea arabica), dwarfness caused by three dominant genes that act non-additively has been reported (Carvalho et al., 1984). The dwarfness has enabled spraying and picking of berries to be easy undertakings.

2.4.2. Dwarf genes in pigeonpea

The traditional pigeonpea types that have been favoured by natural selection in SAT areas have profuse vegetative growth and low harvest indices. Sharma et al. (In press) reported that these types are well adapted to intermittent soil moisture stresses experienced in rainfed subsistence agriculture of SAT areas where they are mainly grown as intercrops. These types have been developed through many years of natural selection for they make effective use of residual soil moisture after the companion crop has been harvested.

Pigeonpea is a potentially high yielding grain legume crop provided that improved varieties are planted (Jain, 1976). For recording high yield levels, however, ease in mechanisation and effective chemical control of pests and diseases are essential features of modern agriculture. ICRISAT (1979) reported that dwarf plants in pigeonpea offer several advantages over the tall plants, including easier spraying, partitioning more

photosynthates to the pods in the absence of large woody stems, and better suitability for mechanical harvesting.

Genetic studies conducted on several traits of pigeonpea by many workers have been summarized by Sharma and Green (1976) and later by Sidhu and Sandhu (1981). In the summaries, plant height was shown to be a quantitative trait under additive and non-additive gene action and with a wide range of heritabilities (27-97 %). The use of different varieties and methods of heritability estimation by various workers in the studies may have contributed to the wide disparity in the heritability estimates.

Various workers have studied the genetics of plant height in pigeonpea. Sharma (1981) reported that both additive and dominance effects are involved in the expression of plant height. He suggested that at least three genes controlling plant height exhibited some degree of dominance, and that the relative numbers of dominant alleles present in a plant determines the final height of that plant.

Shaw (1936) reported a single incompletely dominant gene to be involved in the expression of stature in pigeonpea. He also observed no linkage between type of inflorescence and plant growth habit. Kolhe and Nayeem

(1977) reported incomplete dominance for tallness. They observed that in crosses between tall and dwarf parents, all the F_1 plants were intermediate in height, while the F_2 plants segregated in a ratio of 1 tall : 2 intermediate : 1 short. They further reported that the genes for stature occured in one linkage group with those for stem colour, flower colour, vein colour, and fertility, which they named 'Tht' linkage.

Sen et al. (1966) found a 'dwarf bushy' pigeonpea plant in a plot of the cultivar Brazil P/2. This dwarf had brittle branches, late maturity, low yield, and 70% pollen viability. Dwarfness was shown to be inherited as a monogenic recessive trait. They designated the mutant gene as 'd'. Sheriff et al. (1975) irradiated variety Co 1 and obtained a dwarf mutant. Based on F_1 and F_2 data, they reported dwarfness to be under the control of a single recessive gene. Segregation in the F_2 generation gave a ratio of 3 tall : 1 dwarf, characteristic of a single pair of genes with dominance effects. Marekar et al. (1978) also reported complete dominance for tallness over dwarfness. They observed linkage involving genes for plant height, colour on the dorsal side of the standard petal, and stem colour.

Waldia and Singh (1987) crossed three 3-metre tall indeterminate pigeonpea varieties with a dwarf (D_0)

variety which grows to a height of one metre at Haryana (29°N in India. D_0 was identified from an intergeneric cross of pigeonpea and Atylosia and it is late flowering, bushy and "shy-bearing". Data from the F_1 and F_2 generations of all the three crosses showed that dwarfness was governed by two recessive genes.

Sharma et al. (In press) described seven sources of dwarfness in pigeonpea (D_0, D_1, D_2, D_3, D_4, D_5, and D_6). They reported that on the basis of branching habit and condensation of internodes, dwarfness in one of the dwarfs, D_1, was inherited as a monogenic recessive trait. D_6 and D_2 dwarfs were reported to give good yield. A large number of crosses have been made since 1976 to incorporate the dwarf character in promising early, medium and late lines, and to combine dwarfness with sterility mosaic and wilt resistance. Saxena et al. (1987) reported the identification of high protein dwarf lines from intergeneric crosses involving pigeonpea and Atylosia scarabaeoides, that are 39-76 cm tall. Protein content in these dwarf selections ranged between 25 to 33 percent in contrast to 20-22% for that of standard varieties. But despite the utilization of dwarfs at ICRISAT so far, the inheritance of dwarfness in all the sources, except D_1, and the genetic relationships among them remains to be determined.

III

MATERIALS AND METHODS

3.1. Inheritance and allelic studies (Field experiments)

All the experiments were conducted at ICRISAT Center (18^{O}N, 78^{O}E), located near Patancheru village, 26 km northwest of Hyderabad city in south-central India. ICRISAT Center receives a mean annual rainfall of about 750 mm. The rainy season, also known as monsoon, usually begins in June and extends into early October. More than 80% of the annual rainfall falls in these months. The rainfed crops are raised during this period. The balance of the precipitation is received in the post-rainy winter season (mid-October through January) which has cool, short days. The hot, dry summer season lasts from February until rains begin again in June. The experimental farm includes two major soil types found in the SAT: Alfisols (red soils), which are light, shallow and have low water holding capacity, and Vertisols (black soils), which are deep and have a high water holding capacity.

3.1.1. Materials

The experimental materials used in this study were obtained from the pigeonpea breeding programme of ICRISAT.

3.1.1.1. Inheritance study

The parent material included three dwarf genotypes (D_6, PD_1, and PBNA) and four normal height varieties (ICPL 1, BDN 1, ICPL 366, and NP (WR) 15). Seeds for growing the parents were obtained from isolation plots and were assumed to be homozygous diploid for plant height. Some characteristics of these parents are given in Table 1.

PD_1 and PBNA are dwarfs that have been maintained at ICRISAT. D_6 was identified from a population of BDN 1 irradiated with 25 KR of gamma rays and was described by Sharma et al. (in press). All the three dwarfs used in this study appear similar to each other in respect of height, maturity and branching habit. The dwarfs are medium maturing with indeterminate growth habit and having mean height of about a metre (Table 1). They produce many primary, secondary, and tertiary branches. At ICRISAT Center, the D_6 dwarf trait is being introduced into elite pigeonpea lines to reduce their height so as to facilitate insecticide spraying.

Table 1. Characteristics of the pigeonpea genotypes used in the dwarfism inheritance study at ICRISAT Center.

Genotype	Source	Days to flower	Plant height (cm)	Maturity[1] group
Dwarfs				
D_6	BDN 1 mutant	130	90	Medium
PD_1	Gulbarga collection	129	88	Medium
PBNA	Parbhani collection	131	86	Medium
Tall cultivars				
ICPL 1	ICP 6971	87	133	Early
BDN 1	ICP 7182	109	143	Medium
ICPL 366	ICP 7105	152	228	Late
NP (WR) 15	ICP 6443	156	233	Late

1. < 120 days = Early

   120-200 days = Medium

   > 200 days = Late

Source: ICRISAT's Pigeonpea Breeding Advanced Lines Catalogue.

The tall parents used in the study belong to different maturity groups and have important traits that enable them to be used as checks in various ICRISAT experiments. All the tall parents are of indeterminate growth habit and high yield potential with reasonably good seed size.

ICPL 1 is a semi spreading, early maturing line that was selected from cultivar UPAS 120. It is a widely adapted cultivar with high yield potential. BDN 1 is a semi spreading, medium maturing cultivar that is well adapted to the Alfisols. It has resistance to both wilt and Phytophthora blight diseases. ICPL 366 is a late maturing line with a compact growth habit and high yield potential. This line has resistance to sterility mosaic and Alternalia blight diseases. NP (WR) 15 is a semi spreading, late maturing cultivar that has resistance to wilt disease and high yield potential. It is well adapted to intercropping situations.

For inheritance study, the following six crosses involving tall and dwarf parents were made at ICRISAT Center in 1984 rainy season:

Cross 1: D_6 x ICPL 1

Cross 2: D_6 x BDN 1

Cross 3: PD_1 x ICPL 1

Cross 4: PD_1 x BDN 1

Cross 5: PBNA x 1CPL 366

Cross 6: PBNA x NP (WR) 15

The F_1 plants were grown in 1985 season and selfed to produce F_2 seed. Further crosses were made in 1985 season to produce additional F_1 seed. The F_1 and F_2 populations of these crosses were grown in Vertisols at ICRISAT Center in 1986 rainy season. In order to confirm the deductions made with the F_2 data, fifty tall and nineteen dwarf F_2 plants in each cross were randomly selected and harvested singly for F_3 studies in the 1987 season. F_1s were crossed to the dwarf parent to produce backcross (testcross) seed in the respective crosses. Additional F_1 seed for planting in the 1987 season was also produced.

3.1.1.2. Allelic study

In order to study the allelic relationships among dwarfing genes of the three dwarf genotypes (D_6, PD_1, and PBNA) used in the inheritance study, crosses were made among the three dwarfs in the 1985 rainy season. No reciprocal crosses were made since previous crosses made at ICRISAT had shown non-existence of reciprocal cross differences (Saxena, K.B. 1986, personal communication). The parents and F_1s of these crosses were grown in 1986 season and selfed by covering with muslin cloth bags.

Additional crosses among these dwarfs were made to produce F_1 seed for testing in 1987. The parents, along with their F_1 and F_2 generations were sown for study in 1987.

3.1.2. Methods

3.1.2.1. Inheritance study

The F_1 and F_2 populations of these crosses were grown in Vertisols at ICRISAT center in the 1986 rainy season. One or two rows of the F_1, depending on seed availability, and 50 F_2 rows were sown for each cross. Before sowing the seeds were treated with a mixture of 1.5 g of thiram and 1.5 g of benlate per kg seed to give protection against seedling disease, Schlerotia rolfsii. The seeds were sown on 25 June 1986 at inter- and intra-row spacings of 60 and 30 cm respectively. Sowings were made in four-metre rows without fertilizer or Rhizobium application. Hand weeding was done twice. Spraying with endosulfan 35% EC (2 L a.i./ha) was done during reproductive stages to protect the crop against Heliothis damage. During this season, phenotypic classification and data on plant height were recorded on each individual plant at full flowering, except on the end plants of each row in all the crosses.

During 1987 season, the parents, F_1, F_3, and testcross generations of the six crosses were grown in Vertisols at ICRISAT Center. The number of rows or families sown for each cross are given in Table 2. The genotypes were planted in two blocks in order to reduce environmental effects such as waterlogging which was expected to be high in the Vertisols. During the analysis, however, the results of the two blocks were pooled. The total number of rows sown in different crosses was variable depending on F_1 and testcross seed availability, and on the number of dwarf F_3 families planted. From the F_2 data, the dwarf F_3 families were not expected to segregate, and they were therefore planted only in one block.

The pigeonpea genotypes were sown on 24 June 1987 in a randomised complete block design (RCBD) without fertilizer or Rhizobium inoculation. All the generations in a cross were considered as a unit during the randomisation. Seed treatment was made as in 1986 season.

