

UNIVERSITY OF ILORIN

THE SIXTY-NINETH INAUGURAL LECTURE

GENES IN HIDE-AND-SEEK

By

PROFESSOR J. A. MORAKINYO

B.Sc.; M.Sc.; Ph.D. (Ife)

Professor of Plant Genetics and
Dean Postgraduate School

Thursday, 28th August, 2003

UNIVERSITY OF ILORIN

THE SIXTY-NINETH INAUGURAL LECTURE

GENES IN HIDE-AND-SEEK

By

PROFESSOR J. A. MORAKINYO

B.Sc.; M.Sc.; Ph.D. (Ife)
Professor of Plant Genetics and
Dean Postgraduate School

Thursday, 28th August, 2003

This 69th Inaugural Lecture was delivered
under the Chairmanship of:

The Vice-Chancellor
Professor S. O. O. Amali
B.A (Ibadan), Ph.D. (Wisconsin)

Published by
Library and Publications Committee
University of Ilorin, Ilorin, Nigeria

July, 2003

Printed at
Unilorin Press
University of Ilorin, Nigeria

GENES IN HIDE-AND-SEEK

The Vice-Chancellor, Professor S. O. O. Amali,
Deputy Vice-Chancellors,
Registrar and other Principal Officers of the
University here present,
Deans of Faculties and Student Affairs,
Heads of Departments and other members of
staff,
Gentlemen and women of the press,
Greatest Unilorites!!!,
Our Distinguished Guests,
Ladies and Gentlemen.

INTRODUCTION

All over the world undergraduate admission into the University is coveted by youths because it is a significant milestone in their lives. My admission into the then University Of Ife (now Obafemi Awolowo University), Ile-Ife, in 1971 gave me boundless joy. This was at a time when undergraduate students enjoyed considerable comfort and like there counterparts today, also enjoyed considerable freedom.

PROFESSOR J. A. MORAKINYO B.Sc.; M.Sc.; Ph.D. (Ife)
Professor of Plant Genetics and Dean Postgraduate School

University admission marked for many of us the beginning of independent adult life.

This seemingly comfortable and independent life tended to mask the heavy academic workload and the need for constant study, which was the only panacea for the almighty June examination debacle of those days in the University. The reality of the demand of University education donned on me at the beginning of my second year when many of my friends and classmates were nowhere to be found, only to be told that the previous almighty June examination had shown them the way to road one, the only authorized road that led in and out of Obafemi Awolowo University at that time. I needed no further prompting to brace up to the challenges of the Bachelor Of Science (B.Sc) degree programme in genetics, a subject that attracted me because of its fundamental relevance to all living things. Genetics was, at this time, a relatively young academic discipline in Nigeria. It had just evolved as a first-degree programme at the University of Ife. I was intrigued by the fact that the subject deals with the blueprint of life, the master plan for all life forms.

Genes constitute the blueprint of life and along with the environment, defines the identity and the uniqueness of every organism through their phenotypic effects. In spite of this fundamental importance of genes in determining the physical, physiological and behavioural identities of organisms, their existence is only made known by mutations, the heritable changes in gene functions. Genes therefore exist in-cognito. We are, for example, made aware of the existence and functions of

the gene that is responsible for skin colour in human beings by the mutation that prevents the synthesis of the skin colour pigment called melanin. Similarly, a mutation that prevents the synthesis of the green pigment in plants called chlorophyll exposes the existence of the gene for chlorophyll synthesis. In both man and plant, the results are albinos. Albinism in these two cases is traceable to genes that have lost their functions through mutation and are consequently exposed. Genes are therefore naturally in hide-and-seek.

Genes in Heredity

Mr Vice-Chancellor Sir, man has always known that there is biological similarity between offsprings and their parents, that is, that there is heredity. What was unknown was how it came about. For example when a man's children resemble him, the Yoruba will say about the man "O ni abijo" meaning that he is able to produce children that resemble him. When a child does something that pleases his/her parent, the parent will say "Ọmọ ọkọ niẹ, o kii se ọmọ ale" meaning that the child is not a bastard. However if a child performs below the parent's expectation, the parent would express disappointment by retorting "Şiọ! Ọmọ ẹni iba joni abayo" meaning alas! "One would have been glad if his child resembled him."

Our knowledge of the role of genes in heredity came from the 19th century classical experiments of Gregor Mendel, which was based on the inheritance of contrasting states of characters in the garden pea plant (Pisum sativum). He carried out series of monohybrid crosses (i.e. crosses involving only one character such as

seed colour at a time) and established the classical second generation filial (F_2) phenotypic ratio 3:1. He also carried out series of dihybrid crosses (i.e. crosses involving two characters such as seed colour and seed shape at a time) and established the classical second generation filial (F_2) phenotypic ratio 9:3:3:1.

Gregor Mendel was able to establish from his monohybrid experiments that genes which he called hereditary factors or determinants are responsible for the appearance of characters. Each hereditary factor is particulate in nature and is the basic unit of heredity occurring in two alternative states known as dominant and recessive alleles, and are discrete and unblending. Mendel also deduced that the members (alleles) of the gene pairs segregate (separate) equally into the gametes (eggs and sperms) prior to the random union of gametes from the different sexes to form new progeny. From his dihybrid experiment, he established that the two members (alleles) of a gene pair separate and move into gametes independently of members of other gene pairs (i.e. that different gene pairs assort independently during gamete formation). Mendel's monohybrid and dihybrid experimental results became his two laws of heredity, namely Law of segregation and law of independent assortment respectively. The law of segregation of hereditary factors states that the two particulate members of a gene pair segregate from each other into the gametes, so that half the gametes carry one member of the pair and the other half of the gametes carry the other member of the pair. The law of independent assortment of genes on other hand states that during

gamete formation, the segregation of the alleles of one gene is independent of the segregation of the alleles of another gene.

Although these laws are fundamental to genetics and are true, they are more like the exceptions rather than the rules in nature. We now know that Mendel's hereditary factors were major genes of major discrete clear-cut phenotypic effects, but in reality, nature abounds with hereditary factors whose phenotypic effects are not so clear-cut. For example incomplete dominance, co-dominance, additive gene action and linkages of genes are common in nature. In some of these cases, Mendel's classical ratios of 3:1 (monohybrid phenotypic ratio) and 9:3:3:1 (dihybrid phenotypic ratio) are modified and in others the ratios are completely obliterated. Mendel's second law is also only valid for genes that are on different chromosomes or distantly located on the same chromosome (i.e. not linked). These observations notwithstanding, Mendel's experimental findings and laws of heredity, published in 1865, remain the basic principles of heredity and classical laws of genetics without which our understanding of genetics today would be incoherent. For this reason, Gregor Mendel is regarded as the father of modern genetics. His experiments exposed the existence and function of genes. He brought genes out of hiding.

