

**Development of Drought Tolerant Groundnut (*Arachis hypogaea* L.)
Genotypes with Better Agronomic and Seed Physical Quality traits in
Uganda**

By

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**A thesis submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy (Plant Breeding)**

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March 2018

THESIS ABSTRACT

Groundnut production in Uganda is rain-fed. As such, drought is a major challenge, especially when it occurs in combination with biotic stresses such as groundnut rosette virus disease. The objectives of this study were; (1) to assess smallholder farmers' perceptions of drought in groundnut production, (2) to determine farmers' varietal selection criteria in groundnut, (3) to assess genetic diversity of the Ugandan groundnut collection, and (4) to determine combining ability and gene action controlling drought tolerance traits and physical quality traits under different water regimes, thereby identifying promising parents and crosses for cultivar development. A participatory rural appraisal revealed that groundnut was grown mainly by smallholder farmers under both mono and mixed cropping systems depending on the region. Most of the farmers (>77%) from all regions indicated that the major impact of drought on their farming activity was low yields. The participatory variety selection study showed that farmers have effective methods for selecting varieties based on preferred traits. However, the farmers' selection methods need to be complemented by breeder methods. Results of genetic diversity studies showed that 50% of the 2986 SNPs were polymorphic with a mean PIC of 0.15 for all populations combined, implying low allelic diversity in the groundnut collection. A high level of genetic relatedness was observed at population level, as individuals from all assigned populations aggregated into three clusters based on dissimilarity analysis under principal component analysis (PCA). However, a high level of genetic differentiation existed within individuals rather than among populations based on analysis of molecular variance (AMOVA) and cluster analysis. Based on structure analysis, three gene clusters were found underlying genepools for the groundnut populations used in this study.

The study on genetic analysis for drought tolerance traits revealed that both additive and non-additive gene actions controlled the inheritance of the traits in groundnut. The general combining ability effects (GCA) were more important than the specific combining ability (SCA) for the SPAD chlorophyll meter readings (SCMR) and harvest index (HI). This observation was similar under both drought stressed and non-drought stressed environments and for all the groundnut botanical types. The SCA effects for traits such as drought tolerance index based on pod yield, and biomass were significant. Given such unlikely predominance for either additive or non-additive gene effects, the breeding procedure would require selection to be conducted in the later generations in order to harness both gene effects. In addition, significant associations between drought stressed and non-drought stressed environments were observed for SCMR, harvest index, pod yield, number of pods, leaf length, and leaf width. Therefore, since SCMR and HI are relatively stable and less influenced by environmental conditions, they can thus be measured under both drought stressed and non-drought stressed conditions. However, selection based on these traits can be done more effectively under non-drought

stressed environment. In addition, the best breeding approach would be the one that emphasizes additive gene action such as recurrent selection or simple selection by pedigree breeding.

The study on gene action governing physical quality traits showed the significance of GCA, SCA and maternal effects for various traits. The genetic analysis indicated that expression of the majority of the physical quality traits was regulated by additive gene action suggesting possibility of early generation selection, while non-additive gene action also played an equally important role in the control of the physical seed traits. However, the gene control varied with botanical varieties for some traits. Among the Virginia botanical variety types, non-additive gene action was predominant for all the traits regardless of the test environment implying that botanical classification has a bearing on the parental selection in improving these traits in this subgroup of groundnuts. In cases where both additive as well as non-additive gene effects controlled the expression of the traits, the breeding strategy has to delay selection to later generations or should involve recurrent selection that favours both additive and non-additive gene action. Significant maternal effects for some traits signify the role of the maternal parent in the expression of quality traits and importance of parental selection in quality breeding. Therefore, one of the parents to be used in hybridization should have large pods and seeds for obtaining better segregants. Low but positive or negative association of drought tolerant traits with physical quality traits, regardless of stress regime, can be exploited for improving seed yield without compromising seed size. Thus, the selection of high pod yield potential under no-stress or small reduction in pod yield under drought stress should guarantee high seed size.

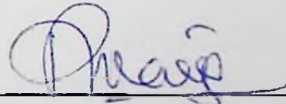
Overall, this study has highlighted the mismatch between the release of new varieties and adoption rates despite the fact that farmers are aware of the new improved materials. Therefore, there is a need for various stakeholders to strengthen their role in the transfer of research outputs to end users (farmers). Among the key recommendations, breeders, extension staff and farmers need to work together to make the technology that has been developed to have relevancy. This study also confirmed that the groundnut genepool in Uganda has a low genetic base. However, from the information obtained from the study, future hybridizations avoiding parents sharing a common ancestry can be done or diversity can be improved by enriching the collection with some introductions from geographically different areas. Identification of genotypes with drought tolerance and/or physical quality traits helps in the quest to develop new varieties, which are well adapted, and with farmer preferred traits. The observation that additive gene effects are involved in governing drought and physical traits, besides, positive correlations between these traits indicates that drought tolerant materials can be improved by accumulating additive genes using methods that favour general combining ability such as recurrent selection breeding procedures. Where possible, molecular techniques such as genomic selection can be applied to shorten the entire process.

Declaration

I, **Ronald Kakeeto**, declare that:

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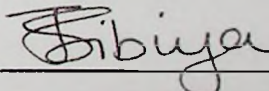
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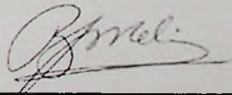
As the candidate's supervisors, we agree to the submission of this thesis:

Signed _____



Dr. Julia Sibiya (Supervisor)

Signed _____



Prof. Rob Melis (Co-supervisor)

Acknowledgements

I am very grateful to my supervisors Dr. Julia Sibiya and Prof. Rob Melis for their counsel, academic input and encouragement right through the research and final thesis write-up. I also thank Dr. Moses Biruma (in-country supervisor) and Dr. Theresa Fulton for their input with regard to molecular biology aspects of the research. Special thanks go to entire ACCI staff, particularly Prof. Mark Laing, Mrs. Lesley Brown, and Mrs. Rowelda Donnelly for their facilitation that enabled successful completion of the study. Institutional facilitation by; National Semi Arid Resources Research Institute (NaSARRI) and Bulindi Zonal Agricultural Research and Development Institute (BUZARDI), funding support from the Alliance for a Green Revolution in Africa (AGRA), Japan International Cooperation Agency (JICA) for providing the drought phenotyping equipment, ICRISAT – Malawi, National Groundnut Improvement Project of Uganda and farmers for providing the germplasm for the study.

My sincere thanks go to Dr. Wellington Ekaya, Dr. Nasser Yao, Mr. Vincent Njunge, and Ms. Blessing Adanta Nwokocha and the entire staff of Biosciences east and central Africa-International Livestock Research Institute (BeCA-ILRI) Hub for their financial, technical support and guidance during my molecular studies.

The diligent contributions by Julius Kaheru, Robert Subire, Beatrice Apenyo, Hellen Asekenye and Josephat Musinguzi in ensuring a successful running of the trials, especially assisting in conducting of groundnut crosses, and field maintenance, are greatly acknowledged.

Special thanks also go to my groundnut farmers David Byaruhanga, Ronald Tekereza, James Kyamanywa, Martin Nek and Stephen Imalingati for providing land, and who besides many other engagements, took time looking after my trials at no cost and were a great encouragement to me during the study.

To the ACCI 2014 cohort; Maurice, Eduardo, Prosy, Lydia, Solomon, Filson, Eluid, Damien and Emmanuel, it was wonderful to have you as friends and colleagues.

I am deeply indebted to my beloved wife Jessica, children, Arianna and Remi for their commitment, support, love, and patience they embraced through the study period.

Lastly, I thank the Almighty God for his grace, mercy and protection that kept me going throughout this period.

Dedication

To my wife Jessica and our children, Arianna and Remigius

Table of Contents

THESIS ABSTRACT	ii
Declaration	iv
Acknowledgements	v
Dedication	vi
TABLE OF CONTENTS	vii
LIST OF TABLES	xiii
LIST OF FIGURES	xviii
Introduction to Thesis	1
1. Importance of groundnuts	1
2. Production constraints	2
2.1. Socio-economic constraints	2
2.2. Biotic constraints	3
2.3. Abiotic constraints	4
3. Groundnut seed quality	4
4. Farmer preferences of groundnut varieties	5
5. Breeding for drought tolerance and grain physical quality	5
6. Problem statement	7
7. Overall goal	8
8. Specific objectives	8
9. Outline of Thesis	9
CHAPTER 1 Literature Review	14
1.1 Introduction	14
1.2 Taxonomy of groundnut	14
1.3 Cultivar development strategies in groundnut	16
1.3.1 Broadening the genetic bases	16
1.3.2 Selection for potential parents	16

1.3.3	Selection based on combining ability effects.....	17
1.3.4	Genetic diversity assessment	17
1.4	Drought tolerance in groundnuts	19
1.4.1	Physiological implications of drought on groundnuts.....	19
1.4.2	Genotypic variability for drought tolerance in groundnut.....	21
1.4.3	Mode of gene action for inheritance of drought tolerance traits	22
1.5	Associations among drought tolerance traits of groundnuts	23
1.6	Association between drought tolerance traits and agronomic traits	24
1.6.1	Breeding for drought tolerance.....	26
1.6.2	Empirical selection approach	26
1.6.3	Physiological selection approach for drought in groundnuts.....	26
1.6.4	DNA marker-assisted selection for drought in groundnuts	27
1.7	Use of early maturity as a selection strategy for drought resistance in groundnuts.....	28
1.7.1	Phenotyping for early maturity in groundnut.....	29
1.8	Groundnut grain quality.....	29
1.9	Variation for grain quality traits and its sources	30
1.9.1	Mode of gene action for grain physical quality traits in groundnut	31
1.9.2	Relationship between physical grain traits and drought tolerance traits	31
1.10	Implications of diseases and insect pests on breeding groundnuts for drought tolerance	32
1.11	Farmers' preferences for groundnut variety adoption	33
1.12	Summary literature review.....	34
CHAPTER 2	Farmer perception of drought, other production constraints and production system, their implication for groundnut breeding in Uganda	55
2.1	Introduction	56
2.2	Materials and methods.....	57
2.2.1	Study areas and their characteristics	57

2.2.2	Sampling procedures, participants and data collection	59
2.2.3	Focus group discussions and survey	59
2.2.4	Survey	59
2.3	Data analysis	61
2.4	Results.....	61
2.4.1	General crop production systems	61
2.4.2	Groundnut production constraints	67
2.4.3	Farmers' perception of drought.....	67
2.5	Discussion	76
2.6	Conclusion	78
CHAPTER 3	Participatory varietal selection criteria for groundnut varieties in selected regions of Uganda.....	83
3.1	Introduction	84
3.2	Materials and methods.....	85
3.2.1	Study sites and their characteristics.....	85
3.2.2	Germplasm collection	86
3.2.3	On-farm evaluation of putative parental varieties	87
3.2.4	Breeder's evaluation of agronomic and morphological traits	88
3.2.5	Data analysis	89
3.3	Results.....	90
3.3.1	Preferred traits of groundnuts	90
3.3.2	Farmers' indigenous variety evaluation technical knowledge (ITK)	91
3.3.3	Breeders' evaluation	92
3.3.4	Farmers' decentralised varietal evaluation	94
3.3.5	Farmers' selection criteria and index.....	96
3.4	Discussion	98
3.5	Conclusion	100

CHAPTER 4	Genome wide SNP diversity and population structure in a Ugandan groundnut (<i>Arachis hypogaea</i> L.) collection	115
4.1	Introduction	116
4.2	Materials and methods.....	117
4.2.1	Genotypes	117
4.2.2	Genotypic characterisation	118
4.2.3	Genotyping and marker analysis.....	119
4.3	Data analysis	120
4.3.1	Population genetic diversity and differentiation	120
4.3.2	Analysis of molecular variance (AMOVA)	120
4.3.3	Phylogenetic and population structure analysis	120
4.4	Results.....	121
4.4.1	Population genetic diversity and SNP Polymorphism.....	121
4.4.2	Genetic differentiation and structure	123
4.5	Discussions and conclusion	132
CHAPTER 5	Gene action governing the inheritance of drought tolerance traits in groundnuts (<i>Arachis hypogaea</i> L.)	144
5.1	Introduction	145
5.2	Materials and methods.....	146
5.2.1	Study sites and genotypes.....	146
5.2.2	Hybridisation using a North Carolina Design II sets mating scheme	147
5.2.3	Evaluation of parents and F ₂ families	148
5.2.4	Data collection	149
5.2.5	Data analysis	149
5.3	Results.....	152
5.3.1	Evaluation of parents and F ₂ families	152
5.3.2	Gene action controlling the drought tolerance traits under drought stress.....	164

5.3.3	Association of drought tolerance traits with agronomic traits under drought stress environment	165
5.3.4	Association among drought tolerance traits under drought stress environment.....	165
5.3.5	Gene action controlling the drought tolerance traits under non-drought stress.....	168
5.3.6	Association of drought tolerance traits with agronomic traits under non-drought stress environment	169
5.3.7	Association among drought tolerance traits under non-drought stress environment.....	169
5.3.8	General combining ability effects	172
5.3.9	Specific combining ability effects for the crosses	175
5.4	Discussion	181
5.4.1	Genetic variability of yield, biomass, and physiological traits	181
5.4.2	Gene action and combining ability effects	182
5.5	Conclusions	183
CHAPTER 6	Gene action and inheritance of seed physical quality traits in groundnut (<i>Arachis hypogaea</i> L.).....	189
6.1	Introduction	190
6.2	Materials and methods.....	191
6.2.1	Study sites and genotypes.....	191
6.2.2	Hybridisation using a North Carolina Design II mating scheme	192
6.2.3	Evaluation of parents and F ₂ families	193
6.2.4	Data collection	193
6.2.5	Data analysis	193
6.3	Results.....	195
6.3.1	Evaluation of parents and F ₂ families	195
6.3.2	Gene action controlling the physical quality traits under drought stress	208

6.3.3	Association of seed physical traits with drought tolerance traits under drought stress	210
6.3.4	Gene action controlling the physical quality traits under non-drought stress	213
6.3.5	Association of seed physical traits with drought tolerance traits under non-drought stress	215
6.3.6	General combining ability effects	218
6.3.7	Specific combining ability effects for the crosses	221
6.4	Discussion	227
6.4.1	Genetic variability of yield and physical-quality traits	227
6.4.2	Genetic action and combining ability effects	228
6.5	Conclusions	228
CHAPTER 7	General overview	233

List of Tables

Table 1 The characteristics of groundnut varieties released in Uganda for period between 1966 and 2002	3
Table 2.1 Land holding used for groundnut production and yields obtained (n=60 respondents per region)	61
Table 2.2 Groundnut production systems in eastern, northern and mid-western Uganda	62
Table 2.3 Sources of seed	62
Table 2.4 Choice of season to grow groundnuts	64
Table 2.5 Groundnut varieties commonly grown	64
Table 2.6 Direct matrix ranking of groundnut production constraints by farmers in the eastern, mid-western and northern regions	67
Table 2.7 Farmers' perception of drought in terms of weather events	68
Table 2.8 Mean occurrence (years) of drought in the study area	69
Table 2.9 Perceived impact of drought on crop yields, food and nutritional security	70
Table 2.10 Perception of stage of groundnut most affected by drought	71
Table 2.11 Farmers' perception of direct effect of drought on groundnut varieties	71
Table 2.12 Farmer perceived % losses under drought across the different groundnut growing regions in Uganda	72
Table 2.13 Perceived drought coping strategies currently used by farmers	73
Table 2.14 Response of farmers for groundnut varieties least affected by drought	74
Table 2.15 Farmers' choice of variety grown last season and variety to be grown next season	75
Table 3.1 Popular groundnut varieties collected from the study districts	87
Table 3.2 Farmer preferred groundnut traits in mid-western, northern and eastern Uganda	90
Table 3.3 Farmer preferred groundnut traits, ranks for preference as given by farmers in mid-western, northern and eastern Uganda	91
Table 3.4 Mean squares for morphological and agronomic traits of parental varieties evaluated by the breeder in Hoima, Masindi, Lira and Kumi districts	93
Table 3.5 Mean squares for groundnut trait scores given by farmers within and across districts	94

Table 3.6 Variety mean rank and overall rank (in parenthesis). before and at harvest in Hoima, Masindi, Kumi and Lira districts	96
Table 3.7 Spearman's rank correlation coefficients between groundnut variety trait scores and ranking before and at harvest in Hoima, Masindi, Kumi and Lira districts	97
Table 4.1 Genetic variability within groundnut populations in the Ugandan collection	122
Table 4.2 Analysis of molecular variance (AMOVA) design and results based on SNP data (Averaged over 2986 loci)	123
Table 4.3 Average Fixation-Statistics over all loci	124
Table 4.4 Populations differentiation: pairwise F_{ST} (below diagonal) and Reynolds' (above diagonal) genetic distance	124
Table 4.5 Effective rate of migration among the study groundnut populations: Based on Slatkin (1995) linearized F_{ST} derivation	124
Table 5.1 Characteristics and type of reaction to drought of the different parental lines used for the North Carolina Design II in sets mating design.	147
Table 5.2 Format of analysis of variance of North Carolina design II repeated over seasons	151
Table 5.3 Wald's statistics for drought tolerance traits and agronomic traits among groundnut parental lines evaluated under drought stress and non-drought stress across two seasons in eastern Uganda	153
Table 5.4 Means for REML combined analysis of drought tolerance traits and selected physiological and agronomic traits for groundnut parents evaluated under drought stress averaged over	154
Table 5.5 Means for REML combined analysis of drought tolerance traits and selected physiological and agronomic traits for groundnut parents evaluated under non- drought stress averaged over seasons 2017A and 2017B	155
Table 5.6 Wald's statistics for drought tolerance traits and selected agronomic traits among groundnut F_2 families evaluated under drought stress and non-drought stress across two seasons in eastern Uganda	157
Table 5.7 Means for REML combined analysis of drought tolerance traits and selected physiological and agronomic traits for F_2 families evaluated under drought stress averaged over seasons 2017A and 2017B	158

Table 5.8 Means for REML combined analysis of drought tolerance traits and selected physiological and agronomic traits for groundnut parents evaluated under non-drought stress averaged over seasons 2017A and 2017B	161
Table 5.9 Summary mean squares and significant tests of combining ability effects for SCMR1, SCMR2, PY, BIO, DTI (PY), DTI (BIO), and HI of groundnut lines evaluated under drought stress for two seasons 2017A and 2017B in eastern Uganda	165
Table 5.10 Pearson's correlation coefficients for association of drought tolerance traits and agronomic traits among 75 F ₂ families of groundnut evaluated under drought stress across two seasons in eastern Uganda	167
Table 5.11 Summary mean squares and significant tests of combining ability effects for SCMR1, SCMR2, PY, BIO, POD, and HI of groundnut lines evaluated for two seasons 2017A and 2017B under non-drought stress in eastern Uganda	168
Table 5.12 Mean squares and relative importance for SCMR1, SCMR2, PY, BIO, DTI(PY), DTI(BIO) and HI of groundnut lines evaluated under drought and non- drought stress conditions for two seasons in eastern Uganda.....	170
Table 5.13 Pair-wise correlation coefficients showing association of drought tolerance traits and agronomic traits 75 F ₂ family groundnut lines tested under non-drought stress for two seasons in eastern Uganda	171
Table 5.14 Estimates of general combining ability (GCA) effects and mean performance for SCMR1, SCMR2, PY, BIO, HI, DTI (PY), DTI(BIO), and POD for 75 F ₂ groundnut families evaluated under drought stress across two seasons in eastern Uganda	173
Table 5.15 Estimates of general combining ability (GCA) effects and mean performance for SCMR1, SCMR2, POD, PY, BIO, and HI for 75 F ₂ groundnut families evaluated under non-drought stress across seasons in eastern Uganda.	174
Table 5.16 Estimates of specific combining ability effects (SCA) and mean performance for SCMR1, SCMR2, POD, PY, BIO, HI, DTI (PY) and DTI(BIO) of F ₂ groundnut families evaluated under drought stress across two seasons in eastern Uganda	176
Table 5.17 Estimates of specific combining ability effects (SCA) and mean performance for SCMR1, SCMR2, POD, PY, BIO, and HI of groundnut families evaluated under non-drought stress across two seasons in eastern Uganda	179
Table 6.1 Characteristics and seed traits of the different parental lines used for the North Carolina Design II mating design.	192
Table 6.2 Format of analysis of variance of North Carolina design II repeated over seasons	194

Table 6.3 Wald's statistics for physical quality traits and agronomic traits among groundnut parental lines evaluated under drought stress and non-drought stress across two seasons in eastern Uganda	197
Table 6.4 Means for REML combined analysis for drought tolerance traits, selected agronomic and seed physical quality traits of groundnut parents evaluated under drought stress averaged over seasons 2017A and 2017B in eastern Uganda.	198
Table 6.5 Means for REML combined analysis for drought tolerance, selected agronomic and seed physical quality traits of groundnut parents evaluated under non-drought stress averaged over two seasons 2017A and 2017B in eastern Uganda.....	199
Table 6.6 Wald's statistics for physical quality traits and agronomic traits among groundnut F2 families evaluated under drought stress across two seasons in eastern Uganda.....	201
Table 6.7 Means for REML combined analysis for drought tolerance, selected agronomic and seed physical quality traits of groundnut F2 families evaluated under drought stress averaged over seasons 2017A and 2017B in eastern Uganda	202
Table 6.8 Means for REML combined analysis for drought tolerance, selected agronomic and seed physical quality traits of groundnut parents evaluated under non-drought stress averaged over seasons 2017A and 2017B	205
Table 6.9 Summary mean squares and significant tests of combining ability effects for HSW, SP, SL, SD and SL/SD of groundnut lines evaluated for two seasons under drought stress in eastern Uganda	209
Table 6.10 Summary mean squares, relative importance ratios and significance tests of maternal effects for KY, POD, HSW, SP, SL, SD and SL/SD of groundnut lines evaluated for two seasons under drought stress in eastern Uganda.....	210
Table 6.11 Pearson's correlation coefficients showing association of PY, DTI (PY), SCMR, KY, HSW, PH, Days, SP, SL, SD, SL/SD and HI for 75 F ₂ family lines tested under drought stress for two seasons in eastern Uganda.....	212
Table 6.12 Summary of mean squares and significant tests of combining ability effects for HSW, SP, SL, SD and SL/SD of groundnut lines evaluated under non-drought stress for two seasons in eastern Uganda	214
Table 6.13 Summary mean squares, relative importance ratio and significance tests of maternal effects for KY, POD, HSW, SP, SL, SD, and SL/SD of groundnut lines evaluated under non-drought stress for two seasons in eastern Uganda	215

Table 6.14 Pearson's correlation coefficients showing association of pod yield, SCMR, HI, Days, PH, PY, KY, POD, SP, HSW, SL, SD, SL/SD for 75 F ₂ family lines evaluated under non-drought stress for two seasons in eastern Uganda	217
Table 6.15 Estimates of general combining ability (GCA) effects and mean performance for KY, POD, HSW, SP, SL, SL/SD for 75 F ₂ groundnut families evaluated under drought stress across two seasons in eastern Uganda.....	219
Table 6.16 Estimates of general combining ability (GCA) effects and mean performance for POD, KY, HSW, SP, SL, SD and SL/SD of 75 F ₂ groundnut families evaluated under non-drought stress across two seasons in eastern Uganda.	220
Table 6.17 Estimates of specific combining ability effects (SCA) and mean performance for KY, POD, HSW, SP, SL, SD, and SL/SD of groundnut F ₂ families evaluated under drought stress in three sets across two seasons in eastern Uganda.....	222
Table 6.18 Estimates of specific combining ability effects (SCA) and mean performance for POD, KY, HSW, SP, SL, SD, and SL/SD of 75 F ₂ groundnut families evaluated under non-drought stress across two seasons in eastern Uganda	224

List of Figures

Figure 2.1 Map of Uganda showing study sites, with the sampled areas represented by black stars	58
Figure 2.2 Land tenure systems for farms owned by small holder farmers in eastern, mid-western and northern regions, Uganda	63
Figure 2.3 Sources of labour used by surveyed households	63
Figure 2.4 Season 1 crops grown	65
Figure 2.5 Production system for season 1	65
Figure 2.6 Season 2 crops grown by farmer	66
Figure 2.7 Production system in season 2	66
Figure 2.8 Seasonal drought occurrence	68
Figure 2.9 Groundnut cultivation season.....	68
Figure 4.1 Histogram for missing individuals	119
Figure 4.2 Histogram for missing loci	119
Figure 4.3 Principal component analysis of the groundnut populations	125
Figure 4.4 Delta K values as inferred by STRUCTURE.....	126
Figure 4.5 Model based clustering of SNP data (from K=2 to K=4) for Ugandan groundnut collection	127
Figure 4.6 Proportion of genotypes allocated by botanical variety (left) and subspecies (right) as inferred by structure from K=2 to K=4).....	128
Figure 4.7 Bayesian clustering analysis with allocation of gene clusters in K=2; K=3; and K=4 for each population in the Ugandan groundnut collection	129
Figure 4.8 Neighbour Joining tree constructed for SNP data based on inferred groups (red, green and blue)	130
Figure 4.9 Phylogenetic network tree based on FST values	131

Introduction to Thesis

1. Importance of groundnuts

Groundnut (*Arachis hypogea* L.) is extensively grown in the tropical, subtropical, and warm temperate regions of the world. It is the fourth most important oilseed crop globally after soybean (*Glycine max* [L.] Merr.), Rape seed (*Brassica napus* L.) and cotton seed (*Gossypium hirsutum* L.) (FAOSTAT, 2012). In addition to oil, groundnut is also important as a food and feed legume. In 2010, 38 million tonnes of groundnut were produced globally from nearly 24 million ha (FAOSTAT, 2012). However, in the last decade, groundnut production has increased only marginally due to a 0.1% and 0.3% increase in yield and area cultivated, respectively; yet demand for the crop has been projected to increase dramatically, especially in Asia (Pasupuleti and Nigam, 2013; Mugisha et al., 2014). Similarly, in Uganda, groundnut is an important legume crop after beans (*Phaseolus vulgaris* L.) (Masette and Candia, 2011), where it is produced mainly in the eastern and northern semi-arid dry regions of Uganda (Kaaya and Warren, 2005). In the last decade, there has been a noticeable increase in the acreage devoted to the groundnuts in Uganda; however, while the productivity has almost stagnated in the same period (FAOSTAT, 2012), the demand for the crop as a source of food is on the increase.