All the materials were sown in four-metre rows at inter- and intra-row spacings of 60 and 50 centimetres respectively. Herbicide mixture at the rate of 1.25 Kg of prometyrin and 2.25 litres of basalin per hectare was sprayed soon after sowing. Hand weeding was done once, two months after sowing.

Table 2. Number of rows/families sown in the dwarf inheritance study of pigeonpea for different crosses, ICRISAT Center, rainy season 1987.

Cross	Block 1						Block 2				
	P1	P2	F_1	TF_3[1]	DF_3[1]	TC	P1	P2	F_1	TF_3[1]	TC
D_6 x ICPL 1	3	3	1	50	19	2	3	3	0	50	2
D_6 x BDN 1	3	3	1	50	19	2	3	3	1	50	2
PD_1 x ICPL 1	3	3	1	50	18	1	3	3	0	50	1
PD_1 x BDN 1	3	3	1	50	17	2	3	3	0	50	2
PBNA x ICPL 366	3	3	2	50	11	0	3	3	1	50	0
PBNA x MP (WR) 15	3	3	1	50	15	0	3	3	1	50	0

P1 = dwarf parent

P2 = normal parent

1. Each family was sown in two rows

TC = Testcross (Backcross of F_1 to the dwarf parent)

TF_3 = F_3 families from tall F_2 plants

DF_3 = F_3 families from dwarf F_2 plants

3.1.2.2. Allelic study

In 1986 season, the parents and F_1 generations were grown in Vertisols. Plant height was recorded on all the parental plants. In 1987 season, five rows of each parent, two rows of F_1 and 40 F_2 rows in each cross were sown for the allelic study. In the cross D_6 x PBNA, however, only 29 F_2 rows were sown. Sowing, weeding and spraying operations were carried out as in the inheritance study.

3.1.3. Observations

Data on days to first 50% flowering were recorded on per plot basis in all the crosses. Data on other traits were recorded on all F_1 and F_2 plants while in the parents, observations were recorded on 10 randomly selected competitive plants at full flowering.

Flowering was determined as the time when 50% of the plants in a plot had at least one open flower.

Plant height was recorded in all the crosses, as the length to the nearest centimetre of a stretched plant from ground level to the tip of the main stem.

In 1987 the number of internodes, number of branches, number of nodes and height from the ground

level to the first primary branch were recorded on the parental lines in order to have their detailed characterisation. Data on yield could not be obtained as a result of high Heliothis attack on the pigeonpea crop despite the intensive spraying undertaken in the field (Appendix 1). W. Reed (1987, Personal communication) estimated that about 80% of ICRISAT's pigeonpea crop was damaged by Heliothis during that year.

3.1.4. Statistical analysis

The F_2 plants in all the crosses were classified phenotypically as either normal or dwarf. This classification was tested by chi-square for goodness-of-fit to various Mendelian ratios to develop a genetic hypothesis of the number of segregating loci. Classifications of testcross and F_3 plants were used to confirm the proposed genetic model.

For comparison, the plants were also classified based on their height. The data on plant height in the F_2 populations were grouped using 10 cm intervals. Histograms of the F_2 population were constructed and plant height groups were determined. The form of the histogram as well as the knowledge of the parental population heights were used to estimate the number of

height genes that were segregating in each cross. The F_2 plant height data were analysed by chi-square for goodness-of-fit to theoretical genetic ratios assumed from the form of the histograms.

3.2. Growth analysis studies (Pot experiment)

3.2.1. Materials

A pot experiment was undertaken in order to understand and generate information on the production and partitioning of dry matter by the dwarf (D_6) and normal tall (BDN 1) genotypes. The two genoytpes chosen were included in the inheritance study discussed earlier.

3.2.2. Methods

The experiment was conducted in plastic pots measuring 23 cm in diameter. Alfisol soil was obtained from the glass house store and sieved with a 2 mm sieve. Seven kg of soil was placed in each pot. A dose of 1.16 g of single-super-phosphate fertilizer was applied to each pot to provide 8 mg P kg^{-1} and 65 mg S kg^{-1} soil and mixed thoroughly. A sample of the soil used in the experiment was analysed for its chemical characteristics.

Sowings were done on 25 July 1987 in a split-plot design, with sampling dates as the main plots and genotypes as sub-plots. The entries (D_6 and BDN 1) were replicated four times. Twenty pots per genotype were planted in order to allow sampling of four pots every 24 days up to flowering. Ten seeds inoculated with IC 3195 Rhizobia slurry were sown in each pot. All the pots were kept outside the glasshouse and watered whenever small cracks started appearing on the soil surface. Thinning was done ten days after seedling emergence leaving four plants in each pot.

3.2.3. Observations

Plant height, branch number, and internode number were recorded on all the plants from four randomly sampled pots for each genotype every 12 days. Four pots from each genotype were sampled every 24 days and data on shoot dry weight, root dry weight, nodule number, and nodule weight were recorded. Root and nodule recovery was done by washing the plants in a bucket and passing the washing water through a 2 mm sieve. The shoot, root, and nodule samples were oven-dried at 80^{o}C for 60 hours and weighed.

3.2.4. Analysis

Graphs were drawn to illustrate the variation of plant height, internode number, and branch number with crop age. Analysis of variance was conducted on the data of other traits.

IV

RESULTS AND DISCUSSION

4.1. Characterisation of the Parents

4.1.1. Field experiments

Mean values of parental characters measured are given in Table 3. The data showed that overall there were wide variations among the parents for all the characters measured. When considered separately, however, the variation for various characters was much less among the dwarf parents as compared to that of the normal parents. The characteristics of each group of parents will be discussed separately.

4.1.1.1. Tall parents

Variations were observed in all the characters recorded, except in the number of nodes to the first branch which were similar in all the genotypes. The data showed that cultivar ICPL 1, which was the earliest in flowering (78 days), was 120 cm tall while ICPL 366 and NP(WR) 15, which were late in flowering (147 and 146 days respectively), attained heights of over two metres.

Table 3. Parental means for characters recorded on pigeonpea cultivars grown at ICRISAT Center, rainy season 1987.

Parent	Days to 50% flowering	No. of branches		Internode no.	Nodes to first branch	Height to first branch (cm)	Plant height (cm)
		Primary	Secondary				
Dwarf parents							
D_6	123	18	63	49	5	12	117
PD_1	127	16	62	47	5	11	113
PBNA	134	25	101	45	2	3	98
Normal parents							
ICPL 1	78	11	5	38	8	20	120
BDN 1	102	16	37	65	8	22	167
ICPL 366	147	27	37	69	9	26	212
NP (WR) 15	146	24	30	63	10	28	216
SE	-	±1	±2	±2	±1	±1	±10
Mean	-	20	48	54	7	17	149
CV(%)	-	13.8	10.4	6.8	16.4	12.7	7.5

BDN 1 which was medium in flowering (102 days), was intermediate in height (167 cm) between the early and the late genotypes. This indicated that plant height increased with days to first flowering. Number of primary branches also increased with days to first flowering. Cultivar ICPL 1, flowering in 78 days, had 11 primary branches, while ICPL 366, flowering in 147 days, had 27 primary branches (Table 3). It was also observed that the first branch in all the genotypes emanated from about the same node number. This helped confirm the observation that differences in primary branch number were a result of differences in days to first flowering.

The medium flowering line BDN 1 had as many internodes as the late flowering genotypes (NP (WR) 15 and ICPL 366), suggesting that the tall stature of the late flowering genotypes did not necessitate the development of more internodes but instead, had longer internodes. This generalisation, however, did not hold true in case of the internodes developed below the first primary branch. On an average, these internodes were 2.7 cm in length, and this was consistent in all the genotypes.

4.1.1.2. Dwarf parents

The dwarf parents generally differed from the tall parents by having a short stature, many secondary branches, and their first branch emanated from a node closer to the ground level (Table 3). As shown in Plate 1, the first 4 or 5 primary branches in the dwarfs were from nodes that were condensed such that the branches appeared as if they were developed from the same node. The primary branches were borne at an acute angle and were brittle and a slight force caused them to be easily detatched from the main stem. This branching habit made them appear as short compact bushes which were easily identifiable.

4.1.1.3. Tall vs dwarf parents

Comparing the dwarf and normal parents (Table 3), the data showed that major differences existed between these two groups of parents in most traits recorded. With respect to height, there was no difference between the early maturing ICPL 1 and the dwarf parents, especially D_6 and PD_1. Plant height, therefore, should not be taken as a character of differentiating the dwarfs from the normal tall genotypes in segregating populations of crosses between ICPL 1 and the dwarfs. The dwarf genotypes had more internodes than ICPL 1.

This was surprising considering the height of ICPL 1 and the dwarf genotypes. The average internode length of the dwarf parents was 2.3 cm and was significantly different to the corresponding value for the normal parents of 3 cm. Internode length below the first primary branch for the dwarf and normal parents were significantly different and were 2 cm and 2.7 cm respectively. It, therefore, can be inferred that the short stature of the dwarfs was due to the reduction in internode length. The data also showed that for the dwarfs as well as the tall, the earlier formed internodes were shorter than the later formed internodes.

Nevertheless, the most striking differences between the talls and dwarfs were their branching pattern (Plate 1). The dwarf parents had more secondary branches than the normal parents which originated at an acute angle, thus making the plants appear like short compact bushes. This branching pattern made the dwarf plants appear phenotypically very distinct from the normal tall types, and was used in the qualitative classification of segregating generations of all crosses.

Plate 1. Normal cultivar, BDN 1, and D_6 dwarf showing variations in plant height and branching pattern.

4.1.2. Pot experiment

Pigeonpea lacks vigour during early vegetative growth and it is difficult to distinguish between dwarf and normal height genotypes. After some time, however, the two types are distinguishable as the normal height genotypes increase in height at a faster rate than the dwarf genotypes due to the development of shorter internodes in the latter. But information is lacking on the production and partitioning of dry matter in the dwarf genotypes as they grow. The available information on the growth analysis of normal pigeonpea genotypes cannot be directly assumed to apply for the dwarf genotypes because the two types appear different in their growth patterns. Growth analysis information is therefore important in the studies on pigeonpea dwarfs and hence the present study was undertaken. The results from that study are given below.

