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INHERITANCE PATTERN OF YELLOW FOLIAGE COLOUR AND ACTIVITIES OF TRANSPOSABLE ELEMENT IN COWPEA *Vigna unguiculata* (L.) Walp

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ABSTRACT

Foliage colour may affect the photosynthetic activities of a plant and consequently yield. Differences in the green foliage colour of plants often reflect differences in chlorophyll concentration of the leaves. This study investigated the inheritance pattern of a yellow foliage mutant in cowpea. Seeds of a nuclear yellow foliage mutant and three green foliage cowpea lines were planted in plastic buckets filled with garden soil on the roof top garden of Department of crop Protection and Environmental Biology, University of Ibadan, Nigeria and crossed to produce six generations per cross comprising parents, F_1, F_2 and BC. The various generations were and on the field at the Teaching and Research Farm of the University of Ibadan, Nigeria and data were collected on phenotypic traits. The nuclear yellow foliage mutant segregated in the ratio 3green:1yellow, thus indicating that the trait was controlled by monogenic recessive gene. Some F_2 and BC plants of the yellow foliage mutant exhibited variegation for leaf colour indicating gene instability resulting from the action of transposable element. The frequencies of reversion from the yellow to green of F_3 progenies vary widely within and between progeny rows. Of a total of 309 individual plants that were scored, 55% were variegated, 23% were green while 22% exhibited the yellow phenotype. The gene symbol *yfc-3* was assigned to the recessive condition, while *yfc-3*^{un} was assigned to the unstable allele of yellow foliage.

Keywords: Cowpea, Yellow foliage, Transposable element, Mutation, and Instability

INTRODUCTION

Heritable changes in foliage colour may affect the photosynthetic activities of a plant and consequently its economic yield. Differences in the green foliage colour of plants often reflect differences in chlorophyll concentration of the leaves. Loomis and William 1963; Palmer *et al*., 2000 reported that the main function of chlorophyll in photosynthesis is to absorb radiant energy from the sun. Therefore chlorophyll concentration of the leaf is one of the factors that determine the photosynthetic capacity of the plant. Nelson, (1967) observed that chlorophyll deficient mutants result from blocks in either the pathway of chlorophyll synthesis or of the synthesis of accessory pigments. Pale green foliage was reported to be monogenically recessive to normal green (Saunders, 1960; Lightbourn *et al*., 2008). Kolhe (1970) however reported that foliage colour in cowpea was controlled by two complementary genes and that light green foliage was dominant to dark green foliage. In contrast, Fawole (2003) reported four chlorophyll deficient mutants controlled by single recessive genes that were neither allelic nor linked.

Transposable elements (TEs) are discrete segments of DNA that rapidly move around the genome sometimes causing a change in DNA function when they insert themselves into a new chromosomal location (McClintock, 1956; Kolade *et al*., 2012). They were originally described as controlling elements in maize due to their ability to modify or control the pattern of gene expression (McClintock, 1951).

The release of a transposable element in an organism had been related to stress or a shock effect within the genome (McClintock, 1953; Kolade *et al*., 2012). Transposable elements (TEs) can be found in virtually all living organisms. A unique and remarkable feature of transposable elements is the insertion and excision activities of these elements in the genome. The presence of these elements in living organisms is a major cause of unusually high mutation frequency leading to instability in gene expression (McClintock, 1951; 1956; Peterson, 1986; Xu and Palmer, 2008). The insertion of a TE at a locus may inhibit the expression of that gene and confer on it the property of high mutability, while the excision of the element from the locus restores the activity of the gene. Reintegration of the element at another locus however may suppress gene action at that locus and cause mutation (McClintock, 1956, Fedoroff, 1983; Nevers *et al*., 1986).