Groundnut in Uganda constitutes an important source of nutrition. For example, the per capita consumption of groundnuts by children and women on a daily basis has been estimated as 37 g and 65 g, respectively (Byemaro, 2010 cited in Mugisha et al., 2014). The crop is consumed raw, roasted, blanched, as peanut butter, and also crushed and mixed with traditional herbs as a cooked pasted sauce to eat with major staples such as "matooke", cassava, sweet potatoes, yams etc. (Okello et al., 2010; Mugisha et al., 2014). Besides being used as a cheap source of protein for the resource-disadvantaged rural populations, the demand for groundnut in urban and peri-urban areas has been attributed to the fact that groundnut sauce is tasty and easier to prepare, saving the urban dwellers time and fuel (Mugisha et al., 2014). Groundnut is also used as a cash crop, making it an excellent income source in the domestic as well as regional markets because of its multiple uses and climatic versatility compared to similar legumes. Like other legumes, groundnut also provides nutrients to the soil and its cultivation improves soil fertility through nitrogen fixation making it an important component for crop rotation (Ghosh et al., 2005). Moreover, the crop has an edge over beans as it can give better returns on a limited area and is also well adapted to the hot, semi-arid conditions typical of groundnut growing areas of Uganda (USAID, 2008; Okello et al., 2010).

2. Production constraints

Despite the ever growing importance and production potential of groundnuts, its productivity has almost stagnated in the recent past. Several causes are responsible for this and these can be categorized as socio-economic (Masette and Candia, 2011; Mugisha et al., 2014), and biotic (Sikuku and Ogemah, 2005; Okello et al., 2010; Kayondo et al., 2014) and abiotic stresses (Okello et al., 2010; Masette and Candia, 2011).

2.1. Socio-economic constraints

Groundnut production in Uganda is characterised by resource-constrained small-scale farmers. These farmers cannot afford inputs such as improved seed and fertilisers and, therefore they rely on fellow farmers, farmer groups, local markets, NGOs and research organisations for these inputs (Mugisha et al., 2014). The decline in the wide use of fertilisers from 1960-1990s has mainly been attributed to the insurgency in the major groundnut production areas. However, the reductions and effects of non-fertiliser usage have even become more pronounced to date. Given the lack of capital resources, the farmers are left with no option but to resort to using traditional farming methods with low levels of mechanisation, and traditional varieties or landraces which compromise yields of the crop despite the existence of a number of released varieties (Table 1).

Table 1 The characteristics of groundnut varieties released in Uganda for period between 1966 and 2010

Variety	Maturity (days)	Yield kg/ha	Year of release	Other remarks
Red beauty [‡]	90-100	1900-2500	1966	Mult-line of Red Valencia
Acholi white	80-90	1900-2500	1966	Valencia
Roxo	100-110	2000-2700	1969	Red Manyema, Spanish
Tatu	100-110	1900-2400	1969	Virginia
Manipintar	110-120	2600-3600	1969	Virginia
Bukene	90-100	1800-2600	1970	Spanish
Mwituude	100-110	2000-2400	1970	Virginia
Makulu Red	110-120	2000-2800	1970	Virginia
Amasoga	110-120	1800-2300	NA	Local
Igola-1	125-130	3000-3500	1995	Virginia
Serenut 1R	100-110	2500-3700	1998	Virginia, Red seeded
Serenut 2	100-110	2500-3500	1998	Virginia, Tan
Serenut 3R	90-100	2500-2900	2002	Spanish, Red seeded
Serenut 4T	90-100	2500-2900	2002	Spanish, Tan
Serenut 5R	100-105	2500-3000	2010	Red seed

Source: Modified from Okello et al. (2010); [‡]Most traded groundnut variety (Mugisha et al., 2014).

3. Biotic constraints

Groundnut is exposed to several pests and diseases that reduce the yields, lower the quality and increase the cost of production. In Uganda, major diseases of groundnuts include rosette (caused by a complex of three viruses; groundnut rosette virus (GRV), groundnut rosette assistor virus (GRAV) and satellite RNA (satRNA) and transmitted by a single species of aphid (*Aphis craccivora* Koch), early leaf spot (*Cercospora arachidicola*), late leaf spot (*Phaeoisariopsis personata*), rusts (*Puccinia arachidis*) and aflatoxin contamination (caused by *Aspergillus niger* and *Aspergillus flavus*). The groundnut rosette virus disease (GRVD) is considered the most important constraint and can cause losses of up to 100% if it occurs before flowering (Okello et al., 2010; Nigam et al., 2012).

The important pests of groundnut are aphids (*Aphis craccivora* Koch), a vector of groundnut rosette disease, leaf miner (*Aproaerema modicella* Deventer), thrips (*Thrips palmi* Karny, *Frankliniella schultzei* Trybom, *Scirtothrips dorsalis* Hood) and termites (Isoptera) (Okello et al., 2010; Okello et al., 2014). Thrips and aphids are considered more important as vectors of viruses than as causing direct damage

to groundnuts. In addition, the groundnut leaf miner, a Lepidopteran defoliater- was reported as an emerging threat to groundnut production areas in Uganda, especially those areas prone to drought (Mukankusi et al., 2000; Okello et al., 2010).

Although, an integrated pest management (IPM) has been proposed for the control of these biotic stresses, host plant resistance seems to be the most feasible approach for groundnut farmers in Uganda. In other words, the use of GRVD resistant varieties is considered the best approach for the management of groundnut pests and diseases by resource-constrained farmers (Nigam et al., 2012). In addition, several biotic constraints are being addressed in the Ugandan groundnut breeding programme. For instance, GRVD resistant cultivars such as Serenut 2, Serenut 3 and Serenut 8 have been released; however, these have a low market value compared to other preferred cultivars or landraces (Kayondo et al., 2014). Besides the biotic constraints for groundnut production, abiotic stresses also cause yield reductions in groundnut cultivars regardless of their reaction to pests and diseases.

3.1. Abiotic constraints

As groundnut is grown in semi-arid regions characterized by erratic rainfall and on predominantly loose sandy loam soils, drought is often a recurring production constraint. This situation also coincides with the climate change phenomenon which projects disturbances such as a decrease in the lengths of the rainy seasons especially in semi-arid tropics (SAT) where most groundnuts are grown (Pasupuleti and Nigam, 2013). It is, therefore, anticipated that the frequency of crop failures is likely to increase, thus threatening food security if not total livelihoods in these sub-climatic regions. In addition, drought has significant implications on groundnut quality which undermines the value of groundnut products especially when it occurs as late season drought. For this reason, there is a need to develop drought tolerant, and/or early maturing groundnut varieties to enable farmers to cope with the unpredictable nature of the imminent droughts. In addition, drought has significant implications on groundnut quality which undermines the value of groundnut products especially when it occurs as late season drought.

4. Groundnut seed quality

The quality of shelled groundnuts is a combination of chemical traits (proteins, amino acid profiles, sugar and fatty acid profiles), physical traits (sound mature kernels percentage, shape of kernels, seed size uniformity, 100-seed mass, colour of the testa, moisture content) and sensory factors (texture, flavour and colour) (Dwivedi et al., 1996; Misra, 2004; Dwivedi and Nigam, 2005). These

characters determine the choice of varieties grown and/or traded, and therefore are of major economic importance and should be the focus of any breeding programme (Dwivedi et al., 1996; Mugisha et al., 2014).

Currently, the improvement of cultivated groundnut for quality attributes, agronomic traits as well as drought traits has focused on the use of germplasm accessions from the international collection in gene banks and more recently the use of wild diploid relatives through development of amphidiploids or autotetraploids (Mallikarjuna et al., 2011; Upadhyaya et al., 2011a). However, in the case of the latter, these may come with undesirable effects such as linkage drag; therefore, repeated back crossing to the cultivated groundnut species is one way of breaking such linkages through recombination and thus broadening the genetic base of cultivated groundnut (Mallikarjuna et al., 2011). Hence there is need to assemble a population of genotypes with a high gene/allele frequency for desirable traits as this is a key requirement for the enhancement of quality through genetic manipulation.

5. Farmer preferences of groundnut varieties

A recent survey by Okello et al. (2014) reported a higher adoption of improved groundnut varieties in the northern and eastern regions of Uganda compared to the rest of the country where landraces are predominantly grown. The increased adoption of improved varieties in these regions was attributed to the high activity of NGOs in the post insurgency period, representing a no-choice situation; in the rest of the country where peace prevailed, free adoption of newly released varieties did not take place and farmers were continuing to grow landraces because they considered them to be of higher quality. Studies conducted by Mugisha et al. (2014) found that the key factors that influence demand for groundnut varieties were taste, colour of testa, moisture content, and size of the seeds among other factors. This illustrates the importance of involving farmers and/or other groundnut value chain actors throughout the breeding processes. Such approaches would ensure that consumer traits are considered, thus popularising those varieties among farmers and causing demand for and eventually enhancing the adoption of these varieties.

6. Breeding for drought tolerance and grain physical quality

The exploitation of both wild diploid relatives through the development of amphidiploids or autotetraploids (synthetic groundnuts) and germplasm accessions in gene banks and landraces are potential sources of germplasm for the development of improved groundnut cultivars with drought tolerance and grain quality traits (Mallikarjuna et al., 2011; Upadhyaya et al., 2011a). Credible sources

for these lines include the International Crops Research Institute for Semi-Arid Tropics (ICRISAT) and the National Agricultural Research Systems (NARS). These lines are known to carry novel alleles for agronomic, nutritional as well as drought tolerance traits (Upadhyaya et al., 2005).

Several studies have investigated the mode of inheritance of drought tolerance traits in the sub-interspecific lines (Nigam et al., 2001; Lal et al., 2005; Suriharn et al., 2005; Lal et al., 2006; Hariprasanna et al., 2008; Upadhyaya et al., 2011b; Lal et al., 2014). Nigam et al. (2001) and Lal et al. (2006) reported significance of additive gene action for harvest index (HI), while Lal et al. (2005), Upadhyaya et al. (2011b) and Suriharn et al. (2005) observed a predominance of additive gene action for soil plant analytical development (SPAD) chlorophyll meter readings (SCMR). Lal et al. (2014) reported a predominance of additive x additive type (i) epistasis for specific leaf area (SLA), and SCMR. Lal et al. (2005), on the other hand, observed maternal effects in the inheritance of SCMR and SLA. Despite all the above findings, drought has the potential to alter the heritability estimates of these traits in a given location; therefore, genetic gains made through conventional selection may be different under drought and well-watered conditions (Songsri et al., 2009). Additionally, genetic variation and heritability estimates have been reported to be unique to a particular population and/or its background, environment and experimental design used (Bergman et al., 1998; Pimratch et al., 2004; Rowland and Lamb, 2009; Chen et al., 2013). Therefore, the information on the inheritance of harvest index (HI), SLA, SCMR and other drought tolerance traits, and the genetic associations among these traits will be useful in planning a suitable breeding strategy for improving drought tolerance in groundnuts.

Studies on the nature of gene action for physical qualities are few and conflicting (Dwivedi et al., 1989; Palmar et al., 2000; Vindhiyavarman, 2000, 2001; Hariprasanna et al., 2008). The majority of the traits governing groundnut grain physical qualities have been reported to be under the control of additive genes, although non-additive genes may also play a role (Hariprasanna et al., 2008). Significant reciprocal effects for all grain physical traits have been related to the maternal parent and the importance of parental selection in quality breeding (Hariprasanna et al., 2008). Palmar et al. (2000) reported on the importance of both additive and non-additive gene action for the control of seed size. Dwivedi et al. (1989) reported both additive and non-additive gene effects for proportion of mature seeds and shelling percentage. However, other authors have also suggested the predominant role of non-additive effects in the control of these traits (Vindhiyavarman, 2000; 2001). Given the conflicting and limited number of reports regarding the inheritance of the physical grain traits in groundnut, there is a need for further investigations. Besides, there are also a few studies regarding the inheritance of grain quality traits in crosses among sub interspecific lines and the correlation of grain quality traits with agronomic traits which warrant further investigations. Furthermore, the role of

maternal effects in the inheritance of grain quality traits in sub interspecific lines needs to be investigated.

Many breeding efforts have not met targets perceived by breeders as farmers often fail to adopt new varieties (Ceccarelli et al., 2007). Various studies (Banziger et al., 2000; Efisue et al., 2008; Sibiya et al., 2013) have expressed the view that the above situation could be improved if farmers' perceptions and preferences are taken into consideration during cultivar development process. According to studies by Mugisha et al. (2014), other value chain actors (traders, consumers, processors etc.) need to be consulted since they can also influence the demand for a given variety with a given combination of traits. Participatory approaches such as participatory breeding and variety selection can be utilised such that a significant proportion of value chain actors are involved. In order to increase production of groundnuts, there is a need to understand and contextualise production constraints including drought, consumer desired qualities and farmer preferred traits to guide development of new groundnut varieties in Uganda.

7. Problem statement

In Uganda, groundnut production is concentrated in rain-fed semi-arid areas, where rainfall is very erratic and inadequate, and is also characterised with loose sandy soil. Drought is thus a frequent problem limiting groundnut yields in those areas (Okello et al., 2010; Masette and Candia, 2011). Currently, no mitigation strategies are available to small holder, resource-constrained famers to alleviate this constraint which has also been described as unpredictable (Reddy et al., 2003). Most groundnut farmers in the region are still growing drought susceptible, improved varieties, and low yielding drought and disease susceptible landraces (Okello et al., 2010; Mugisha et al., 2014; Okello et al., 2014) as they have desired farmer- and consumer-preferred traits. Given the importance of the traditional landraces in Uganda, and the fact that improved cultivars are often associated with a narrow genetic base (Upadhyaya et al., 2002) for improvement of traits of economic importance, it is thus necessary to carry out a genetic diversity study to facilitate the improvement of drought tolerance and grain quality traits among these landraces and improved varieties in the farmer domain. Genetic variability and heritability of traits for drought, like any other trait of interest, depends on the breeding population in use and also on the fact that these properties are subject to variation due to the environment and genetic background of the breeding population (Pimratch et al., 2004; Chen et al., 2013) and the experimental design used (Bergman et al., 1998 cited in Khodadadi et al., 2011). Given the paucity of information on inheritance for drought tolerance traits, it is aptly necessary to determine variability and heritability for drought tolerance traits as tools for crop improvement aimed at longer term drought management.

Several studies have also indicated the existence of a wide genetic variability for grain quality traits (Upadhyaya et al., 2005; Upadhyaya et al., 2011a) which can be exploited for improvement of groundnuts. However, published information regarding the inheritance of physical grain quality traits in crosses within and among botanical varieties of groundnut (Hariprasanna et al., 2008) is limited; this, therefore, calls for investigations to study the mode of inheritance of groundnut grain physical traits.

Information regarding adoption of improved groundnuts varieties, validation of production constraints and farmer preferred traits by region of production is limited (Masette and Candia, 2011; Mugisha et al., 2014; Okello et al., 2014). Okello et al. (2014) reported skewed adoption levels for improved varieties in favour of the northern and eastern regions compared to the rest of the country. In addition, productivity of the crop has stagnated at an average of 650 kg/ha in the past one decade compared to the potential yields of 3000-3500 kg/ha, even though the area under production has been increasing over the same period (FAOSTAT, 2012). The explanations regarding the status quo are scanty (Okello et al., 2010; Masette and Candia, 2011; Okello et al., 2014). Therefore, there is an urgent need to redefine and contextualise consumer and agronomic traits, production constraints including drought and their implications for breeding in groundnut in a bid to enhance groundnut productivity and production in Uganda.

8. Overall goal

The overall goal of this study was to alleviate poverty, food and nutritional insecurity and improve food safety by ensuring that resource-constrained farmers have access to diverse groundnut cultivars that are high yielding, early maturing, with good consumer qualities and also tolerant to droughts typical of the semi-arid dry zones of Uganda.

9. Specific objectives

The specific objectives of the study were;

1. To assess smallholder farmers' knowledge and perceptions of drought and other production constraints, how it influences the choice of varieties grown and/or the cropping patterns adopted, and the implications for groundnut breeding in Uganda.
2. To determine farmers' selection criteria for groundnut varieties grown in selected regions of Uganda
3. To determine the genetic diversity of Ugandan landraces and selected improved varieties as revealed by morphological and molecular markers.

4. To determine the combining ability and gene action, and the association between drought tolerance traits and agronomic traits in diverse groundnut germplasm under different water regimes.
5. To determine combining ability and gene action, and the association between drought tolerance traits and physical quality traits in diverse groundnut genotypes under different water regimes.

10. Outline of Thesis

The chapters in this thesis are written in form of research articles. Some overlap and unavoidable repetition of references and some introductory information between chapters may, therefore, exist. The referencing system used in the thesis is based on the Crop Science Journal referencing style. The thesis is divided into the following chapters;

Thesis introduction

Chapter 1: Literature review

Chapter 2: Farmer perception of drought, other production constraints and production system, their implication for groundnut breeding in Uganda

Chapter 3: Participatory varietal selection criteria for groundnut varieties in selected regions of Uganda

Chapter 4: Genome wide SNP diversity and population structure in a Ugandan groundnut (*Arachis hypogaea* L.) collection

Chapter 5: Gene action governing the inheritance of drought tolerance traits in groundnuts (*Arachis hypogaea* L.)

Chapter 6: Gene action and inheritance of seed physical quality traits in groundnut (*Arachis hypogaea* L.)

Overview of the research findings

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CHAPTER 1 Literature Review

1.1 Introduction

This literature review covers research topics related to the objectives of the thesis and also serves as the theoretical context on which the research methodology of this study will be based. The literature addresses; the taxonomy, botanical, ecological, physiological responses of the crop to drought, progresses in the genetics of drought tolerance, genetic control of seed physical quality traits, challenges and critical limitations in improving drought tolerance and grain quality traits through breeding. In addition, farmers' preferences and variety selection criteria in conjunction with indigenous technical knowledge (ITK) is also reviewed as a basis for enhanced adoption of groundnut varieties. Knowledge gaps identified in this report are highlighted.

1.2 Taxonomy of groundnut

The genus *Arachis* is composed of 80 species divided into nine sections according to morphological traits, ploidy levels and chromosome number, namely *Arachis*, *Caulorrhizae*, *Erectoides*, *Extranervosae*, *Heteranthae*, *Procumbentes*, *Rhizomatosae*, *Trierectoides*, and *Triseminate*. The species of genus *Arachis* are perennial or annual legumes and made up of a large and diverse group of diploid ($2n = 2x = 20$ or 18) and allotetraploid ($2n = 4x = 40$) species according to Stalker (1997) and Ceccarelli et al. (2004) cited in Burrow et al. (2008). All species, except the cultivated species (*A. hypogaea* and *A. monticola*) are in section *Arachis*, and certain species in section *Rhizomatosae*, are diploid ($2n = 2x = 20$). The diploid progenitors, *A. duranensis* and *A. ipaensis*, contributed "AA" and "BB" genomes, respectively, to the cultivated groundnut (Kochert et al., 1996). A rare chromosome doubling (polyploidization), subsequent to a single hybridization event is believed to have occurred between the diploid progenitors about 3500 years ago leading to the origin of the cultivated groundnut. As a result, reproductive isolation of one or a few natural interspecific hybrids is believed to have occurred (Moretzsohn et al., 2005). These tetraploid hybrids were unable to produce fertile offspring with surrounding diploid ($2n = 2x = 20$) *Arachis* species because of the difference in chromosome number (Singh, 1985; Singh and Gibbons, 1986). The result of this sexual isolation was a disruption in the gene flow from the few reproductively isolated mutant plants that probably gave rise to all the cultivated peanut landraces (Hopkins et al., 1999). The natural variation observed within *A. hypogaea* resulted from mutation, recombination, and selection that occurred after the polyploidization event, a short period compared with the age of the highly variable diploid species.

Owing to the large amount of variability of growth habits and morphological traits of agronomic importance, the cultivated groundnuts (*A. hypogaea*) is the most studied and most described species of the genus *Arachis*. The cultivated groundnut is classified into two subspecies, subsp. *Fastigiata* Waldron and subsp. *hypogaea* Krap. et Rig. While subsp. *fastigiata* contains four botanical varieties, var. *vulgaris*, var. *fastigiata*, var. *peruviana* and var. *aequatoriana*, the subsp. *hypogaea* contains two varieties, var. *hypogaea* and var. *hirsuta*. Each of these botanical types differ in terms of growth habit, branching patterns, pubescence, stem colour, and pod and seed size and shape (Krapovickas and Gregory, 1994).

Of the six botanical varieties, only three are widely cultivated in Africa, Americas, and Asia (Ferguson et al., 2004). The *A. hypogaea* subsp. *hypogaea* has alternate pairs of vegetative and reproductive axes on branches (alternate branching) and does not bear flowers on the main axis. The inflorescence is simple, and it generally has two seeds per pod, with a moderate seed dormancy. The seed coat is generally tan in colour and the species is medium to late maturing. Var. *hypogaea*, is comprised of cultivars with a medium seed size and are runner market types, but those with large seeds are Virginia market type. In contrast, *A. hypogaea* subsp. *fastigiata* var. *vulgaris* (Spanish market type) has floral axes on the main stem, an irregular pattern of vegetative and reproductive branches with reproductive branches predominating on branches (sequential branching). The inflorescence is compound, and the species has mostly two seeds per pod and with little or no dormancy. The *A. hypogaea* subsp. *fastigiata* var. *fastigaita* (Valencia market type) has floral axes on main stem, sequential branching, an inflorescence that is usually simple. It has two or four seeds per pod and little or no seed dormancy. These varieties have also been reported to have differential responses to drought (Reddy et al., 2003).

While Virginia type cultivars are associated with better water use efficiencies, Spanish and Valencia cultivars are superior in partitioning dry matter to pods (ICRISAT, 1992 cited in Reddy et al., 2003). In addition, the Virginia bunch and Virginia runner types with smaller and darker leaves were found to be drought resistant based on their wilting score. Moreover, Spanish bunch types were reported to have a faster recovery rate from drought. Further evidence from Erickson and Ketring (1985), also in Reddy et al. (2003), alludes to the fact that Spanish types are more tolerant to drought than Virginia types under severe stress and high evaporative demand. On that account, the use of all these marketable botanical varieties will provide scope for exploiting a large source of drought tolerance and grain physical traits for improvement of farmer preferred cultivars.

1.3 Cultivar development strategies in groundnut

1.3.1 Broadening the genetic bases

Identification of superior parents with high yield and desirable traits is the basis of a breeding programme. A wide genetic base is important in order to choose the best parents for breeding, and to design proper crossing schemes and selection strategies (Carputo et al., 2013). However, modern groundnut breeding is constrained by a narrow genetic base in the cultivated groundnut.

Groundnut wild relatives have long been identified as important sources of traits of interest to breeders (Holbrook and Stalker, 2000; Simpson, 2001). However, utilization of the wild germplasm in breeding programmes has received little attention due to the reproductive barriers between wild and cultivated species caused by ploidy differences, which has hampered the use of wild diploid relatives in groundnut breeding programmes (Fonceka et al., 2009). Nonetheless, several successful stories do exist from other crops such as tomato (Lippman et al., 2007), rice (Zhao et al., 2008), wheat (Liu et al., 2006) and barley (Schmalenbach et al., 2009) where wild relatives have been used to introgress important traits.

In groundnut, examples of genome wide introgressions made into the background of a cultivated variety have been done for traits such as resistance to cercospora leafspot (Stalker, 1984), root-knot nematode (Garcia et al., 1996; Sharma et al., 1999), peanut bud necrosis virus (PBNV) (Reddy et al., 2000), late leaf spot disease (Pande and Rao, 2001), and tolerance to abiotic stresses (Nautiyal et al., 2008). However, all these cases represent only a small number of wild species that have been used compared with the large natural genetic diversity available in the wild relatives, which is yet to be exploited for useful alleles. Genetic breeding barriers associated with many wild species are the major challenges to exploitation of these resources (Fonceka et al., 2009). Approaches such as ploidy manipulations and bridge crosses, embryo rescue and hormone treatment have been the methods used to overcome the difficulty of hybridization between sexually incompatible species (Acquaah, 2012). Understanding these barriers and developing techniques to allow for introgression are fundamental to utilize the wealth of genetic resources in several domesticated crops (Acquaah, 2012; Weber et al., 2012).

1.3.2 Selection for potential parents

Since the cultivated groundnut is an allotetraploid ($2n = 4x = 40$), but highly homozygous, crosses are made between parents with complementary features, and the selection of parents is more often based on phenotype rather than genotype (Acquaah, 2012). In recent years, major progress has been made in the use of molecular technologies for the identification of genes to enable the implementation of marker-assisted selection in crop improvement programmes (Varshney et al., 2012). This may help

to accelerate breeding of several diploid and polyploid crops. Conventional breeding, which is the main method used to develop new improved cultivars, includes hybridization and selection (Sleper and Poehlman, 2006). The procedure starts with the identification of desirable parents, followed by crossing selected superior genotypes for the trait under consideration. Several methods are used by groundnut breeders for selection of desirable parents, including, the use of mid-parent values, combining ability effects, estimated breeding values, progeny tests and genetic diversity analysis (Gopal, 2015).

1.3.3 Selection based on combining ability effects

Combining ability analysis is a type of progeny test which predicts the performance of parents in crosses. This is the factor determining genotype's potential for cultivar development (Hallauer et al., 1988; Acquaah, 2012). Combining ability effects are partitioned into two types: general combining ability (GCA) and specific combining ability (SCA). The GCA depends predominantly on additive effects of the genes. Where GCA predominates, progeny performance can be reliably predicted from the performance of the parents. The SCA effect depends predominantly on non-additive effects of the genes (Acquaah, 2012). In case the SCA effect predominates, specific combinations of parents would have to be evaluated to find progeny with the desired characteristic and considerably more testing would be required (Machado et al., 2002). Diallel and North Carolina Design II are the most widely used mating designs for an efficient estimation of combining ability effects (Acquaah, 2012).