4.1.2.1. Plant height

The changes recorded in plant height of D_6 dwarf and the normal cultivar, BDN 1, with their growth are illustrated in Figure 1a. Both the genotypes started showing differences in height by the 12^{th} day after sowing. BDN 1 was found to be consistently taller than D_6 throughout the study. BDN 1 attained a plateau in

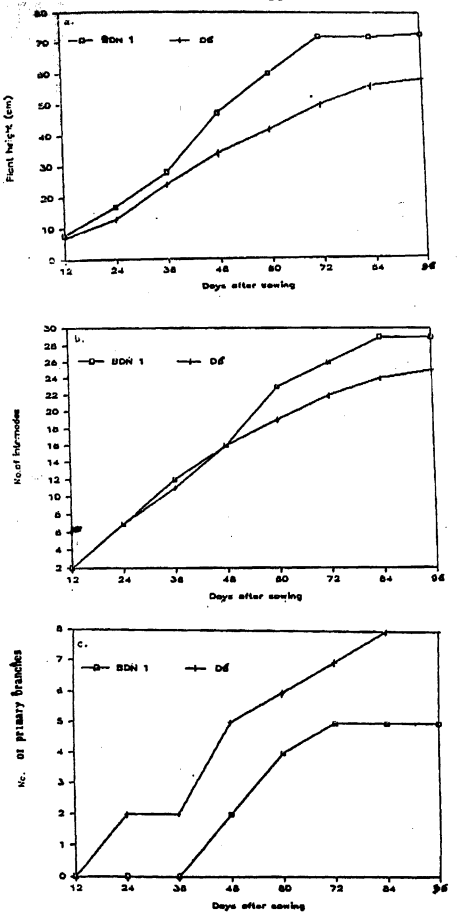


Fig 1. Variation in (a) plant height, (b) no. of internodes, and (c) no. of primary branches with crop age in the genotypes D_6 and BDN 1.

its plant height in 72 days after sowing as it approached the reproductive stage. D_6 was slower than BDN 1 by 24 days in aproaching the plateau in plant height.

4.1.2.2. Internode numbers

Internode numbers in the two genotypes remained similar up to about 48 days after sowing (Figure 1b). This observation suggested that the taller stature of BDN 1 relative to D_6, despite similar internode numbers in the two genotypes, could only have been caused by the development of shorter internodes in D_6. Sampling on the 96^{th} day after sowing showed that BDN 1 had 29 internodes while D_6 had 18. This showed that in the period from 48 to 96 days after sowing, BDN 1 developed more internodes than D_6. These results suggested that besides shorter internodes, the short stature of a full grown D_6 plant relative to BDN 1 was also a result of the development of fewer internodes.

4.1.2.3. Number of branches

The number of branches were counted on the plants. It was observed that D_6 had more primary branches than BDN 1 (Figure 1c). Branching in D_6 was initiated before it was 24 days old. Secondary branches were initiated in D_6 48 days after sowing. As mentioned earlier, D_6

had lower internode numbers than BDN 1 in sampling done later than 48 days after sowing.

4.1.2.4. Nodulation

The nodules in the two genotypes were found mainly on the primary roots and only a few were on the secondary and tertiary roots. The nodule number and nodule weight in BDN 1 and D_6 were similar (Table 4) which could be attributed to their common origin. (D_6 was identified from irradiated material of BDN 1). This then implies that, the irradiation treatment on the parental BDN 1 material did not affect the loci influencing nodulation. The nodule number increased with crop age up to about 72 days after sowing. Sampling 96 days after sowing gave lower nodule counts and some nodules were found to have senescenced. This reduction in number was attributed to senescence and nodule predation by a dipteran larvae, Rivellia angullata (Sithanantham et al, 1981). Nodule weight increased consistently with crop age, despite the drop in their numbers during the last sampling. Wallis et al (1976) and Thompson et al (1981) reported that nodule number per plant increased with crop age up to about 75 days after sowing and then start declining. Both groups of workers reported that nodule weight in the pigeonpea genotypes continued increasing even with a drop in

Table 4. Characteristics of a D_6 dwarf and the normal cultivar, BDN 1, of pigeonpea grown in pots at ICRISAT Center, rainy season 1987.

Genotype	DAS	Height (cm)	Internode No.	Branch No.	Nodule No.	Nodule dry mass (mg)	Root dry mass (g)	Shoot dry mass (g)	Shoot/root ratio[1]
D_6	24	13	7	2	7	(0)	0.05	0.08	1.60
	48	34	16	5	34	22	0.82	1.64	1.95
	72	50	22	7	61	90	1.49	3.76	2.37
	96	58	25	8	43	127	2.47	7.31	2.79
BDN 1	24	17	7	0[2]	10	(0)	0.05	0.08	1.60
	48	47	16	2	39	21	0.99	2.04	2.02
	72	72	26	5	56	91	1.53	4.07	2.51
	96	73	29	5	47	129	2.59	8.19	3.01
SE		±0.7	±0.4	±0.3	±3	±2	±0.05	±0.09	±0.18
CV(%)		3.7	5.2	5.8	15.5	8.4	6.5	5.3	15.2
LSD 0.05		1	1	1	6	4	0.11	0.20	0.39
0.01		2	1	1	9	6	0.15	0.27	0.55

DAS Days after sowing

1. Nodule mass included in the calculation

2. Zero values not used in SE calculation

() Quantities were very low for accurate weighing

nodule numbers which could be attributed to an increase in nodule size.

4.1.2.5. Total dry matter production

Shoot and root dry mass for the two genotypes increased progressively during the 96-day period (Table 4). Dry matter accumulation in both the roots and shoots were significantly and consistently higher in BDN 1 on all sampling dates except on the first when both the genotypes recorded similar weights. The similarity in shoot mass during the first sampling date was attributed to the possession of more branches in D_6 which counteracted the effects of differences in height in the two genotypes. The similarity in root mass during this period was attributed to age whereby differences in the two genotypes had not yet set in.

4.1.2.6. Shoot/root ratio

The shoot/root ratio was similar in both genotypes and it increased with crop age (Table 4). Slight differences which were not significant were observed in the last two samplings where BDN 1 had a slightly higher ratio. The faster growth rate associated with the period prior to flowering may have caused these slight differences in shoot/root ratio, where BDN 1 was earlier (78 days) in flowering than D_6 (88 days).

The shoot/root ratio was initially low and increased with crop age. The results suggested that in the initial stages of growth, the roots constitute a higher proportion of the dry matter, but with time, the plant directs more of the assimilates to the shoot. Brakke and Gardner (1987) reported that the shoot/root ratios in pigeonpea, soybean and cowpea are similar during the early seedling stages of these crops. They reported that the ratios are initially high soon after germination and decrease progressively until 25 days after sowing when they start increasing. The first sampling in the present study was done 24 days after sowings and earlier comparisons were not possible.

Madhusudana Rao et al. (1981) reported that dry stem yield in cultivars T.21 and BDN 1 grown in Alfisols ranges from 7 to 23 grams/plant at harvest. The total dry matter produced by the genotypes in this study at flowering was generally low. This was partly as a result of late planting where the shorter photoperiod reduced growth and the genotypes flowered about one month earlier than that for normal planting. The resultant plants were short in stature and had only a few branches. In addition, the fallen leaves were not collected for inclusion in the analysis. Madhusudana Rao et al. (1981) reported that leaf fall in cultivars

T.21 and BDN 1 grown in Alfisols may be as high as 0.5 to 1.8 tonnes/ha. This suggested that the total dry matter produced by the genotypes in this study was actually higher than the reported figures, although not to the magnitudes of the values reported by Madhusudana Rao et al. (1981). In the case of the roots from the second sampling, dry matter produced by the genotypes was almost one gram which was similar to what Brakke and Gardner (1987) had reported.

The soil analysis report showed that the soil used for the pot experiment had a neutral pH and a normal electroconductivity (EC) of 0.92 m.mhos/cm. The soil also had a high content of the major nutrients (NH_4-N = 3.2 ppm; NO_3-N = 90 ppm; P = 38.75 ppm; K = 399 ppm). The high nutrient status of the soil suggest that the addition of SSP fertilizer would have caused P-toxicity on the growing plants. But this problem was not encountered because most grain legumes require a large amount of phosphorus for good growth (Kumar Rao and Dart, 1981). However, the high nitrogen content may have affected the nodulation capacity of the genotypes in this study. Thompson et al. (1981) reported that when medium duration genotypes are grown in Alfisols and sampled 20, 40, 60, 80, 100, and 140 days after sowing, they give an average of 16, 24, 32, 118, 60 and 75

nodules per plant respectively. However, Table 4 shows that for equivalent sampling dates, the nodule counts in this study were lower than the numbers reported by Thompson *et al.* (1981). On the other hand, the low numbers obtained with the two genotypes in this study may have been due to low nodulating ability of the genotypes, a factor that was beyond the scope of this study.

4.1.2.7. Conclusion

The data from the growth analysis showed that D_6 dwarf, which was derived from normal cultivar BDN 1, was short in height as a result of the development of fewer and shorter internodes. This was accompanied by the production of more branches. D_6 dwarf also produced less total dry matter than BDN 1 although the shoot/root ratio and nodulation ability remained similar in both the genotypes. The implications of the study were that, despite having a shorter height and lower dry matter production, D_6 dwarf had similar dry matter partitioning as the normal cultivar BDN 1.

4.2. Inheritance study

Observations on plant type (dwarf/tall) and plant height were recorded on the parents, F_1, F_2, F_3, and the testcross generations of each cross. In the segregating generations (F_2, F_3, and testcross), the plants were phenotypically classified based on the parental characteristics (dwarf or tall). The results of the phenotypic classification are given in Tables 5 to 17. Measurements of plant height of F_2 populations were made and the frequency distributions given in Figures 2 to 7. The segregation and chi-square analysis were carried out to test genetic hypotheses for the different crosses. The results from the crosses are discussed below:

4.2.1. Cross D_6 x ICPL 1

Results of the phenotypic classification of the segregating generations of the cross are given in Tables 5 and 6. All the F_1 plants were phenotypically classified as normal (Table 5). Segregation in the F_2 generation gave 153 dwarfs out of a total of 545 plants grown. The chi-square test indicated that segregation in the F_2 progenies gave a good fit to the monogenic ratio of 3 normal : 1 dwarf (Table 5).

Table 5. Phenotypic classification of the parents, F_1, F_2, F_3 and testcross generations from the cross D_6 x ICPL 1 grown at ICRISAT Center, rainy season 1987.

Parent/ generation	Total families	Total plants	Observed		Expected		Ratio tested	Chi-square	(P)
			Normal	Dwarf	Normal	Dwarf			
D_6 (P_1)	-	41	0	41	0	41	-	-	-
ICPL 1 (P_2)	-	40	40	0	41	0	-	-	-
F_1	-	8	8	0	8	0	-	-	-
F_2	-	545	392	153	408.75	136.25	3:1	2.76	0.05 - 0.10
F_3[1]- Normal[2]	17 (TT)	118	118	0	118	0			
	31 (Tt)	1076	823	253	807	269	3:1	1.27	0.25 - 0.50
- Dwarf[2]	19 (tt)	133	0	133	0	133	-	-	-
Testcross[3]		34	17	17	17	17	1:1	0	1

1. Plants pooled for all the families

2. F_2 condition before selection

3. F_1 x P_1

P_1 = dwarf parent, P_2 = tall parent

TT = homozygous tall, Tt = heterozygous tall, tt = homozygous dwarf

TT:Tt fit the 2:1 ratio, $\chi^2 = 0.08$, $(0.75 < P < 0.90)$

Table 6. Segregation for the 3:1 ratio within F_3 families obtained from heterozygous tall F_2 single plants from the cross D_6 x ICPL 1 grown at ICRISAT Center, rainy season 1987.