The unstable expression and consequent reversion of the organism to the wild-type may occur in the somatic or germinal tissue, and may consequently lead to distorted Mendelian ratio in crosses involving a mutable allele (Nevers *et al*., 1986; Fawole, 2001b). A gene influenced by a transposable element remains stable until a regulatory element is introduced via crossing (McClintock, 1956; Peterson, 1986). In autonomous or one-element systems, the TEs transpose regardless of the genetic background, due to the fact that control of instability resides at the locus and does not require a second factor. However, in two-element or non-autonomous systems, the element that suppresses gene action, called the operator, (McClintock, 1956) or receptor (Fincham and Sastry, 1974) is itself controlled by another element known as the regulatory element, located elsewhere in the genome. In such cases, mutability occurs only when a regulatory element is introduced into the system by crossing. Transposable elements were first genetically characterized in maize (McClintock, 1951; 1953; 1956; and Peterson, 1986) and later reported in many organisms including, *Pisum sativa* (Vershinin *et al*., 2003; Lee *et al*., 2005); *Circer arietinum* (Stagginus *et al*, 2001); *Oryza sativa* (He *et al*., 2000); *Antirrhinm majus* (Delool and Tilney-Bassett, 1986). In leguminous species mutations attributable to the action of TEs have been reported in *Gylcine max* (Peterson and Weber, 1969; Palmer *et al*., 2000); *Phaseolus vulgaris* (Garber *et al*., 1999), and *Vigna unguiculata* (Kolade *et al*., 2012; Oluwatosin, 1997).

In order to utilize both nuclear mutants effectively in crop improvement, a thorough understanding of their inheritance pattern is necessary. The objective of this study therefore, was to; determine the inheritance pattern of a yellow foliage mutant of cowpea.

MATERIALS AND METHODS

The yellow foliage mutant arose spontaneously in a field planting of the cowpea cultivar, Ife-Brown. Ife-Brown is an early maturing, semi-upright and day length neutral cowpea cultivar with good pod productivity. Normal plants of Ife-Brown subtend an average of 4 semi-erect branches on the main stem. The leaves are alternate, stipulate and trifoliolate. Flowers are arranged on distal ends of unbranched peduncles, which arise in leaf axils. The flowers are borne on alternate pairs and although many pairs may occur per inflorescence, only three or four flowers develop into mature pods. Plants of the yellow mutant have similar morphological characteristics to Ife-Brown except for the foliage colour. Ife-Brown foliage is characteristically green, but the mutant leaves posses a peculiar yellow colouration that appears as fine speckles distributed evenly over the entire leaf surface (Figure 1). The mutant bred true for the yellow colour phenotype. Inheritance study of the yellow foliage colour mutant was conducted in crosses between normal lines (green foliage colour) and the mutant (yellow foliage colour), at the rooftop garden of Department of Crop Protection and Environmental Biology in plastic buckets filled with garden soil. The inheritance study of the yellow foliage mutant was carried out with the following lines:

G10603 x IF-BR-Y-2
Ife-BPC x IF-BR-Y-2
IBS 4474 (Septa) x IF-BR-Y-2

F_1 and reciprocal F1 seeds were easily obtained in crosses involving the yellow mutant and the normal green foliage lines. Backcrosses to both parents were also produced for each of the crosses. Six families viz: P_1, P_2, F_1, BC_1, BC_2 and F_2 were produced for each cross. Crosses involving normal and yellow foliage lines were evaluated at the Teaching and Research Farm, University of Ibadan, Ibadan, Nigeria. Field plantings were made on 4m rows at spacing of 60cm between rows and 30cm within the rows. The weeding was carried out at 2 weeks, 4 weeks and 6 weeks after planting, while spraying to control insect pest was achieved using Cyperforce 40EC at the rate of 500g ai/ha. The number of rows planted to each generation was determined by seed availability. The plants were scored for the qualitative traits of interest at the appropriate stages of plant development. Data were collected on the following qualitative traits; leaf colour (green vs yellow), stem pigmentation (pigmented vs non-pigmented), peduncle type (branched peduncle vs normal peduncle). Data on qualitative traits were classified into distinct phenotypic classes and tested for goodness-of-fit to appropriate genetic ratios using the Chi-square test.