Varying reports on the importance of GCA (Lal et al., 2005; Suriharn et al., 2005; and Upadhyaya et al., 2011) and SCA (John et al., 2012) effects for drought tolerance traits in groundnut exist in the literature. These conflicting views may be the result of the use of different mating designs and/or different genetic parent materials for evaluation (Hallauer et al., 2010). Despite the differences, the studies showed that both GCA and SCA effects are important for choosing drought resistant parents for use in breeding. Groundnut breeding work in Uganda has focused on the introduction and testing of advanced lines developed by ICRISAT for disease resistance and productivity. However, little work has been done in identifying parents, and generating and selecting progenies which combine drought tolerance, disease resistance and good physical quality traits.

1.3.4 Genetic diversity assessment

Genetic diversity study is an important method that can contribute to the selection of parents for breeding. A genetic diversity assessment provides an understanding of the genetic variation of a germplasm collection (Varshney et al., 2008). Besides, it is also a measure of the genetic deviation between and genetic diversity within the major genetic clusters that comprise the crop germplasm.

Among other methods, DNA-based techniques are most suitable for genetic diversity assessment, and evolutionary and conservation studies for germplasm accessions.

In groundnut, the genetic bottlenecks caused by spontaneous hybridization, polyploidisation, and reproductive isolation from wild relatives have largely affected the development of optimum genetic and genomic resources for molecular breeding (Varshney et al., 2013). Nonetheless, large scale genomics resources with the arrival of genome sequences from the ancestors of peanut *A. duranensis* and *A. ipaensis*, implies the onset of several genetic studies including molecular diversity, genetic mapping and utilisation of modern breeding strategies in groundnut (Pandey et al., 2012, Varshney et al., 2013; Bertioli et al., 2016)

In the last decade, SSR markers have been favoured for genetic mapping in groundnut (Gautami et al., 2012; Qin et al., 2012; Shirasawa et al., 2013; Huang et al., 2015). However, polymorphic SSR markers are limited in number, time consuming, and expensive to assay. Therefore, the use of high-throughput markers like those based on single nucleotide polymorphisms (SNPs) is much needed for efficient application of genomics data for marker assisted breeding, quantitative trait locus (QTL) mapping, and genomic selection.

Although, SNP arrays have been used in wild relatives of groundnut (Nagy et al., 2012; Bertioli et al., 2014), their development to assay the tetraploid ($2n = x = 40$) cultivated groundnut (*A. hypogaea*) and has lagged behind other polyploids including oat (Tinker et al., 2014), wheat (Wang et al., 2014), and strawberry (Bassil et al., 2015). However, recent progress in sequencing has enabled timely detection of large numbers of SNPs at a much lower cost. More recently, an innovative approach known as genotyping-by-sequencing (GBS) has been developed to perform simultaneous SNP discovery and genotyping (Elshire et al., 2011). This approach is a united one-step procedure of SNP discovery and genotyping and constitutes a rapid, high throughput and cost-effective tool for a genome-wide analysis of genetic diversity, especially for non-model species and germplasm sets. These features make GBS an encouraging and advantageous tool for genetic diversity studies in plants with informative sets of markers (Peterson et al., 2014). Among the several processes advanced to cut down genome complexity, the DArT-Seq method has become a significant influence through the intelligent selection of the genome fraction corresponding predominantly to active genes. Classic DArTs markers have been substituted by DArT-Seq markers based on genotyping by sequencing. DArT-Seq and single nucleotide polymorphism (SNP) markers based on genotyping by sequencing (GBS) technology have been successfully applied for linkage mapping, quantitative trait locus (QTL) identification in bi-parental mapping population, genome wide association studies (GWAS), and genetic diversity studies in a range of crops (Grzebelus et al., 2014; Brinez et al., 2012) as well as in marker-assisted genomic selection. Given the shortcomings of conventional breeding for groundnut improvement, there is need to apply molecular tools for groundnut breeding in Uganda.

However, genetic diversity and population structure of the of Ugandan groundnut materials, as revealed by SNP markers, have not been undertaken. Therefore, the proposed study seeks to uncover the underlying genetic diversity and genetic relatedness in the Ugandan collection using SNP markers.

1.4 Drought tolerance in groundnuts

1.4.1 Physiological implications of drought on groundnuts

In the event of water stress, plant species often activate various physiological and biochemical mechanisms to cope with the stress (Munns, 2002). These include changes in water relations, photosynthesis, metabolism, growth and yield.

Relative water content (RWC), leaf water potential, stomatal resistance, rate of transpiration, leaf temperature and canopy temperature determine water relations under water stress (Reddy et al., 2003). The RWC is considered a measure of plant water status, reflecting the metabolic activity in tissues and can thus be used as an index for dehydration tolerance. It is normally higher in the early stages of leaf development and reduces as dry matter accumulates as the leaf matures (Anjum et al., 2011). The RWC is often associated with water uptake by the roots as well as water loss through transpiration.

An elaborate root system is considered good for early crop growth and extraction of water from shallow soil layers, which could have otherwise been lost by evaporation. There are conflicting reports in general regarding the effect of drought on root growth. While Jaleel et al. (2008) reported increased growth rates due to water stress, Sacks et al. (1997) reported that root growth was not significantly affected by drought. However, other studies have concluded that in the presence of water stress, the root:shoot ratio of plants increases due to the differential effects of low plant water potential favouring roots more than the shoots (Wright and Rao, 1994; Wu and Cosgrove, 2000; Furlan et al., 2012). Therefore, an increased root/shoot ratio can be considered as an index that shows changes induced by drought stress as differential rates of growth between these organs is crucial for crop drought tolerance (Puangbut et al., 2009; Furlan et al., 2012). Moreover, drought conditions also induce a signal torrent to the shoots through the xylem flow that results in further physiological changes which can also determine the level of plants adaptation to drought stress; for example, through stomata closure, although this has implications for photosynthetic apparatus (Anjum et al., 2011).

Environmental stresses including drought have a direct impact on the photosynthetic machinery. These stresses have been reported to disrupt all major components of the photosynthetic pathway including electron transfer, carbon reduction cycle and stomatal control of carbon dioxide supply. This results in the accumulation of carbohydrates, peroxidative destruction of lipids, and alteration of plant

water balance. Reduced photosynthetic capacity may be caused by both stomatal and non-stomatal mechanisms under water deficit conditions (Del Blanco et al., 2000; Samarah et al., 2009). Stomata are the points of water loss and carbon dioxide entry into the plant, in fact, stomata closure is one of the first responses to drought stress with a direct negative implication for photosynthesis, but this also increases photorespiration. Stomata conductance is related to leaf water status and a good association normally exists between these two parameters even under drought stress, to enhance the fitness of crops through drought stress (Anjum et al., 2011). Besides the stomatal causes, non-stomatal causes of reduction in photosynthesis are also important as mechanism as physiological response to drought stress.

Chlorophyll is one of the major chloroplast components for photosynthesis, and the relative chlorophyll content has a positive association with the photosynthetic rate. Chlorophyll is important in plants for harvesting light and production of reducing powers. It has been reported to be susceptible to soil dehydration (Farooq et al., 2009). Many studies have reported a decreased or unchanged chlorophyll content during drought stress in many plant species depending on the duration and severity of drought (Zhang and Kirkham, 1996; Songsri et al., 2009). Loss of chlorophyll under drought stress is regarded as a main cause of inactivation of photosynthesis (Anjum et al., 2011). Reduction in chlorophyll may be attributed to a loss of chloroplast membranes, excessive swelling, distortion of the lamellae vesiculation, and appearance of lipid droplets as a result of formation of highly reactive oxygen species (ROS) in plant cells triggered by an increased photorespiration in the leaves (Imlay, 2003; Azevedo Neto et al., 2008; Anjum et al., 2011). On the other hand, stability in chlorophyll also has implications for the plants' ability to cope with drought.

Stability in chlorophyll content is associated with drought tolerance through its ability to maintain constant biomass production, despite the harsh conditions. Furlan et al. (2012) related chlorophyll stability to the need to maintain higher root biomass to scavenge enough soil volume to improve water uptake. In addition, studies have also indicated that chlorophyll stability is also instrumental in helping plants to deliver sufficient energy to deal with the energy-consuming drought stress adaptations (Arunyanark et al., 2008; Furlan et al., 2012). Another possibility is that chlorophyll has a role in the control of redox homeostasis, in other words, it participates in heat dissipation of excess excitation energy within light collecting chlorophyll and the carotenoid-binding protein complexes of photosystem (PS) II, which are considered major photo protective mechanisms (Niyogi, 1999). Furlan et al. (2012) found a negative association between shoot N and chlorophyll content, although these were considered tightly related (Bojović and Marković, 2009). This was attributed to water stress induced re-translocation of shoot N to roots or volatilisation of foliar N (Heckathorn et al., 1997). Therefore, the ability of the plant to tolerate drought can also be considered to depend on its ability to adapt at

the level of photosynthesis which in turn affects biochemical and physiological processes leading to growth and yield of the whole plant (Chandra, 2004; Anjum et al., 2011).

Groundnut, like other legumes, exhibits reduced nodulation and biological nitrogen fixation (BNF) under drought stress (Pimratch et al., 2008; Furlan et al., 2012). Within the nodule, a water deficit enhances soluble sugar and reduces solute potential in cells to maintain cell turgor at a low water potential. As a result of this and also because of the high sensitivity of nodules to phloem volumetric flow, BNF is significantly reduced in groundnut depending on genotype (Pimratch et al., 2008). Several mechanisms are considered to play a role, including carbon shortage and nodule carbon metabolism, oxygen limitation, and feedback regulation by the accumulation of N fixation products (Serraj, 2003). Somasegaran and Hoben (1994) and Furlan et al. (2012) reported a high correlation between N content, nodule dry weight (NDW) and shoot dry weight (SDW), and concluded that the latter could be used as a basis for N₂-fixation effectiveness (Somasegaran and Hoben, 1994). Therefore, the ability to maintain a high nitrogen fixation under drought stress is key in order to maintain high yields under water stress conditions (Pimratch et al., 2008)

1.4.2 Genotypic variability for drought tolerance in groundnut

Genetic variability in groundnut is low as the species is believed to have emerged from a single crossing event between two diploid species followed by a chance chromosome doubling, resulting in crossing barriers with wild diploid species after these events (due to ploidy differences) (Singh, 1985; Singh and Gibbons, 1986). Therefore, the cultivated groundnut is an allotetraploid, while all the wild *Arachis* species are diploid except *A. monticola* and a few species in section *Rhizomatosae* (Stalker, 1997; Burrow et al., 2008). The low genetic variability for traits of importance and the polyploidy nature are a bottle neck to the groundnut improvement efforts in general (Janila and Nigam, 2013). However, useful genetic variation in morpho-physiological traits associated with drought tolerance have been reported by several workers, such as total root dry mass, chlorophyll density (Nigam et al., 2001; Upadhyaya, 2005; Nigam and Aruna, 2008), root length density (RLD) (Taiz and Zeiger, 2006; Songsri et al., 2009), stomata conductance (Ober et al., 2005; Songsri et al., 2013), water up take capability (Wright and Rao, 1994; Taiz and Zeiger, 2006), SLA (Rao Nageswara and Wright, 1994), specific leaf nitrogen-SLN (Nigam et al., 2001), canopy temperature depression (Bhatnagar-Mathur et al., 2007), water use efficiency-WUE (Passioura, 2002; Nigam et al., 2005; Sheshshayee et al., 2006), water uptake capability and WUE (Hebbar et al., 1994), and harvest index-HI (Velu and Gopalkrishnan, 1985; Sharma and Varshney, 1995) among others. The repository of all this variation is found in the germplasm accessions of cultivated groundnut in gene banks. Wild *Arachis* species are also reported to possess desirable alleles for several economically important traits including abiotic stress (Dwivedi et al., 2003; Kalyani et al., 2007; Dwivedi et al., 2008; Nautiyal et al., 2008) and, therefore can be potential sources for use in improvement of groundnut (Mallikarjuna et al.,

2011). However, a large proportion of cultivated and wild genetic resources of groundnut are yet to be studied and characterized for traits of economic importance (Janila and Nigam, 2013).

Some of the traits contributing to drought resistance/tolerance have not always been fully exploited for improving groundnuts for drought tolerance because of lack of effective phenotyping tools (Janila et al., 2013). However, studies on character associations provide scope for identification of associated traits that would result in maximizing gains through selection of both targeted and its associated traits (Gomes and Lopes, 2005; Janila et al., 2013). For example, pod yield was reported to be positively associated with the number and mass of mature pods per plant, the number and mass of mature kernels per plant, shelling-out-turn, 100-seed mass, primary and secondary branches per plant, and harvest index. Thus, selection for these associated traits simultaneously affects pod yield (Janila et al., 2013). Character association studies have also made it possible to use robust, low-cost, and convenient surrogate traits as alternatives to laborious traits for phenotyping in making selections (Janila et al., 2015). For instance, SPAD chlorophyll meter reading (SCMR) and specific leaf area (SLA) are highly correlated with water-use efficiency-WUE (Sheshshayee et al., 2006) and hence SPAD and SLA are used as the surrogate traits for WUE. Several groundnut breeding programmes for drought tolerance have adopted the trait-based approach, where selections are based on surrogate traits of WUE, such as SPAD and SLA, in combination with an empirical approach in order to maximize the genetic gains for drought tolerance in groundnuts.

It is evident that a number of physiological traits and their surrogates for drought tolerance have been widely studied. However, these traits have not been fully exploited by breeders for developing drought tolerant varieties, because in most cases, only a few contrasting genotypes are used, while the bulk of useful genetic variability remains unknown. In addition, only a few of the modern groundnut cultivars are drought tolerant. Furthermore, studies that investigate genetic variability for drought tolerance among the Ugandan landraces and improved cultivars are very limited. Therefore, there is a need to search for sources of drought tolerance among the available elite cultivars and local landraces in Uganda and introgress drought tolerance into the farmer preferred cultivars.

1.4.3 Mode of gene action for inheritance of drought tolerance traits

The genetic approach to improvement of traits of economic importance relies on knowledge of the genetic system controlling the trait. Understanding the nature of variability of the trait is important because it determines the breeding scheme to be followed for improvement of that trait. In groundnut, both qualitative and quantitative inheritance has been reported for traits of importance (Janila and Nigam, 2013). However, in most of the cases preponderance of additive genetic variance for quantitative traits such as drought tolerance has been reported (Nigam et al., 2001; Lal et al., 2005; Suriharn et al., 2005a; Lal et al., 2006b; Hariprasanna et al., 2008; Upadhyaya et al., 2011; Lal et al.,

2014a). Nigam et al. (2001) and Lal et al. (2006a) reported significance of additive gene action for harvest index (HI), while Lal et al. (2005), Upadhyaya et al. (2011) and Suriharn et al. (2005b) reported predominance of additive gene action for soil plant analytical development chlorophyll meter readings (SCMR). On the other hand, Lal et al. (2014b) reported predominance of additive x additive type (i) epistasis for specific leaf area (SLA) and soil plant analytical development (SPAD) chlorophyll meter readings (SCMR), while dominance and epistasis variance were also reported for quantitative traits due to the allotetraploid nature of the crop for control of SCMR. John et al. (2012), using diallel, reported the predominance of non-additive gene control for days to 50% flowering, days to maturity, specific leaf area, specific leaf weight, leaf area index, transpiration rate, photosynthetic rate, stomatal conductance, water use efficiency, dry haulm weight per plant and harvest index. The influence of maternal effects in the inheritance of soil plant analytical development (SPAD) chlorophyll meter readings (SCMR) and specific leaf area (SLA) was also reported (Lal et al., 2005). The above studies contradict with each other regarding whether additive or non-additive gene action is important for the control of drought tolerance traits in groundnut. Thus, there is need to determine the nature of gene action for drought tolerance traits in the available germplasm to enable successful of improvement groundnut for these traits in the farmer preferred cultivars.

1.5 Associations among drought tolerance traits of groundnuts

The breeding progress for improving drought tolerance in groundnut on the basis of yield as selection tool has often been slow due to large genotype x environment (G x E) interactions (Holbrook and Stalker, 2003; Songsri et al., 2008). As a result, breeding methodologies using physiological traits have become popular. This is because physiological traits have a high heritability and a non-significant G x E interactions. Therefore, utilisation of these traits can greatly improve selection efficiency for superior drought resistant genotypes in addition to the yield-based or empirical approach (Blum, 1988; Falconer and Mackay, 1996).

Several studies (Wright and Rao, 1994; Craufurd et al., 1999; Nigam et al., 2005) identified alternative selection criteria that could be used in indirect selection to increase drought tolerance in groundnut. Drought tolerance might be enhanced by improvement of soil water extraction capability or improvements in WUE, or integration of both (Hebbar et al., 1994; Wright and Rao, 1994). Improvement of WUE could potentially lead to increased yield under limited moisture availability (Passioura, 1986). However, WUE is not easy to measure and may not be a feasible selection criterion for segregating breeding populations. Wright and Rao (1994) found WUE to be negatively correlated to SLA over a wide range of varieties and environments, and it was simple to measure. However, SLA was found to depend on the environment, thus it couldn't be used *per se*. Significant negative correlations between SLA and SCMR have been reported by several researchers (Nageswara Roa et al., 2001; Upadhyaya, 2005; Nigam and Aruna, 2008; Songsri et al., 2009; Upadhyaya et al., 2011).

This implies that SCMR could be used as a rapid and reliable measure for identifying genotypes with low SLA and hence high WUE in groundnut. In addition, HI was also found to be correlated with SLA and SCMR under both well-watered and long-term drought conditions (Songsri et al., 2008; Girdthai et al., 2012). Therefore, measurement of these three traits would guarantee breeding gains for drought tolerance traits in groundnuts.

1.6 Association between drought tolerance traits and agronomic traits

Correlations between drought resistance traits and yield and yield components provide information on expected responses of yield and yield components to selection for drought tolerance traits. Songsri et al. (2008) found high correlation between HI and PY, and low genetic correlation between SCMR, PY and HI, and based on lower GXE for HI and SCMR than yield. Wright et al. (1996) concluded that it would be possible to improve yield by selecting for high HI and high SCMR.

Yield parameters are important benchmarks for sustaining yields under drought. Genotypes with increased yield under drought are also associated with a high number of mature pods under both stress and non-stress conditions (Songsri et al., 2008; Boontang et al., 2010). Several studies reported that SCMR was positively correlated with pod number per plant (Painawadee et al., 2009; Wunna et al., 2009; Puangbut et al., 2010; Koolachart et al., 2013b). In contrast, Boontang et al. (2010) reported that SCMR was not related to number of pods per plant, number of seeds per pod and seed size evaluated under terminal drought. In addition, under severe drought stress, Wunna et al. (2009) did not find relationship between SCMR and pod yield. These findings are conflicting and seem to be related to a given set of drought parameters. That being the case, further investigation is needed.

Nonetheless, the SCMR is related to the photosynthetically active light-transmittance characteristics of the leaf and is positively correlated with chlorophyll content (Akkasaeng et al., 2003), chlorophyll density (Arunyanark et al., 2008) and WUE (Sheshshayee et al., 2006), and, therefore, contributes to the yield of the crop (Koolachart et al., 2013b). Therefore, the incorporation of physiological traits (or their surrogates) in the selection scheme would be advantageous in selecting genotypes that are more efficient water users (SCMR) and with better partitioning ability of photosynthates into economic yield (Nigam et al., 2005). On that account, the SMCR provides an easy opportunity to integrate a surrogate measure of WUE with PY, in the selection scheme of a drought resistance breeding programme in groundnut.

Rooting characteristics of the crop play an important role for maintaining high photosynthesis during drought stress. Studies by Puangbut et al. (2009) and Furlan et al. (2012) have indicated the differential growth of shoots and roots in favour of the latter under drought conditions to support the

plant to draw more moisture for photosynthesis. Rooting characteristics related with drought tolerance are important for identifying drought resistant mechanisms of plants. Rooting traits such as deep rooting, root length density (RLD) and root distribution have been identified as drought adaptive traits, and can be used as selection criteria for drought resistance (Taiz and Zeiger, 2006; Songsri et al., 2008). Genotypes with higher root length density in the deeper soil layers are considered to have drought tolerance resulting in the higher potential to obtain high pod yield and harvest index under long term drought conditions (Jongrunklang et al., 2008; Songsri et al., 2008). However, other studies (McPhee, 2005; Painawadee et al., 2009) found that root characters were positively and significantly correlated with biomass and, to a lesser extent, to the number of pods per plant, and that root dry weight was not significantly correlated with pod yield and pods per plant but it was negatively and significantly associated with the harvest index. These findings may point to the fact that different drought response mechanisms work in association with root traits to determine pod yield under drought conditions. These factors include stomata conductance, WUE and HI, and are considered to play a modifying role (Koolachart et al., 2013a).

Stomata conductance and WUE have consequences for pod yield of groundnut under moisture stress conditions. Several studies reported that photosynthesis was reduced by water stress due to the reduction in stomata conductance (Del Blanco et al., 2000; Samarah et al., 2009; Koolachart et al., 2013a) and leaf area (Koolachart et al., 2013a). Increased water stress resulted in closure of stomata as a mechanism to reduce transpiration. Consequently, carbon dioxide diffusion into the plant was curtailed thus causing reduction in photosynthesis (Reddy et al., 2003). Therefore, under a given set of drought conditions, yield may be undermined.

The effects of drought on yield attributes were also related to the period during the growth of groundnut when drought occurs. Random drought, occurring at any stage of growth of groundnut led to more reductions in pods/plant than in the number of seeds per pod and seed size. Conversely, small reductions in pods/plant and reduction in seed size were not severe under terminal drought (Boontang et al., 2010). However, under early season drought, reductions for pods/plant were moderate to high, high for seed size and moderate for seeds/pod (Wunna et al., 2009). But under long term, drought studies, high reductions for pods/plant and seed size and low for seeds/pod were observed. Therefore, the reductions in yield parameters were more or less similar in most studies but were only different in terms of magnitude of reductions among different studies. The differences could be associated with materials used and experimental conditions peculiar to each study.

Reductions in pod/plant can be associated with the type of groundnut. Studies have indicated that groundnut typically produces 2-5 pods depending on the type (Young, 2006). Spanish and Virginia have fewer seeds/pod than Valencia types (Kottapalli et al., 2008). In addition, late season drought reduced pod yield in Virginia type more severely than Spanish because of reductions in pods/plant

and kernel size (Wright et al., 1991). Besides this, the subterranean nature of groundnut pods also has implications for the crop's response to drought.

The groundnut pod has a capacity to absorb nutrients (calcium) and water and this ability depends on the genotypes (Tillman et al., 2010). In general, small pods imbibe Ca better than large pods (Walker, 1975; cited in Koolachart et al., 2013b). Under drought stress, greater reduction in seed size was seen in large seeded as opposed to small seeded seed types (Vorasoet et al., 2003). These findings have shown that pod number per plant contributes more to yield under any drought condition than seeds/pod and seed size. A high number of pods/plant under drought could be obtained either by selecting the groundnut genotypes with a high number of pods/plant under non-stress conditions or selecting the peanut genotypes with a low reduction in number of pods/ plant under drought.

1.6.1 Breeding for drought tolerance

1.6.2 Empirical selection approach

This is selection based on superior performance for primary traits under a given drought environment, which involves selection for high pod yield and other desirable agronomic traits on segregating populations as well as advanced breeding lines in replicated trials under stress and non-stress conditions (Nigam et al., 2002; Rao et al., 2003; Zhang et al., 2011). This approach however has limitations in that it is less efficient and requires many resources which more often than not are unavailable to most groundnut breeding programmes in Africa. Additionally, like other traits of economic importance, pod yield is a polygenic trait affected by large and uncontrollable G x E interactions and, as the result of this, breeding progress is often slowed (Nigram et al., 1991; Cooper and Hammer, 1996; Songsri et al., 2008).

1.6.3 Physiological selection approach for drought in groundnuts

The trait based approach involves selection for traits such as transpiration (T), transpiration efficiency (TE), WUE and HI. The WUE and TE traits are difficult to measure directly. Consequently, surrogate traits are instead used to measure WUE and TE. For example, SCMR and WUE have been reported to have strong and positive correlation (Nageswara Roa et al., 2001; Sheshshayee et al., 2006). Stomata density and conductance (SC) have also been associated with WUE (Songsri et al., 2013); Leaf relative water content (LRWC) has been used in sorghum and wheat as an index for dehydration avoidance (McCraing 1982; cited in Abdalla et al., 2007). A strong negative correlation between pod yield and canopy air temperature (CT) (Greenberg and Ndurugu, 1989; cited in Abdalla et al., 2007) has been reported. However, SCMR and SLA were found to be negatively correlated (Nageswara Rao et al., 2001; Upadhyaya et al., 2011). In addition, significant and positive correlations between SCMR and chlorophyll content (Akkasaeng et al., 2003) and chlorophyll density (Arunyanark et al.,

2008; Arunyanark et al., 2009) have been reported. On the above account, selection for consistently higher SCMR, and lower SLA under drought stress condition could be good selection criteria for genotype performance when used as surrogate traits for phenotyping for WUE and TE in groundnuts. In addition, other selection criteria such as higher LRWC, SC and lower CT are equally good selection for WUE and TE.

1.6.4 DNA marker-assisted selection for drought in groundnuts

Altered gene expression has been documented as one of the responses of plants to water stress (Ranganayakulu et al., 2012). Significant information has been assembled in regard to the role of various genes, transcription factors, cellular macromolecules and components of signal transduction cascades in plants under stress (Xiong et al., 2002). As such, identification and characterization of these genes is crucial for improving crops for drought tolerance through genetic and/or transgenic approaches.

Significant progress has been made in the identification of genes with a potential role in water stress tolerance (Sunkar et al., 2003; Zhuang et al., 2010; Ranganayakulu et al., 2012). Thus, introgression of these genomic regions (gene/QTLs) into genetic backgrounds of farmer preferred cultivars is key to sustaining yields under drought-prone conditions. However, drought is a complex trait conditioned by many genes under strong environmental influences making selections based on phenotype difficult (Collins et al., 2008). The application of DNA markers for indirect selection provides scope for phenotyping such traits (Sharma et al., 2002). In addition, molecular breeding methodologies such as using marker assisted backcrossing (MABC) through background and foreground selection procedures may be applied (Janila and Nigam, 2013). However, this approach is limited due to the fact that it cannot handle multiple traits/QTLs/genes in a single attempt due to necessity of large back-cross populations, which become unmanageable (Ribaut and Hoisington, 1998; Varshney et al., 2012). Therefore, the method becomes less useful for traits that are controlled by many genes/ QTLs.