	No.of plants				
	Total	Tall	Dwarf	Chi-square	(P)
1	34	28	6	0.98	0.25 - 0.50
2	34	30	4	3.18	0.05 - 0.10
3	34	26	8	0.04	0.75 - 0.90
4	34	20	14	4.74	0.01 - 0.05
5	36	28	8	0.15	0.50 - 0.75
6	36	22	14	3.70	0.05 - 0.10
7	32	24	8	0.00	1
8	34	28	6	0.98	0.25 - 0.50
9	36	26	10	0.15	0.50 - 0.75
10	36	24	12	1.33	0.10 - 0.25
11	34	30	4	3.18	0.05 - 0.10
12	34	28	6	0.98	0.25 - 0.50
13	36	26	10	0.15	0.50 - 0.75
14	36	28	8	0.15	0.50 - 0.75
15	36	30	6	1.33	0.10 - 0.25
16	34	26	8	0.04	0.75 - 0.90
17	32	24	8	0.00	1
18	36	30	6	1.33	0.10 - 0.25
19	34	24	10	0.35	0.50 - 0.75
20	36	30	6	1.33	0.10 - 0.25
21	36	20	16	7.26	< 0.01
22	34	22	12	1.92	0.10 - 0.25
23	34	28	6	0.98	0.25 - 0.50
24	34	30	4	3.18	0.05 - 0.10
25	34	30	4	3.18	0.05 - 0.10
26	34	28	6	0.98	0.25 - 0.50
27	36	26	10	0.15	0.75 - 0.90
28	36	24	12	1.33	0.10 - 0.25
29	34	26	8	0.04	0.75 - 0.90
30	36	28	8	0.15	0.50 - 0.75
31	34	29	5	1.92	0.10 - 0.25
Pooled	1076	823	253	1.27	0.25 - 0.50

Table 7. Mean plant height, range, and heterosis[1] of the F_1 generation from crosses involving dwarf and normal (tall) pigeonpea genotypes grown in 1986 and 1987

Cross	1986 season			1987 season					
	No. of plants	Mean	Range	No. of plants	Mean	Range	P1	P2	Heterosis (%)
D_6 x ICPL 1	14	117	105 - 131	8	132	120 - 145	117	120	10.0
D_6 x BDN 1	10	124	115 - 148	12	165	156 - 170	117	167	-1.2
PD_1 x ICPL 1	11	144	120 - 170	5	147	142 - 154	113	120	22.5
PD_1 x BDN 1	17	153	136 - 170	7	197	170 - 225	113	167	18.0
PBNA x ICPL 366	-	-	-	15	216	200 - 235	98	212	1.9
PBNA x NP (WR) 15	-	-	-	15	222	210 - 235	98	216	2.8

1. Calculated based on the tall parent

P1 = Dwarf parent, P2 = Tall parent

Genetic testing of the segregation pattern was confirmed in the F_3 families grown from selected F_2 plants and in the testcross. The testcross progenies fit the expected ratio of 1 normal : 1 dwarf plants (Table 5). In the F_3 generation raised from tall F_2 plants, 31 families produced both normal and dwarf progenies while 17 families produced only tall plants which fit the expected ratio of 2 segregating : 1 non-segregating families (Table 5). All F_3 families raised from dwarf F_2 plants bred true for dwarfness (Table 5). Further classification done within the segregating tall F_3 families showed that the majority of the families and the pooled analysis over the families fit the expected ratio of 3 normal : 1 dwarf (Table 6). These results confirmed the monogenic recessive system for the expression of the D_6 dwarf.

Plant height measurements showed that both parents were within the same height range (Table 3). The F_1 plants showed a heterosis of 10% (Table 7). Frequency distribution of plant height in the F_2 generation gave a continous curve that was difficult to separate into distinct classes (Figure 2). Consequently, no genetic ratios could be tested with the F_2 plant height data. The normal tall parental genotype (ICPL 1) was early flowering (Table 3) and it was within the height range

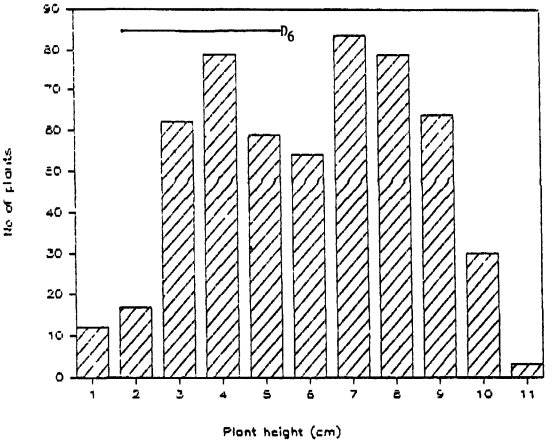


Fig 2, Plant height frequency distribution of the F_2 generation from the cross D_6 x ICPL 1.

1 = 50-60 cm
2 = 61-70 "
3 = 71-80 "
4 = 81-90 "
5 = 91-100 cm
6 = 101-110
7 = 111-120 "
8 = 121-130 "
9 = 131-140 cm
10 = 141-150
11 = 151-160 "

of the dwarf parent. Variation in plant height observed in the F_2 generation was attributed to environmental and/or modifiers present in the two genotypes.

4.2.2. Cross D_6 x BDN 1

Results of the phenotypic classification are given in Tables 8 and 9. All the F_1 plants were phenotypically classified as normal (Table 8). Segregation in the F_2 generation gave 392 normal plants and 138 dwarf plants. Chi-square tests gave a good fit to the monogenic ratio of 3 normal : 1 dwarf (Table 8).

The segregation pattern was confirmed in the F_3 and testcross generations. The testcross progenies fit the expected ratio of 1 normal : 1 dwarf (Table 8). In the F_3 generation raised from tall F_2 plants, 37 families produced both normal and dwarf plants while 12 families produced only normal plants. This fit the expected ratio of 2 segregating : 1 non-segregating F_3 family (Table 8). All the 19 families obtained from dwarf F_2 plants bred true for dwarfness (Table 8). Classification within all the segregating tall F_3 families and the pooled analysis for these families fit the expected ratio of 3 normal : 1 dwarf (Table 9). The results from the cross gave a good fit to the monogenic genetic system.

Table 8. Phenotypic classification of the parents, F_1, F_2, F_3 and testcross generations from the cross D_6 x BDN 1 grown at ICRISAT Center, rainy season 1987.

Parent/ generation	Total families	Total plants/	Observed		Expected		Ratio tested	Chi-square	(P)
			Normal	Dwarf	Normal	Dwarf			
D_6 (P_1)	-	42	0	42	0	42	-	-	-
BDN 1 (P_2)	-	40	40	0	42	0	-	-	-
F_1	-	10	10	0	10	0	-	-	-
F_2	-	530	392	138	397.50	132.50	3:1	0.30	0.50 - 0.75
F_3[1] - Normal[2]	12 (TT)	85	85	0	85	0	-	-	-
	37 (Tt)	1281	985	296	960.75	320.25	3:1	2.45	0.10 - 0.25
- Dwarf[2]	19 (tt)	131	0	131	0	131	-	-	-
Testcross[3]	-	31	16	15	15.5	15.5	1:1	0.03	0.75 - 0.90

1. Plants pooled for all the families

2. F_2 condition before selection

3. F_1 x P_1

P_1 = dwarf parent, P_2 = tall parent

TT = homozygous tall, Tt = heterozygous tall, tt = homozygous dwarf

TT:Tt fit the 2:1 ratio, $\chi^2 = 1.70$ $(0.10 < P < 0.25)$

Table 9. Segregation for the 3:1 ratio within F_3 families obtained from heterozygous tall F_2 single plants from the cross D_6 x BDN 1 grown at ICRISAT Center, rainy season 1987.

Progeny No.	No. of plants			Chi-square	(P)
	Total	Tall	Dwarf		
1	36	28	8	0.15	0.50 - 0.75
2	35	26	9	0.01	0.90 - 0.95
3	34	26	8	0.04	0.75 - 0.90
4	34	28	6	0.98	0.25 - 0.50
5	35	27	8	0.09	0.75 - 0.90
6	35	26	9	0.01	0.90 - 0.95
7	33	27	6	0.82	0.25 - 0.50
8	35	29	6	1.15	0.25 - 0.50
9	35	28	7	0.47	0.25 - 0.50
10	36	26	10	0.15	0.50 - 0.75
11	34	27	7	0.35	0.50 - 0.75
12	36	29	7	0.59	0.25 - 0.50
13	35	28	7	0.47	0.25 - 0.50
14	36	27	9	0.00	1
15	26	20	6	0.05	0.75 - 0.90
16	34	28	6	0.98	0.25 - 0.50
17	36	29	7	0.59	0.25 - 0.50
18	36	26	10	0.15	0.50 - 0.75
19	35	28	7	0.47	0.25 - 0.50
20	36	29	7	0.59	0.25 - 0.50
21	35	28	7	0.47	0.25 - 0.50
22	34	28	6	0.98	0.25 - 0.50
23	33	27	6	0.82	0.25 - 0.50
24	34	24	10	0.35	0.50 - 0.75
25	35	25	10	0.24	0.50 - 0.75
26	35	26	9	0.01	0.90 - 0.95
27	34	24	10	0.35	0.50 - 0.75
28	34	25	9	0.04	0.75 - 0.90
29	34	27	7	0.35	0.50 - 0.75
30	36	27	9	0.00	1
31	35	26	9	0.01	0.90 - 0.95
32	35	26	9	0.01	0.90 - 0.95
33	35	25	10	0.24	0.50 - 0.75
34	34	26	8	0.04	0.75 - 0.90
35	35	24	11	0.77	0.25 - 0.50
36	36	28	8	0.15	0.50 - 0.75
37	35	27	8	0.09	0.75 - 0.90
Pooled	1281	985	296	2.45	0.10 - 0.25

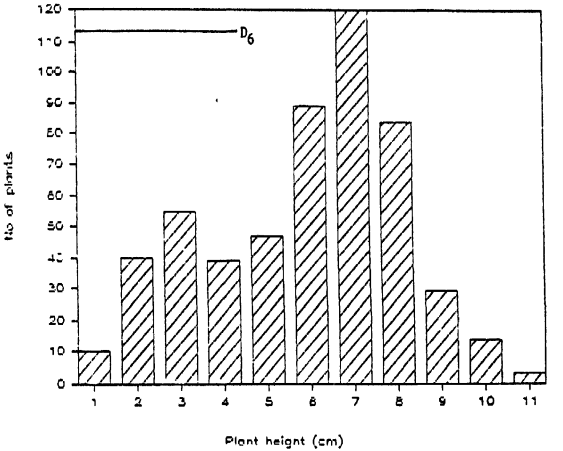


Fig 3, Plant height frequency distribution of the F_2 generation from the cross D_6 x BDN 1.

1 = 60-70 cm
2 = 71-80 "
3 = 81-90 "
4 = 91-100 "
5 = 101-110 cm
6 = 111-120 "
7 = 121-130 "
8 = 131-140 "
9 = 141-150 cm
10 = 151-160 "
11 = 161-170 "

There was a large difference in height between the two parental genotypes (Table 3). Their F_1 generation in 1987 were slightly taller than the recorded height in the 1986 season, a factor that was attributed to the environmental variation in the two years (Table 7). The F_1 plants in 1987 were not significantly different in height from the tall parent. Frequency distribution of plant height in F_2 plants gave a continous curve that was skewed towards taller height (Figure 3). The frequency distribution curve did not have distinct breakpoints to divide the plants into different classes a factor that was attributed to environment and/or modifiers. This was surprising considering that the parents had large differences in height (Table 3).