Figure 1: Plants of Ife Brown yellow-2 (IF-BR- Y- 2) a foliage colour mutant derived from the cowpea cultivar Ife-Brown

Allelism Test

IF-BR-Y-2 and two previously described yellow foliage mutants, designated Solojo-3-Yellow (IB-Y-1), Yellow coiled (IB-Y-2) according to Fawole (2003) were crossed in all possible combinations. The resulting F1 seeds were planted on the Teaching and Research Farm of the University of Ibadan, Nigeria. Individual F1 plants were scored for foliage colour at the onset of flowering.

Linkage Analysis

For all categories of two-factor joint segregation ratios, contingency Chi-square was used to test for linkage. If the calculated Chi-square was greater than the tabulated, then linkage was indicated between the two traits. After detecting linkage by test of independence, linkage intensities were calculated using F_2 data. A computer programme, Linkage-1 was used to calculate recombination fractions and map distances (Suiter *et al*., 1983). However, this was possible only in cases where the F_2 single-factor segregation for each character fitted the monogenic inheritance model. Where epistasis is involved in one of the traits, the recombination fraction and map distances can not be determined for the F_2 generation (Kehinde *et al*., 1997).

RESULTS

Inheritance of yellow foliage colour

Data on the inheritance of yellow leaf colour in three cowpea crosses are shown in Table 1. The leaves of all plants of the normal parent were green, while leaves of plants of the mutant parent were yellow in colour (Figure 1). Leaves of F_1 and reciprocal F_1 plants were green in colour indicating that neither maternal nor cytoplasmic factors were involved in the control of leaf colour in these crosses. The progeny of backcrosses to the green parents were also green in colour. Thus the F_1 and the backcross to the green parent data suggest that the gene controlling the expression of foliage colour is completely dominant to that controlling the expression of yellow foliage colour. In the two crosses, data on the backcross to the yellow mutant gave a good fit to the 1 green: 1 yellow ratio. The F_2 plants segregated for three different phenotypes, namely, green, variegated and yellow. When the data were tested for a goodness-of-fit to the 1 green: 2 variegated: 1yellow genetic ratio, there was a highly significant deviation from this tested ratio. However, when the data on the variegated and yellow plants were combined into a phenotypic class and tested for goodness-of-fit to the 3 green: 1 yellow monohybrid ratio, a good-fit was obtained. For the cross G10603 x IF-BR-Y-2, however, data on the backcross to the mutant parent and the F_2 deviated significantly from the 1:1 and 3:1 segregation ratios respectively.

Instability at the yellow leaf locus

Seeds obtained from the variegated plants of the F_2 generation of the different crosses were advanced to the F_3 generation. Four different phenotypes namely, green, slightly variegated, highly variegated and yellow were observed in the F_3 progenies. Variegation appears to result from reversion of the recessive yellow condition to the wild-type. The frequencies of reversion from the yellow to green vary widely within and between progeny rows. Of a total of 309 individual plants that were scored for foliage colour, 55% were variegated, 23% were green while 22% exhibited the yellow phenotype (Table 2).

Table 1: Inheritance of yellow leaf colour in three cowpea crosses

Cross and generation	No. of plants/class						
IBS 4474 x IF-BR-Y-2	Green	Varie-gated	Yel-low	Total	Ex-pected ratio	X2	P
IBS 4474(Septa) P_1	56	-	-	56			
IF-BR-Y-2 (P_2)	-	-	62	62			
F_1	50	-	-	50			
BC_1	70	-	-	70			
BC_2	56	19	31	106	1:1	0.34	0.70-0.50
F_2	865	124	188	1177	1:2:1	266.79	>0.005
F_2 (pooled)	865	124	188	1177	3:1	1.43	0.30-0.20
IF-BPC x IF-BR-Y-2							
IF-BPC (P_1)	50	-	-	50			
IF-BR-Y-2 (P_2)	-	-	46	46			
F_1	93	-	-	93			
BC_1	32	-	-	32			
BC_2	30	4	42	76	1:1	3.37	0.10-0.05
F_2	567	18	162	747	1:2:1	256.54	>0.005
F_2 (pooled)	567	18	162	747	3:1	0.21	0.70-0.50
G10603 x IF-BR-Y-2							
G10603 (P_1)	65	-	-	65			
IF-BR-Y-2 (P_2)	-	-	62	62			
F_1	48	-	-	48			
BC_1	169	-	-	169			
BC_2	126	47	42	215	1:1	6.37	0.01-0.001
F_2	1006	101	182	1289	1:2:1	415.72	>0.005
F_2 (pooled)	1006	101	182	1289	3:1	6.37	0.01-0.001