The majority of the economically important traits including drought, are quantitative in nature and controlled by numerous genomic regions (genes/QTLs) each with small effects distributed throughout the whole plant genome (Janila and Nigam, 2013). Consequently, QTL analysis targeting improvement of such complex traits, involves the identification of several small-effect QTLs (Ravi et al., 2011; Gautami et al., 2012). Use could be made of the QTL analyses using a molecular breeding approach called marker-assisted recurrent selection (MARS) (Ribaut and Ragot, 2007), which can target several minor as well as major QTLs. The MARS has been proposed for improvement of drought tolerance in groundnut due to the discovery of more than 100 main and epistatic effect QTLs, however, it is not applied due to lack of dense linkage maps in groundnut, limiting the applicability of MARS (Ravi et al., 2011). Therefore, there is scope for use of molecular and genomic tools for

Improving drought tolerance in groundnut, however, all this will depend on successful improvement of the molecular genetic base of the cultivated groundnut and developing dense linkage maps which can be used for gene/QTL mapping and marker-assisted breeding. Thus, conventional breeding using empirical as well as physiological approaches is still useful for drought tolerance breeding.

1.7 Use of early maturity as a selection strategy for drought resistance in groundnuts

Adaptation of drought mitigation strategies calls for careful consideration of the various attributes of drought such as timing, intensity and duration (Cattivelli et al., 2008a). There are various mechanisms by which plants respond to drought and these may be categorized as escape, avoidance or postponement, and tolerance (Levitt, 1980; Ludlow and Muchow, 1990). Crop plants normally use more than one of these mechanisms to cope with drought at a time (Mitra, 2001). Tailoring crop phenology to soil available moisture in a drought prone area is called drought escape, and it is associated with rapid growth (early flowering and maturity), phenological plasticity and remobilization of assimilates to the economic yield. In areas where the growing season is short and also where terminal droughts are prevalent, deployment of early maturing crop genotypes is more feasible in order to optimally exploit soil available moisture (Turner et al., 2001; Passioura, 2007; Janila and Nigam, 2013). However, other studies (Kumar et al., 1985; Roa et al., 1992) support the opinion of using early maturing groundnut genotypes only as a short term strategy especially for drought prone areas because they are generally related to low yields.

There are reports that indicate low seed yields and/or yield because the grain filling period was greatly reduced when extremely early maturing groundnut genotypes were selected, although this may not be true in all cases (Karamanos and Papatheohari, 1999; Cattivelli et al., 2008). Earlier studies by Fereres et al. (1986) also disproved the maturity strategy because such early genotypes may have shallow roots which are not appropriate for rainfall dependent production systems making them prone to intermittent droughts and ultimately low yields. Roa et al. (1992), however, argue that higher yields in early maturing groundnuts are possible and perhaps more so when combined with good crop management practices on genotypes that have synchronized pod setting. Early maturity as a drought escape strategy in crops is once again getting more attention and is projected to gain even more importance in the wake of the predicted increases in temperature and the shortening of growing seasons of up to 5% or more in the tropics where groundnut is predominantly grown (Janila and Nigam, 2013).

1.7.1 Phenotyping for early maturity in groundnut

Optimization of crop adaptation and yield at different water availability levels depends on the time of flowering (Tuberosa, 2012). The relative changes in flowering time can affect level of yields in many crops (Sandras et al., 2009; cited in Tuberosa, 2012). Thus, the ability of a crop's phenological stage duration to change under stress may provide an opportunity to manage drought.

Groundnut is an indeterminate legume with a long flowering period, producing a high number of flowers, although only a few mature into pods (Krishna Sastry et al., 1985). Days to flowering initiation and duration for accumulation of first 25 flowers in a genotype have been proposed as important traits for early maturity in groundnut (Upadhyaya and Nigam, 1994). However, earliness based on early flowering is affected by large G x E variation (Khan et al., 2010) and would require testing in multiple environments making it less effective as a selection strategy for drought management.

Rao et al. (1992) proposed the use of the concept of thermal time or degree days (CTT or °Cd), based on temperature, which was neutral to both location and season to breed for early maturing varieties with stable maturity duration across locations. Taking 10 °C as base temperature for groundnuts cumulative thermal time or cumulative degree days (CTT or °Cd) is calculated from the maximum and minimum temperatures daily. The daily thermal time is accumulated each day from planting to harvest to arrive at the CTT or °Cd. The standard CTTs of 1240 and 1470 Cd corresponding to 75-day and 90- day crop growing cycles, respectively, have been used to predict the harvest dates for early-maturing groundnut breeding materials and trials in each season (Janila and Nigam, 2013). The CTT

or °C d for other locations can also be worked out using the formula: $\sum_P^H [(T_{max} + T_{min}) / 2] - T_{base}$,

where Tmax is daily maximum temperature, Tmin is daily minimum temperature, Tbase is mean base temperature for groundnut, P is planting date and H is harvest date.

In breeding for early maturity, the segregating progenies, and preliminary and advanced yield trials are harvested at 1,470 °Cd and selection is practiced based on number of mature pods per plant and yield. The selection is stricter in the elite trial and is harvested more than one time, first when the crop is sampled at 1,240 °Cd and next at 1,470 °Cd. The selection for early maturity is based on the increase in pod yield, shelling outturn and 100-seed weight from 1,240 and 1,470 °Cd, and the genotypes recording the least increase are selected for early maturity (Janila and Nigam, 2013).

1.8 Groundnut grain quality

Quality of shelled groundnut can be explained by a combination of chemical and physical traits and sensory factors (Dwivedi et al., 1996; Misra, 2004). Key physiochemical characteristics that are of

major economic importance and, therefore, of concern to any breeding programme include sound mature kernels percentage, shape of kernels, seed size uniformity, 100-seed mass, colour of the testa, moisture content, sensory factors (seed colour, texture, flavour) and nutritional factors (oil, protein, sucrose, reducing sugar, and free amino acid among others) (Dwivedi et al., 1996; Mugisha et al., 2014)

Until recently, breeding efforts for groundnut improvement had been mainly geared towards increasing pod yield and oil content as the crop was mainly regarded as oilseed crop (Bishi et al., 2013; Okello et al., 2013). But, recent reports indicate a changing pattern perhaps due to factors ranging from urbanization to increasing availability of cheaper alternative sources of oil (Bishi et al., 2013). Many long-term health benefits can be obtained by consumption of groundnuts due to concentration and availability of bio-functional components like tocopherol, niacin and folic acid; mineral components like Cu, Mn, K, Ca, and P; dietary fibres, phytosterols like resveratrol, beta-sitosterol; flavonoids and phenolic acids (Francisco and Resurreccion, 2008). Peanut oil is also rich and composed of oleic (monounsaturated fatty acid) and linoleic acids (polyunsaturated acid) which make up 80% of the total fatty acid profile of groundnut seeds (Treadwell et al., 1983). Additionally, the confectionery type groundnut is increasingly becoming important as a snack in the domestic and international markets (Bishi et al., 2013).

In Uganda, groundnut consumption has gained more ground as a cheap source of protein especially for the rural poor (Okello et al., 2013). As the demand for confectionery peanut type increases, there is a need to re-direct the breeding strategy so as to focus on both confectionery and oil extraction end-use equally. Much as the physical (shape, size and colour) qualities are considered critical for direct consumption; chemical attributes also need to be considered so as to improve the sensory as well as the nutritive qualities of groundnut. This further demonstrates the fact that the quality requirements of groundnut for confectionery use are quite different from those for oil extraction. Characters that are a must-have for confectionery grade varieties are high protein and sugar, low oil and aflatoxin contamination, attractive seed size and shape, pink or tan seed colour, ease of blanching and high oleic/linoleic acid (O/L) ratio (Dwivedi and Nigam, 1995 cited by Ajay et al., 2011).

1.9 Variation for grain quality traits and its sources

Groundnut quality is influenced by factors that are under genetic and environmental control (Upadhyaya and Nigam, 1999; Noubissié et al., 2012). Several studies have revealed genetic variation among breeding germplasm and landraces for several quality traits such as: hundred kernel weight (Dwivedi et al., 1990; John et al., 2008); seed size, oil content and fatty acid profile (Treadwell et al., 1983 cited by Dwivedi et al., 1996; Norden et al., 1987; Dwivedi et al., 1998); nutritional factors (Norden et al., 1987; Upadhyaya et al., 2005) in cultivated groundnut, and even higher variation in

other *Arachis* species (Cherry, 1977). Existence of this variation offers opportunity to breed for grain quality to meet specific market requirements.

1.9.1 Mode of gene action for grain physical quality traits in groundnut

Genetic improvement of traits of interest largely depends on the existence of variation and knowledge of the nature of genetic control underlying the traits. Understanding the nature of variability of the trait is important because it determines the breeding scheme to be followed for improvement of that trait. Studies on the nature of gene action for physical qualities are few and conflicting (Dwivedi et al., 1989; Palmar et al., 2000; Vindhiyavarman, 2000, 2001; Hariprasanna et al., 2008). Recent studies (Venuprasad et al. 2011) reported predominance of additive genes for seed weight, seed length, seed width, and length-width ratio. Earlier studies found that the traits governing groundnut grain physical qualities are under the control of additive genes although non-additive genes also played a role (Dwivedi et al., 1989; Palmer et al., 2000; Hariprasana et al., 2008). In addition, significant reciprocal effects for all grain physical traits have been related to the role of the maternal parent and the importance of parental selection in quality breeding (Hariprasana et al., 2008; Venuprasad et al., 2011).

However, other authors have also suggested the predominant role of non-additive effects in the control of these traits (Vindhiyavarman, 2000; 2001). Furthermore, more recent studies (Lal et al., 2014) have found inter-allelic gene control for physical traits such as shelling out turn, 100-pod weight, 100-seed weight, sound mature kernels, pod length, seed diameter and the ratio of seed length to seed diameter. Given the conflicting and rare reports regarding the inheritance of the physical grain traits in groundnut, there is a need for further investigations. Besides, there are also a few studies regarding the inheritance of grain quality traits in crosses among sub-interspecific lines and the correlation of grain quality traits with agronomic traits which warrant further investigations. Furthermore, the role of maternal effects in the inheritance of grain quality traits in sub- interspecific lines needs to be investigated.

1.9.2 Relationship between physical grain traits and drought tolerance traits

The relationship between drought tolerance traits is best expressed through seed yield under stress and non-stress conditions. Seed yield was highly significant and positively correlated with 100-kernel weight, seed length and seed width in several studies (Roy et al., 2003; Kavani et al., 2004; Gopal Reddy, 2008). Other studies have also reported moderately significant correlation of drought tolerance traits with yield components such as seed size, shelling percentage, sound mature kernels, and pod size under non-stress conditions (Songsri et al., 2009). However, under stress conditions, there were weak or negative correlations between drought tolerant traits and seed quality traits. In addition, some

studies reported that seed quality traits such as sound mature kernel percentage, 100-seed weight, shelling percentage and percentage maturity level (Clavel et al., 2004) and 100-seed weight (Vorasoot et al. 2003) were negatively affected by water deficit stress. This has implication for indirect selection of drought tolerance traits for physical seed traits of groundnuts.

The weak association of drought tolerant traits with seed physical traits implies independent genetic control for their expression (Reddy, 2008). Such weak association also points to ample possibility of simultaneous improvement of drought tolerance and physical grain traits through enhanced seed yield under stress and non-stress conditions. Such relationship would be advantageous for improving seed yield without compromising seed size. Consequently, the selection of high pod yield potential under no-stress or small reduction in pod under drought stress should guarantee high seed size.

1.10 Implications of diseases and insect pests on breeding groundnuts for drought tolerance

Besides its narrow genetic base, groundnut productivity is heavily undermined by both abiotic and biotic stresses which have been reported to occur together in most of the cases, causing significant reduction in both quantity and quality of groundnut. Drought rarely occurs in isolation, but interacts with biotic stresses (pests and diseases) (Wheatley et al., 1989; Ceccarelli et al., 2007), agronomic management and soil types (Sadras and Angus, 2006), and its effects are more felt by resource constrained farmers (Ceccarelli et al., 2007). For example, leaf miner (*Aproaerema modicela*) was found to be more devastating on drought stressed groundnuts especially when canopy temperature was high. In addition, biochemical changes in drought stressed groundnut crop leading to increase in levels of soluble carbohydrates and amino acids in leaves caused an increase in growth and reproductive rates of phloem feeding insects such as aphids (Wheatley et al., 1989). Therefore, drought can never be handled in isolation, especially in a system dominated by resource constrained small-holder farmers. This situation presents a challenge to efforts aimed at making groundnut a more competitive (at least in terms of yield and trade volumes) and nutritionally superior crop (Upadhyaya et al., 2014). It is thus necessary to select cultivars with enhanced host plant resistance for diseases and pests, adaptation to abiotic stresses, input use efficiency and yield potential. Identification and use of such cultivars should maximise gains, while minimising inputs and thus enable groundnut to compete favourably with other crops. In relation to this, selection of genetically diverse germplasm with several valuable traits should be the aim of any successful breeding programme. Therefore, this study aims to identify groundnut genotypes with not only drought tolerance, but rather those with drought tolerance in combination with acceptable resistance to groundnut rosette and its putative vectors, and also with acceptable consumer qualities for further development and eventual release to farmers.

11 Farmers' preferences for groundnut variety adoption

Several studies have documented farmer's preferences for groundnut varieties in areas where the crop is grown. Generally, farmers prefer varieties that provide a high and stable yield (Adu-Dapaah et al., 2007; Masette and Candia, 2011; Chintu, 2013); however, their choices for varieties are dictated not only by personal preferences but also by other factors such as interest of consumers and processors (Chintu, 2013; Mugisha et al., 2014), and also by traders (Shiferaw et al., 2010). In the case of groundnuts, studies by Mugisha et al. (2014) reported that consumers have high culinary preferences, especially regarding physical and eating qualities. Physical (shape, size and colour) qualities were considered critical for direct consumption in addition to sensory attributes such as taste, which also influenced the choice of traded variety on the market. This would imply that a popular variety is expected to have preferred grain and eating qualities (Tan et al., 1999). However, quality is often difficult to identify as it is defined by end users and their preferences are highly variable (Traore, 2005).

Different end uses for groundnut dictate different attributes of groundnut grain (Ajay et al., 2011). Groundnuts meant for direct consumption or confectionery types are normally larger seeded, have a low oil content, and a high sugar and high protein (Ajay et al., 2011). By contrast, those meant for oil extraction are small seeded with high oil content and low protein content (Chintu, 2013). Therefore, careful selection for groundnuts with desired traits for each end-use has positive implications for adoption of such varieties. Besides yield and quality attributes, other attributes that influence choice of varieties include tolerance to pests and diseases, early maturity and tolerance to drought (Nutsugah et al., 2007; Chintu, 2013; Jnr et al., 2014). However, of all these traits, drought tolerance is the least investigated.

The low rate of adoption of released varieties reflects the lack of involvement of farmers prior to development of putative varieties (Virk et al., 2002). The primary goal of participatory plant breeding (PPB) is developing locally adapted cultivars with diverse traits that are valued by farmers in the farmers' locality (Bellon, 2006; Joshi et al., 2007). Participatory rural appraisal (PRA) techniques have been applied in PPB to understand farmer's priorities, preferences for variety choice, and to set breeding objectives that meet these requirements (Adu-Dapaah et al., 2007). In addition, this approach enables breeder to collect key information on the physical environment where the crop is grown, the existing varietal diversity, the size of market, and the essential traits (Witcombe et al., 2005). Therefore, to ensure increased adoption, both farmers' preferences and physical parameters that define the target environment have to be taken into consideration during the process of developing varieties.

farmers' preferences can guide breeders in the development of new groundnut varieties (Ajay et al., 2011). This was found to be the case in the breeding of groundnut in Ghana (Adu-Dapaah et al., 2007). In Uganda, there is limited information on farmer variety preferences for guiding breeders in groundnut improvement. In addition, only a few studies highlight the implications of imminent droughts on groundnut productivity and its ramifications on groundnut quality caused by climate change, farmers' perception of drought per se, its ranking among production constraints, how current cultivars respond and the ranking of farmer and/or consumer preferred traits across different regions of Uganda. This information is urgently needed for guiding breeders for groundnut improvement.

1.12 Summary literature review

The literature review demonstrated that the exploitation of genes for tolerance to several biotic and abiotic constraints has been through intraspecific breeding and lately, interspecific breeding using materials collected at international repositories (or gene banks). It also noted the increasing need to exploit the huge variation that is found in the wild relatives of groundnut to improve various traits including tolerance to droughts.

The review provided information on farmers' groundnut variety preferences, the state of groundnut breeding in terms of tools for breeding, and also highlighted the importance of physical grain traits for direct consumption of groundnuts and that breeding for tolerance to drought and optimum seed physical attributes could be enhanced. In addition, the review established that progress has been made in improving groundnut for drought tolerance using biotechnology approaches. However, most of the biotechnology approaches have limited use at the moment because of poor repeatability of results due to limited genetic variation in groundnut in part and also due to the fact that dense genetic linkage maps for groundnut are still limiting. Therefore, much work for the improvement of groundnut for drought tolerance and physical seed quality lies in its genetic improvement using conventional breeding by means of empirical and physiological approaches. In order to exploit the genetic potential of the crop, studies to understand the genetic function of genes involved in drought tolerance mechanisms and inheritance for drought tolerance and physical seed quality in landraces and sub-specific groundnut lines, are required.

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CHAPTER 2 Farmer perception of drought, other production constraints and production system, their implication for groundnut breeding in Uganda

Abstract

Drought is among the major constraints limiting groundnut productivity in the smallholder farming in Sub-Saharan Africa. The major objectives of this study were, therefore, to; i) determine how smallholder farmers perceive and cope with drought, and ii) to identify farmers' other production constraints and production systems in Uganda. Data were collected from a total of 247 farmers from three major groundnut growing regions in Uganda using surveys and participatory rural appraisal (PRA) methods. The results revealed that groundnut in Uganda is primarily grown by small scale farmers mainly for subsistence under both mono and mixed cropping systems. Unpredictable weather, pests and diseases, rodents, soil exhaustion and lack of access to improved varieties were the most important constraints identified. All farmers surveyed agreed that drought was a major production constraint, although its rank among production constraints varied with location and season. The local perceptions of drought included hot sunny weather, and poorly distributed and little rainfall. Almost 48.3% to 82.5% of the farmers, depending on the region, perceived drought as warm/hot windy conditions, little rainfall or just hot sunny weather. The majority of farmers surveyed, from eastern (81.7%), northern (77.6%) and mid-western regions (86.6%), indicated that the major impact of drought was low yields, showing clearly that farmers understood the effects and consequences of drought. Several drought mitigation measures are used by farmers including early planting and growing drought tolerant varieties or, using either short maturing varieties or simply not growing groundnut in the season associated with drought. Nonetheless, a large percentage of farmers would like drought tolerance to be bred into their preferred varieties providing an entry point for improving farmers' preferred varieties for tolerance to drought.

2.1 Introduction

About 90 % of the world's groundnut production occurs in the tropical and semi-arid tropical regions. Much of these regions are characterized by high temperature and low or erratic rainfall and drought is a familiar occurrence. In addition, the crop is mostly grown by small scale farmers with no capacity to adequately optimize production in these areas (Pasupuleti et al., 2013)

In Uganda, groundnut is the second most important food legume after common beans (*Phaseolus vulgaris* L.) (Okello et al., 2014; Kabeere and Wulf, 2008; UBOS, 2013). The crop is popular, especially in the eastern and northern regions of the country where it has become a part of the peoples' culture (Rooney and Giller, 2012; Mahmoud et al., 1991 cited in Mugisa et al., 2015). It is grown throughout the country in diverse environments including both dryland and rain fed conditions (Rooney and Giller 2012) and by small holder farmers with little or no inputs (Shiferaw et al., 2010; Mugisha et al., 2011; 2014). Studies have indicated yields in Uganda average 0.8 t ha⁻¹ of dried pods which is in sharp contrast to yields at research stations ranging from 2.5 to 3.0 t ha⁻¹ (Kaizzi et al., 2013; Okello et al., 2014). This is due to several production constraints.

Amongst the major constraints limiting groundnut productivity are abiotic and biotic stresses (Okello et al., 2010, 2014). These constraints vary among growing areas and between cropping seasons (Rooney and Giller, 2012). For example, disease epidemics and insect pest outbreaks frequently occur as a result of the warm climate and/or high rainfall common to many groundnut production zones in sub Saharan Africa (SSA) (Vivek et al., 2010). Several diseases are widespread in most SSA groundnut production areas and these include groundnut rosette virus (GRVD), early and late leaf spot (ELS/LLS) and rust (Naidu et al., 1999; Okello et al., 2010). As a result of favourable seasons with high rainfall, diseases also become more prevalent and damaging, yet the majority of small scale farmers do not control the diseases due to limited access to pesticides. The abiotic stress, drought, has the potential to amplify already existing risks such as diseases resulting in increased yield losses (Mubaya et al., 2012). This trend is likely to cause significant damage on groundnut production. Although there are a few commercial cultivars available with some level of resistance to some of these stresses, the intermittent occurrence of drought has been increasing (Kassie et al., 2011). Therefore, research is urgently needed to develop groundnut cultivars with enhanced levels of disease resistance and high abiotic stress tolerance to ensure a sustainable increase in groundnut yields, especially in the smallholder farming sector.

It is imperative that high priority research be given to these constraints in all the important groundnut production areas of Uganda. To achieve this, it is important to understand how smallholder farmers recognize the production constraints in their environments and what mechanisms they have to cope with some of these constraints. This will aid in developing relevant cultivars that meet the farmers' needs.

Participatory methods have been used to gather information on important traits, and in facilitating breeding programmes for these traits to achieve a greater impact (Witcombe et al., 2005, Asfaw et al., 2006). Farmers can provide important information on plant types, desired traits and insight into trade-offs they are willing to make among traits in designing new cultivars (Sperling et al., 2001). Therefore, if the farmers' priorities, needs and capacities are valued and better understood by researchers, then appropriate and sustainable recommendations can be made and thus, increase the chances of adoption of new technologies (Horne and Stur, 1999; Scoones et al., 2009; Sibiya et al., 2013). The objectives of this study were therefore to; (i) assess farmers' perceptions on drought and (ii) identify and validate other constraints in groundnut production (ii), identify groundnut production systems in a selected smallholder farming area of Uganda.

2.2 Materials and methods

A participatory rural appraisal (PRA) approach was adopted and this involved the use of focus group discussions (FGD) and household interviews. The PRA was conducted in 2015.

2.2.1 Study areas and their characteristics

The mid-western, north and eastern regions were selected for their importance in groundnut production in Uganda. Hoima, Masindi, Lira, Dokolo, Amuria and Kumi were selected as the key groundnut producing districts representing different ethnic communities and agro-ecological zones (AEZ) (Figure 2.1). The western zone (Hoima and Masindi) is predominantly inhabited by the Bantu speaking Banyoro ethnic group. This area receives two rainfall peaks (1200-2000mm), April/May and August/September, respectively. The major economic activity in this area is agriculture with much prominence given to food crops.

The Lira and Dokolo districts are part of the Lango sub region in Northern Uganda. The majority of the population are ethnic Langi and the predominant language is Luo. This region has got a diversified and vibrant economy. The region receives between 1000-1400 mm of rainfall annually in a bimodal rainfall pattern - from March to May and again from August to October.

The Amuria and Kumi districts are part of the Teso sub-region. It is home to Iteso and Kumam ethnicities. This region receives annual rainfall of about 1100-1200 mm, distributed between two seasons of March to May and September to November. Late February/early March is usually the long dry season period while Mid-June to late July is the short one. Two sub-counties were sampled from each district based on ethnic community and AEZ. In these, five neighbouring villages were randomly sampled.



Figure 2.1 Map of Uganda showing study sites, with the sampled areas represented by black stars

2.2.2 Sampling procedures, participants and data collection

2.2.3 Focus group discussions and survey

A research team comprising the breeder, research assistant, agricultural extension staff and key village elders was established to facilitate this activity. Participatory methodologies used included focus group discussions, matrix scoring and pair-wise ranking. The discussions were guided by two facilitators in the local language (depending on district) and notes were written down in English on a flip chart. The discussions involved key informants made up of individuals who had great knowledge about the villages, the farms, crops and local conditions and production problems in the district. The groups were a mixture of farmers (both men and women) who planted many crop varieties including groundnut, farmers with a reputation for good workmanship, young and old farmers, and farmers with large or small land holdings (Plate 1). Farmers identified the "core problems or constraints" to groundnut production, listed them and ranked them according to the most important constraints. In addition, the farmers listed and ranked the essential traits and indigenous technical knowledge skills (ITKS) for their evaluation. The facilitators used various visual aids including pictures showing drought symptoms and cards that had drawings representing various constraints to assist the farmers during the discussions. Later, the farmers who did not participate in the FGDs were randomly selected from a list of households compiled by village heads and interviewed using a structured questionnaire. A total of 128 farmers (68 females and 60 males), were interviewed (Plate 2).

2.2.4 Survey

The structured survey served as a control for checking or comparing information obtained through participatory methods. The survey was conducted through field visits, observation and assessment. In each of the sub-counties, 30 farmers were selected randomly among growers with the assistance of agricultural extension officers, principal investigator (breeder) and production officers at each district who were familiar with the farmers and fields concerned. In each district, sub counties were selected based on their performance and history of groundnut production.



Plate1: Partial view of FGD panel in Hoima district



Plate 2: Partial view of enumerator interviewing a farmer in Alebtong district

2.3 Data analysis

Data collected from the six districts were analysed and descriptive statistics were generated using SPSS (Release 15.0). The study results were presented using percentages, means, frequencies and standard deviations.