Separation of the F_2 population into dwarf and tall classes was done by considering the plant height range of the dwarf parent (65-100 cm) grown in the 1986 rainy season (Fig. 3). There were 387 plants taller than, and 143 plants shorter than 100 cm. The hypothesis to test the ratio of 3 tall: 1 dwarf gave a chi-square value of 1.11 ($0.25 < P < 0.50$) from the total of 530 plants. These data suggested that although the breakpoints on the frequency distribution curve were not very clear, the data fit the ratio of 3 tall : 1 dwarf.

In general, data from the two crosses involving the D_6 dwarf line confirmed that dwarfism in D_6 was controlled by a single recessive gene pair.

4.2.3. Cross PD_1 x ICPL 1

Results of the phenotypic classification are given in Tables 10 and 11. Phenotypic classification showed that all the F_1 plants were normal (Table 10). Segregation in the F_2 generation gave 51 dwarf plants out of a total of 204 plants. Despite the low population size, the chi-square test gave a good fit to the monogenic ratio of 3 normal : 1 dwarf (Table 10).

The proposed genetic system was confirmed with the F_3 and testcross generations. The testcross generation fit the expected ratio of 1 normal : 1 dwarf (Table 10). In the F_3 generation raised from tall F_2 plants 30 families produced both normal and dwarf plants while 20 families produced only normal tall plants. This segregation fit the expected ratio of 2 segregating : 1 non-segregating F_3 families (Table 10). All families grown from dwarf F_2 plants gave dwarf progenies (Table 10). Further classification within all the segregating F_3 families and the pooled analysis for these families fit the expected ratio of 3 normal : 1 dwarf (Table 11).

Table 10. Phenotypic classification of the parents, F_1, F_2, F_3 and testcross generations from the cross PD_1 x ICPL 1 grown at ICRISAT Center, rainy season 1987.

Parent/ generation	Total families	Total plants/	Observed		Expected		Ratio tested	Chi-square	(P)
			Normal	Dwarf	Normal	Dwarf			
PD_1 (P_1)	-	40	0	40	0	40	-	-	-
BDN 1 (P_2)	-	42	42	0	42	0	-	-	-
F_1	-	7	7	0	7	0	-	-	-
F_2	-	204	153	51	153	51	3:1	0	1
F_3[1] - Normal[2]	20 (TT)	137	137	0	137	0	-	-	-
	30 (Tt)	1036	789	247	777	259	3:1	0.74	0.25 - 0.50
- Dwarf[2]	17 (tt)	117	0	117	0	117	-	-	-
Testcross[3]	-	18	10	7	9	9	1:1	0.22	0.50 - 0.75

1. Plants pooled for all families

2. F_2 condition before selection

3. F_1 x P_1

P_1 = dwarf parent, P_2 = tall parent

TT = homozygous tall, Tt = heterozygous tall, tt = homozygous dwarf

TT:Tt fit the 2:1 ratio, $X^2 = 0.89$ $(0.25 < P < 0.50)$

Table 11. Segregation for the 3:1 ratio within F_3 families obtained from heterozygous tall F_2 single plants from the cross PD_1 x ICPL 1 grown at ICRISAT Center, rainy season 1987.

Progeny No.	No.of plants			Chi-square	(P)
	Total	Tall	Dwarf		
1	34	26	8	0.04	0.75 - 0.90
2	33	27	6	0.82	0.25 - 0.50
3	34	26	8	0.04	0.75 - 0.90
4	34	27	7	0.35	0.50 - 0.75
5	35	30	5	2.14	0.10 - 0.25
6	35	29	6	1.15	0.25 - 0.50
7	33	27	6	0.82	0.25 - 0.50
8	35	23	12	1.61	0.10 - 0.25
9	36	29	7	0.59	0.25 - 0.50
10	36	27	9	0.00	1
11	36	28	8	0.15	0.50 - 0.75
12	35	28	7	0.47	0.25 - 0.50
13	34	22	12	1.92	0.10 - 0.25
14	36	27	9	0.00	1
15	36	22	14	3.70	0.05 - 0.10
16	32	22	10	0.67	0.25 - 0.50
17	34	26	8	0.04	0.75 - 0.90
18	35	25	10	0.24	0.50 - 0.75
19	34	26	8	0.04	0.75 - 0.90
20	34	29	5	1.92	0.10 - 0.25
21	35	24	11	0.77	0.25 - 0.50
22	36	31	5	2.37	0.10 - 0.25
23	35	28	7	0.47	0.25 - 0.50
24	33	23	10	0.49	0.25 - 0.50
25	34	25	9	0.04	0.75 - 0.90
26	35	27	8	0.09	0.75 - 0.90
27	33	27	6	0.82	0.25 - 0.50
28	36	28	8	0.15	0.50 - 0.75
29	34	26	8	0.04	0.75 - 0.90
30	34	24	10	0.35	0.50 - 0.75
Pooled	1036	789	247	0.74	0.25 - 0.50

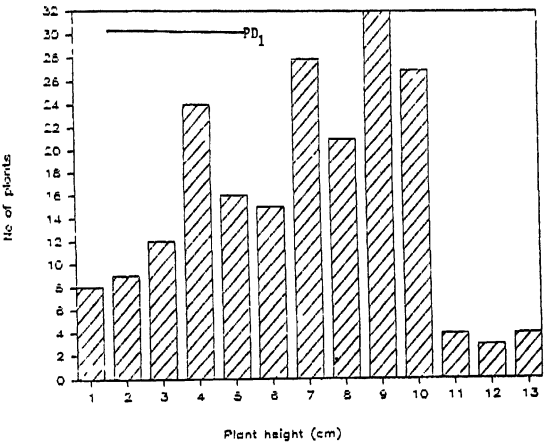


Fig 4. Plant height frequency distribution of the F_2 generation from the cross PD_1 x ICPL 1.

1 = 50-60 cm
2 = 61-70 "
3 = 71-80 "
4 = 81-90 "
5 = 91-100 "
6 = 101-110 cm
7 = 111-120 "
8 = 121-130 "
9 = 131-140 "
10 = 141-150 cm
11 = 151-160 "
12 = 161-170 "
13 = 171-180 "

As in the cross D_6 x ICPL 1, both parents in this cross were within the same height range. Heterosis of 18% was expressed in the F_1 generation in 1987 season (Table 7). Segregation in the F_2 generation gave a continous curve which was skewed towards taller height. This was attributed to the masking effect of the environment and/or modifiers in the population. The curve also did not show distinct classes (Figure 4), thus making it difficult to classify the F_2 generation on the basis of height.

4.2.4. Cross PD_1 x BDN 1

Results of the phenotypic classification are given in Tables 12 and 13. All F_1 plants had the normal tall phenotype (Table 12). Segregation in the F_2 generation gave 129 dwarf out of a total of 463 plants. The chi-square test gave a good fit to the monogenic ratio of 3 normal : 1 dwarf (Table 12).

Genetic testing of the segregation pattern was confirmed with the F_3 and testcross generations. The testcross generation fit the expected ratio of 1 nrmal : 1 dwarf plant (Table 12). In the F_3 generation raised from tall F_2 plants, there were 29 heterozygous and 19 homozygous tall families which fit the expexted ratio of 2 segregating : 1 non-segregating F_3 families (Table

Table 12. Phenotypic classification of the parents, F_1, F_2, F_3 and testcross generations from the cross PD_1 x BDN 1 grown at ICRISAT Center, rainy season 1987.

Parent/ generation	Total families	Total plants	Observed		Expected		Ratio tested	Chi-square	(P)
			Normal	Dwarf	Normal	Dwarf			
PD_1 (P_1)	-	39	0	39	0	39	-	-	-
BDN 1 (P_2)	-	41	41	0	41	0	-	-	-
F_1	-	10	10	0	10	0	-	-	-
F_2	-	463	334	129	347.25	115.75	3:1	2.02	0.10 - 0.25
F_3[1] - Normal[2]	19 (TT)	135	135	0	135	0	-	-	-
	29 (Tt)	1032	789	243	774	258	3:1	1.16	0.25 - 0.50
- Dwarf[2]	17 (tt)	117	0	117	0	117	-	-	-
Testcross[3]	-	26	19	7	13	13	1:1	5.54	0.01 - 0.05

1. Plants pooled for all families

2. F_2 condition before selection

3. F_1 x P_1

P_1 = dwarf parent, P_2 = tall parent

TT = homozygous tall, Tt = heterozygous tall, tt = homozygous dwarf

TT:Tt fit the 2:1 ratio, $\chi^2 = 0.84$ $(0.25 < P < 0.50)$

Table 18. Segregation for the 3:1 ratio within F_3 families obtained from heterozygous tall F_2 single plants from the cross PD_1 x BDN 1 grown at ICRISAT Center, rainy season 1987.

Progeny No.	No.of plants			Chi-square	(P)
	Total	Tall	Dwarf		
1	36	28	8	0.15	0.50 - 0.75
2	36	24	12	1.33	0.10 - 0.25
3	36	30	6	1.33	0.10 - 0.25
4	34	30	4	3.18	0.05 - 0.10
5	36	26	10	0.15	0.50 - 0.75
6	36	24	12	1.33	0.10 - 0.25
7	36	24	12	1.33	0.10 - 0.25
8	36	28	8	0.15	0.50 - 0.75
9	36	22	14	3.70	0.05 - 0.10
10	34	28	6	0.98	0.25 - 0.50
11	36	26	10	0.15	0.50 - 0.75
12	34	26	8	0.04	0.75 - 0.90
13	36	28	8	0.15	0.50 - 0.75
14	36	28	8	0.15	0.50 - 0.75
15	36	30	6	1.33	0.10 - 0.25
16	36	30	6	1.33	0.10 - 0.25
17	36	30	6	1.33	0.10 - 0.25
18	36	28	8	0.15	0.50 - 0.75
19	36	28	8	0.15	0.50 - 0.75
20	34	28	6	0.98	0.25 - 0.50
21	36	28	8	0.15	0.50 - 0.75
22	36	28	8	0.15	0.50 - 0.75
23	36	20	16	7.26	< 0.01
24	36	30	6	1.33	0.10 - 0.25
25	36	28	8	0.15	0.50 - 0.75
26	34	26	8	0.04	0.75 - 0.90
27	36	28	8	0.15	0.50 - 0.75
28	34	28	6	0.98	0.25 - 0.50
29	36	27	9	0.00	1
Pooled	1032	789	243	1.16	0.25 - 0.50

12). All families from dwarf F_2 plants gave dwarf plants (Table 12). Further testing within the segregating F_3 families showed that the majority of the families and the pooled analysis for these families fit the expected ratio of 3 normal : 1 dwarf (Table 13).