Genes and Reproduction

Mr. Vice Chancellor Sir, the fact that inheritance of characters is an inherent attribute of living organisms has never been in doubt. That like begets like is an

incontrovertible fact. This is established in the Yoruba proverb that says “Bi ọmọ o jọ ẹ̀kòtò yio jọ kípá, ẹ̀ni bini lajọ” meaning that if a child does not resemble his/her father he/she will resemble his/her mother, it is mandatory to resemble one’s biological parents. In the African marriage institution therefore, the two families whose children are coming together in marriage would investigate each other to be sure that there are no undesirable familial traits in their pedigree. This is because they are aware that such undesirable familial traits may be transmitted to the children of the new couple. This investigation is particularly important in some African traditional settings where the grandparents are more possessive of their grandchildren than the actual parents. The possessiveness has genetic justification because the reproductive success of a pair of organisms is measured by the viability and reproductive ability of their offsprings. Thus if the F1 generation of Mendel’s crosses were sterile, then the mating of the true breeding parents would have been futile. Also, consanguinous mating, the extreme case of which is incest, is an abomination in Africa. This is another cultural belief that has sound genetic basis because consanguinous matings (inbreeding) have high likelihood of exposing the worst of human genetic complements in the form of undesirable homozygous recessives. Africans therefore have genetically sound culture.

Similarly, subsistence farmers save the best of their crops for next season planting in order to retain good crop yield. This practice is based on the belief that whatever is responsible for good crop yield would be

transmitted to the next generation of crops, all things being equal.

Thus, genetics has been appreciated since man learnt to raise crops and flocks and live in organized societies in family units. The systematization of the knowledge of heredity however received major impetus with the rediscovery of Gregor Mendel's work in 1900, 35 years after the work was published. In the cases cited above, namely the African marriage institution and subsistence farming, the concern is about maintaining desired qualities generation after generation. This is where sexual reproduction becomes pertinent as a bridge between generations (Figures 1 & 2).

Fig. 1: Reproduction in maize (a monoecious plant).

Fig. 2: Reproduction in human beings.

The appearance of an organism in respect of a particular character is a result of gene expression. Genes are located on chromosomes. Chromosomes occur in definite ($2n$) number in the nucleus of somatic cells. In eukaryotic organisms, some of these cells develop into sex cells through the process of meiosis that takes place in the anthers and ovaries of plants, or in the testes and ovaries of animals including human beings. Genes are reshuffled and chromosome number is reduced from the diploid ($2n$) to haploid (n) in the sex cells during meiosis.

In the course of sexual reproduction, male and female sex cells unite and the diploid chromosome number is restored in the single-cell zygote which by repeated mitotic division becomes the embryo. As the new individual develops, its identity which is encoded in its gene complement unfolds. The fusion of the two haploid sex cells in the process of fertilization to form the zygote marks the beginning of a new life in both plants and animals including man. The zygote develops into the new organism. The characteristics of the new organism are hidden in the gene complement of the zygote and it takes life developmental processes in the zygote through embryogenesis and growth in the appropriate environment to unfold the identity of the individual by the expression of its genes.

Variability is inherent in the way sex cells are produced because their formation is preceded by the reshuffling of the genes that were received from the previous generations. Thus the genes received by a sexually reproducing organism are the genes from his/her grandparents reshuffled in his/her parents. This is the reason why some traits (good or bad), run in families and are therefore called familial traits. If such traits are recessive as in the Mendelian recessive character, two carrier (heterozygous) spouses have a one-in-four likelihood of producing affected children. A common example here is the sickle cell anaemia in human beings where the 'AA' genotype is normal, 'AS' is the carrier and 'SS' is the sickler. 'AS' is perfectly normal, in fact, more normal than 'AA' in malaria endemic regions because 'AS' has some resistance against malaria, while 'AA' does not.

Intended marriage partners should therefore know their genotypes and the possible genotypes of their children. This allows them to identify their hidden genes and take appropriate decisions.

A very important aspect of sexual reproduction is the formation of sex cells through meiosis. During this process, chromosomes behave in particular ways that ensure reshuffling of the genes on them and the reduction of chromosome number by half in the resulting sex cells. The new organism (zygote) grows to become an adult through repeated mitosis and differentiation. Since genes are on chromosomes, their fate during sexual reproduction is tied to the fate of meiotic chromosomes. The behaviour of chromosomes during meiosis is therefore an important area of study when the fertility of the individual is concerned. Any abnormal chromosome behaviour such as abnormal chromosome pairing, non-pairing, pre-cocious chromosome movement, lagging chromosomes or non-disjunction of chromosomes will lead to defective sex cells and result in sterility. This was established in Hparrhenia by Olorode and Morakinyo, (1980) and in the chilly peppers (Capsicum spp) by (Morakinyo and Falusi, (1992). Fertility or sterility is therefore determined in plants, animals and humans by determining the viability of the sex cells, particularly pollen grains in plants or sperms in animals and humans. The viability or non-viability of the sex cells is however a direct result of the meiotic process that produced them. (Fig. 3a-d). Pollen viability was practically reduced to zero in some of these plants because of meiotic

irregularities in them and are therefore male sterile.

(a)

(b)

(c)

(d)

Fig. 3: Abnormal Meiotic chromosome behaviours that lead to the production of non-viable sex cells and sterility. (a) Anaphase I in triploid hybrid of Hyparrhenia involucrata and H. Subplumosa showing lagging chromosomes and a non-disjunction bridge; (b) Anaphase I in interspecific Hybrid of pepper (Capsicum spp) showing non-disjunction bridge and chromosome fragments; (c & d) Anaphase II in interspecific hybrid of pepper showing non-disjunction bridges. (From Olorode and Morakinyo, 1980; Morankinyo and Falusi, 1992)

Genes in qualitative inheritance

Heritable characters are characters that can be reproductively passed from parents to offspring's because they are controlled by hereditary factors (genes), which are transmitted through the germline (through the sex cells) from parents to offspring's. Heritable characters may be qualitative when conditioned by major genes (Oligogenes) of pronounced clear-cut phenotypic effect or quantitative when controlled by multiple genes or polygenes of small individual phenotypic effects. Recessive qualitative characters abound in plants and animals including human beings. Examples are determinate growth and uniform fruit ripening in tomato,

sickle-cell anaemia, phenylketonuria (PKU) and cystic fibrosis in human beings and albinism in plants, animals and humans. Fig. 4(a & b) shows albinism in human beings and plants.

(a)

(b)

Fig. 4: Albinism in (a) human beings (b) maize plants

The inheritance pattern is Mendelian.