2.4 Results

2.4.1 General crop production systems

Across all regions, there were no significant differences in the land owned per household and yields of groundnuts. However, significant ($P \leq 0.001$) differences were observed for the land that was dedicated to groundnut cultivation. Mean land ownership per household was 2.13, 2.10, and 2.41 ha in the eastern, northern and mid-western regions, respectively (Table 2.1) and the majority of the farmers owned the land as opposed to other land tenure systems (Figure 2.2). Mean farm size under groundnut was 0.46, 0.35 and 0.38 ha in the eastern, northern and mid-western regions, respectively. The majority of farmers in eastern (62.9%) and northern (62.1%) region prepared land by ox-plough while in mid-western region, 73.8% use hand digging (Table 2.2). The major source of labour for farm work was contract labour in the mid-western and the eastern Uganda, while in the northern Uganda, family labour is the major source of labour (Figure 2.3). During group discussions, farmers indicated that the major source of groundnut seed for planting was farmer's saved and village markets. While a majority of groundnut farmers in the eastern (45.3%) and the mid-western region (70.4%) used their own seed, those in the northern Uganda (77.8%) get the seed from local markets (Table 2.3). This may pose a risk of disease spread, though it enhances variety diffusion and adoption.

Table 2.1 Land holding used for groundnut production and yields obtained (n=60 respondents per region)

Parameter	Eastern	Northern	Mid-western	mean	P value
Total land per household	2.13	2.10	2.41	2.17	
Area for groundnut (ha)	0.46	0.35	0.38	0.40	0.001
Yield (bags harvested)	10.73	11.19	11.82	11.25	
Yield (kg/acre)	423.5	578	571.7	527	

Table 2.2 Groundnut production systems in eastern, northern and mid-western Uganda

Description	Type	Region		
		Eastern (n=62)	Northern (n=58)	Mid-western (n=65)
Land preparation methods used (% farmers)	Hand digging	35.5	37.9	73.8
	Ox-plough	62.9	62.1	3.1
	Tractor	1.6	0	23
Cropping system (% farmers)	Inter cropping	33.3	42	48.6
	Sole cropping	66.6	58	51.4
Crops intercropped with Groundnuts (% of farmers)	Pearl millet	0	23.3	0
	Maize	89.3	76.7	76.6
	Sorghum	7.1	0	0
	Cassava	0	0	17
	Beans	0	4.7	0
	Pigeon peas	0	5	0
	Field peas	0	2.3	0
	Cowpeas	0	2.3	0

Table 2.3 Sources of seed of groundnut among respondents

Source of seed	% of respondents		
	Eastern (n=64)	Northern (n=54)	Mid-western (n=54)
Own farmers saved	45.3	18.5	70.4
Bought from market	43.8	77.7	25.9
Given by NGO	1.5	1.8	3.7
Gov't agency	6.2	1.8	0

Owned Rented Borrowed Share cropped

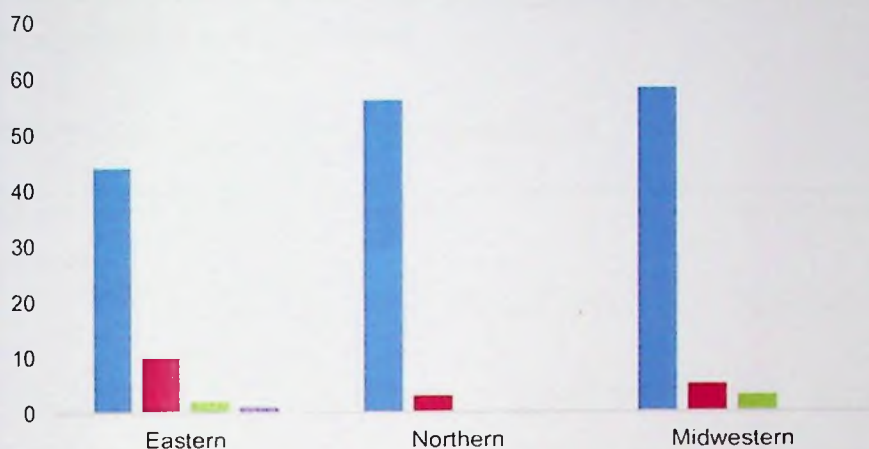


Figure 2.2 Land tenure systems for farms owned by small holder farmers in eastern, mid-western and northern regions, Uganda



Figure 2.3 Sources of labour used by surveyed households

The majority of farmers in the eastern (95.2%) and northern (80.3%) regions grow groundnut in the first season, while in the mid-western region a majority of farmers grow the crop in second season (Table 2.14). According to the farmers surveyed, the choice of season was primarily determined by the availability of sufficient rainfall.

Table 2.4 Choice of season to grow groundnuts

Season for cultivation of groundnuts	% of respondents		
	Eastern (n=63)	Northern (n=56)	Mid-western (n=67)
Season one	95.2	80.4	31.3
Season two	1.5	3.6	41.8
Both	3.2	16.1	26.9

2.4.1.1 Groundnut varieties grown by farmers in the study areas

Farmers grow only a small number of varieties (Table 2.5). In the eastern region, the most popular variety is Serenut 2 (42.2%), while in northern Uganda, the most popular variety is Olwok-olwok-Arema (37.0%), and in mid-western Uganda, the majority of farmers (81.5%) grow Red beauty, a landrace.

Table 2.5 Groundnut varieties commonly grown in the various regions

Varieties grown	% of respondents		
	Eastern (n=64)	Northern (n=54)	Mid-western (n=54)
Serenut 2 (Igola)	42.2	14.8	0.0
Serenut 4	10.9	0.0	0.0
Serenut 6	9.4	0.0	0.0
Red beauty	4.6	22.2	81.5
Oluk-olwok-arema	0.0	37.0	0.0
Erudurudu	20.3	0.0	0.0
Etosot/egoromoiti	9.4	0.0	0.0
Oluk-oluk-Atar	0.0	18.5	0.0
Alur	0.0	3.7	0.0
2-seeded (Poland)	0.0	0.0	9.0

2.4.1.2 Other crops grown

In season 1, besides groundnut, the major crops grown are sim sim, maize and sorghum in eastern region. In the northern and mid-western regions, the major crops grown are maize and beans (Figure 2.4). In the eastern and northern regions, the majority of farmers practice sole cropping, while in the mid-western region, almost all farmers practice mixed cropping (Figure 2.5)

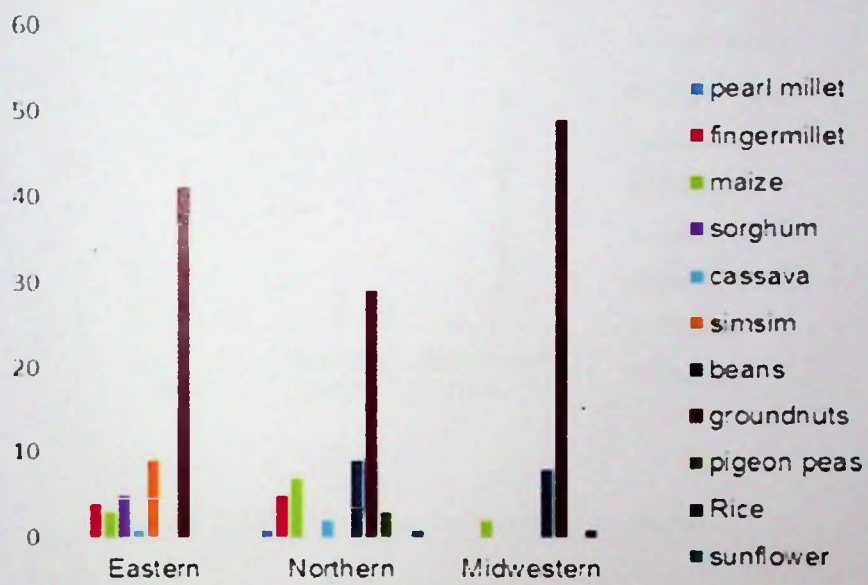


Figure 2.4 Crops grown in season 1

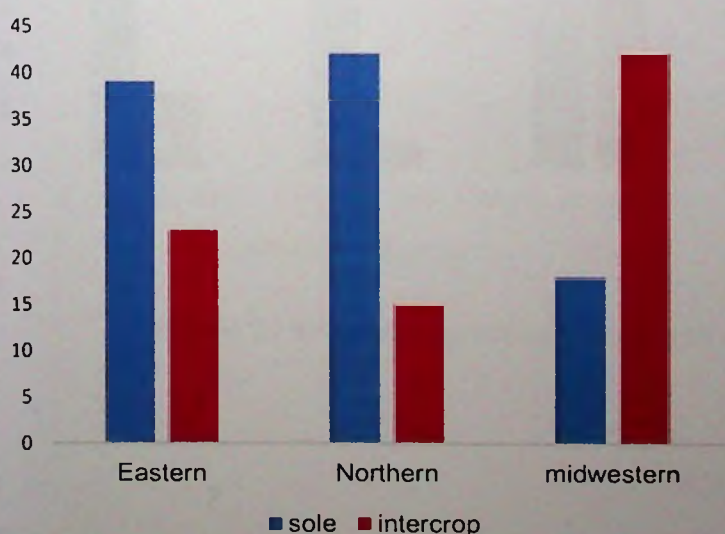


Figure 2.5 Production systems practised by farmers in season 1

Figure 2.6 and Figure 2.7 present the major crops grown and cropping systems under which they are grown in season 2. Besides groundnut, the major crops grown are sorghum, sim sim, cassava and finger millet in the eastern region. In the northern region, the major crops grown were sim sim, cassava and beans. In the mid-western region, maize, beans and sweet potato. As in season 1, in the eastern and northern regions, the majority of farmers practice sole cropping while in the mid-western region, almost all farmers practice mixed cropping.

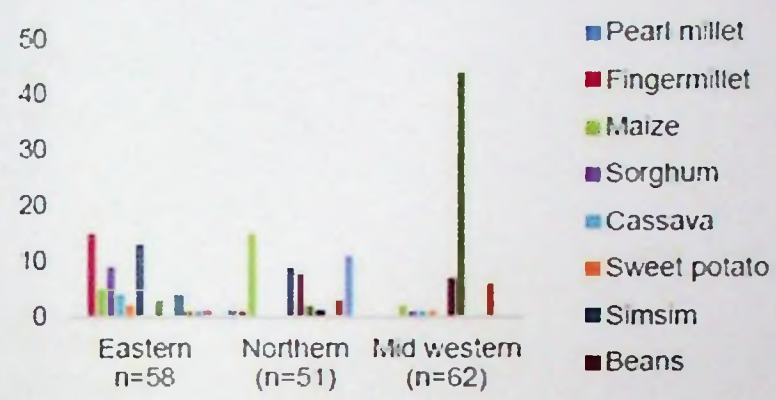


Figure 2.6 Crops grown by farmers in season 2

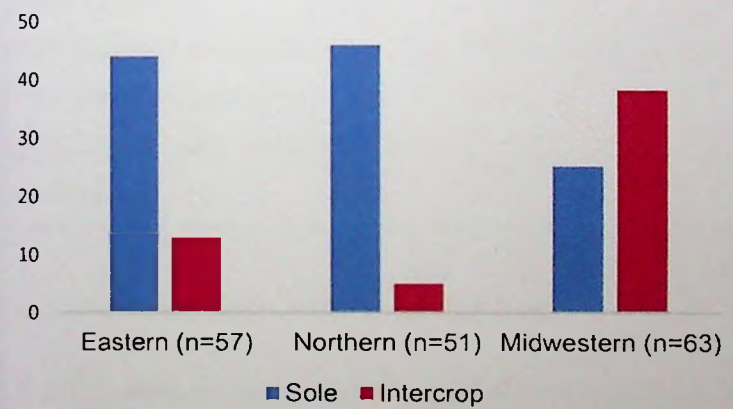


Figure 2.7 Production systems practiced by farmers in season 2

2.4.2 Groundnut production constraints

A total of eight groundnut production constraints were identified and ranked during the FGDs across all the three study regions (Table 2.6). Unpredictable weather, lack of access to improved varieties, limited access to extension services and pests and diseases were identified as the most important production constraints and were consequently ranked, first, second, third and fourth, respectively, across the study sites.

Table 2.6 Direct matrix ranking of groundnut production constraints by farmers in the eastern, mid-western and northern regions

Constraint	Rank			Mean Rank
	Mid-western	Eastern	Northern	
Unpredictable weather	1	5	3	3.0 (1)
Pests and diseases	2	3	8	4.3 (4)
Lack of access to improved varieties	3	1	6	3.3 (2)
Post maturity/post-harvest pests – Rodents	8	6	5	6.3(7)
Poor soils/soil exhaustion	6	4	4	4.7(5)
Poor markets/low prices	4	9	1	4.7(5)
Limited access to extension services	6	2	4	4.0 (3)

2.4.3 Farmers' perception of drought

2.4.3.1 Farmers' perception of drought in terms of weather events

The majority of the farmers in this study perceive drought as hot sunny weather, poorly distributed rainfall and little rainfall (Table 2.7). In the eastern region, most farmers (55.74%) perceived drought as warm/hot windy conditions. In the northern region, most farmers (82.5%) perceive drought as little rainfall while in the mid-western region, majority (48.39%) perceive drought as hot sunny weather.

Table 2.7 Farmers' perception of drought in terms of weather events

Meaning of drought in terms of weather events	% of respondents		
	Eastern (n= 61)	Northern (n= 40)	Mid-western (n= 62)
Hot sunny weather	26.2	35.0	48.4
No rainfall for a long time	80.3	12.5	37.1
Warm/hot windy conditions	55.7	5.0	27.4
Hard soil	0.0	0.0	9.7
Poorly distributed rainfall	22.9	52.5	22.6
Little rainfall	27.9	82.5	11.3
Misty weather	0.0	0.0	16.1

In all regions, there is no significant difference in the perception of farmers about the occurrence of drought in either season 1 or 2 (Figure 2.8). However, there are differences in the perception of farmers about drought occurrence in both seasons in the eastern and mid-western regions. In the northern region, farmers did not report any occurrence of drought in both seasons per se.

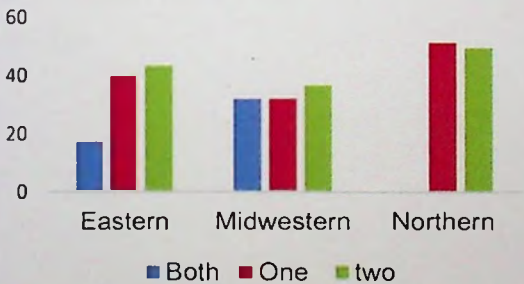


Figure 2.8 Seasonal drought occurrence

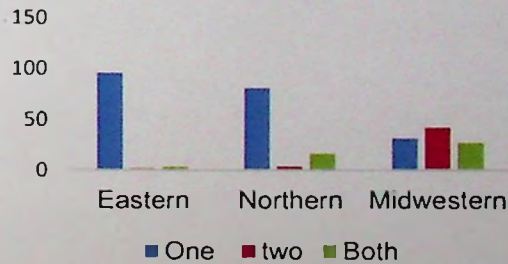


Figure 2.9 Groundnut cultivation season

Although there were no differences in the response of farmers on the occurrence of drought in either season 1 or 2 in all regions (Figure 2.8), most farmers in the eastern (95.2%) and northern (80.4%) region grow groundnuts almost exclusively in season 1 because of the presence of more reliable rainfall in that season (Figure 2.9). On the other hand, farmers in mid-western region grow groundnuts in any or both seasons and this result agrees with their response/perception of drought occurrence (Figure 2.8).

2.4.3.2 Occurrence of drought in the last 10 years

In the last 10 years, the farmers expressed highly varied responses to the occurrence of drought in their areas. Farmers in the eastern region reported drought to have occurred close to four times in the reporting period, followed by mid-western as three times and the least occurrence of drought was reported by farmers from the northern region (Table 2.8).

Table 2.8 Mean occurrence (years) of drought in the study area

	Eastern	Northern	Mid-western
Mean	3.8	2.5	3.4
S.D	1.9	1.3	1.7
Min.	1	0	1
Max	10	6	10

The majority of farmers surveyed, namely 81.7%, 77.6% and 86.6% from the eastern, northern and mid-western region, respectively, indicated that the major impact of drought on their farming activity is low yields (Table 2.9). Besides this, other perceived impacts include, no yield at all and shortage of sufficient food. This perception shows clearly that farmers understood the effects and consequences of drought.

Table 2.9 Perceived impact of drought on crop yields, food and nutritional security

Effect of drought on crop yield/food and nutritional security	% of respondents		
	Eastern (N=60)	Northern (N=58)	Mid-western (N=67)
Low yields	81.7	77.6	86.6
No yield	38.3	21.0	28.4
Shortage of sufficient food	26.7	55.2	19.4
Famine	46.7	34.5	17.9
Malnutrition	6.7	3.5	3.0
Low income	1.7	0.0	3.0
High food prices	0.0	0.0	1.5

This study also found that farmers believed that drought does not affect all stages of growth equally. The farmers indicated that the critical stages at which drought is most significant was at flowering, pegging and pod development (Table 2.10). The majority of the farmers, 75.4% and 62.2% in the eastern and northern, respectively, indicated that drought was most destructive at the pegging stage. In the two regions, these results agree with their perception of the direct effect of drought on groundnut such as poor pod filling (Table 2.11). However, the farmers from the mid-western region noted that drought was most destructive at flowering (Table 2.10), although this was not supported by results on the direct effect of drought on groundnut (Table 2.11). Instead, the farmers in the mid-western, indicated that drought's direct effect on groundnut was mainly stunted leaf growth (53.9%) and leaf abortion (52.3%).

Table 2.10 Perception of stage of groundnut most affected by drought

Stage of groundnut most affected by drought	% respondents		
	Eastern (N= 61)	Northern (N=58)	Mid-western (N=66)
Germination	0.0	0.0	0.0
Before flowering	0.0	0.0	4.6
Flowering	54.1	34.5	69.7
Flower fall	3.3	3.5	3.0
Pegging	75.4	62.1	36.4
Pod development	13.1	20.7	10.6
Pod filling	3.3	3.5	0.0

Table 2.11 Farmers' perception of direct effect of drought on groundnut varieties

Characteristics of groundnut varieties affected by drought	% of respondents		
	Eastern (N=58)	Northern (N=57)	Mid-western (N=65)
Have small seeds	20.7	22.8	10.8
Leaves dry-up and fall off	50.0	50.9	52.3
Stunted growth	34.5	63.2	53.9
Yellowing of leaves due to premature aging	51.7	49.1	24.6
Withering of flowers	34.5	24.6	3.1
Poor pod filling	48.3	35.1	44.6
Light weight of harvest	19.0	26.3	3.1

2.4.3.3 Farmers' perception of the quantity of losses incurred due drought occurrence

Generally, across regions, all farmers were able to distinguish between the losses that could be incurred under mild (19.1%), moderate (42.1%) and severe (71.4%) drought (Table 2.12). Drought losses in the northern (24.0%-63.0%) and mid-western (20.0%-76.5%) region were similar, while those observed in the eastern region were higher than those in mid-western and northern regions. These results agree with those of the mean occurrence of drought in each region in the last 10 years (Table 2.8).

Table 2.12 Farmer perceived % losses under drought across the different groundnut growing regions in Uganda

Region		Losses under mild drought	Losses under moderate drought	Losses under severe drought
Eastern (n=57)	Mean	13.7	43.4	72.6
	S.D	13.0	22.8	28.7
Northern (n=47)	Mean	24.4	40.0	63.0
	S.D	17.1	22.6	29.0
Mid-western (n=65)	Mean	20.1	42.3	76.5
	S.D	27.0	18.2	20.1
Total (n=169)	Mean	19.1	42.1	71.4
	S.D	20.8	21.0	26.3

S.D = standard deviation

2.4.3.4 Farmers' drought mitigation/ coping strategies

Several drought mitigation approaches are used by farmers in the study areas (Table 2.13). While farmers in the eastern and northern regions use early planting and drought tolerant varieties, farmers in mid-western region use early maturing varieties (98.5%), drought tolerant varieties (89.4%), select good seed that produce vigorous plants (100%) and/or simply avoid planting groundnuts in seasons associated with terminal drought (100%). Although there is a high likelihood of drought occurrence in the eastern region (Table 2.8), only a small proportion of farmers (26.9%) use a few drought tolerant groundnut varieties for mitigation of drought. However, all the farmers irrespective of the region, 96.8%, 94.6% and 92.9% for eastern, northern and mid-western, respectively, would like drought tolerance to be bred into their preferred varieties (Data not shown).

Table 2.13 Perceived drought coping strategies currently used by farmers

Drought coping strategies used by farmers	% of respondents		
	Eastern (n=52)	Northern (n=57)	Mid-western (n=66)
Irrigation	3.9	3.5	28.8
Early planting	90.4	77.2	12.1
Use drought tolerant groundnut varieties	26.9	35.1	89.4
Selection of good seed that produce vigorous plants	0.0	7.0	100.0
Use early maturing varieties	0.0	5.3	98.5
Do not plant groundnuts in that season	0.0	0.0	100.0

2.4.3.5 The influence of drought on the choice of variety grown

Drought had a profound influence on the choice of variety grown in all the regions. There was high agreement between the variety least affected by drought, grown in the previous season, and variety to be grown next season (Table 2.14 and Table 2.15). In the eastern region, Serenut 2, an improved variety, was the variety of choice for most farmers. It is known to be drought tolerant and resistant to pests and disease, and also high yielding. In the northern and mid-western regions, landraces such as Red beauty, Oluk-oluk-atar and oluk-oluk-Arema are popular varieties because they are said to be drought tolerant, tasty, oily and high yielding.

Table 2.14 Response of farmers for groundnut varieties least affected by drought

Varieties	% of respondents		
	Eastern (n=60)	Northern (n=53)	Mid-western (n=35)
Serenut 2	61.7	7.6	0.0
Serenut 3	0.0	1.9	0.0
Serenut 4	3.3	0.0	0.0
Serenut5	5.0	0.0	2.9
Serenut6	3.3	0.0	0.0
Serenut 7	1.7	0.0	0.0
Red beauty	3.3	8.0	65.7
Oluk-olwok-arema	0.0	13.2	0.0
Erudurudu	1.7	0.0	0.0
Etosot/egoromoiti	3.3	0.0	0.0
Igola	16.7	13.2	0.0
Oluk-oluk-atar	0.0	37.7	0.0
Gambia	0.00	13.21	0.00
2-seeded (Poland)	0.00	1.89	31.43

Table 2.15 Farmers' choice of variety grown last season and variety to be grown next season

	Variety grown last season			Variety to be grown in the next season		
	% of respondents			% of respondents		
			Mid-			
Variety	Eastern (n=61)	Northern (n=40)	western (n=61)	Eastern (n=58)	Northern (n=50)	Mid-western (n=61)
Serenut1	1.6	0.0	0.0	0.0	0.0	0.0
Serenut 2	41.0	2.5	0.0	36.2	2.0	0.0
Serenut 3	1.6	2.5	0.0	1.7	2.0	0.0
Serenut 4	8.2	0.0	0.0	10.3	0.0	0.0
Serenut5	1.6	0.0	1.6	1.7	0.0	1.0
Serenut6	9.8	0.0	0.0	8.6	0.0	0.0
Red beauty	4.9	30.0	88.7	3.4	28.0	86.9
Oluk-olwok-arema	1.6	30.0	0.0	0.0	42.0	0.0
Erudurudu	18.0	0.0	0.0	17.2	0.0	0.0
Etosot/egoromoiti	3.3	0.0	0.0	3.5	0.0	0.0
Igola	6.6	2.5	0.0	8.6	0.0	0.0
Oluk-oluk-atar	1.6	15.0	0.0	1.7	8.0	0.0
Gambia	0.0	17.5	0.0	0.0	8.0	0.0
Poland (2-seeded)	0.0	0.0	8.2	0.0	8.0	11.5

2.4.3.6 The influence of drought on agronomic practices used for groundnut cultivation

Like other crops, several agronomic practices are carried out during the growth cycle of the groundnuts. In the wake of drought, farmers revealed that they carry out several practices such as early planting, use early maturing varieties, conduct timely weeding and also apply dead season. In all regions surveyed, the farmers practice early planting as the major strategy against end of season drought in eastern (87.5%), northern (68.5%) and mid-western (53.6%) regions, respectively (Table 2.13)

Despite the high rank given to drought as a major production constraint in all regions (Table 2.6), and high knowledge which they have on the stage, direct symptoms and impact of drought (Table 2.10, Table 2.11 and Table 2.9), they are not utilising all the known drought mitigation measures to counteract drought such as use of drought tolerant and early maturing varieties. The farmers do not use these varieties either because they are not aware of these varieties (mid-western region) or because the drought tolerant varieties lack other desirable traits such as oil content, good and

attractive testa colour (northern). The desirable traits by farmers are also highly influenced by the market. In eastern Uganda, drought tolerant varieties are grown because they are high yielding and are, therefore, grown as sources of income but landraces such as Erudu-rudu are preserved for home use, in fact, they refer to this variety as "super variety" because it is early maturing, oily, tasty and easy to harvest.

2.5 Discussion

The study aimed at collecting information on groundnut production systems, utilization, preferred traits and variety adoption, production constraints and perception of drought in selected groundnut producing regions of Uganda. The study area covered diverse production, agro-ecological and ethnic niches in the regions. Understanding the groundnut production and utilization landscape (target production environments), and the variation that exists between them, will provide vital information which will guide the setting of breeding objectives, variety development, testing and promotion.

The results showed that groundnut is produced by small scale farmers with a mean land size of 2.1 ha. These results concur with reports by Shiferaw et al. (2010); Pasupuleti et al. (2013); Ronner and Giller (2012) that groundnut in Africa is produced by small scale farmers. In this study, the mean area under groundnut production was 0.42 ha, representing 20% of the land owned by each farmer. The majority of farmers prepare groundnut fields by using ox-ploughing except in the mid-western region where hand digging is popular. These results suggest that land is a limiting factor in groundnut production. Therefore, production can be increased by developing high yielding varieties that will increase yield per unit area and decrease the unit capital spent on labour.

Okello et al. (2010) reported that groundnut is often produced under mixed cropping systems in Uganda with maize, pearl millet and cassava or as sole crop. In this study, the majority of farmers (> 51%) practice the sole cropping system. Farmers practice mixed cropping system so as to minimize the risk of crop failure and ensure household food security. The decision for sole or mixed cropping is also dictated by the type of groundnut grown. In areas where erect types are grown (Midwestern) mixed cropping is the major production system, while sole cropping is often associated with runner or bunchy types of groundnut. Therefore, it can be concluded that the system of production adopted depends on location, purpose (small vs commercial scale) and the type of groundnut grown.