The two parents had large differences in plant height (Table 3). F_1 plants grown in the 1986 season were shorter than those grown in the 1987 season (Table 7). This was attributed to environmental differences in the two years. Heterosis of 22% was expressed in the 1987 season (Table 6). Plant height frequency distribution of the F_2 generation gave a wide range of plants. The frequency distribution curve was continous and skewed towards taller height (Figure 5). It was difficult to classify the plants into different classes from the frequency distribution due to its continuity. However, the population was separated into tall and dwarf classes by considering the plant height range of the dwarf parent (70-100 cm) grown in the 1986 season (Figure 5). There were 387 plants taller than and 112 plants shorter than 100 cm. The hypothesis to test the ratio of 3 tall : 1 dwarf gave a chi-square value of 0.16 ($0.50 < P < 0.75$) from the total of 463 plants.

Data from the two crosses involving PD_1 dwarf line confirmed that dwarfism was controlled by a single recessive gene pair.

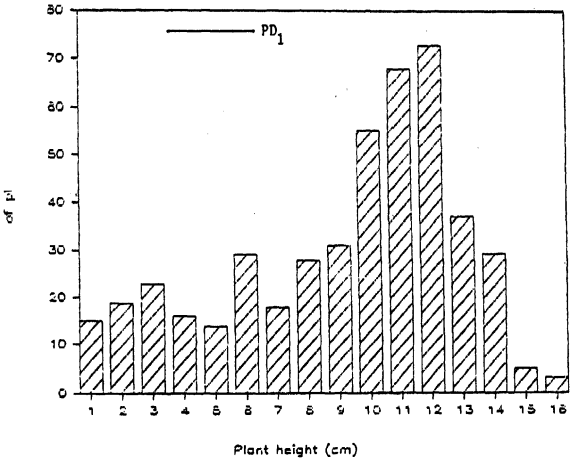


Fig 5. Plant height frequency distribution of the F_2 generation fro the cross PD_1 x BDN 1.

1 = 40-50 cm
2 = 51-60 "
3 = 61-70 "
4 = 71-80 "
5 = 81-90 "
6 = 91-100 "
7 = 101-110 cm
8 = 111-120 "
9 = 121-130 "
10 = 131-140 "
11 = 141-150 "
12 = 151-160 cm
13 = 161-170 "
14 = 171-180 "
15 = 181-190 "
16 = 191-200 "

4.2.5. Cross PBNA x ICPL 366

Results of the phenotypic classification are given in Tables 14 and 15. Segregation in the F_2 generation gave 1124 normal and 321 dwarf plants. The chi-square test gave a good fit to the monogenic ratio of 3 normal : 1 dwarf although with a low probability (Table 14). Genetic testing was made with the F_3 generation. In the F_3 raised from tall F_2 plants, there were 31 families that gave both normal tall and dwarf progenies and 19 families that gave only normal progenies. These data fit the expected ratio of 2 segregating : 1 non-segregating F_3 families (Table 14). All the progenies from the 11 dwarf F_2 plants gave dwarf plants (Table 14). Classification within all the segregating F_3 families and the pooled analysis for all these families fit the expected ratio of 3 normal : 1 dwarf (Table 15).

The two parents had large differences in height (Table 3). The F_1 plants were within the height range of the tall parent (Table 7). The frequency distribution of the F_2 population was bimodal (Figure 6). One peak of the histograms coincided with the dwarf parent, and the other peak coincided with the normal parent. The division between the peaks was at 90 cm. The mean of the peak coinciding with the dwarf parent was less than the dwarf parent's mean, a factor

Table 14. Phenotypic classification of the parents, F_1, F_2, and F_3 generations from the cross PBNA x ICPL 366 grown ICRISAT Center, rainy season 1987.

Parent/ Generation	Total families	Total plants	Observed		Expected		Ratio tested	Chi-square	(P)
			Normal	Dwarf	Normal	Dwarf			
PBNA (P_1)	-	40	0	40	0	40	-	-	-
ICPL 366 (P_2)	-	41	41	0	41	0	-	-	-
F_1	-	15	15	0	15	0	-	-	-
F_2	-	1445	1124	321	1083.75	361.25	3:1	5.98	0.01 - 0.05
F_3[1] - Normal[2]	19 (TT)	130	130	0	130	0	-	-	-
	31 (Tt)	1066	820	246	799.50	266.5	3:1	2.10	0.10 - 0.25
- Dwarf[2]	11	74	0	74	0	74	-	-	-

1. Plants pooled for all families

2. F_2 condition before selection

P_1 = dwarf parent, P_2 = tall parent

TT = homozygous tall, Tt = heterozygous tall, tt = homozygous dwarf

TT:Tt fit the 2:1 ratio, $\chi^2 = 0.48$ $(0.25 < P < 0.50)$

Table 15. Segregation for the 3:1 ratio within F_3 families obtained from heterozygous tall F_2 single plants from the cross PBNA x ICPL 366 grown at ICRISAT Center, rainy season 1987.

Progeny No.	No. of plants			Chi-square	(P)
	Total	Tall	Dwarf		
1	35	28	7	0.47	0.25 - 0.50
2	34	29	5	1.92	0.10 - 0.25
3	34	27	7	0.35	0.50 - 0.75
4	34	28	6	0.98	0.25 - 0.50
5	36	29	7	0.59	0.25 - 0.50
6	36	30	6	1.33	0.10 - 0.25
7	33	27	6	0.82	0.25 - 0.50
8	34	25	9	0.04	0.75 - 0.90
9	35	28	7	0.47	0.25 - 0.50
10	35	29	6	1.15	0.25 - 0.50
11	34	22	12	1.92	0.10 - 0.25
12	35	27	8	0.09	0.75 - 0.90
13	32	23	9	0.17	0.50 - 0.75
14	34	27	7	0.35	0.50 - 0.75
15	34	25	9	0.04	0.75 - 0.90
16	34	27	7	0.35	0.50 - 0.75
17	36	27	9	0.00	1
18	35	29	6	1.15	0.25 - 0.50
19	35	26	9	0.01	0.90 - 0.95
20	34	27	7	0.35	0.50 - 0.75
21	36	29	7	0.59	0.25 - 0.50
22	34	27	7	0.35	0.50 - 0.75
23	36	27	9	0.00	1
24	32	26	6	0.67	0.25 - 0.50
25	34	25	9	0.04	0.75 - 0.90
26	35	26	9	0.01	0.90 - 0.95
27	33	22	11	1.22	0.25 - 0.50
28	33	23	10	0.49	0.25 - 0.50
29	34	25	9	0.04	0.75 - 0.90
30	36	25	11	0.59	0.25 - 0.50
31	34	25	9	0.04	0.75 - 0.90
Pooled	1086	820	246	2.10	0.10 - 0.25

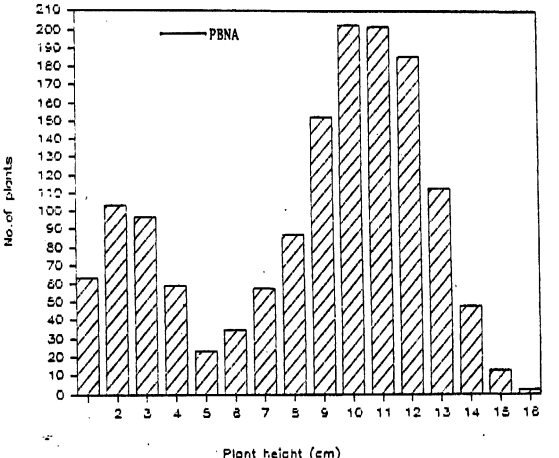


Fig 6. Plant height frequency distribution of the F_2 generation from the cross PBNA x ICPL 366.

1 = 40-50 cm		7 = 101-110 cm		12 = 151-160 cm	
2 = 51-60 "		8 = 111-120 "		13 = 161-170 "	
3 = 61-70 "		9 = 121-130 "		14 = 171-180 "	
4 = 71-80 "		10 = 131-140 "		15 = 181-190 "	
5 = 81-90 "		11 = 141-150 "		16 = 191-200 "	
6 = 91-100 "					

that was attributed to modifiers that may have been contributed by the normal parent. The hypothesis to test the ratio of 3 normal : 1 dwarf in the F_2 gave a chi-square value of 0.80 ($0.25 < P < 0.50$) from the total of 1443 plants.

It was observed that chi-square values of both the phenotypic classification and classification based on plant height fit the same genetic ratio. This was attributed to the large differences in height between the two parents.

4.2.6. Cross PBNA x NP(WR) 15

Results of the phenotypic classification are given in Tables 16 and 17. Segregation in the F_2 generation gave 372 normal plants and 144 dwarf plants (Table 16). The chi-square test gave a good fit to the monogenic ratio of 3 normal : 1 dwarf (Table 13). Genetic testing was made with the F_3 generation. In the F_3 families raised from tall F_2 plants, 31 families produced both dwarf and normal plants while 19 families gave only normal plants. These data fit the expected ratio of 2 segregating : 1 non-segregating F_3 families (Table 16). All progenies from the 15 selected dwarf F_2 plants were dwarf (Table 16). Classification within the segregating F_3 families showed that the majority of the families and

Table 16. Phenotypic classification of the parents, F_1, F_2, and F_3 generations from the cross PBNA x NP (WR) 15 grown at ICRISAT Center, rainy season 1987.

Parent/ Generation	Total families	Total plants	Observed		Expected		Ratio tested	Chi-square	(P)
			Normal	Dwarf	Normal	Dwarf			
PBNA (P_1)	-	40	0	40	0	40	-	-	-
NP (WR) 15 (P_2)	-	42	42	0	42	0	-	-	-
F_1	-	14	14	0	14	0	-	-	-
F_2	-	516	372	144	387	129	3:1	2.32	0.10 - 0.25
F_3[1] - Normal[2]	19 (TT)	128	128	0	128	0	-	-	-
	32 (Tt)	1102	845	257	826.5	275.5	3.1	1.66	0.10 - 0.25
- Dwarf[2]	15 (tt)	104	0	104	0	104	-	-	-

1. Plants pooled for all families

2. F_2 condition before selection

P_1 = dwarf parent, P_2 = tall parent

TT = homozygous tall, Tt = heterozygous tall, tt = homozygous dwarf

TT:Tt fit the 2:1 ratio, $\chi^2 = 0.48$ $(0.25 < P < 0.50)$

Table 1[illegible]. Segregation for the 3:1 ratio within F_3 families obtained from heterozygous tall F_2 single plants from the cross PBNA x NP (WR) 15 grown at ICRISAT Center, rainy season 1987.