Inheritance pattern in albinism:-

True breeding normal parent: x Albino parent

CC

cc

Heterozygous normal offspring

Cc

Heterozygous normal
normal

x

Heterozygous

Cc

Cc

1CC : 2Cc : 1cc

1 Homozygous normal: 2 Heterozygous normal: 1 albino

One albino is expected out of four offsprings. The one albino out of every four expectation may, however, not be realized with a single mating or with a single couple because, by chance (sampling variation) alone, the number of albinos from a single couple of heterozygous parents may be above or below the expected number. However, when the offsprings of many couples are pooled together, the 3:1 ratio (i.e. one albino out of every four children) is realized. Mr. Vice-Chancellor Sir, it is obvious from this explanation that we can absolve the witches and wizards of complicity in the birth of human albinos.

There are also many dominant qualitative characters in living organisms. In this case, the normal allele is recessive and the abnormal allele is dominant. Examples are shown in Fig. 5a-d. Achondroplasia is a type of dwarfism in human beings where the normal human stature is recessive (dd) and dwarfism is dominant (DD or Dd) (Fig. 5a). It is however believed that the homozygous DD condition is lethal and the living dwarfs are Dd. Two dwarfs (Dd x Dd) may therefore produce children with normal stature. Polydactyly (extra digits), brachydactyly (short digits) and piebald spotting are other Mendelian dominant characters that are visible in human beings. It must be noted however that not all skin spots are due to piebald spotting. Some may be caused by reaction to drugs.

(a)

(b)

(c)

(d)

*Fig. 5: (a) Achondroplasia, (b) Polydactyly,
(c) Brachydactyly, (d) Piebald.*

Seed shattering is an important qualitative character of seed plants. It is desirable in nature because it helps plants to disperse their propagules. It is found to be dominant in the wild grain sorghums (Morakinyo, 1993). Seed shattering is however undesirable in crop plants where seeds (i.e. grains) represent the yield. In soyabean (Glycine max) and benniseed (Sesamum indicum; Ceratotheca sesamoides) the plants are cultivated for their seeds, most of which are lost to shattering of the pods at maturity. In many seed or grain crops such as guinea corn, millet, rice and beans, man has selected for non-shattering seeds and developed cultivars that do not shatter their seeds at maturity by incorporating the genes for “non-shattering” into them. For other crop plants such as soyabean and benniseed, the search for the “non-shattering” genes and breeding of non-shattering cultivars continues.

A gene may be lethal when its expression results in the death of the individual expressing it. Such gene may be dominant or recessive. Some lethals are expressed as deaths in utero, where they either go unnoticed, or are noticed as spontaneous abortions. Other lethals such as those responsible for Duchenne muscular dystrophy, pku and cystic fibrosis, exert their

effects at childhood while Huntington's disease, expresses itself by killing the sufferer at adulthood. The total of all the deleterious and lethal genes that are present in all individuals of a population, is called genetic load, a kind of genetic burden that the population has to carry as an insurance for the future survival of the population as a whole. For example the gene for sickle cell anaemia is deleterious to an individual carrying the two recessive alleles (SS), but in the heterozygous (AS) it is advantageous and superior to (AA) the homozygous normal (AA) in malaria endemic areas. The S allele is therefore part of the genetic load that we in the malaria endemic areas have to carry for our collective survival. The superiority of the heterozygous AS in this case is comparable to the superiority of the F1 hybrid maize over its inbred parents.

All human populations have their shares of genetic load, the nature and "weight" of which may differ from one population to the other. They also have their share of genetically mediated congenital abnormalities. In all cases, sufferers should be considered as part of God's creation whose existence is for a good purpose and they should not be perceived as some kind of demons as some people would want to believe them to be. We must look hard enough at this segment of God's creation to identify their beauty and ability which quite often stares us in the face, but we fail to appreciate because of our bias against them. After all, according to the motto of Ibadan Boys' High School, my alma mater, "Domino opera, pro bono publico, the work of God is for the good of the people."

Genes in Quantitative Inheritance

This is the inheritance of measurable and continuously varying characters. Just as Mendel had noted and studied the more obvious qualitative characters that occurred in clear-cut states, smaller and less striking almost imperceptible quantitative differences were also noted especially with regard to measurable characters such as size. These quantitative variations had continuous phenotypic range and lacked distinct steps that could be accounted for by distinct genes. In fact, most measurable characters follow a normal distribution curve ranging from low to high values.

The analysis of quantitative inheritance is complicated by the fact that the expression of polygenes that are responsible for the inheritance is influenced by the environment (i.e. GxE interaction is significant). The pioneering work of Eberhart and Russell (1966) as well as those of many others after them (Duddley and Moll, 1969; Obisesan, 1986; Morakinyo and Ajibade, 1998; Ajibade and Morakinyo, 2000; Aliero and Morakinyo, 2001) have shown the significance of G x E interaction in the inheritance of quantitative characters.

This reminds me of my encounter with a friend and his son. The fact that my friend is the biological Father of this boy is not in doubt because of obvious resemblance of Father and son in all features except height. The boy is much taller than both his parents. In a casual conversation with me, my friend expressed surprise at the height of his son and wondered aloud where the boy got so much height from. I told my friend

that both himself and his wife gave the genes for height to the boy and provided him with a conducive environment for the genes to be expressed by giving the boy good nourishment and proper health care compared to himself, (my friend), who grew on fermented pounded yam in the morning, roasted yam in the afternoon and another round a pounded yam in the evening. So the fault of my friend's short height is not in his genetic make-up but in the environment that inhibited the expression of his genes for height.

Hybrid maize is improved by accumulating the genes for grain yield in them and are therefore very high yielding in the appropriate environment with adequate water, fertilizer, weed control, adequate insolation, disease control etc. In the absence of suitable environment the yield drops drastically. The polygenes that are responsible for quantitative characters are therefore more in hiding than the oligogenes (major genes) and require the appropriate environment to expose them through their observable phenotypic effects. The observable phenotype for quantitative traits is a product of the interplay between genotype and the environment.

Using quantitative genetic principles and methods, mating designs and experimental designs, genetic and environmental variances can be partitioned and estimated (Cochran and Cox, 1964 Mather and Jinks, 1971; Singh and Chaudhary, 1977). A major preoccupation of plant quantitative geneticist and breeders is therefore to partition the total variance δ_{ph}^2 in desirable quantitative characters of crop plants into the genetics

and environmental components (i.e. $\delta_{ph}^2 = \delta_G^2 + \delta_{G \times E}^2 + \delta_E^2$) using appropriate mating designs. The higher the genetic variance (δ_G^2), the higher, the proportion of the observed variability that is due to genetic cause (i.e. $\delta_G^2 = \delta_A^2 + \delta_D^2 + \delta_I$; where δ_A , δ_D , δ_I are additive, dominance and epistatic variances respectively). The relationship between the total variance for a character and the variance components can be quantified as heritability (the proportion of total variance of a character that is due to genetic causes). This may be broad or narrow sense i.e. $h_{bs}^2 = \delta_G^2 / \delta_{ph}^2 \times 100\%$, or $h_{ns}^2 = \delta_A^2 / \delta_{ph}^2 \times 100\%$ respectively.