Small scale farmers have several sources of technological information at their disposal. Shiferaw et al. (2008) and the present study concur that the majority of farmers acquire knowledge about improved varieties from neighbours or fellow farmers. Although the acquisition of knowledge (technology) from neighbours has an advantage of enhancing technology diffusion in communities (Katungi et al., 2008;

Shiferaw et al., 2010; Bonabana-Wabbi et al., 2015), it has the disadvantage in exposing farmers to distorted information and spread of seed borne diseases (Okello et al., 2014). This shows that the methods of variety promotion and dissemination in the study are lacking. Therefore, a decentralized participatory plant breeding (PPB) approach would suffice to remedy the poor technology dissemination. PPB has an advantage of enhancing promotion and dissemination of new varieties (Fukuda and Saad, 2001; Gyawali et al., 2007), especially in low input crops such as groundnut in which private seed companies have no interest (Ntare et al., 2008).

Like other low input crops, groundnut production faces several constraints. In this study, unpredictable weather, groundnut diseases and pests, lack of access to improved varieties, post maturity-harvest pest/rodents, soil exhaustion, poor markets/low prices and limited access to extension services, lack of planting materials, and drought were identified as the major groundnut production constraints. These results corroborate those of Bonabana-Wabbi et al. (2006), Kassie et al. (2011) and Rooner and Giller (2012). Therefore, all efforts to address them would imply higher yields for the farmers. This study focused on understanding the farmers' perception of the drought constraint as a basis for developing mitigation strategies with farmers.

Drought has often been cited as one of the major production constraints in rain-fed small holder farming sectors. In this study, farmers perceived drought as a reduced or lack of rainfall for a long time, poorly distributed rainfall and hot sunny weather. These results agree with those from several reports (Mapfumo et al., 2008; Nhemachena and Hassan, 2008; Gbetibouo, 2009; International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), 2009;). The farmers clearly indicated that the critical stages at which drought is most significant is at the flowering and pegging stage and pod development. The majority of the farmers, 75.4% and 62.1% in eastern and northern region, respectively, indicated that drought is most destructive to groundnut at pegging stage. Overall, regardless of region, the farmers agreed that drought impacts groundnut production through reduced yields. This observation concurs with that of Singh and Kumar (2015). Several drought mitigation approaches were found to be applied by farmers in these study areas. These included early planting, use of drought tolerant varieties, selection of good seed to produce vigorous plants and also simply avoiding seasons suspected to be associated with drought.

The study also found that there is a high likelihood of drought occurrence in the eastern region because of the prolonged dry season. This agrees with the observation by Rooner and Giller (2012). However, only a small proportion of farmers (26.92%) were using drought tolerant groundnut varieties for mitigation of drought, and the rest grow landraces. This mismatch implies either the farmers are not aware (mid-western and northern) or the drought tolerant varieties lack farmer preferred traits (eastern). Although the improved varieties may have desired traits such as drought tolerance and higher yields, farmers also want other traits that fit their utilisation needs, especially when targeted for

home consumption. All the farmers, irrespective of the region, would like drought tolerance to be bred into their preferred varieties. The lack of farmers' preferred traits in improved varieties could be a consequence of the conventional plant breeding approach (CPB) under which they were developed. The CPB approach mainly focuses on high yield and disease and pest resistance (Witcombe et al., 1996; Ceccarelli and Grando, 2007), often neglecting other farmer preferred traits. The traits in which landraces are superior are certain plant and kernel quality traits which are preferred by farmers. These traits are farmer specific depending on how, where and for what groundnut is grown. They cannot be evaluated by the breeder on-station (Woyengo, 2010). Therefore, a participatory plant breeding (PPB) approach, where farmers are involved in development of breeding objectives and variety selection, provides an opportunity that ensures such traits are incorporated and improved using both the landraces and improved varieties (Witcombe et al., 2006; Woyengo, 2010).

2.6 Conclusion

In conclusion, the PRA study has provided an insight into groundnut production systems in different agro-ecologies, and production and utilization niches in selected regions of Uganda. The majority of groundnut farmers in these regions are small scale farmers growing groundnut under both mixed and sole cropping system for food and income. Groundnut production constraints and preferences are prioritized, and drought stood out. There is a need to develop high yielding, disease and pest resistant varieties which are also drought tolerant. In addition, it is equally important to develop systems that can provide clean planting materials to farmers. Groundnut productivity and adoption in these regions can be improved by developing varieties with preferred traits under the prevailing production system, and which can alleviate the production and utilization bottlenecks. However, this can be achieved through the approach of decentralized PPB, which takes into account differences in ethnicity culture, production systems, agro-ecologies and utilization methods.

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CHAPTER 3 Participatory varietal selection criteria for groundnut varieties in selected regions of Uganda

Abstract

One of the fundamentals of plant breeding is the identification of suitable parents. A study was conducted to understand the basis of farmers' selection of groundnut varieties in selected regions of Uganda. Ten popular groundnut varieties (parents) were planted by farmer groups from Hoima, Masindi, Kumi and Lira districts. The districts represented four distinct production and utilization niches. Farmers evaluated and ranked the varieties using indigenous technical knowledge (ITK) for the preferred traits. The results showed that there were significant differences between the parental varieties in the mean scores of traits in all districts, except for quality (greenness) of leaves, number of flowers per node, seed size, plant vigour, drought tolerance, oil content and ease of drying, implying that farmers' evaluation uncovered genotypic differences between varieties, and that farmers' ITK alone cannot be used to evaluate varieties. Therefore, there should be complementation between farmers' ITK and breeder's conventional methods of variety evaluation. The farmers' variety scores varied between districts for most of the traits evaluated demonstrating regional differences in farmers' priorities, environments and/or genotype x environment interaction effects, highlighting the need to decentralize parental variety selection. Parental variety ranking positively and significantly correlated with the percentage of sound mature kernels (SMK%) and groundnut rosette virus disease (GRVD) severity only in Hoima and Masindi, respectively. Correlation between parental variety ranking with leafspot severity, GRVD severity, GRVD prevalence, and SMK% in Hoima was positive but not significant. In Masindi, the parental variety ranking high and positively correlated with leafspot, GRVD severity, GRVD prevalence, seed length (SL) and SMK%. In Kumi district, parental variety ranking was high and positively correlated with GRVD prevalence and seed width (SD). In Lira, parental variety ranking high and positively correlated with GRVD severity, GRVD prevalence, dry pod weight, seed width (SD), seed length (SL), seed length to width ratio (SL/SD) and SMK%. The above positive correlations indicate that the traits are important farmers' selection criteria for preferred groundnut varieties. Simple selection indices were developed for each district using the correlation coefficients as weightings.

3.1 Introduction

The success of a plant breeding programme is determined by several stages ranging from setting objectives to the eventual release of a variety. Routinely, breeders single-handedly implement all the activities involved in variety development on-station, in most cases, using their own selection criteria (Sperling et al., 2001). The breeders' testing environments are often different from the target environments where the potential varieties are to be grown. In addition, by avoiding involvement of farmers, breeders miss out on information and skills/techniques that may be deemed important by the farmers (Manu-Aduening et al., 2006).

The participatory plant breeding (PPB) approach promotes the involvement of farmers in cultivar development (Gyawali et al., 2007). It is well documented that farmers' participation through variety evaluation, in target environments enhances breeding efficiency and effectiveness making sure that the final products are adapted not only to physical environment, but also to the socio-economic environment and to the actual needs of the clients (Sall et al., 2000; Bellon, 2006; Joshi et al., 2007; Virk and Witcombe, 2007). However, involving farmers in breeding may not necessarily guarantee breeding efficiency and effectiveness. Mustafa et al. (2006) found that PPB would cost 2.66 more than conventional breeding. It is only when farmers' participation complements the efforts of the breeder that breeding efficiency is increased (Ceccarelli et al., 2007; Ceccarelli, 2015). This is because some stages of breeding may be carried out much better by the farmers than the breeders and vice-versa. Similarly, some traits can be evaluated better by the farmer, using traits about which little is known from classical genetics, than by the breeder using conventional methods and vice-versa.

Variety testing and selection is one of the most important stages of variety development. In PPB, involvement of farmers in variety testing and selection provides an opportunity for farmers to identify and select what they prefer (Morris and Bellon, 2004; Ceccarelli et al., 2007). Farmers intuitively select varieties based on a number of preferred traits using their own ITK (Odendo et al., 2002), which may be hard for breeders to mimic. Participatory variety selection increases genetic diversity of the crop since farmers from different niches select varieties suitable for their conditions (Witcombe et al., 1996; Joshi et al., 2007). In addition, such a level of agro-biodiversity creates an almost insurmountable barrier to pests and diseases, and allows for a rapid and continuous adaptation to climatic changes.

In order to reap most of the benefits of PPB programmes, farmers should be involved early in the process of developing varieties (Sunberg and Reece, 2004; Witcombe et al., 2005). However, selecting from large plant populations is time consuming and confusing to farmers (Joshi et al., 2007). This limitation can be alleviated by employing a simple selection index formula that can help in ranking large populations of varieties based on farmers' preferences.

Selection indices have been used in plant breeding to rank and select genotypes based on a range of traits for a long time (Sleper and Poehlman, 2006). In many PPB programmes, when selecting for many traits, farmer preferences are used as weightings in the development of selection indices (Odendo et al., 2002). Correlation analysis of trait scores and farmer variety ranking provides information on important traits considered during ranking. The correlation coefficient values indicate the direction and strength of the association between the two variates (Steel and Torrie, 1960). These correlation coefficient values can be used as weightings (coefficients for the trait) in the selection index formula (Witcombe, personal communication). The selection index formula is used to compute a selection index which is used by the breeder to rank and select varieties. To increase breeding effectiveness and efficiency, it is important to determine how best the developed varieties can be evaluated for preferred traits. It is also important to determine who between the farmers using ITK, and the breeders using conventional methods, can evaluate which trait(s). A research study was therefore, conducted in three major groundnut growing regions in Uganda with the objectives to: i) determine farmers' variety selection criteria, ii) identify parental lines, and iii) develop selection index formula.

3.2 Materials and methods

This study involved the interaction of farmer groups with popular groundnut varieties in three regions. These regions represented different production and utilization niches of Uganda.

3.2.1 Study sites and their characteristics

Four districts namely, Hoima, Masindi, Kumi and Lira were purposefully selected. Hoima and Masindi were selected from mid-western while Kumi and Lira were selected from eastern and northern Uganda, respectively, as the main groundnut producing areas that also represent different ethnic communities and production niches. From each district, one active farmer group with experience in groundnut production was identified with the help of agricultural extension staff.

Hoima district receives a bimodal rainfall pattern (March to June and August to December) with an average rainfall of 1000 mm per year. Soils in the district are classified as acidic ferralsols (FAO system, 2004) with low exchangeable bases and organic matter. Soils are predominantly clay (heavy textured), acidic and with a low level of available phosphorus and total nitrogen. The major ethnic group is the Bantu speaking Banyoro. Hoima district was represented by the Mairirwe farmers' cooperative with 25 members (10 men and 15 women).

Masindi district has a bimodal rainfall pattern as described in Hoima district. The district has an annual long-term average rainfall of 1304 mm with three main climatic zones according to rainfall levels: (i)

high rainfall zones, which are areas which receive more than 1000 mm of rainfall per annum, (ii) medium rainfall zones, which are areas with a total amount of rainfall ranging from 800 mm to 1000 mm per annum; and (iii) lower rainfall zones, which refers to areas receiving less than 800mm of rainfall per annum. Soil types in Masindi District, determine the type of crops grown in various areas. The major ethnic groups include Banyoro, Langi, and Lugubara. In this district, the Batereine farmers' group with a membership of 60 farmers (20 men and 40 women) was selected.

The continental climate of Lira district is modified by the large swamp area surrounding the southern part of the district. The rainfall in the district is bimodal with one peak during April to May and the other in August to October. The average annual rainfall in the district varies between 1200-1600 mm decreasing northwards. The rainfall is mainly convectional and normally comes in the afternoons and evenings. The soils can best be described as basement complex (mainly undifferentiated acid gneiss) covering most of the district. The ethnic group is the Langi. In the Lira district, the Barr-oppur farmers group with a membership of 31 farmers (12 men and 19 women) was selected.

Kumi district climate is the modified equatorial type. The rainfall pattern in the district is bi-modal with peaks in April to May and July to August. The annual mean rainfall amount is 800 – 1000 mm. However, recently, the rainfall pattern has become erratic and unpredictable, which has resulted in frequent food shortages. More than half of the district soils are sandy posing a great risk of leaching and erosion especially when poor cultivation methods are used. With continuous cultivation of such soils, soil fertility is lost and yet the farmers hardly add nutrients to the soil. The water carrying capacity of the sandy soil is low compared to the loam clay soils. The major tribe is the Itesot. In this district, farmers from Kellim community with 10 women and 24 men were selected.

3.2.2 Germplasm collection

The germplasm collection team comprised of the breeder, crop technician and extension staff. Popular groundnut varieties were selected from key production areas within these districts based on secondary data from each district's crop production records, and information from extension staff and farmers. During the germplasm collection, the cultivar's local name, utilization and any other special attributes of the collected materials were described. Six most widely grown landraces and four improved varieties were selected for the study (Table 3.1).

Table 3.1 Popular groundnut varieties collected from the study districts

Variety name	Source/special traits	Main utilization form
Farmer (landraces)/		
Improved varieties		
Arema	Lira	Paste
Etesot	Kumi	Paste
Gambia	Lira	paste
Igola	Igola	Paste
Red beauty	Hoima	Paste/flour
Two seeded type	Masindi	flour
Improved varieties		
Serenut 11T	Released drought tolerant, rosette and leaf spot resistant; giant pod and seeds)	Confectionery use
Serenut 2T	Released Rosette and leaf spot resistant and highly drought tolerant	Paste
Serenut 6T	Released rosette resistant, early maturing (90 days)	Confectionery use
Serenut 8R	Released drought tolerant, rosette and leafspot resistant	Good for butter

3.2.3 On-farm evaluation of putative parental varieties

Each farmer group was guided to identify a research plot centrally located and accessible to all group members. On this piece of land, the 10 parental varieties were planted under concealed identity using a completely randomised design (CRD) with three replications. Plots consisted of four rows that were 15 cm apart, each consisting of 10 plants spaced 20 cm from one to another. All these trials were managed by group members.

Farmer preferred groundnut traits identified during the participatory rural appraisal (PRA) (Chapter 2) were used to evaluate the 10 selected parental varieties. In addition, farmers also used their ITKs to evaluate these varieties. Before the evaluation, the farmers listed and described the ITKs they use to evaluate each of the preferred groundnut varieties. Using a simple tool (Appendix 3.1), each farmer in the group independently evaluated each variety for the traits by scoring on a scale of 0 to 5 (0 = the

variety is lacking the trait: 5 = the variety expresses the trait at a satisfactory level). Variety evaluation was conducted at two stages; vegetative to flowering stages and at harvesting.

At the onset of flowering, farmers scored for traits related to plant growth. These included uniformity of germination, time to floral initiation, branches level, leaves level, pests and diseases, quantity/quality of leaves, vigour of the plant, plant height, number of flowers, and number of flowers per node. Besides scoring for preferred traits, farmers ranked the varieties based on their overall visual assessment, without considering the scores already awarded for preferred traits (ranking at vegetative to early reproductive stages).

Groundnut plants were harvested at two dates, 90 and 120 days after sowing by uprooting or digging out the plants depending on the availability of moisture in the soil. Using a simple tool (Appendix 3.2), farmers evaluated all the varieties by scoring for traits related to yield and kernel quality. These included; pod yield (g/plot), size of kernels, size of pods, number of pods per plot, number of seeds per pod, time to maturity, and colour of the kernels. To score taste and texture, farmers tasted dried raw seeds. After the above exercise, farmers were asked to give overall ranking without considering scores for the traits.

3.2.4 Breeder's evaluation of agronomic and morphological traits

Data on selected agronomic and morphological traits were recorded by the breeder. These included; groundnut rosette virus disease (GRVD) and early and late leaf spot resistance, and yield parameters such as fresh pod yield, number of pods, dry pod yield, shelling %, weight of 100 seeds, seed colour, number of seeds per pod, seed length, seed width, and seed length to width ratio.

3.2.4.1 Disease severity score ratings for leafspot diseases

The groundnut leafspot disease severity (DS) data was carried out 40 DAP and was subsequently collected at 30-days interval until maturity. The severity of early and late leafspot infections was scored on 1-9 scale (Subrahmanyam et al. 1995) as follows: 1= no disease, 2 = 1-5% leaf area damaged, 3=6-10% leaf area damaged, 4 =11-20% leaf area damaged, 5=21-30% leaf area damaged, 6=31-40% leaf area damaged, 7= 41-60% leaf area damaged, 8=61-80% leaf area damaged and 9=81-100% leaf area damaged.

3.2.4.2 Groundnut rosette virus disease severity rating

Visual assessments and scoring of groundnut rosette disease severity (DS) was carried out thrice, at 30, 60 and 90 DAP. Groundnut rosette disease severity on each individual plant, was rated using a quantitative scale adapted from Waliyar et al. (2007) as follows: no visible symptoms on leaf (highly

resistant), rosette symptoms covering 1- 20% area of leaf but no obvious stunting (resistant), rosette symptoms on 21-50% area of leaf with stunting (moderately resistant), severe rosette symptoms on 51-70% area of leaf with stunting (susceptible), and severe symptoms on 71-100% area of leaf with stunting (highly susceptible).

3.2.4.3 Groundnut rosette prevalence

The percentage disease incidence (PDI) was measured as described by Waliyar et al. (2007). A total number of five plants along two diagonals were randomly selected in each plot and counted. Plants showing GRVD symptoms were selected from this sample and counted. Percentage disease incidence (PDI) was then computed using the formula below;

$$\text{PDI} = (\text{Number of plants infected along 2 diagonals} / \text{Total number of plants along 2 diagonals}) \times 100$$

3.2.4.4 Agronomic data

Data on selected agronomic traits were collected on plot basis. Yield data were recorded from the middle rows excluding plants at the end of rows for each of the germplasm collection to record data on the following traits; pod yield per plot (g), number of pods per plot, 100-kernel weight (g), shelling percentage. All plants were clipped at the soil surface, the pods were dug up and pods were then detached, bulked together and weighed to get fresh pod weight and converted into fresh pod yield. Pods were sundried for two weeks, weighed and recorded as dried pod weight. Seed size traits (shelling percentage, percentage of sound mature kernels, length, seed width, and ratio of seed length to seed width) were measured according to the method of Lal et al. (2014).

3.2.5 Data analysis

All data collected were subjected to analysis of variance using both parametric and non-parametric (Kruskal-Wallis) methods using Genstat version 14 (Payne et al., 2011) to detect differences between varieties within and between districts. Variety mean scores for all traits were computed and the groundnut varieties were ranked for each trait per district. A Spearman's rank correlation analysis was conducted between farmer variety ranks and mean trait scores as measured by the breeder in each district. Correlation coefficients were used to determine the importance of each trait to farmers when selecting varieties (selection criteria) and to generate a simple selection index.

3.3 Results

3.3.1 Preferred traits of groundnuts

During the focus group discussion (FGD), farmers listed a total of 11 traits they prefer in groundnut varieties (Table 3.2). These ranged from pod yield, ease of post maturity/harvest handling, pest and disease resistance, drought tolerance or escape to appeal of the kernels (appearance of kernels upon shelling). In addition, they described the form in which the trait was preferred.

Table 3.2 Farmer preferred groundnut traits in mid-western, northern and eastern Uganda

Trait	Preferred form and reason
Yield	• High yielding varieties. (yield is assessed by farmers as the number of pods and weight of kernels per plant)
Diseases and pests resistance	• Dark green clean leaves indicate healthy plants. (clean plants are considered appealing in the field).
Time to maturity	• Varieties that can mature early to release land for other crops
Drought responsiveness	• Varieties that can produce some yield even in case of drought for food security
Taste (sweetness)	• Kernels with sweet taste. (this is appealing for home consumption and also for marketing)
Easy to shell	• Easy to shell. (this is associated with high efficiency of utilization for planting and processing for home consumption).
Oil content	• High oil content. (farmers associate this with suitability of variety for the purpose of making paste).
Seed size	• Medium to large seeds/kernels. (these are attractive to market)
Easy to uproot	• Erect or semi-erect varieties. (these are easy to harvest)
Easy to pound	• Easy to pound. (these varieties are easily broken down upon pounding for extraction of flour or paste)
Testa colour	• Appealing colour. (red colour is associated with sweet taste and market)

Some traits were highly preferred in one region, but not in others. The most preferred trait was high yielding, which was ranked first and second in the mid-western and eastern regions, respectively. The second most preferred trait across the regions is resistance to diseases and pests. In addition, drought tolerance was ranked first and second in the eastern and mid-western regions, respectively. Overall

drought responsiveness was ranked fourth across all regions. However, early maturity was only highly ranked by FGD in the mid-western region (Table 3.3).

Table 3.3 Farmer preferred groundnut traits, ranks for preference as given by farmers in mid-western, northern and eastern Uganda

Traits	Eastern		Northern		Mid-western		Average Ranks
	FGD	Survey	FGD	Survey	FGD	Survey	
High yielding	2	1	-	1	1	1	1
Diseases and pests resistance	3	3	1	2	4	2	2
Early maturity	4	4	7	3	2	3	3
Drought responsiveness	1	2	9	6	2	4	4
Taste (sweetness)	7	5	3	5	5	5	5
Ease of shelling	6	9	-	7	-	11	8
Oil content	8	10	4	4	9	7	6
Seed size	10	10	6	11	-	6	10
Ease of uprooting	5	6	12	6	8	8	7
Ease of pounding	9	7	11	9	-	9	11
Testa colour	11	8	5	10	7	9	9

FGD = Focus group discussions

3.3.2 Farmers' indigenous variety evaluation technical knowledge (ITK)

During FGD, farmers described and listed the ITK methods they use to evaluate preferred groundnut traits. In this study, the different ITKs that farmers use to evaluate different preferred traits were described as;

- i) **Cleanliness of plants:** Was evaluated by observing the health and appearance of leaves. Plants with deformed, few and/or discoloured leaves are considered susceptible and undesirable. They believe that the poor health of plants is expressed by yellowing, curling, dropping of leaves and stunted growth of plants are due to poor soils, and water stress or bad weather conditions is associated with bad omen.
- ii) **Branchness of the plant:** Was observed by observing the appearance of plants. Plants with less branches are considered less productive. They believe that with more branches, more pegs can be formed and all this would translate into high yields.

- iii) **Number of flowers/number of flowers per node:** This was observed by observing the flowering rate and number of flowers present. They believe that the more flowers produced, the higher the expected yield of the cultivar.
- iv) **Size and colour of seeds.** This was observed by shelling pods and looking at the appearance of the kernels. Generally, farmers prefer medium to large seeds. Colour was an additional criterion that farmers like and as such, they associate it with quality and market value.

3.3.3 Breeders' evaluation

The 10 parental varieties were significantly ($P \leq 0.05$ to $P \leq 0.001$) different for all the traits evaluated, except prevalence of rosette disease (Table 3.4; Appendix 3.4). There were significant differences among the three districts for all traits ($P \leq 0.05$ to $P \leq 0.001$), except for groundnut rosette disease severity, seed diameter, seed length, and seed length to width ratio (Table 3.4). There were no significant ($P > 0.05$) interaction effects between varieties and districts for all traits, except weight of 100 seeds, unshelled dried pod weight and shelling percentage.

Table 3.4 mean squares for morphological and agronomic traits of parental varieties evaluated by the breeder in Hoima, Masindi, Lira and Kumi districts

SOV	Df	Pod No.	Fresh pod wt	HSW	Dried Pd_wt	Shelling (%)	GRD	Severity scores				SL	SL- SD
								GRD	Leafspots	SMK%	SD		
Variety (V)	9	296295"	0.38"	2534.25"	7437.5"	44.17"	0.19	2.57"	8.62"	725.9"	0.05**	0.33*	0.12*
District (D)	4	332531"	6.81"	184.07"	575.1"	147.11"	3.34"	3.19	23.65"	1190.8"	0.02	0.06	0.03
V x D	36	41167	0.24	40.60*	243.5*	14.02*	0.05	0.40	0.28	335.9	0.01	0.04	0.06

* and ** significant at $P \leq 0.05$ and $P \leq 0.01$, respectively; SOV = source of variation; Df = degrees of freedom; D = district; V = variety; Pod no. = number of pods per plot; Fresh pod wt = fresh pod weight; HSW = hundred seed weight; Dried Pd_wt = unshelled pod weight (g/plot); GRD = groundnut rosette virus disease; GRD Prev. = GRD prevalence ; SMK % = percentage of mature kernels; SD = seed width (cm); SL = seed length (cm); SL/SD = seed length to width ratio;

3.3.4 Farmers' decentralised varietal evaluation

Results of farmer's evaluation are presented in Table 3.5, Figure 3.1 and Appendix 3.3. There were significant differences ($P\leq0.05$ to $P\leq0.001$) between varieties for some traits evaluated in all districts (Table 3.5, Appendix 3.3). The varieties performed differently ($P\leq0.05$) across districts for branching level, quantity of leaves, time to initial flowering, number of flowers, plant height, pest and disease, plant vigour, ease of shelling, seed coat colour, size of pods, size of seeds and taste of grains.