Progeny No.	No.of plants				
	Total	Tall	Dwarf	Chi-square	(P)
1	36	26	10	0.15	0.50 - 0.75
2	32	24	8	0.00	1
3	34	24	10	0.35	0.50 - 0.75
4	36	30	6	1.33	0.10 - 0.25
5	34	28	6	0.98	0.25 - 0.50
6	34	26	8	0.04	0.75 - 0.90
7	34	30	4	3.18	0.05 - 0.10
8	36	27	9	0.00	1
9	34	25	9	0.04	0.75 - 0.90
10	36	28	8	0.15	0.50 - 0.75
11	32	20	12	2.67	0.10 - 0.25
12	32	22	10	0.67	0.25 - 0.50
13	34	26	8	0.04	0.75 - 0.90
14	34	28	6	0.98	0.25 - 0.50
15	34	28	6	0.98	0.25 - 0.50
16	35	24	11	0.77	0.25 - 0.50
17	34	26	8	0.04	0.75 - 0.90
18	36	28	8	0.15	0.50 - 0.75
19	36	30	6	1.33	0.10 - 0.25
20	36	26	10	0.15	0.50 - 0.75
21	35	27	8	0.09	0.75 - 0.90
22	34	28	6	0.98	0.25 - 0.50
23	36	28	8	0.15	0.50 - 0.75
24	36	28	8	0.15	0.50 - 0.75
25	34	26	8	0.04	0.75 - 0.90
26	36	30	6	1.33	0.10 - 0.25
27	34	28	6	0.98	0.25 - 0.50
28	32	22	10	0.67	0.25 - 0.50
29	34	25	9	0.04	0.75 - 0.90
30	34	26	8	0.04	0.75 - 0.90
31	34	27	7	0.35	0.50 - 0.75
32	34	24	10	0.35	0.50 - 0.75
Pooled	1102	845	257	1.66	0.10 - 0.25

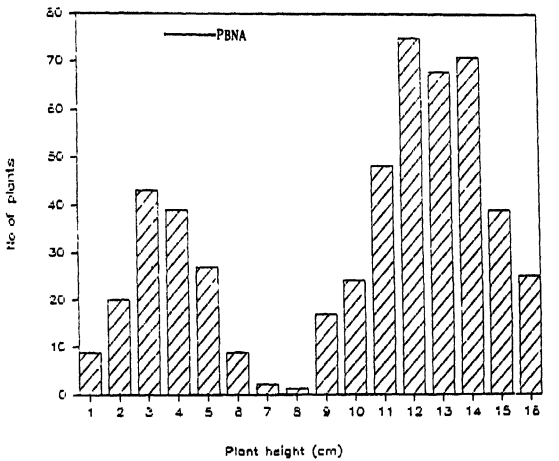


Fig 7. Plant height frequency distribution of the F_2 generation fro the cross PBNA x NP(WR) 15.

1 = 40-50 cm
2 = 51-60 "
3 = 61-70 "
4 = 71-80 "
5 = 81-90 "
6 = 91-100 "
7 = 101-110 cm
8 = 111-120 "
9 = 121-130 "
10 = 131-140 "
11 = 141-150 "
12 = 151-160 cm
13 = 161-170 "
14 = 171-180 "
15 = 181-190 "
16 = 191-200 "

the pooled analysis for all the (segregating) families fit the ratio of 3 normal : 1 dwarf (Table 17).

Plant height measurements showed that there were large differences in height between the parents (Table 3). Frequency distribution of the F_2 population was bimodal with a division between the peaks at 110 cm (Figure 7). Chi-square test for the 3 normal : 1 dwarf mutant ratio gave a value of 4.13 ($0.05 < P < 0.10$) which fit the monogenic hypothesis. Again in this cross, the phenotypic and the plant height classifications gave the same genetic ratios as a result of the large differences in height between the parents.

The crosses involving PBNA dwarf line also confirmed that dwarfism was controlled by a single recessive gene pair.

4.2.7. General discussion for the inheritance study

A 3 normal : 1 dwarf mutant F_2 segregation ratio was observed in all the crosses. The chi-square tests in all the crosses fit the proposed genetic systems. The data suggested the presence of one segregating gene pair with complete dominance for normal plant height. The data also suggested that the dwarf character was inherited as a monogenic recessive. These results were

confirmed with the F_3 and testcross data. The results of this study were in conformity with the findings of earlier workers (Kolhe and Nayeem, 1977; Marekar et al., 1978; Sen et al., 1966; Shaw, 1936; Sheriff et al., 1975) who reported that dwarfness in pigeonpea behaves like a monogenic recessive trait relative to tall stature. But Waldia and Singh (1987) reported two recessive genes to be involved in the expression of dwarfness. The dwarf genotype in their study was about one metre and was an intergeneric selection, while the tall varieties were over three metres tall. The large differences in height between the parents in their study helped in the identification of dwarf and tall plants in the segregating populations. Since plant height is a quantitative trait, it would not be ruled out that dwarfs which are recessive at two loci could be obtained.

Phenotypic classification of all generations gave a good fit to the proposed genetic model of monogenic inheritance in all the crosses. But F_2 plant height data of crosses D_6 x ICPL 1, D_6 x BDN 1, PD_1 x ICPL 1, and PD_1 x BDN 1 gave continous frequency distributions from which genetic ratios could not be fit. Separation into tall and dwarf classes was attempted by considering the dwarf plant height of < 100 cm in the crosses D_6 x BDN 1 and PD_1 x BDN 1, and it was possible to fit the 3 tall:

1 dwarf ratio in these crosses. In the crosses D_6 x ICPL 1 and PD_1 x ICPL 1, classification on the basis of dwarf plant height could not be made since the parents in the crosses were similar in height (Table 3). The short stature of ICPL 1 suggested that for genetic studies of dwarf lines, parents having diverse maturity groups which may influence the expression of plant height, should not be used. However, in the crosses PBNA x ICPL 366 and PBNA x NP (WR) 15, the F_2 frequency distribution curves gave two distinct classes which fit a monogenic ratio as in the phenotypic classification. The identification of distinct classes was attributed to the large differences in height and maturity of the two parents involved in those crosses. Waldia and Singh (1987) using parents with large differences in height were also able to study the inheritance of dwarfness using plant height as the basis of classification.

The complete dominance of the genes for tallness over the genes for dwarfness was also reported in pigeonpea (Marekar et al., 1978; Sen et al., 1966; Sheriff et al., 1975). However, some workers (Kolhe and Nayeem, 1977; Shaw, 1936) reported incomplete dominance for tallness over dwarfness. The differences in these reports could be attributed to the use of different parental materials by the various workers and to differences in the test environments. The results in

this study showed complete dominance of the genes for tall plant stature in the crosses D_6 x ICPL 1, D_6 x BDN 1, PBNA x ICPL 366, and PBNA x NP(WR) 15. In the crosses PD_1 x ICPL 1 and PD_1 x BDN 1, a heterosis of about 20% was expressed suggesting the presence of overdominance of tallness.

Allard (1960) reported that although plant height is a quantitative trait, both dwarf and giant strains dependent upon single gene differences have been found in nearly all plant species in which a search has been made. He suggested that in view of this, the distinction between qualitative and quantitative characters is not absolute. Sharma (1981) reported that the relative numbers of dominant alleles for height present in a plant determines the final height of that plant. When crosses are made, therefore, the plants in the segregating generations receive varying numbers of dominant and recessive alleles which then influence the final height expressed by the plant. From this wide array of plants, a breeder can select plants of a desired height.

The traditional pigeonpea types have been useful in intercropping systems of subsistence agriculture in the SAT where intermittent soil moisture stresses are important. These types are able to give a yield when

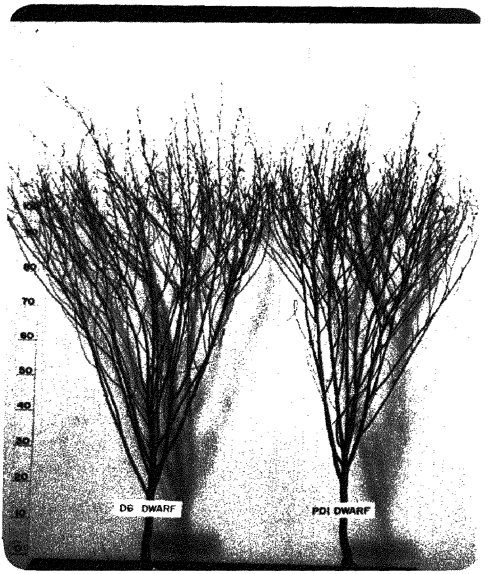
all other crops have failed. Also they have been important as a source of firewood and building material. But the population pressure in the SAT areas has built up and food self-sufficiency is of vital importance in these areas. However, for intensive pigeonpea production, it is essential that the crop be protected from pod-boring insects. The traditional tall pigeonpea varieties pose a problem in that they cannot be effectively covered with insecticide because of their height. Short statured pigeonpea varieties that pose no problems in the management of the crop have been suggested. But there are limitations to their use in that they may produce smaller stems that do not satisfy the building requirements. The use of dwarf varieties in order to allow higher plant populations per unit area and thus resulting in higher yields would be more appreciable. This would be possible with the dwarf mutants in this study which have short stature and many branches.

4.3. Allelic study

The plants were classified phenotypically based on the differences observed among the dwarf genotypes (Plates 2 and 3). Two types of dwarfs were identified phenotypically (Plate 3). One type of dwarf was slightly taller than one metre, with fewer secondary and tertiary branches than the other type and named PD_1/D_6 type. This type of dwarf had been described by Sharma et al. (In press). The other type, named PBNA type, was slightly shorter than one metre in height and had relatively more secondary and tertiary branches. It also was slightly later maturing than PD_1/D_6 type of dwarf. The results of the phenotypic classification of the F_1 and F_2 generations of the crosses made among the three dwarfs in this study are given in Table 18.

4.3.1. Cross D_6 x PD_1

Measurements made on the parents showed that these two dwarfs were similar with respect to all characteristics recorded (Table 3). These plants looked phenotypically similar (Plate 2). On crossing, all their F_1 progenies were similar to the parents. There was no phenotypic segregation in the F_2 generation and all progenies were similar to the parents (Table 18). The lack of segregation in F_2 suggested that both D_6 and PD_1



D6 and PD

Table 18. Phenotypic classification of F_1 and F_2 generations from crosses involving three pigeonpea dwarf mutants grown at ICRISAT Center, rainy season 1987.

Cross/ generation	Total plants	D_8/PD_1 type	PBNA type	Ratio tested	Chi-square	(P)
D_8 x PD_1						
F_1	17	17	0	-	-	-
F_2	313	313	0	-	-	-
D_8 x PBNA						
F_1	16	16	0	-	-	-
F_2	229	172	57	3:1	0.001	0.90 - 0.95
PD_1 x PBNA						
F_1	16	16	0	-	-	-
F_2	265	186	79	3:1	3.27	0.05 - 0.10

Table 19. Range, variance, mean and standard error of three dwarf pigeonpea parents and their F_1 and F_2 populations in respect of plant height (cm) grown at ICRISAT Center, rainy season 1987.