Heritability is an important parameter that is usually considered in making a choice of breeding method in crop improvement programmes. For example early generation selection will be appropriate where narrow sense heritability is high (h_{ns}^2). This is because greater genetic advance is expected under selection when h_{ns}^2 is high. This is in turn due to the fact that h_{ns}^2 measures the proportion of the total variability in a character that is transmissible to the next generation. Dominance and epistasis are gene interactions that are not transmissible. In this connection, heritability was estimated for various characters in populations of Okra, guinea corn and cowpea to serve as guide in choosing breeding methods for these crop plants (Morakinyo and Makinde, 1991; Morakinyo, 1996a; Ajibade and Morakinyo, 1999). In the guinea corn population under reference the expected genetic advance under selection for grain yield was also estimated. This approach shows that quantitative inheritance is about the inheritance of differences that

are of degrees and not of kinds and therefore requires specialized mathematical approach in its study as done by Morakinyo, 1996a.

Multiple alleles (i.e. forms) of genes

Mendel reported hereditary factors with only two forms each (e.g. Y and y) but it has since been found that in a population, a gene may contain or “hide” itself in more than two forms. This is known as multiple allelism. There are four blood types (i.e. phenotypes) in the ABO blood group system. The allelic series includes three major alleles namely, i, I^A and I^B out of which any person has only two. In this allelic series, the alleles I^A and I^B each determines a unique antigen in the red blood cell, namely, antigen A and antigen B respectively. Allele i confers on a person inability to produce any antigen. Each of the alleles I^A and I^B is dominant to allele i but are co-dominant to one another such that the blood group AB is recognizable (see table below):

ABO Blood group system in Humans;

Blood group (Phenotype)	Genotype (Combination of alleles)	Antigen on red blood cell	Antibody in the blood serum
O	ii	None	A and B
A	I ^A I ^A or I ^A i	A	B
B	I ^B I ^B or I ^B i	B	A
AB	I ^A I ^B	A and B	None

This information has implication for blood transfusion in human beings and may also be useful in resolving disputed paternity.

Self-incompatibility in plants is also controlled by multiple alleles. This is the inability of a plant with functional female and male gametes to produce a zygote by self-pollination and it is an effective mechanism for promoting cross-pollination in some plant species. Self-incompatibility is based on the genotypic and phenotypic relationship between the female and male reproductive organs. Alleles in cells of the pistil determine its receptability to pollen. The phenotype of the pollen which is expressed as its inability to effect fertilization, may be determined by its own alleles (i.e. gametophytic incompatibility) or by alleles of its maternal parent (i.e. sporophytic incompatibility).

A male gamete is able to effect fertilization in a species with gametophytic incompatibility if the allele it possesses at the 'S' locus differs from both alleles of the pistil as in the figure below (Fig. 6).

Fig. 6: Gametophytic incompatibility controlled by multiple alleles in plants. (From Griffiths et al., 1996)

Kola nut trees (cola species) were found to exhibit sporophytic self-incompatibility with differential dominance relationship in the pistil and the pollen. Cola clones also show specific cross compatibilities on the basis of which field layouts could be designed to enhance

the yield of kolanut trees (Town, 1967; Jacob,1971; Jacob and Okoloko, 1974, Morakinyo et al., 1981).

Molecular nature of the gene and gene expression

The presence of Deoxyribonucleic Acid (DNA) in chromosome is revealed by the characteristic reddish-purple staining reaction that occurs with Schiff's reagent. This reaction by Feulgen (1912) is specific for DNA. Other stains are now known that stain chromosomes. When the nuclei of dividing cells are therefore subjected to the Feulgen's reaction, the chromosomes stain reddish-purple indicating the presence of DNA in them. Although chromosomes are made up of protein and DNA, only DNA has been shown to be the genetic material (Griffiths, 1928; Avery, Macleod and McCarty, 1944; Hershey and chase, 1952).

Using clues from x-ray diffraction data that were amassed by Franklin and Wilkins, Watson and Crick (1953) established that a DNA molecule is made up of two strands that form a double helix (Fig. 7a & b) each strand consisting of nucleotides as the building units. Each nucleotide consists of a nitrogen base, a deoxyribose sugar and a phosphate group (Fig. 7a & b).

(a)

Fig. 7, (a) DNA double helix unrolled to show the sugar-phosphate backbones and the base-pair runs

(b)

(b) A simplified DNA double helical structure

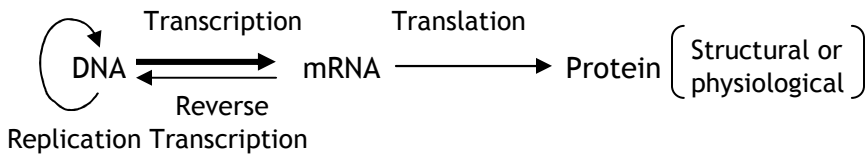
The Watson and Crick model of DNA suggests orderly replication of DNA, which is a prime requirement for genetic material.

Secondly, the molecular structure of DNA suggests that the sequence of nucleotides in DNA dictates the sequence of amino acids in proteins.

Thirdly, inherent in the DNA structure is the potential for gene mutation.

Fourthly, the structure of DNA (i.e. the chemical nature of the gene) makes possible DNA analysis and manipulation.

Genetic information in an organism is therefore stored in the double helix of DNA. The information is encoded in the sequence of bases along the DNA strands. The expression of this information begins with the transcription of the DNA base sequence from the template strand into a strand of mRNA. The mRNA is translated by each triplet of bases, a codon, coding for a particular amino acid (except the chain terminating codons) and specifying its incorporation into the growing polypeptide chain (growing protein molecule). There are the start (initiation) and terminating codons at the beginning and end respectively of each translation process in the mRNA. The protein thus made may be structural (in hairs, muscles or skin) or physiological (as a regulator of the body chemistry such as enzymes, haemoglobin or hormones). The replication, transcription and translation of the genetic information in DNA is summed up in the modified central dogma below:-



These processes of biological information storage, replication, transcription and translation are fundamentally similar in all living organisms because of the universality of the genetic code. The chemical nature and structure of the gene make these processes possible and form the basis for gene manipulation. The production of designer cells, tissues and whole organisms is now possible through recombinant DNA technology.