Table 3.5 Mean squares for groundnut trait scores given by farmers within and across districts

Source	Districts				
	Hoima	Masindi	Kumi	Lira	Across districts
Branching	0.54	1.85 [*]	4.06 ^{**}	1.27 ^{**}	6.23 ^{**}
Quantity/ greenness of leaves	0.75	4.05 ^{**}	5.71 ^{**}	0.81	6.97 ^{**}
Time to initial flowering	0.62 [*]	0.78	2.03 [*]	0.60	16.45 ^{**}
Number of flowers	1.28 ^{**}	1.60 [*]	1.87 [*]	1.05 [*]	10.05 ^{**}
Plant height	1.73 ^{**}	2.85 ^{**}	3.34 ^{**}	1.69 [*]	7.04 ^{**}
Pest and disease infestation	2.08 ^{**}	2.87 ^{**}	5.18 ^{**}	0.73	9.21 ^{**}
Plant vigour	0.43	5.29 ^{**}	3.14 ^{**}	0.80	8.20 ^{**}
Ease of shelling	1.65	4.09 ^{***}	3.93 ^{**}	2.26 [*]	5.39 ^{**}
Number of pods	4.00 ^{**}	4.36 ^{**}	4.19 ^{**}	2.82 ^{**}	1.47
Number of seeds/pod	1.54	1.93	2.16 ^{**}	1.60 [*]	1.08
Seed coat colour	5.89 ^{**}	10.05 ^{**}	0.64	2.17 [*]	9.60 ^{**}
Size of pods	2.47 [*]	2.52 [*]	1.95 ^{***}	2.83 [*]	14.12 ^{**}
Size of seeds	1.60	0.58	2.82 ^{**}	3.36 ^{**}	3.84 [*]
Taste of grains	4.04 ^{**}	8.88 ^{**}	2.81 ^{***}	2.86 ^{***}	4.81 [*]
Time to maturity	7.79 ^{**}	2.14 [*]	11.76 ^{**}	2.92 [*]	3.26
Total plot yield	3.95 ^{**}	3.38 ^{**}	3.64 ^{**}	1.40	0.67

^{*}, ^{**} and ^{***} = significant at $P\leq0.05$, $P\leq 0.01$, and $P\leq 0.001$, respectively.

The differences in variety performance between districts could be due to either differences in farmers' rating, growing environments or genotype x environment interaction effects.



Fig. 3.1A: Evaluation of groundnut at vegetative stage (before harvest)



Fig.3.1B: Evaluation of groundnut after harvest (after harvest)

The results for farmer ranking of varieties are presented in Table 3.6. and Appendix 3.3. There were substantial differences amongst districts in variety ranking at the harvest and before harvest stages. The varieties ranked first before harvest were Poland in Hoima, Serenut 8R in Masindi, Serenut 6T in Kumi and Serenut 2T in Lira. The poorly ranked varieties before the harvest stage were Serenut 2T, Arema, Red Beauty and Serenut 6T for Hoima, Masindi, Kumi and Lira districts, respectively. At the harvest stage, Arema in Hoima and Kumi and Red Beauty in Lira and Masindi districts were ranked last. All the varieties ranked last were landraces. Among the improved varieties, Serenut 6T and Serenut 2T were best in Hoima district before and at harvest stages, respectively. Serenut 8R and Serenut 6T were ranked top in Masindi before and at harvest stages, respectively. In Kumi district, the best among improved varieties was Serenut 6T before and at harvest stage. In Lira, the best among improved varieties were Serenut 2T and Serenut 8R before and at harvest, respectively.

Table 3.6 Variety mean rank and overall rank (in parenthesis) before and at harvest in Hoima, Masindi, Kumi and Lira districts

Variety	Hoima		Masindi		Kumi		Lira	
	BH	AFH	BH	AFH	BH	AFH	BH	AFH
Red beauty	7.0 (2)	6.8 (9)	6.2 (6)	7.2 (10)	9.9 (10)	6.4 (9)	3.8 (3)	9.3 (10)
Serenut 6T	5.7 (4)	4.6 (4)	8.0 (9)	4.4 (2)	2.1 (1)	4.4 (2)	7.2 (10)	3.9 (3)
Serenut 11T	3.3 (9)	4.5 (3)	2.5 (2)	5.2 (5)	2.9 (3)	4.5 (3)	5.4 (6)	5.5 (6)
Polandi	8.3 (1)	7.9 (10)	7.8 (8)	5.2 (4)	8.4 (9)	5.7 (7)	4.7 (4)	4.6 (4)
Serenut 8R	3.6 (8)	4.7 (5)	1.4 (1)	5.8 (8)	2.3 (2)	4.7 (4)	5.8 (8)	3.1 (1)
Serenut 2T	3.0 (10)	4.2 (2)	4.0 (4)	4.5 (3)	3.3 (4)	5.5 (6)	1.7 (1)	5.6 (7)
Gambia	4.5 (5)	5.0 (6)	5.6 (5)	6.2 (9)	3.5 (5)	4.1 (1)	7.1 (9)	5.6 (7)
Igola	4.1 (7)	5.9 (7)	3.3 (3)	5.4 (7)	6.3 (6)	5.1 (5)	3.3 (2)	3.6 (2)
Etesot	4.2 (6)	2.6 (1)	6.8 (7)	3.6 (1)	7.7 (8)	5.9 (8)	5.3 (5)	4.7 (5)
Arema	6.8 (3)	6.2 (8)	8.1 (10)	5.3 (6)	6.7 (7)	6.4 (10)	5.6 (7)	6.1 (9)

BH and AH = variety ranking before and at harvest stages, respectively.

The varieties were ranked differently for the various traits in the districts (Appendix 3.3). Serenut 6T was the most resistant variety to foliar diseases, ranked first in Hoima district and second in Masindi and Kumi, but ranked eighth in Lira district (Appendix 3.3). Polandi was ranked the best for drought tolerance in Kumi, second in Lira, third in Hoima and fourth in Masindi. This implies that when breeding for drought tolerance, Polandi would be the best parent to be used, while when breeding for foliar disease resistance, Serenut 6T would be the best parent to be selected.

3.3.5 Farmers' selection criteria and index

There were no significant ($P > 0.05$) correlations between farmers' overall variety ranking by visual assessment before harvest and the traits' values as measured by the breeder in all districts except for ground rosette disease severity in Masindi district (Table 3.7). Overall variety ranking at harvest stage was also not significantly ($P > 0.05$) correlated with all trait's values as measured by the breeder, except for percentage of sound mature kernels in Hoima district.

Significant correlations between certain variety trait scores, as measured by the breeder, and variety ranking done by farmers, imply that these traits form the basis on which farmers rank varieties and provide information on the importance attached to the traits considered by the farmers during variety ranking. Thus, correlation coefficients can be used as weighting for traits that form the selection criteria.

By using these correlation coefficients, simple linear selection indices can be developed. Given that variety ranking before and at harvest were not significantly correlated, and that varieties scores for most of the traits differed significantly ($P \leq 0.05$ to $P \leq 0.001$) across districts (Table 3.5 and Table 3.7, and Appendix 3.5), selection indices were developed for each district separately.

Table 3.7 Spearman's rank correlation coefficients between groundnut variety trait scores and ranking before and at harvest in Hoima, Masindi, Kumi and Lira districts

Trait	Hoima		Masindi		Kumi		Lira	
	BH	AH	BH	AH	BH	AH	BH	AH
Leaf spot severity	-0.31	-0.61	0.06	0.35	-0.11	-0.24	-0.02	0.29
GRD severity	0.36	0.09	0.75**	-0.16	-0.02	-0.13	0.16	0.38
GRD prevalence	0.37	0.35	0.41	-0.04	0.50	0.53	0.17	0.47
Dry pod weight(g/plot)	-	0.19	-	0.04	-	-0.10	-	0.51
HSW weight (g)	-	0.26	-	0.04	-	-0.15	-	-0.02
Shelling %	-	-0.02	-	0.04	-	-0.25	-	-0.30
SD (cm)	-	0.17	-	-0.18	-	0.34	-	0.56
SL (cm)	-	0.17	-	-0.37	-	0.35	-	0.43
SL:SD	-	-0.04	-	0.01	-	0.29	-	0.30
SMK %	-	-0.75**	-	-0.50	-	0.21	-	0.30

* and ** = significant at $P \leq 0.05$ and $P \leq 0.01$ respectively; BH = variety ranking before harvest; AH = variety ranking at harvest and after harvest; - = not assessed at that stage; SMK = Percentage of sound mature kernels; GRD; = Groundnut rosette virus disease; HSW = hundred seed weight; SD= seed width; SL = Seed length; SL-SD=seed length to width ratio.

All the correlation coefficients, as expected were negative or low since the rank of the best variety, as determined by the farmers, is numerically lower than the worst variety yet the reverse is true for variety scores as measured by the breeder. In the selection indices, positive correlation coefficients were used for each trait as weightings since the scores are positively awarded. Preferred traits had high positive scores, while less preferred traits had lower scores (appendix 3.1 and appendix 3.2). The best variety is one with the highest positive selection index.

$$SI_{Hoima} = (0.31+0.61)^{\dagger} LS + (0.36+0.09) GRDs + (0.37+0.35) GRDp + 0.19DPW + 0.26HSW + 0.02SP + 0.17SD + 0.17SL + 0.17SD + 0.04SL/SD + 0.75SMK$$

$$SI_{Masindi} = (0.06+0.35) LS + [(-0.75) + 0.16]] GRDs + (0.41+0.04) GRDp + 0.04DPW + 0.04HSW + 0.04SP + 0.18SD + 0.37SL + 0.01SL/SD + 0.5SMK$$

$$SI_{Kumi} = (0.11+0.24) LS + (0.02+0.13) GRDs + [(-0.50) + (-0.53)] GRDp + 0.10DPW + 0.15HSW + 0.25SP + 0.34SD + 0.35SL + 0.29SL/SD + 0.21SMK$$

$$SI_{Lira} = 0.02+0.29) LS + (0.16+0.38) GRDs + (0.17+0.47) GRDp - 0.51DPW + 0.02HSW + 0.30SP - 0.56SD + 0.43SL + 0.30SL/SD + 0.30SMK$$

Where: LS = leaf spots prevalence, GRDs = groundnut rosette disease severity, GRDp = groundnut rosette disease prevalence, DPW= dried pod weight, HSW= hundred seed weight, SP= shelling percentage, SD = seed width, SL= seed length, SL/SD = ratio of seed length to seed width ratio, SMK = percentage of sound mature kernels; ± = values in brackets represents Pearson's correlation coefficient for trait score as measured by breeder with variety ranking by farmer before (BH) and at harvest (AH), respectively.

Based on the above selection indices, the best two varieties for Hoima district were Serenut 11T and Igola, while for Masindi district, the best two varieties were Serenut 11T and Etesot. The top two varieties for Kumi district were Serenut 11T and Serenut 8R, while Arema and Polandi were the best varieties in Lira district.

3.4 Discussion

Participatory plant breeding entails the participation of farmers in the breeding processes (Witcombe et al., 2005; Woyengo, 2010) with the aim of increasing the adoption of varieties and thus improve efficiency and effectiveness of a breeding programme. When farmers are able to apply their selection criteria accurately on large population, using limited resources and time, breeding efficiency and effectiveness is achieved. Farmers have their own way of selecting varieties that they eventually grow. They select varieties based on their own traits using informal ITK. Some of these ITKs lack any alternative formal scientific methods of evaluation. As such, these traits cannot be assessed by the breeder on-station without the participation of farmers (Woyengo, 2010). In this study, the farmers used ITK, in addition to the yield traits to evaluate potential parental varieties. Significant differences were observed between varieties for all traits evaluated, except for ease of drying and number of seeds per pod. This indicates that the ITKs used were able to show genotypic differences and can be employed in groundnut variety evaluation. These results are in agreement with those of other studies (Mkumbira et al., 2003; Woyengo, 2010) who reported that farmers were able to distinguish between cassava landraces with higher precision than scientists.

Some of the ITKs used in this study have been used in similar studies elsewhere. Ndejeunga et al. (2010) reported that colour of leaves, maturity (short cycle), number of pods, pod size, pod constriction, pod yield, pod filling and taste were the important attributes explaining farmers ranking for varieties in Mali. In Niger, the colour of leaves, the number of pods per plant, pod filling, pod beak,

and pod yield were the most important traits sought by farmers. In Nigeria, plant vigour, plant maturity, plant type, number of pods per plant, pod size, haulm yield and pod yield were the preferred traits. Therefore, local farmers' knowledge (ITK) is an important benchmark that need to be borne in mind while defining precise criteria to be used for evaluation of genotypes depending on the crop species and the location where study is taking place (Bellon, 2001; Kamara et al., 2006)

Significant differences observed between varieties in trait scores in the different districts indicate the different preferences by farmers from different districts. These differences may be a result of socio-economic conditions, physical environment, and genotype x environment interaction effects. Environmental effects are at play when the same genotype reacts differently in different environments (Sleper and Poehlman, 2006) leading to differences in scoring and ranking in those environments. The evaluation by the breeder of the morphological and agronomic traits revealed significant differences between environments and their interaction with genotypes. Although broad adaptation is part of the legal frameworks for variety deployment in many countries (Halewood et al., 2007), such blanket recommendations often mask the specific adaption of some varieties to given locations, and the varied preferences displayed by farmers from the different locations. This, therefore, calls for better targeting of varieties, implying that the four districts need to be considered as different target environments that require decentralized participatory variety evaluation and selection.

In order to increase breeding efficiency and effectiveness, parental selection is key. Participatory plant breeding requires that at least one of the parents used in the development of varieties should be a local variety, adapted to the targeted production environment and widely grown by farmers (Witcombe and Virk, 2009). These varieties are normally already popular in the target locations because they have farmer-preferred traits. Witcombe and Virk (2009) noted that the most ideal parental varieties are those selected through participatory variety selection (PVS). Woyengo (2010) reported that, using their own criteria, farmers were able to select preferred cassava varieties among landraces and improved varieties in Kenya. In the current study, the following varieties were selected by farmers; Arema and Red Beauty, among the land races, and Serenut 6T among the improved varieties. However, selection of varieties based on ranking alone, may be misleading. Thus, it is more logical to select parental varieties based on traits to be improved. If from this study, the breeding objective was to increase the number of pods per plant, the best parents would be Gambia from Hoima and Lira districts, and Arema from Kumi district. In addition, significance across districts in variety scoring, as measured by the breeder and farmers, imply that parental varieties need to be selected per district.

Variety ranking by visual assessment is a quick method based on a few observable traits. Traits that farmers highly consider during variety selection express large significant correlation between variety ranking by visual assessment (farmer ranking) and trait score, as measured by the breeder. Traits that are highly and significantly correlated with overall variety ranking form the selection criteria (a

combination of traits that influence variety ranking and selection). The results of this study show that percentage of mature kernels (SMK %) and seed length form part of the most important selection criteria in most of the districts. Also to note, dried pod weight, seed width (SD) in Lira; groundnut rosette disease prevalence in Kumi and groundnut rosette disease severity in Masindi, and hundred seed weight (HSW) in Hoima, were part of the selection criteria in each district.

Development of a simple selection index formula to aid in the quick selection from a large number of varieties is important. Correlation coefficients indicate the direction and degree of association between traits. Correlation coefficients of traits that significantly correlate with variety ranking are used to develop selection index formula (Witcombe personal communication). The correlation coefficients represent the direction and contribution of the trait to the ranking. In this study, most of the traits assessed had very little variability, implying limited varietal differentiation. A similar observation was also noted by Ndjeunga et al. (2010). As such, only SMK (%) and seed length (SL) significantly contributed to variety rank in most of the districts. Therefore, based on the selection index formulae, the best variety is one with highest positive selection index. For instance, the top variety in Hoima, Masindi and Kumi district was Serenut 11T, while the top variety in Lira was Arema.

3.5 Conclusion

Farmers, using their own selection criteria have the capacity to select suitable parental varieties. The selection differs between target production environments and is based on farmers' preferences. As a result, breeding efficiency and effectiveness will be enhanced when farmers are involved in selection of parental varieties. However, this must be decentralized if the target environments are different and based on the traits to be improved (breeding objectives) and not just overall performance of the variety. Despite the ability of farmers to select suitable varieties, their ability to evaluate certain traits is limited. Therefore, there should be complementation between the breeders and farmers in parental variety selection especially for traits where local farmers' knowledge-based methods cannot be used alone.

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Appendix 3.1 Groundnut variety evaluation sheet at vegetative and early reproductive stage (V0 – R2)

Name of farmer: _____ Name of Sub County: _____ Date: _____

Name of village: _____ Gender: _____ Group member: YES NO

Instruction: For each plot, award 'marks' for each trait based on your level of satisfaction

(To what level of satisfaction is the trait expressed by the variety?)

Traits	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Plot 8	Plot 9	Plot 10
1 Uniform germination										
2 Pests and disease resistance										
3 Height of main stem										
4 Branches level										
5 Leaves level										
6 Time to initial flowering										
7 No. of pegs/flowers										
8 No. of pegs/flowers/node										
9										
10										
Overall rank										

Key: Score out of 5: 5= variety has the trait to satisfactory level; 0 = Variety does not have the trait; Overall score =

Give a rank for the overall performance of the variety.

Appendix 3.2 Groundnut variety evaluation sheet at harvest stage

Name of farmer: _____ Name of Sub County: _____ Date: _____

Name of village: _____ Gender: _____ Group member: YES NO

Instruction: For each variety, award 'marks' for each trait based on your level of satisfaction (To what level of satisfaction is the trait expressed by the variety?)

Traits	VAR 1	VAR 2	VAR 3	VAR 4	VAR 5	VAR 6	VAR 7	VAR 8	VAR 9	VAR 10
1 Time to maturity										
2 Ease of drying										
3 Number of pods										
4 Number of seeds/pod										
5 Total plot yield (unshelled)										
6 Size of the pods										
7 Size of the seed										
8 Seed coat colour										
9 Taste of the grain										
10 Ease of shelling										
11 Drought tolerance (% of green leaves)										
12										
13										
Overall rank										

Key: Score out of 5: 5 = variety has the trait to satisfactory level; 0 = Variety does not have the trait; Overall score = Give a rank for the overall performance of the variety; VAR = Variety

Appendix 3.3: Variety mean scores rank (besides value) and H-values for farmer preferred traits in Hoima, Masindi, Kumi and Lira districts

Trait	District	Variety										Ht-values										
		V-1	V-2	V-3	V-4	V-5	V-6	V-7	V-8	V-9	V-10											
Branching	H	4.0	5	3.5	1	4.1	7	4.1	7	4.3	10	4.0	5	3.9	4	3.7	2	3.8	3	4.1	7	7.2
	M	3.5	5	3.2	2	3.7	8	4.1	10	3.8	9	3.5	5	3.6	7	2.5	1	3.4	4	3.2	2	10.67
	K	4.3	9	3.2	3	3.2	3	4.0	7	3.6	6	4.6	10	4.2	8	3.0	2	2.7	1	3.2	3	36.40**
	L	4.5	10	4.0	6	4.2	7	3.9	5	4.3	9	4.2	7	3.7	4	3.5	1	3.5	1	3.6	3	19.51**
Pest-diseases	H	4.2	10	2.9	1	3.2	3	3.2	3	4.0	8	3.1	2	3.9	7	3.5	5	4.0	8	3.8	6	21.39*
	M	3.0	4	2.8	2	3.7	7	3.9	9	3.3	6	3.8	8	3.2	5	2.4	1	2.9	3	4.0	10	26.03**
	K	4.4	8	3.0	2	3.3	5	4.4	8	3.4	6	4.7	10	3.6	7	3.1	3	2.5	1	3.1	3	41.31***
	L	4.1	5	4.2	8	4.0	3	4.0	3	4.4	10	3.8	2	4.2	8	4.1	5	3.4	1	4.1	5	5.94
Quantity/quality of leaves	H	3.6	2	6.6	10	4.0	5	4.1	7	4.2	8	4.2	8	4.0	5	3.8	3	3.4	1	3.9	4	9.63
	M	3.6	8	2.9	2	4.0	9	4.0	9	3.4	6	3.5	7	3.2	5	1.8	1	3.0	3	3.1	4	27.27**
	K	4.1	8	2.9	2	4.0	6	4.2	9	4.0	6	4.7	10	3.8	5	2.9	2	2.4	1	2.9	2	37.35***
	L	3.5	2	3.8	7	4.0	9	4.2	10	3.7	5	3.7	5	3.8	7	3.5	2	3.2	1	3.5	2	9.46
Time to initial flowering	H	3.3	2	3.3	2	3.7	8	3.6	7	4.0	10	3.4	5	3.5	6	3.2	1	3.7	8	3.3	2	9.43
	M	3.0	5	2.8	3	3.0	5	3.1	7	3.3	10	3.2	9	2.6	2	2.4	1	3.1	7	2.8	3	3.91
	K	3.8	7	2.7	1	3.5	4	3.8	7	3.7	6	4.3	10	3.8	7	3.2	3	3.1	2	3.5	4	17.69*
	L	3.4	3	3.1	1	3.8	8	3.4	3	3.4	3	3.4	3	3.1	1	3.4	3	3.8	8	3.8	8	2.9
Vigour	H	3.9	2	3.7	1	4.2	8	4.3	9	4.4	10	4.0	4	3.9	2	4.0	4	4.1	7	4.0	4	7.79
	M	3.2	5	2.8	2	3.9	7	3.9	7	3.7	6	4.2	10	3.0	4	1.9	1	2.9	3	4.1	9	29.80***
	K	4.6	10	3.2	3	3.1	2	4.1	8	4.0	6	4.5	9	4.0	6	3.6	4	3.0	1	3.8	5	23.57**
	L	3.8	6	4.1	10	3.6	3	3.8	6	3.8	6	3.5	2	3.7	4	3.7	4	3.0	1	3.8	6	5.72
Number of flowers	H	3.3	6	3.5	7	3.7	8	3.7	8	3.7	8	3.0	3	3.1	4	2.8	1	3.2	5	2.8	1	14.89
	M	2.8	7	2.1	1	2.3	2	3.0	8	3.3	10	3.2	9	2.4	3	2.4	3	2.5	5	2.7	6	9.07
	K	3.4	6	2.9	2	2.7	1	3.8	9	3.5	7	4.2	10	3.5	7	3.3	5	3.2	4	3.1	3	17.70*
	L	3.0	5	3.0	5	3.4	9	2.9	4	3.1	8	2.7	2	2.8	3	3.0	5	2.3	1	3.4	9	8.64

Appendix 3.3: Continued.

Trait	District	Variety										H-values										
		V-1	V-2	V-3	V-4	V-5	V-6	V-7	V-8	V-9	V-10											
Height	H	3.2	1	3.3	2	4.4	10	3.7	4	4.3	9	3.5	3	4.1	7	3.9	5	4.2	8	3.9	5	21.96**
	M	3.9	9	2.8	2	3.4	5	4.2	10	3.6	8	3.5	6	3.3	4	2.3	1	3.2	3	3.5	6	20.98*
	K	3.7	8	2.9	2	2.8	1	4.2	9	3.6	6	4.6	10	3.6	6	3.3	4	2.9	2	3.5	5	31.85***
	L	4.0	5	4.5	10	3.8	3	4.0	5	4.4	9	3.8	3	4.1	8	4.0	5	3.1	1	3.6	2	18.95*
Germination	H	3.9	4	2.7	1	4.1	8	3.9	4	4.1	8	3.7	3	3.4	2	3.9	4	3.9	4	4.1	8	33.60**
	M	3.7	5	3.5	3	4.6	10	4.0	8	3.9	6	4.5	9	3.9	6	3.1	1	3.3	2	3.6	4	30.00***
	K	4.1	8	2.6	1	2.7	2	4.6	9	3.9	7	4.9	10	3.8	6	3.3	4	3.3	4	2.9	3	53.30***
	L	4.1	8	3.9	6	3.7	3	4.1	8	4.5	10	3.8	5	3.7	3	3.4	2	2.4	1	3.9	6	23.90**
Flowers/node	H	3.2	3	3.4	6	3.6	8	3.6	8	3.6	8	3.1	2	3.2	3	3.0	1	3.4	6	3.2	3	5.8
	M	3.2	7	2.5	4	2.6	5	2.9	6	3.4	9	3.4	9	2.2	1	2.4	3	2.2	1	3.2	7	12.04
	K	3.4	6	3.2	5	2.8	1	4.1	9	3.5	7	4.3	10	3.7	8	3.0	3	3.1	4	3.0	2	24.35**
	L	2.9	4	3.3	9	2.9	4	2.7	3	3.0	6	2.4	2	3.0	6	3.2	8	2.3	1	3.3	9	5.5
Disease free	H	2.8	2	3.5	7	3.2	3	3.9	9	4.3	10	3.3	6	3.5	7	3.2	3	3.2	3	2.6	1	16.03
	M	2.3	2	4.5	10	4.0	7	3.0	4	2.6	3	1.8	1	3.3	5	4.1	9	4.0	7	3.9	6	48.82**
	K	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Drought tolerance	H	3.5	7	3.3	4	3.8	9	3.2	3	3.9	10	3.5	7	3.4	6	3.3	4	3.0	1	3.0	1	8.74
	M	1.8	2	4.1	8	4.0	7	2.6	4	1.8	2	1.6	1	3.2	5	3.5	6	4.1	8	4.3	10	68.40***
	K	3.8	9	3.5	4	3.0	1	3.0	1	3.7	8	3.5	4	3.6	7	4.1	10	3.5	4	3.4	3	14.32
	L	3.0	1	3.4	3	4.0	8	3.2	2	4.1	9	3.4	3	3.5	5	4.4	10	3.7	7	3.5	5	19.90*
Ease dry	H	3.0	2	3.1	3	3.3	6	4.0	10	3.7	9	3.5	8	2.8	1	3.1	3	3.4	7	3.1	3	10.96
	M	3.9	10	2.9	2	2.9	2	3.5	7	3.4	6	3.5	7	2.9	2	2.8	1	3.1	5	3.7	9	14.2
	K	2.9	3	2.4	1	3.2	5	4.7	10	2.4	1	4.1	8	4.0	7	3.1	4	3.7	6	4.1	8	56.37***
	L	3.2	2	4.1	10	2.9	1	3.6	6	3.5	5	3.3	4	3.7	7	3.7	7	3.2	2	3.7	7	13.5

Appendix 3.3: Continued.