Table 2: Percentage of plants in different classes of F_3 progeny rows following reversion of F_2 variegated plants

S/No	Green (%)	Slightly variegated (%)	Highly variegated (%)	Yellow (%)	No. of plants
1	21.05	52.63	10.53	15.79	19
2	-	84.62	7.69	7.69	13
3	52.94	5.88	41.18	-	17
4	32.00	28.00	28.00	12.00	25
5	-	75.00	-	25.00	24
6	16.67	-	33.33	50.00	06
7	70.00	20.00	-	10.00	10
8	40.00	10.00	40.00	10.00	10
9	-	15.38	-	84.62	13
10	-	57.14	28.57	14.29	14
11	11.11	22.22	11.11	55.56	09
12	41.94	9.68	35.48	12.90	31
13	32.00	28.00	28.00	12.00	25
14	12.50	56.25	12.50	18.75	32
15	31.04	24.48	24.14	10.35	29
16	12.50	25.00	12.50	50.00	32
Total	23.30 %	34.95 %	19.74 %	22.01 %	309

Allelic relationship between three foliage colour genes in cowpea

Results of all cross combinations among the three yellow foliage mutants show that all the 48 F_1 progeny of the cross Solojo-3 Yellow x Ife- Brown Yellow-2 and the 60 F_1 progeny of the cross Yellow colied x Ife-Brown Yellow-2 were all green. Similarly, 34 F_1 plants produced from the cross Solojo-3 Yellow x Yellow coiled were green. Thus, the genes controlling each of the three mutants were non-allelic.

Linkage tests of F_2 generation in three cowpea crosses

Linkage analyses of four different genes were done using Linkage-1 a computer programme for the detection and analysis of genetic linkage. The results, presented in Table 3, showed that of the two linkage tests between gene pairs, suggested independence. The gene *Yfc* showed independence with respect to the gene *Bp* with a map distance of 122.47cM and recombination frequency of 49.26%, while map distance of 64.59cM and recombination frequency of 42.98% was recorded for the gene *Pg.*

Table 3: Linkage tests of the F_2 generation of cross involving two cowpea mutants for foliage colour

Alleles				No. of plant/class							
				a	b	c	d	Total	$\chi2$ Linkage	Recombination (%) ±S.E	Map distance (cM) ± S.E
Yfc-3	Yfc-3	Pg	Pg	589	417	111	172	1289	33.24	42.98±0.02	64.59±2.25
Yfc-3	Yfc-3	Bp	Bp	429	138	138	42	747	0.08	49.26±0.03	122.47±2.77

DISCUSSION

In contrast to the cytoplasmic yellow foliage mutant, the IF-BR-Y-2 arose spontaneously from the mutation of a nuclear gene in the cultivar Ife Brown. Neither maternal nor cytoplasmic factors were involved in the expression of this yellow foliage phenotype. Inheritance data obtained from crosses between normal green and the yellow foliage mutant showed that the trait is controlled by a single homozygous recessive gene. However, the recessive gene exhibited unstable expression in some plants of the F_2 and backcross generations. Instability is characterized by reversion from a stable yellow condition to the wild-type phenotype. The frequencies of reversion from the yellow to the green foliage colour vary widely within and between progeny rows resulting in various degrees of variegation in the plants.

Several authors have reported on the inheritance of mutations resulting in chlorophyll deficiency in cowpea. Saunders (1960) and Kirchhoff *et al*. (1989) concluded that chlorophyll deficiency in their mutant cowpea lines was controlled by single recessive genes. Sen and Bhowal (1961) proposed that an allelic series for dark green, green and yellow green pod colours condition similar colours in the leaf, calyx and dorsal surface of the standard petal respectively but the pattern of inheritance of chlorophyll deficiency in the leaf was not indicated. However, Kolhe (1970) observed that foliage colour in cowpea was controlled by two complementary genes. In contrast, Fawole (2003) studied the inheritance patterns of four foliage colour mutants consisting of two yellow and two variegated phenotypes, and showed that they were each controlled by single recessive genes that were neither allelic nor linked. The gene controlling the yellow foliage phenotype reported in this study is nonallelic to the two yellow foliage mutants reported earlier by Fawole (2003).