Genes and chromosomes

Mendel showed that genes are responsible for the appearance of characters in living organisms and although the process of meiosis during which haploid sex cells (gametes) are formed was unknown to him, his segregation and independent assortment of genes are parallel to and based on the separation during meiosis of members of each chromosome pair and the independent meiotic behaviour of different chromosome pairs. This parallel behaviour of genes and chromosomes led to the concept that genes are located on chromosomes which is the kernel of the chromosome theory of inheritance by Sutton and Boveri. It showed the role of chromosomes in heredity and firmly established the field of cytogenetics (Sutton, 1903). It was however, Morgan (1922) who experimentally demonstrated that chromosomes are indeed the vehicles of gene transmission from generation

to generation and that their behaviour at meiosis determines patterns of inheritance.

A chromosome is essentially one long DNA molecule and genes are functional regions of this DNA molecule. Each cell in a living organism has one or more sets of the basic DNA complement called the genome. The genome (represented by x) is made up of one or more extremely long molecules of DNA, which are packaged, one per chromosome. Genes are the functional regions of these DNA molecules and are therefore simply the active segments along chromosomes. The number of chromosomes in each cell of an organism may be equal to the basic chromosome number or a multiple of it. The basic chromosome number contains the basic DNA complement. The number, structure and behaviour of these chromosomes in an organism are important genetic considerations in the life of the organism and has been a subject of intensive research in plants.

Morakinyo and Adebola (1991), showed that the diploid chromosome number in Pennisetum americanum (the pearl millet) is 14, in P. purpureum (elephant or napier grass) is 28, with the basic chromosome number (x) equals 7 in both species. Thus in P. americanum, $2n=2x=14$ and in P. purpureum $2n=4x=28$ showing the latter to be a tetraploid (Fig. 8a-d).

(a)

(b)

(c)

(d)

Fig. 8: (a) Mitotic metaphase cell in Pennisetum americanum (2n=14); (b) Diakinesis in P. americanum showing the nucleolus and 7 II; (c), Mitotic metaphase in P. purpureum (2n=28) (d), Metaphase I in P. purpureum showing 14 II chromosomes in secondary quadrivalent associatoin.(From Morakinyo and Adebola, 1991)

On the basis of these chromosome numbers the pathway for the evolution of pearl millet and its wild relatives has been described and the prospect of further genetic improvement of millet and elephant grass as cereal crop and as fodder grass respectively through interspecific hybridization similar to the development of the hexaploid bread wheat, was shown (Hanna and Morison, 1980; Morakinyo and Adebola, 1991).

Morakinyo and Olorode (1988a) established through cytogenetic studies that guinea corn (Sorghum bicolor) is a segmental allotetraploid that evolved through interspecific hybridization and polyploidization on a basic chromosome number of five i.e. $2n=4x=20$ (Fig. 9 a-d).

(a)

(b)

Fig. 9: (a), Mitotic metaphase cell in Sorghum bicolor (2n=20); (b), Metephase I in S.bicolor showing 5 IV chromosomes. (From Morakinyo and Olorode, 1988a)

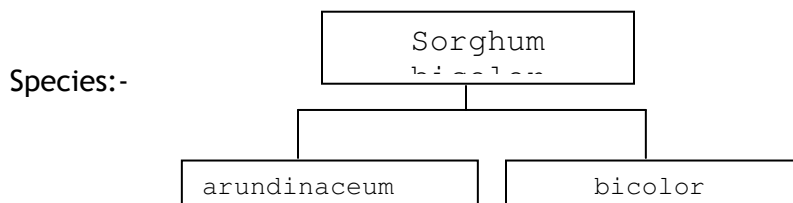
Cola nitida, C. acuminata, (the sources of kolanut) and C. milleni, “monkey kola”, were found to have the same chromosome number i.e. $2n=2x=20$. A cross between C. nitida and C. acuminata produced a viable but sterile interspecific hybrid while a cross between C. nitida and C. milleni produced a non-viable interspecific hybrid (Morakinyo and Olorode 1984, Morakinyo, 1995; 1996b). These results showed that there are effective barriers to gene exchange among the species of cola and these constitute impediments to cola improvement. A step towards removing these impediments through the rescue of the interspecific embryo in cola has recently been taken by the development of a protocol for the in-vitro growth of cola embryo (Adebola, 2003).

Genes in Germplasm

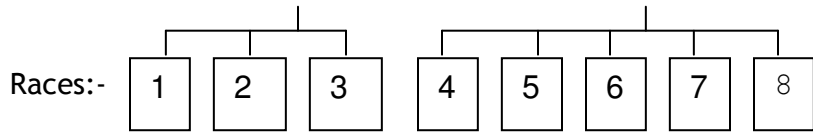
Mr. Vice-Chancellor Sir, the world is endowed with enormous genetic variability. This natural endowment is however being threatened by the wanton destruction of vegetation and wild life. By the destructive activities of man, genetic variability and the genes that bring it about are lost for ever. The different fauna and flora (animals and plants respectively) that make up the world biodiversity also constitute the world genetic resources. The conservation of these resources is vitally important for a stable biosphere and sustainable supply of human needs. Conservation of biodiversity and safety of the gene has therefore become a major pre-occupation of man on the planet earth.

It is in this connection that the International Board for Plant Genetic Resources (IBPGR) was created through an agreement between the Consultative Group on International Agricultural Research (CGIAR) and Food and Agricultural Organization (FAO), an agency of United Nations, leading to a major international effort in collecting, conserving and utilizing the germplasms of major economic plant species. Collection, characterization and conservation of germplasm is therefore a genetic imperative because landraces and wild relatives of cultivated plants, which are fast disappearing, are reservoirs of desirable genes for resistance or tolerance to certain biotic and abiotic stresses.

Morakinyo and Olorode (1988b) examined the germplasm collections of Sorghum species (guinea corn and its wild relatives) in Nigeria and showed that there is free exchange of genes among them in nature. On the basis of results of hybridization, cytology and electrophoresis, all sorghums in Nigeria were reclassified as members of the species Sorghum bicolor with two subspecies created within it, namely arundinaceum (for the wild sorghums) and bicolor (for the cultivated sorghums). Races were then identified within the subspecies (Fig. 10). The possibility of utilizing desirable genes in the wild sorghums for the development of new sorghum cultivars is thereby enhanced.



Sub species:-



1 = arundinaceum, 2 = lanceolatum, 3 = aethiopicum,
4 = colorans, 5 = durra, 6 = caudatum, 7 = roxburghii,
8 = bicolor

Fig. 10: The subspecies and races of Sorghum bicolor in Nigeria. (From Morakinyo and Olorode, 1988b)

The work cited above provides a glimpse into the store of plant genetic variability that is available to us in this part of the world, the custody of which we must keep for our present and future needs.