Parent/ cross	Plants (No.)	Range	Mean ±SE	Variance	CV(%)
Parents					
D_6	50	94-134	117 ± 9	75.2	7.4
PD_1	50	88-131	113 ±10	101.4	8.8
PBNA	50	80-115	98 ± 9	76.8	8.9
F_1 population					
D_6 x PD_1	17	114-130	121 ± 6	21.2	3.8
PD_1 x PBNA	16	110-134	124 ± 7	29.6	4.7
D_6 x PBNA	16	110-134	119 ± 6	33.3	4.8
F_2 population					
D_6 x PD_1	313	80-150	121 ±12	151.2	10.2
PD_1 x PBNA	265	75-158	121 ±19	346.0	15.3
D_6 x PBNA	229	70-149	118 ±17	273.7	14.0

had the same alleles for dwarfness although the two dwarfs had been identified from different sources.

Plant height in the parents, F_1 and F_2 generations is reported in Table 19. The data showed that there was a wide range in the parental heights, 94-134 cm for D_6 and 88-131 cm for PD_1, which could be attributed to the environment. The mean heights of the parents, F_1 and F_2 generations were within the same ranges. Frequency distribution of plant height of the F_2 generation were constructed (Fig. 8). It was difficult to classify the plants into classes since the distribution was continous with no obvious breakpoints.

4.3.2. Cross D_6 x PBNA

Measurements made on the parents had shown that these two dwarfs were different in all characteristics recorded (Table 3) and they could be differentiated phenotypically (Plate 2). When these two dwarfs were crossed with one another, all the F_1 plants were phenotypically classified as being like $PD1/D_6$ dwarf (Table 18). Phenotypic segregation in F_2 gave 172 progenies which were like D_6 dwarf and 57 progenies similar to PBNA. Chi-square tests indicated that segregation in the F_2 generation gave a good fit to the monogenic ratio of 3 PD_1/D_6 type : 1 PBNA type

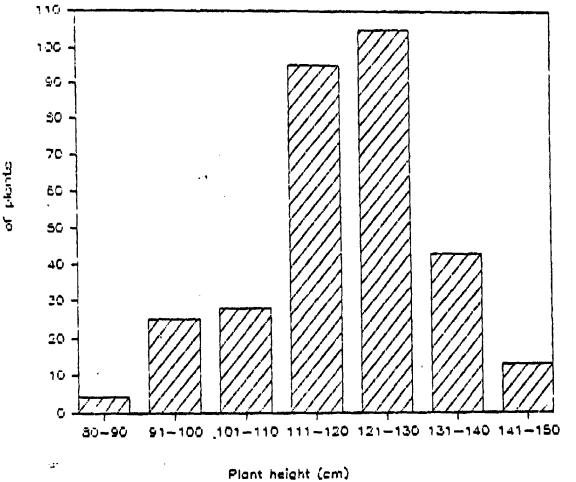


Fig 8. Plant height frequency distribution of the F_2 generation from the cross $D_6 \times PD_1$

phenotype. The segregation showed that one locus with dominance was involved in the differences observed in the two dwarfs. The D_6 type of phenotype was dominant to the PBNA type of phenotype as shown in the F_1 and F_2 generations.

Plant heights recorded on the parents showed that PBNA (98$\pm$ 9 cm) was significantly shorter than D_6 (117 $\pm$ 9 cm) although the difference was not large (Table 19). The plant height of the F_1 was 119 cm and hence similar to that for D_6. The mean height of the F_2 generation (121 $\pm$ 17 cm) was similar to that for D_6 but the range (70-149 cm) was outside the ranges for both parents. Because of the little difference in height between the two dwarf parents, different classes of plants could not be differentiated on the basis of height (Figure 9). In this cross, phenotypic classification of the F_2 generation was a better criterion for the F_2 classification.

4.3.3. Cross PD_1 x PBNA

The recorded characteristics showed that the two parents were different in all characteristics (Table 3). All the F_1 progenies from this cross were phenotypically classified as being like the PD_1/D_6 dwarf (Table 18).

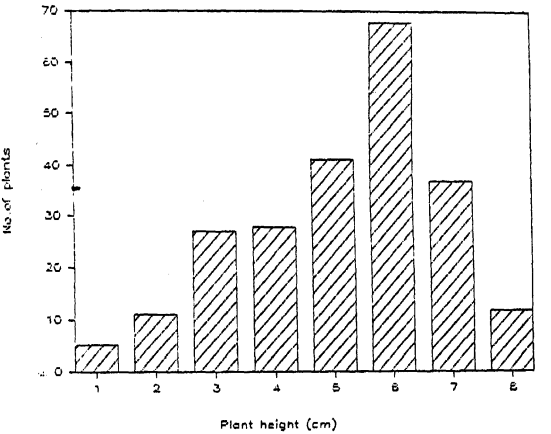


Fig 9. Plant height frequency distribution of the F_2 generation from the cross D_6 x PBNA.

1 = 70-80 cm
2 = 81-90 "
3 = 91-100 "
4 = 101-110 "
5 = 111-120 cm
6 = 121-130 "
7 = 131-140 "
8 = 141-150 "

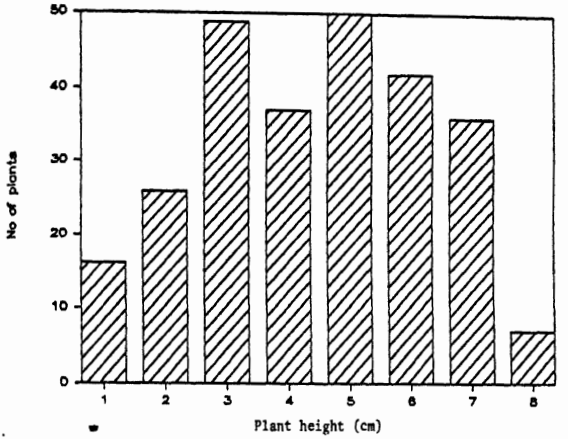


Fig 10. Plant height distribution of the F_2 generation from the cross PD_1 x PBNA.

1 = 70-80 CM
2 = 81-90 "
3 = 91-100 "
4 = 101-110 CM
5 = 111-120 "
6 = 121-130 "
7 = 131-140 CM
8 = 141-150 "

Segregation in the F_2 gave 186 progenies that were of the PD_1/D_6 type and 79 progenies of the PBNA type. The chi-square tests showed that segregation in F_2 fit to a monogenic ratio of 3 D_6 type : 1 PBNA type typical of a single locus with dominance. This classification showed that this cross was segregating in a similar manner with the cross D_6 x PBNA. This was expected considering that the two dwarfs (D_6 and PD_1) had been classified as having the same alleles for dwarfness.

Plant height measurements showed that PBNA (98$\pm$9 cm) was significantly shorter than PD_1 (117$\pm$9 cm) (Table 19). Mean plant heights of the F_1 and F_2 generations were similar to that for PD_1. The frequency distribution in the F_2 gave a continous curve that could not be used to classify the two types of dwarfs (Figure 10).

Although the results showed that the PD_1/D_6 type of phenotype is dominant to the PBNA type of phenotype, both phenotypes were recessive to the tall (normal) plant phenotype. Their expression suggested the presence of a multiple allelic system designated as TT or Tt for the tall phenotype, t_3t_3 for the PD_1/D_6 type of phenotype and $t_3't_3'$ for the PBNA type of phenotype. Dominance hierarchy followed the order $T > t_3 > t_3'$. For the development of the PD_1/D_6 type of phenotype, the presence of the t_3 allele either in the homozygous or

heterozygous condition was essential; while expression of the PBNA type of phenotype required the presence of t_3' allele in the homozygous condition only. From this reasoning it would be expected that the parental genotypes were t_3t_3 for PD_1 and D_6, and $t_3't_3'$ for PBNA. On crossing, all their F_1s were 't_3t_3'' and they expressed the PD_1/D_6 type of phenotype. Segregation occured in the F_2 resulting in 3 PD_1/D_6 type : 1 PBNA type of phenoytpe thus confirming the hypothesis of a multi-allelic locus with dominance hierarchy.

V

SUMMARY AND CONCLUSIONS

A study was carried out to determine the nature of dwarf inheritance in three dwarf sources of pigeonpea (D_6, PD_1 and PBNA). Four normal tall parents (ICPL 1, BDN 1, ICPL 366, and NP (WR) 15 were used in the study. Allelic relationships were studied in crosses among the three dwarfs not including the reciprocals. In addition, a pot experiment was conducted to determine the total dry matter production and its partitioning by the dwarf plants as compared to the normal tall genotypes. The crosses D_6 x ICPL 1, D_6 x BDN 1, PD_1 x ICPL 1, PD_1 x BDN 1, PBNA x ICPL 366 and PBNA x NP (WR) 15 were studied for the mode of dwarf inheritance in the F_1 and F_2 in the 1986 rainy season. The parents, F_1, F_3, and testcross generations were studied in the 1987 rainy season. A phenotypic classification of the segregating generations was made. The plant height were obtained and the F_2 height frequency distribution was used to classify the plants for comparison with the phenotypic classification.

From the studies, the following conclusions were drawn:

1. Dwarfness was expressed in the form of shorter and fewer internodes. The mutants had many secondary and tertiary branches that were loosely held at an acute angle thus making them appear as short compact bushes. This property was used in the phenotypic classification of segregating generations. The dry matter partitioning and nodulation were similar in both dwarf and tall genotypes.

2. The three dwarfs, which were identified from different sources, were mutants at the same locus. The locus was expressed in a multi-allelic system with dominance hierarchy ($T > t_3 > t_{3'}$). D_6 and PD_1 had t_3 alleles while PBNA had $t_{3'}$ alleles.

3. There was no difference in height among the dwarf mutants and the early normal parent. This caused problems in the classification of segregating generations.

4. Dwarfness was inherited as a monogenic recessive trait relative to normal plant type.

5. Tall plant stature was completely dominant to dwarf plant stature.

6. Enviromental conditions and/or modifiers were indicated as being involved in the expression of plant height.

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Appendix 1. BP 3C PLOT HISTORY RECORD (1987K) : INPUTS

I N P U T S				
NAME	DOSES/HA (KG/L/HA)	DATE	METHOD	AREA (LOCATION)
ZN SO4	40 KG	27.4.87	SPRAYING	1.2Ø
PROMETRYN +	2 LIT			
DECONIL	0.15%	18.7.87	SPRAYING	1.2ØHA.
BASALIN	2.25 LIT	26.8.87	SPRAYING	1.2ØHA.
DITHANE	0.22%	27.7.87	SPRAYING	1.2ØHA.
FENVALRATE	0.1%	26.9.87	SPRAYING	0.7ØHA-MIDDLE.
THIODON	0.35%	10.10.87	SPRAYING	1.2ØHA.
NUVACRON	0.1%	28.10.87	SPRAYING	1.2ØHA.
THIODON	0.17%	30.10.87	SPRAYING	1.2ØHA.
NUVACRON	0.15%	2.11.87	SPRAYING	1.2ØHA.
THIODON	0.35%	7.11.87	SPRAYING	1.2ØHA.
FENVALERATE	0.06%	11.11.87	SPRAYING	1.2ØHA.
EKALUX	0.06%	30.11.87	SPRAYING	1.2ØHA.
THIODON	0.17%	11.12.87	SPRAYING	1.2ØHA.
THIODON	0.17%	23.12.87	SPRAYING	1.2ØHA.