The unstable behaviour of the recessive gene controlling the yellow foliage phenotype of IF-BR-Y-2 affected the segregation ratio of some generations in the crosses. In two crosses, the backcross to the recessive yellow parent gave a good fit to the expected 1green: 1yellow ratio while the F_2 generation deviated significantly from the 1green: 2variegated: 1yellow expected on the basis of incomplete dominance of green over yellow. However, when yellow and variegated F_2 plants were combined into a single phenotypic class, the expected 3green: 1yellow goodness-of-fit was obtained. In the third cross, data on the backcross to the recessive parent and the F_2 generation deviated significantly from all expected monohybrid ratios. This deviation probably resulted from the reversion of some yellow plants from the recessive mutant condition to the wild-type (green) phenotype.

Instability of gene expression in living organisms is often caused by transposable elements. A prominent feature of most unstable genes is their reversion to a phenotypically wild-type condition in somatic and/or germinal tissue (McClintock, 1956; Lightbourn *et al.* (2008). The degree of variegation of a mutable organism depends on whether reversion occurs early or later in development. Frequent reversions to wild-type in germinal tissue will result in distorted Mendelian ratio in crosses involving a mutable allele. Wild-type or near wild-type individuals may occur in the progeny of variegated plants or an excess of wild-type individuals may be observed (Nevers *et al*., 1986; Xu and Palmer, 2006). The behaviour of the backcross and F2 generations of the crosses involving the yellow foliage mutant IF-BR-Y-2 strongly indicates that the mutant gene controlling the yellow phenotype is mutable and capable of frequent reversions to the wild-type condition.

The inheritance data obtained from crosses involving normal green and the yellow foliage mutant suggested the presence of transposable elements in the expression of the yellow phenotype. Two systems of transposable elements have been identified in higher plants. In one-element or autonomous systems, the control of instability resides at the locus and does not require a second factor. However, in non-autonomous two-element systems, the gene influenced by the transposable elements remains stable until a regulatory element is introduced into the system by crossing (McClintock, 1953; 1956). The transposable element present in the yellow foliage mutant reported here is probably the one-element type capable of autonomous transposition.

Transposable elements were first genetically characterized in maize (McClintock, 1951; 1953; 1956; Peterson, 1986) but their widespread occurrence in many plant species has been documented. Comprehensive reviews of maize and cowpea transposable elements were given by Finchan and Sastry, 1974; Fedoroff, 1983; Porbeni, J.B. and I. Fawole, 2009; and Kolade *et al*. (2012). Nevers *et al*. (1986) included in their review a list of plant species in which the presence of transposable elements has been reported. An update list of other plant species can be found in (Galum, 2003). Gene instability attributable to the activity of transposable elements has been found in some leguminous species such as *Glycine max* (Peterson and Weber, 1969; Groose *et. al*. 1988); *Phaseolus vulgaris* (Coyne, 1966), Alfalfa (Talbert and Bingham, 1989). In cowpea, a two-element system of transposable elements affecting many genes has been reported (Fawole, 1988; 2001a; Porbeni, J.B. and I. Fawole, 2009. The transposable element affecting the expression of the yellow foliage mutant reported in this study is a one-element system and the first to be reported in cowpea.

Allelic tests showed that the new yellow foliage mutant is nonallelic to the yellow foliage mutants described by Fawole (2003), therefore the symbol *yfc-3* is assigned to the stable recessive gene controlling yellow foliage colour in the mutant IF-BR-Y-2. Thus, the genotypes *YFc-3 YfC-3 YFC-3* give normal green colour while the genotype *yFc-3 yFC-3* determines yellow foliage colour. The symbol *yfc-3*^{un} is proposed for the unstable allele for yellow foliage colour.

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