DNA Manipulation and Analysis

Mr. Vice-Chancellor Sir, Genetics has come a long way since the time of Mendel in 1865. The gene is now known to be a functional segment of DNA molecule. The gene can therefore be directly manipulated without going through the conventional breeding procedures of mating. The DNA molecule can be cut at specific sites using restriction endonucleases to get an array of segments, some of which represent genes that can be inserted and integrated into different genomes using the restriction enzymes, ligases and appropriate vectors. Thus restriction endonucleases are used as molecular scalpels to cut DNA in a precise and predictable manner while ligases are used to join cut ends of DNA together. Once integrated into the genome the DNA segment can express itself and give the appropriate phenotypic effect in the organism that receives the foreign DNA segment. These are the basic events in generating recombinant DNA and

the basic principles of recombinant DNA technology (genetic engineering). These basic steps are shown in Fig. 11.

Fig. 11: Basic technique of Recombinant DNA Technology. (From Ogden and Adams, 1989a)

A number of plants have been genetically transformed using recombinant DNA Technology. The process involved is the co-cultivation of the soil bacterium, Agrobacterium tumefaciens with plant tissue after the foreign DNA segment (gene) has been cloned in the T- DNA part of the tumour inducing plasmid, pTi, a plasmid that is naturally associated with Agrobacterium tumefaciens. The foreign DNA segment cloned into the vector can be from any source, man, animals, plants or bacteria. One particularly striking foreign DNA that has been inserted into a plant using T- DNA is the gene for the enzyme luciferase which was isolated from fireflies, flies that flash light at night ((Yor. Tanatana). The enzyme catalyzes the reaction of a chemical called luciferin with Adenosine Triphosphate (ATP) in fireflies and in the process emits light which makes the fireflies to glow in the dark. The gene for the luciferase enzyme has been transferred into the genome of tobacco plant where it is expressed to produce a transgenic tobacco plant that glows in the dark (just like the firefly), when the tobacco plant is watered with a solution of luciferin (the substrate). The glowing tobacco plant is transgenic, containing a gene from an animal, the firefly (Figs 12 and 13).

Fig. 13: The glowing transgenic tobacco plant containing the firefly's luciferase gene.

(From Ogden and Adams, 1989b)

Apart from the possible aesthetic effect of the luciferase gene such as producing glowing Christmas trees without electricity, it is also useful as a reporter gene to monitor the functions of other genes during development by emitting light in various tissues at different stages of development depending on the regulatory sequence of these other genes (Griffiths et al., 1996).

Recombinant DNA Technology provides the unique opportunity of directly transferring foreign genes such as genes for disease resistance, from plant germplasm collections (genebanks) to improved crop cultivars. The completion of the human genome project which now lays bare the functions of the genes that make up the human genome, has opened new ways of curing previously incurable genetic diseases by adding exogenous wild type genes to correct the defective function of mutations in the process of gene therapy.

Direct DNA manipulation and analysis hold great opportunities for important advances in Research, Medicare, Agricultural production, environmental protection and crime detection. The determination through DNA analysis of the real mother of the so called Nigerian wander baby who was stolen from her mother after birth somewhere in Lagos State in 1990s is still fresh in our minds. Restriction enzyme digests contain DNA fragments that produce DNA finger-prints which are unique to individuals and are therefore useful in forensic medicine. The DNA fingerprint is the autoradiographic

banding pattern produced when DNA is digested with restriction enzyme. In criminal investigations, blood stain, siemen stain or hair follicle cells can be used to prepare DNA fingerprints and the fingerprint pattern compared with those of suspects (Fig. 14). In Fig. 14, a comparison of the DNA fingerprint from the blood stain obtained at the site of a crime and the DNA fingerprints of the suspects proved suspect number three to be the culprit because all the bands in the DNA fingerprints of suspect number three are identical with all the bands in the DNA fingerprint from the bloodstain.

*Fig. 14: DNA fingerprint for crime detection.
(From Griffiths et al., 1996).*

DNA analysis has also been used in characterizing plant populations and determining identity of plants. Ajibade, Weeden and Morakinyo (1999) used inter simple sequence repeats (ISSR) of DNA to determine the identity of cowpea plants in advanced generations (F_5) of varietal crosses. In this study (which was carried out in Cornell, USA) AG repeats dinucleotide primers were found to be useful in detecting polymorphism in cowpea. Two of such primers UBC 811 and UBC 836 were used to differentiate between two parents of a cross and to see how differences in DNA fragments of the parents were expressed by their F_5 selected progenies. By the use of these ISSR markers, closely related cowpea lines were differentiated (Fig. 15a & b). Fig. 15a shows that Ife brown and TVu3067 were differentiated by a DNA

fragment length of about 900bp which is present in Ife brown but absent in TVu3067 and their F₅ selected progeny. Another faint band of about 1000bp was observed in TVu3067, but absent in Ife brown and the F₅ progeny.

Fig. 15b. shows a polymorphic DNA fragment at about 650bp which is present in TVu16006 and the F₅ select progeny but absent in IT84S-2246. Another band at about 380bp was also observed in TVu16006, but absent in IT84S-2246 and the selected F₅ progeny. This differentiation is important in characterizing plant populations and in cultivar development.

(a)

(b)

Fig. 15: (a), DNA profiles of Ife brown (lanes 1-5), TVU 3067 (lanes 5-10) and Ife brown XTVu 3067 (lanes 11-15) amplified by primer UBC 811 (100bp marker). (b) DNA profiles of IT 84S-2246 (lanes 1-5), Tvu 16006 (lanes 6-10) and IT 84S - 2246 X Tvu 16006 (lanes 11-15) amplified by primer UBC 836 (100 bp marker). (From Ajibade, Weeden and Morakinyo, 1999)

Conclusion

Mr. Vice-Chancellor Sir, Genetics has come a long way since the time of Gregor Mendel when genes

(hereditary factors) were appreciated as mere abstract entities whose existence was only in the minds of geneticists. Today, genes are known to be real as functional segments of DNA, a chemical compound of large molecular weight whose structure and mode of action have been thoroughly elucidated. We have shown in this lecture some aspects of plant and human lives in which genes play hide-and-seek game. In this hide-and-seek game of the gene, I have been an active participant in seeking out the genes involved in qualitative and quantitative inheritance in plants particularly crop plants and in the direct use of DNA as population markers. At the level of qualitative and quantitative inheritance we have looked at the genes in masticatory cola, guinea corn, okra, pepper, cowpea etc and at the molecular level we have used Inter Simple Sequence Repeats of DNA to differentiate cowpea genotypes.

The knowledge of these genes that we have gathered over the years either at the qualitative, quantitative or molecular levels is assisting in the improvement of these crop plants for better productivity.

If we know all the genes that exist today in all living things (and this is an obvious impossibility) the gene would still be in hiding because of the potential for change that is inherent in its very nature and our inadequate knowledge of the mechanism of gene expression. As the search for the existence and functions

of genes continues in our germplasm collections, through characterization, evaluation and genome projects, new alleles emerge (through mutations) whose functions or dysfunction are waiting to be found. In the meantime, these mutations create the raw material for selection (natural or artificial) and along with the environment mediate organic evolution or crop and animal improvement. The hide-and-seek game between man, gene and nature therefore continues.

Recommendations

1. Our theoretical understanding of molecular genetics in Nigeria is flawless, but our genetic research environment in terms of facilities is not much better than that of Mendel in the 19th Century and a far cry from what obtains elsewhere in the world. However, the opportunity to bridge this gap now exists with the emergence of computational biology (i.e. bioinformatics) which reduces emphasis on conventional laboratories and concentrates on access to and analysis of the databases of published gene and protein sequences. According to Bewaji (2003) “The advent of Bioinformatics has suddenly brought research at the cutting edge to a level playing field”. We can however, only take advantage of this level playing field if we embrace Bioinformatics. This is why I support Professor Bewaji’s advocacy of Bioinformatics Centre in this University that will be the nucleus of the Nigerian National Bioinformatics Institute.

2. Nigeria should be actively involved in the IBPGR coordinated plant germplasm collection and conservation efforts through persons, NGOs and governmental bodies. This will enable us take full advantage of world germplasm collections in our crop plant development efforts.
3. Afflicted persons who suffer various types of genetic disabilities and diseases should be statutorily cared for because they are bearing the brunt of our collective genetic load as a people. This will enable us take full advantage of their potentials which are often very strong in some aspects. In any case the terms “useful” and “useless” are relative terms depending on the prevailing environment. This is why in plant germplasm collections all types are important.
4. Parents should make the care of their children a priority by providing the conducive environment for their growth and development right from the womb to ensure that their genetic potentials are fully realized. This is necessary because many aspects of the human personality including intelligence are under quantitative genetic control and require the enabling environment for their full realization.

ACKNOWLEDGEMENTS

I wish to thank the Almighty God who has made this day possible. I also wish thank the following for their

contributions towards my achievements in life up-to-date.

- My paternal grandparents Mr. And Mrs. Idowu of blessed memory, who nurtured me in my early life and thought me the rudiments of responsible living.
- My parents, Elder James Morakinyo Idowu of blessed memory and Deaconess Deborah Olagbemijo Idowu who, despite their lack of formal school education, saw education as beacon of light and did all that was within their capacity to give me a functional formal education.
- My uncle Mr. Samuel Tunji Oke who was instrumental to my secondary school education and provided a home out of home for me and my siblings.
- My sister Mrs. S. A. Adedokun and brother, Mr. D. A. Morakinyo, for being there for me at all times.
- My teachers at various levels of education particularly, Professor Omotoye Olorode, who literally transferred his first class knowledge of Genetics and Plant Biology to me.
- My past and present students, particularly at the Postgraduate level, who have been sources of joy and fulfillment to me.
- The University of Ilorin for giving me the opportunity to prove my self by providing me with the environment for productive teaching and research.

- My Colleagues and friends particularly in the Department of Biological Sciences, University of Ilorin, with whom I have painstakingly but successfully traversed the difficult academic terrain.
- The staff of Postgraduate School for their moral support in the course of preparing this lecture particularly Mr. Nathaniel Pamdaya who did the computer production of the manuscript.
- My friends and relatives from far and near who have continued to believe in me and therefore make me believe in myself.
- Mr. Vice-Chancellor Sir, the month I had in mind for this inaugural lecture was June 2003 but August turned out to be the month available to me on the university inaugural lecture roster. This is fortuitous because the month of August happens to be the month for my silver jubilee wedding anniversary, so today as I give my Inaugural lecture, I also celebrate my silver jubilee wedding anniversary with my sweetheart and the love of my life Deaconess Dorcas Aderonke Morakinyo, and our beloved children Toluwalope, Oluwatosin, Oluwarogbayimika and Oluwagbemileke Morakinyo.

I thank you all for your patience and kind attention.

REFERENCES

Adebola, P. O. (2003). Genetic characterization and

Biosystematic studies in the Genus Cola Schott and Endlicher. A Ph.D. thesis for the University of Ilorin, Ilorin.

- Ajibade, S. R. and Morakinyo, J. A. (1999) Heritability and Correlation studies in cowpea. Nigerian Journal of Genetics 14: 29- 33.
- Ajibade, S. R. and Morakinyo, J. A. (2000) Pedigree selection in cowpea. Nigerian Journal of Botany 13:1 - 12
- Ajibade, S. R., Weeden, N. F. and Morakinyo, J. A. (1999) Identification of polymorphic inter simple sequence repeat primers (ISSRs) in cowpea. Nigerian Journal of Genetics 14 : 8 - 13.
- Ajibade, S. R., Weeden, N. F. and Chite, S.M. (2000). Inter-Simple Sequence Repeat Analysis of Genetic Relationships in the Genus Vigna. Euphytica 111:47-55.
- Aliero, A. A. and Morakinyo, J. A. (2001). Varietal Characterization of Digitaria exilis Stapf and D. iburua Stapf. Nigerian Journal of Genetics 16:10-21.
- Avery, O. T.; Macleod, C. M. and McCarty, M. (1944). Studies on the chemical nature of the substance inducing transformation of pneumococcal types. Induction of transformation by a deoxyribonucleic acid fraction isolated from pneumococcus Type II. J. Exp. Med. 79:137-158.

- Bewaji, C. O. (2003). The sickle cell membrane: Tip of the Iceberg. The 64th Inaugural lecture of the University of Ilorin.
- Cockran, W. G. and Cox, G. M. (1964). Experimental Designs. John Wiley & Sons. Inc. London pp 611.
- Comstock, R. E. and Robinson, H. F. (1948). The components of genetic variance in populations. Biometrics 4:254-26.
- Dudley, J. T. and Moll, R. H. (1969) Interpretation and use of estimates of heritability and genetic variances in plant breeding. Crop Science 9:257:262.
- Fillippone E. and Penza, R. (1992). Agrobacterium tumefaciens - mediated gene transfer. In. Biotechnology: Enhancing Research on Tropical Crops in Africa. Eds. Thottaphilly G.; Monti, L. M. Mohan Raj, D. R. and Moore, A. W. CTA/IITA Co-publication, IITA Ibadan.
- Griffith, F. (1928). Significance of pneumococcal types. J. Hygiene 27:113-159.
- Griffiths, A. J. F.; Miller, J. A.; Suzuki, D.T. Lewontin, R.C. and Gelbart, W. M. (1996). W. H. Freeman and Company, New York pp 916.
- Hershey, A. D. and Chase, M. (1952). Independent functions of viral protein and nucleic acid in growth of bacteriophage. J. Gen. Physiol 36:39-

56.

Jacob, V. J. 1971. Self-incompatibility in Cola nitida
CRIN Annual Report for 1969/70 pp 16-18.

Jacob, V. J. and Okoloko, G. (1974). Compatibility
studies in Cola nitida (Vent) Schott and Endl.
Ghana Journal of Science, 4(2):143-146.

Mather, K. and Jinks, J. L. (1971). Biometrical genetics
2nd edition. Chapman and Hall Ltd. London.

Morakinyo, J. A., N. E. Egbe and Y.A.O. Olaniran (1981)
Compatibility studies and yield components of
recent Cola nitida selections. Cafe cacao The
XXIV: 121-126

Morakinyo, J. A. And O. Olorode (1984). Cytogenetic
and Morphological studies on Cola nitida (vent.)
Schot & Endl. and C. acuminata X C. nitida F1
hybrid. Cafe Cacao The XXVIII: 251 - 256

Morakinyo, J. A. And Olorode (1988a). Cytogenetic
studies in Sorghum bicolor (L.) Moech. Cytologia
53: 653 - 658.

Morakinyo, J. A. And O. Olorode (1988b). Biosystematic
studies in the genus Sorghum (L.) Moech in
Nigeria. Ife Journal of Science. 3:29-38

Morakinyo, J. A. And P. O. Adebola (1991). Karyotype
analysis and meiotic chromosome behaviour in
Pennisetum americanum (L.) Leeke, P.

purpureum schum and P. pedicellatum Trim.
Nigerian Journal of Botany 4: 127 - 134.

Morakinyo, J. A. And C. O. Makinde (1991). Variability and heritability in some cultivars of Okra (Abelmoschus esculentus (L.) Moench. Nigerian Journal of botany. 4. 33 - 40

Morakinyo, J. A. And A. O. Awojobi (1991). Cytogenetics and Morphology of Digitaria exillis (Kipp) stapf, Digitaria horizontalis Wild and Digitaria leptorhachis Stapf. Nigerian Journal of Botany 4: 199 - 212

Morakinyo, J. A. And O. A. Falusi (1992). Chromosome behaviour in Capsicum annum L. , C. frutescens L. And Their Intra - And Interpsecific Hybrids. Nigerian Journal Of Botany 5: 135 - 143

Morakinyo, J. A. (1993). Inheritance of head and grain characters in Sorghum bicolor (L.) Moech. Nigerian Journal Of Pure and Applied Science 8: 245 - 252

Morakinyo, J. A (1995). Mitosis in Cola lepidota, Cola millenii and Sterculia tragacantha, Biosciences Research communications 7: (2) 147 - 150

Morakinyo, J. A (1996a). Heritabilities, correlation and expected responses to selection of some yield components in grain sorghum (Sorghum bicolor

(L.) Moech Nigeria Journal of Genetics (XI) 48 - 54

Morakinyo, J. A (1996b). Gene exchange between Cola millenii and Cola nitida: hybridization and hybrid seed viability., Biosciences Research communications 7: (2) 151- 153

Morakinyo, J. A (1997). Morphology and cytogenetics of Corchorus tridens Biosciences Research Communications (9): 9 - 13.

Morakinyo J. A. and A. O. Baderinwa. (1997) Karyotype analysis and meiotic chromosome behaviour in Corchorus olitorius, C. tridens and C. aestuans. Nigerian Journal of Genetics XII : 20 - 28

Morakinyo, J. A and A. Adekun (1997). Effect of gamma radiation on meiosis and pollen grain viability in Digitaria exilis. Nigeria Journal of Genetics (XII) 29 - 36

Morakinyo, J. A and S. R. Ajibade (1998a). Effect of Seasons and Genotype X Season interactions on vegetative and Yield Parameters of Cowpea (Vigna unguiculata (L.) Walp). Nigeria Journal of Science 32 : 21-25

Morakinyo, J. A and S. R. Ajibade (1998b). Characterization of the segregants of an

improved cowpea line IT84E - 124 - 6 . Nigeria Journal of Science 32 : 27-32

Morakinyo, J.A. 1998. Recombinant DNA Technology In: Genetics in the 90's ed. B.A. Ogunbodede and G. Olaoye published by Genetic Society of Nigeria.

Morakinyo J. A. (1999) Cytogenetic Research in Cereal Improvement in Nigeria. In: Genetics and Food Security in Nigeria in the Twenty first century. Ed: D. O. Ladipo and G. Olaoye Published by Genetic Society of Nigeria.

Obisesan, I. O. (1986). Genotype X Environment interaction and plant breeding. Paper presented at 13th Annual conference of the Genetic Society of Nigeria, FRIN, Ibadan.

Ogden, R. and Adams, D.A. (1989a). Recombinant DNA Technology: Basic Techniques. Carolina tips. 52(4):13-16.

Ogden, R. and Adams, D.A. (1989b). Recombinant DNA Technology: Applications. Carolina tips. 52(5):17-19.

Olakojo, S. A. And J. A. Morakinyo (1998) Morphological characterization of some cultivars of guinea corn (Sorghum bicolor L. Moench). Nigerian Journal of Genetics XIII: 13-18

Olorode, O. And J. A. Morakinyo (1980) Hybridization Studies in the Hyperrhenia involucrata - H. subplumosa (Gramineae) complex in Nigeria.

Cytologia 45: 189 - 196

Perrino, P. and Monti, L. M. (1991). Characterization and evaluation of Plant Germplasm: A problem of organization and collaboration. In. Crop Genetic Resources of Africa Vol. II - Proceedings of an international conference on Crop Genetic Resources of Africa eds: Ng. N.Q; Perrino, P; Attere, F. and Zedan, H. IITA, IBPGR, UNEP Publication.

Singh, R. K. and Chaudhary, B.D. (1977) Biometrical Methods in Quantitative Genetic Analysis. Kalyani Publishers, New Delhi, India.

Stickberger, M. W. (1976). Genetics. Macmillian Publishing Co., Inc. New York pp 914.

Sutton, W. S. (1903) Biol. Bull. 4:231-251.

Town, P. A. (1967). Studies on the fruitfulness in Cola nitida M. Phil. Thesis, University of Reading.

Watson, J. D. and Crick, F. H. C. (1953) A structure for deoxyribose nucleic acid. Nature 171:737-738.