Trait	District	Variety										H-values										
		V-1	V-2	V-3	V-4	V-5	V-6	V-7	V-8	V-9	V-10											
Ease shelling	H	3.4	7	3.0	3	4.1	10	3.4	7	3.5	9	3.1	5	2.8	2	3.1	5	3.0	3	2.7	1	11.60ns
	M	4.4	10	2.5	1	2.7	2	2.7	2	3.4	8	3.2	6	3.2	6	2.7	2	2.8	5	4.1	9	24.59**
	K	4.1	8	2.9	3	3.8	4	3.8	4	2.8	1	4.5	10	4.0	7	2.8	1	3.8	4	4.3	9	24.87**
	L	3.6	8	3.5	6	3.1	5	3.0	4	2.9	2	2.7	1	3.5	6	3.8	9	2.9	2	4.2	10	17.61*
Number of pods	H	3.6	7	3.2	4	3.0	3	3.2	4	3.5	6	4.7	10	2.5	1	4.1	9	3.7	8	2.9	2	29.3***
	M	2.7	3	2.7	3	2.5	1	2.9	5	3.7	8	3.6	7	3.2	6	4.5	10	3.7	8	2.5	1	32.66***
	K	2.8	2	3.0	3	3.9	8	4.6	10	3.9	8	3.7	7	3.6	6	3.3	4	3.5	5	2.3	1	36.52**
	L	3.1	4	2.9	2	3.7	7	3.4	5	2.9	2	3.7	7	2.7	1	4.2	9	4.2	9	3.5	6	24.50**
Seeds/pods	H	3.1	2	2.8	1	4.0	9	3.1	2	3.3	5	3.4	6	4.0	9	3.2	4	3.6	7	3.6	7	14.89
	M	4.2	10	2.9	2	2.7	1	3.5	8	3.4	7	3.2	4	3.0	3	3.2	4	3.3	6	3.8	9	13
	K	3.8	7	2.7	1	3.4	3	3.6	5	4.3	10	3.8	7	3.6	5	4.0	9	3.5	4	3.0	2	19.11**
	L	3.4	4	4.1	10	3.1	2	3.6	7	3.1	2	3.6	7	2.8	1	4.0	9	3.4	4	3.4	4	19.21**
Oil content	H	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	M	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	K	4.2	8	4.0	5	3.0	3	4.1	7	2.7	2	4.6	9	4.0	5	2.0	1	3.7	4	4.8	10	45.36***
	L	3.1	1	4.3	10	3.3	3	3.6	6	3.3	3	3.1	1	3.6	6	4.0	9	3.3	3	3.9	8	17.60*
Seed coat	H	3.4	7	2.9	5	4.0	8	4.4	9	4.4	9	2.7	3	2.6	2	2.8	4	2.9	5	2.3	1	37.52***
	M	4.8	9	2.7	6	2.5	1	2.6	4	4.2	8	4.9	10	2.5	1	2.8	7	2.6	4	2.5	1	59.14***
	K	3.9	6	3.8	4	4.0	7	3.7	3	3.6	2	4.2	9	4.3	10	3.8	4	4.0	7	3.5	1	6.79ns
	L	3.1	2	3.3	3	3.4	5	3.5	6	2.7	1	3.3	3	3.5	6	4.4	10	3.9	9	3.8	8	20.64*
Size pods	H	2.5	1	3.2	8	3.8	9	2.7	2	3.0	6	2.7	2	4.0	10	2.7	2	3.0	6	2.8	5	16.99*
	M	3.9	9	3.2	5	3.4	8	3.3	6	2.9	3	3.3	6	2.7	2	2.6	1	3.0	4	4.2	10	17.86*
	K	4.3	8	4.0	5	4.0	5	3.3	1	4.3	8	3.3	1	4.1	7	4.6	10	3.8	4	3.5	3	22.87**
	L	2.8	2	3.4	5	3.5	6	3.8	9	2.8	2	3.7	7	3.2	4	4.2	10	3.7	7	2.5	1	21.48*
Size of seeds	H	3.6	5	4.4	10	3.2	2	3.9	9	3.8	8	3.6	5	2.9	1	3.5	3	3.5	3	3.6	5	14.22
	M	3.5	7	3.7	10	3.6	8	3.1	2	3.0	1	3.4	5	3.3	4	3.6	8	3.4	5	3.1	2	7.56ns

Appendix 3.3: Continued.

Trait	District	Variety										H-values										
		V-1	V-2	V-3	V-4	V-5	V-6	V-7	V-8	V-9	V-10											
Size of seeds	K	4.2	7	4.3	9	4.2	7	2.8	1	4.0	5	3.1	2	4.1	6	4.3	9	3.7	4	3.5	3	24.68**
	L	3.7	7	3.6	5	4.5	10	3.6	5	2.9	2	3.4	4	2.3	1	3.7	7	3.7	7	3.2	3	20.88**
Taste of grains	H	3.5	7	3.2	3	4.1	8	4.1	8	4.2	10	3.3	4	3.3	4	3.3	4	2.9	2	2.1	1	26.81**
	M	4.7	10	2.4	3	2.7	6	2.4	3	4.1	8	4.4	9	2.6	5	2.3	2	2.2	1	3.0	7	42.03**
	K	4.5	10	4.1	9	3.8	7	3.3	3	2.8	1	3.7	6	3.8	7	2.8	1	3.5	4	3.6	5	20.77***
	L	2.8	1	3.2	4	3.3	5	3.3	5	3.3	5	2.8	1	3.5	8	4.3	9	3.0	3	4.3	9	26.06*
Time to maturity	H	3.4	4	3.5	5	4.4	7	4.8	10	4.5	8	3.0	3	4.5	8	2.8	2	3.9	6	2.1	1	43.00***
	M	3.9	9	3.2	4	2.6	1	3.6	6	3.9	9	3.7	8	3.1	3	3.3	5	2.7	2	3.6	6	18.16*
	K	1.9	1	3.2	4	2.9	3	4.9	9	2.6	2	4.9	9	4.8	8	3.3	5	4.3	6	4.5	7	72.07*
	L	3.8	1	3.8	4	3.4	5	2.6	5	3.1	5	2.7	1	3.5	8	4.4	9	3.5	3	3.7	9	26.06**
Yield	H	3.2	5	2.7	2	3.3	6	2.6	1	3.0	3	4.3	10	3.6	7	4.2	8	4.2	8	3.1	4	34.48***
	M	3.5	7	3.3	6	3.0	2	3.2	5	2.3	1	3.0	2	3.8	9	4.5	10	3.6	8	3.1	4	26.83***
	K	2.9	2	3.6	7	3.3	3	3.6	7	4.2	10	3.3	3	3.4	6	3.7	9	3.3	3	1.9	1	30.99***
	L	2.5	1	3.2	5	3.5	7	3.3	6	2.9	2	3.0	3	3.6	9	3.7	10	3.5	7	3.0	3	10.72

*, ** and ***, significant at $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$, respectively; V-1 = Red beauty, V-2 = S6T, V-3 = S11T, V-4 = Poland, V-5 = Serenut 8R, V-6 = Serenut 2T, V-7 = Gambia, V-8 = Igola, V-9 = Elsoot, V-10 = Arema; H = Hoima district, M = Masindi district, K = Kumi district, L = Lira district; () = rank in bold font; H value = Kruskal-Wallis H-values.

Appendix 3.4: Morphological and agronomic performance of parental varieties in Hoima, Masindi and Kumi and Lira districts

Variety	GRVDsev.				GRVDprev.				SD				SL_SD				SL				SMK			
	H	M	K	L	H	M	K	L	H	M	K	L	H	M	K	L	H	M	K	L	H	M	K	L
V1	2.89	2.47	2.94	1.85	1.45	1.8	1.84	1.85	0.76	0.73	0.71	0.79	1.55	1.62	1.48	1.5	1.17	1.15	1.06	1.19	1.88	1.81	1.87	1.93
V2	2.42	2.53	3.33	1.85	1.32	1.85	1.83	1.85	0.76	0.77	0.77	0.81	1.66	1.67	1.66	1.63	1.26	1.29	1.27	1.31	1.79	1.81	1.78	1.83
V3	2.61	2.78	2.94	1.87	1.65	1.93	1.92	1.87	0.89	0.91	0.93	0.89	1.59	1.72	1.76	1.85	1.41	1.55	1.63	1.65	1.77	1.96	1.94	1.92
V4	3.11	3.06	3.08	1.9	1.33	1.8	1.88	1.9	0.72	0.69	0.65	0.73	1.59	1.73	1.68	1.53	1.15	1.18	1.09	1.12	1.84	1.68	1.87	1.92
V5	2.43	3	3.11	1.87	1.62	1.95	1.9	1.87	0.87	0.85	0.82	0.88	1.59	1.65	1.67	1.68	1.37	1.4	1.37	1.48	1.64	1.92	1.88	2.00
V6	2.22	2.69	2.75	1.8	1.49	1.92	1.95	1.8	0.8	0.83	0.85	0.86	1.82	1.74	1.69	1.9	1.46	1.45	1.43	1.64	1.76	1.90	1.91	1.93
V7	2.33	2.36	2.78	1.9	1.33	1.76	1.93	1.9	0.75	0.7	0.69	0.77	1.66	1.69	1.68	1.49	1.24	1.18	1.15	1.44	1.90	1.85	1.85	1.97
V8	2.03	2.5	2.67	1.92	1.48	1.84	1.93	1.92	0.81	0.82	0.82	0.79	1.85	1.58	1.86	2.02	1.49	1.29	1.53	1.59	1.89	1.80	1.86	1.90
V9	1.92	2.19	2.25	1.85	1.32	1.71	1.78	1.85	0.79	0.82	0.85	0.84	1.7	1.59	1.63	1.71	1.35	1.3	1.39	1.43	1.69	1.86	1.91	1.90
V10	2.97	2.56	3.19	1.91	1.52	1.88	1.89	1.91	0.81	0.77	0.69	0.75	1.46	1.47	1.55	1.46	1.17	1.14	1.07	1.09	1.94	1.94	1.94	1.93
Mean	2.49	2.64	2.91	2.72	1.45	1.84	1.88	1.87	0.80	0.79	0.78	0.81	1.65	1.65	1.67	1.68	1.31	1.29	1.30	1.36	1.81	1.85	1.88	1.92
LSD _{0.05}									0.07	0.10	0.06	0.05	0.22		0.16	0.13	0.11	0.18	0.13	0.09	0.15			
CV(%)	35.8	24.2	18.7	22.8	49.1	9.6	6.7	7.4	4.9	7.6	4.5	3.3	7.7	7.8	5.5	4.4	5.1	7.9	5.7	3.9	4.7	6.7	4.6	2.7

GRD sev. = Groundnut rosette severity score on a scale (1-5), GRD prev = Groundnut rosette disease percentage prevalence, SD = Seed diameter, SL_SD = Ratio of seed length to seed diameter, SL = Seed length, SMK = Sound Mature Kernels; V1 = Red beauty; V2 = S6T; V3 = S11T; V4 = Poland; V5 = Serenut 2T; V6 = Serenut 8R; V7 = Gambia; V8 = Igola; V9 = Etesot; V10 = Arema; H = Hoima district, M = Masindi district, K = Kumi district, L = Lira district; LSD(0.05) = least significant difference at 5%; CV = coefficient of variation.

Appendix 3.4: Continued.

Variety	Pd wt			Shelling %				Pod. no.				Wt_100				ELS Sev.				
	H	M	K	L	H	M	K	L	H	M	K	L	H	M	K	L	H	M	K	L
V1	136.2	126.6	137.4	137.4	67.83	74.24	70.5	70.5	2.90	2.98	2.89	2.89	35.9	33.7	33.3	40.7	2.75	4	3.19	3.19
V2	110.2	106.8	101.0	101.0	62.20	71.44	66.4	66.4	3.10	3.02	2.87	2.87	42.5	42.9	34.9	41.5	2.81	3.75	3.47	3.67
V3	151.4	151.0	156.6	156.6	68.94	71.79	71.5	71.5	1.87	2.91	2.78	2.78	67.9	69.7	61.1	69.1	2.14	2.97	2.92	3.83
V4	96.0	85.8	99.2	99.2	69.94	67.63	68.2	68.2	3.11	3.05	2.81	2.81	36.9	33.4	32.9	35.3	2.58	3.92	3.69	4.19
V5	136.7	139.0	140.3	140.3	62.98	71.69	70.4	70.4	3.03	3.03	2.86	2.86	58.7	64.7	56.5	60.5	2.00	3.22	2.58	3.72
V6	138.0	117.7	139.0	139.0	63.25	71.23	66.8	66.8	3.05	2.96	2.81	2.81	55	53.7	62.2	63.7	1.89	3.08	2.5	3.28
V7	141.5	127.3	112.1	112.1	64.28	65.32	66.2	66.2	2.86	2.86	2.82	2.82	39.7	37.7	33.2	36.6	2.42	3.61	3.42	3.92
V8	146.9	130.9	134.1	134.1	68.38	68.89	67.1	67.1	1.97	3.01	2.95	2.95	59	52.5	59.5	58.1	2.19	3.42	2.69	3.69
V9	137.5	151.3	152.5	152.5	66.71	72.25	71.7	71.7	3.00	2.98	2.93	2.93	51.6	57	42.7	54.4	2.28	2.97	2.83	3.83
V10	107.2	92.8	86.0	86.0	68.41	69.83	66.1	66.1	3.02	3.06	2.98	2.98	41.9	31.5	31.9	37.1	2.69	3.89	3.75	3.89
Mean	130.20	123.00	125.80	125.80	66.29	70.43	68.5	68.5	2.79	2.99	2.87	2.87	48.9	47.7	44.8	49.7	2.38	3.48	3.11	3.72
LSD _{0.05}	16.78	26.99	20.08	20.08	3.06	-	3.67	3.67	-	0.09	-	-	0.043.7	0.16	0.05	0.05	-	-	-	-
CV(%)	7.40	12.80	9.30	9.30	2.70	5.30	3.10	3.10	29.40	1.80	4.20	4.20	1.20	5.50	1.80	1.80	49.7	62.4	51.3	55.6

Pd wt = Dry Pod weight (g), Shelling % = Shelling percentage; Pod No. = Pod number per plant; Wt_100 = Weight of 100 seeds (g); ELS severity = ELS severity score on a scale (1-9); V1 =Red beauty; V2 = S6T; V3 = S11T; V4 = Poland; V5 = Serenut 8R; V6 = Serenut 2T; V7 = Gambia; V8 = Igola ; V9 = Elesot; V10 = Arema; H= Hoima district, M = Masindi district; K = Kumi district; L = Lira district; LSD_{0.05} = least significant difference at 5%; CV = coefficient of variation.

Appendix 3.5: Spearman's rank correlation coefficients between breeder evaluation of morphological and agronomic traits and farmers' variety scores in Hoima, Masindi, Kumi and Lira districts.

Traits evaluated		Traits evaluated by farmers in Hoima district																	
by breeder	Br	PDZ	QLLVS	TIFLO	VIG	FLON	HT	GEM	NFN	SDPD	SDCTC	SDSZ	DTR	TSE	TMTY	Yld	SHE	RH	RB
Dpw	-0.09	0.46	-0.2	0.22	0.18	0.58	-0.15	0.36	-0.77**	0.16	-0.15	-0.77**	0.46	0.16	0.06	0.74**	0.22	-0.03	0.19
Shg	-0.39	-0.29	0.12	0.22	-0.23	0.22	0.15	-0.25	-0.23	0.16	0.15	-0.23	-0.29	0.16	0.02	-0.1	0.22	0.24	-0.02
Pdno	0.52	-0.23	0.55	-0.09	0.11	-0.56	0.2	-0.22	0.88***	-0.02	0.2	0.88	-0.23	-0.02	0.18	-0.52	-0.09	-0.01	0.13
Wt100	0.06	0.37	0.31	0.36	0.29	0.33	0.09	0.3	-0.26	0.17	0.09	-0.26	0.37	0.17	-0.13	0.4	0.36	-0.01	0.13
ELSSv	-0.22	-0.49	-0.49	-0.41	-0.41	-0.45	-0.1	-0.05	0.36	-0.37	-0.1	0.36	-0.49	-0.37	-0.1	-0.56	-0.41	-0.31	-0.61
GRDsv	-0.01	0.05	0.12	0.28	-0.53	-0.2	0.35	-0.2	0.43	0.37	0.35	0.43	0.05	0.37	0.2	0.76**	0.28	0.36	0.09
GRDprev	-0.16	0.54	0.27	0.52	-0.02	0.38	0.15	-0.07	-0.15	0.46	0.15	-0.15	0.54	0.46	-0.15	0.08	0.52	0.37	0.35
SD	-0.2	0.38	0.2	0.32	0.12	0.38	0.04	0.19	-0.19	0.13	0.04	-0.19	0.38	0.13	-0.32	0.23	0.32	0.19	0.17
SL_SD	0.22	-0.13	0.08	-0.17	0.54	0.03	-0.26	0.04	-0.27	-0.19	-0.26	-0.27	-0.13	-0.19	-0.06	0.65*	-0.17	-0.44	-0.04
SL	0.04	0.41	0.16	0.26	0.55	0.23	-0.08	0.13	-0.32	0.09	-0.08	-0.32	0.41	0.09	-0.27	0.66*	0.26	-0.2	0.17
SMK%	-0.42	-0.39	-0.67*	-0.51	-0.47	0.05	-0.57	-0.09	-0.21	-0.34	-0.57	-0.21	-0.39	-0.34	-0.36	-0.08	-0.51	0.43	-0.75*

Traits evaluated		Traits evaluated by farmers in Masindi district																	
by breeder	Br	PDZ	QLLVS	TIFLO	VIG	FLON	HT	GEM	NFN	SDPD	SDCTC	SDSZ	DTR	TSE	TMTY	Yld	SHE	RH	RB
Dpw	0.04	-0.46	-0.12	-0.12	-0.36	-0.18	-0.36	-0.1	-0.33	-0.34	-0.02	0.19	0.05	-0.2	-0.4	0.1	0	-0.27	-0.24
Shg	-0.02	-0.24	0.16	0.42	-0.04	0.05	0.1	-0.05	0.21	0.14	0.33	0.3	0	0.28	0.08	-0.24	0.24	0.01	0.26
Pdno	-0.1	0.26	-0.14	0.1	0.11	0.33	0.33	-0.3	0.4	0.6	0.08	-0.37	0.22	-0.03	0.49	-0.23	0	-0.27	-0.24
Wt100	0.18	-0.27	0.03	0.4	-0.1	-0.08	-0.31	0.21	-0.02	-0.56	0.18	0.25	-0.13	-0.07	-0.3	-0.31	-0.24	0.02	-0.33
ELSSv	-0.99***	-0.02	0.13	0.1	-0.33	0.13	0.44	-0.15	0.19	0.59	0.08	-0.13	-0.06	0.24	0.5	0.22	0.27	0.06	0.35
GRDsv	0.58	0.64*	0.5	0.5	0.62*	0.42	0.56	0.63*	0.66**	0.05	0.09	-0.34	-0.29	0.29	0.34	0.79**	-0.13	0.75*	-0.16
GRDprev	0.19	0.39	0.23	0.34	0.5	0.22	0.19	0.49	0.69*	-0.19	0.19	-0.08	-0.16	0.47	0.28	-0.83*	0.02	0.41	0.04
SD	0	0.02	0.02	0.4	0.21	0.07	-0.19	0.2	0.28	-0.33	0.17	0.12	-0.01	0.16	-0.11	-0.54	0.01	0.09	0.01
SL_SD	0.67*	0.35	0.65*	0.42	0.43	0.15	0.32	0.82**	0.21	-0.4	0.13	0.01	-0.53	0.21	-0.03	0.39	-0.29	0.65*	-0.5

Appendix 3.5: Continued.

Traits evaluated		Traits evaluated by farmers in Masindi district																	
By breeder	Br	PDZ	QLLVS	TIFLO	VIG	FLON	HT	GEM	NFN	SDPD	SDCTC	SDSZ	DTR	TSE	TMTY	Yld	SHE	RH	RB
SL	0.22	-0.12	0.12	0.45	0.07	-0.04	-0.26	0.38	0.07	-0.64*	0.21	0.26	-0.2	-0.03	-0.28	-0.41	-0.35	0.16	-0.37
SMK (%)	0.1	0.43	0.15	0.28	0.51	0.03	0.01	0.37	0.31	-0.22	-0.28	-0.17	0.22	0.37	-0.16	-0.64*	0.3	0.19	-0.06
Traits evaluated by farmers in Kumi district																			
Dpw	0.36	-0.33	0.1	0.19	-0.74*	-0.19	-0.19	0.14	-0.43	-0.24	0.08	0.32	0.46	-0.07	-0.2	0.46	-0.38	0.03	0.33
Shg	-0.09	-0.35	-0.06	0.29	-0.12	-0.16	0.59	0.66*	-0.34	0.31	0.17	-0.06	0.04	0.08	-0.46	-0.1	-0.3	0.53	0.03
Pdno	-0.51	0.19	-0.76**	0.24	0.26	0.14	-0.14	-0.31	0.46	0.26	0.46	0.03	0.18	0.33	0.73*	-0.02	0.62*	0.53	0.03
Wt100	0.24	-0.25	-0.02	0.18	-0.51	-0.06	-0.07	0.05	-0.31	0.11	-0.18	0.38	0.46	-0.29	-0.12	0.13	-0.49	-0.12	0.08
ELSSv	0.38	0.58	0.58	-0.1	0.88**	0.64*	0.47	-0.29	0.61	0.09	-0.45	-0.31	-0.27	0.18	-0.006	-0.5	0.27	-0.07	-0.13
GRDsv	-0.18	-0.39	-0.4	-0.28	-0.38	-0.45	-0.34	-0.54	-0.24	-0.9***	0.04	-0.13	-0.56	0.43	0.31	-0.43	0.37	0.02	-0.28
GRDprev	-0.3	-0.16	-0.25	-0.1	-0.11	-0.09	-0.11	0.54	-0.32	0.08	-0.41	0.09	0.06	-0.45	0.16	0.27	-0.24	0.47	0.47
SD	-0.09	-0.1	0.09	-0.14	-0.32	-0.21	-0.34	-0.15	-0.17	0.15	0.15	0.25	0.06	0.05	-0.46	0.13	-0.22	0.46	-0.32
SL_SD	0.26	-0.09	0.06	-0.17	0.29	0.01	-0.21	0.03	-0.09	0.36	0.27	0.22	0.17	-0.35	-0.06	0.38	-0.37	-0.37	-0.32
SL	-0.12	-0.01	0.15	-0.08	-0.27	-0.1	-0.27	-0.05	-0.15	0.32	0.39	0.32	0.16	-0.1	-0.28	0.25	-0.26	0.02	-0.1
SMK%	0.1	-0.47	-0.24	0.88***	0.36	0.32	-0.76**	0.02	-0.28	-0.3	0.03	0.15	0.16	-0.04	-0.33	-0.3	-0.17	0.02	-0.5

Appendix 3.5: Continued.

Traits evaluated		Traits evaluated by farmers in Lira district																	
By breeder	Br	PDZ	QLLVS	TIFLO	VIG	FLON	HT	GEM	NFN	SDPD	SDCTC	SDSZ	DTR	TSE	TMTY	Yld	SHE	RH	RB
Dpw	-0.1	-0.02	0.09	-0.02	-0.27	-0.1	-0.28	0.03	-0.15	0.3	0.47	0.16	0.13	-0.02	-0.42	0.03	-0.16	-0.21	-0.29
Shg	-0.21	-0.06	0.09	-0.1	-0.22	-0.12	-0.23	0.1	-0.18	0.23	0.16	0.07	0.02	-0.09	-0.46	0.03	-0.27	-0.19	-0.31
Pdno	-0.5	-0.58	-0.68*	-0.49	-0.22	-0.31	-0.22	-0.31	-0.44	-0.05	-0.46	0.22	0.43	-0.2	-0.19	-0.13	-0.1	0.01	0.47
Wt100	-0.15	-0.08	0.09	-0.13	-0.29	0.19	0.31	-0.13	-0.26	0.24	0.23	0.26	0.1	-0.1	-0.36	0.11	-0.19	-0.02	0.01
ELSSv	-0.35	-0.16	-0.23	-0.09	-0.24	0.04	-0.1	-0.09	-0.13	-0.05	-0.2	-0.17	-0.21	-0.55	0.49	0.32	-0.25	-0.2	0.52
GRDsv	-0.18	-0.39	-0.4	-0.28	-0.38	-0.45	-0.34	-0.54	-0.24	-0.9***	0.04	-0.13	-0.56	0.43	0.31	-0.43	0.37	0.16	0.37
GRDprev	-0.3	-0.16	-0.25	-0.1	-0.11	-0.09	-0.11	-0.2	-0.32	0.08	-0.41	0.09	0.06	-0.45	0.16	0.27	-0.24	0.15	0.6
SD	-0.09	-0.1	0.09	-0.14	-0.32	-0.21	-0.34	-0.15	-0.17	0.15	0.3	0.25	0.06	-0.46	0.13	-0.22	-0.22	0.1	-0.16
SL_SD	-0.26	-0.09	0.06	-0.17	-0.29	0.01	-0.21	0.03	-0.09	0.36	0.27	0.22	0.17	-0.35	-0.06	0.38	-0.37	-0.39	0.12
SL	-0.12	-0.01	0.15	-0.08	-0.27	-0.1	-0.27	-0.05	-0.15	0.32	0.39	0.32	0.16	-0.1	-0.28	0.25	-0.26	-0.19	-0.02
SMK%	0.66*	0.62*	0.49	0.72*	0.64*	0.54	0.59	0.52	0.41	0.51	0.02	-0.3	0.25	-0.03	0.01	-0.03	0.36	0.36	0.25

*, ** and *** = significant at Ps0.05, Ps0.01 and Ps0.001, respectively; DFW= Dry pod weight; Shg = Shelling out turn; Pdno = Pod number; wt100 = weight of 100 seeds; ELSSv = leaf spot (ELS+LLS) severity score; GRDsv = groundnut rosette severity score; GRD prev= Groundnut rosette prevalence; SD = Seed diameter; SL_SD=Ratio of Seed length to seed diameter; SL= Seed length; SMK%=Proportion of sound mature kernels; Br= Level of branching, PDZ, Prevalence of pests and/or diseases; QLLVS = Quantity/quality of leaves; TIFLO = Time to initial flowering; VIG= Plant vigour; FLON=flower number; HT=plant height (cm); GEM = germination percentage; NFN = number of flowers per node; SDPD = Number of seed per pod; SDTC = Seed coat colour; SDSZ = Seed size; DTR = Drought tolerance; TSE= Taste of raw kernel; TMTY = Time to maturity; SHE = Shelling out turn; RB = Ranking before harvest; RH = Ranking at harvest.

CHAPTER 4 Genome wide SNP diversity and population structure in a Ugandan groundnut (*Arachis hypogaea* L.) collection

Abstract

Information on genetic diversity and population structure among germplasm collections is essential for crop genetic improvement schemes, as well as in supporting conservation. In this study, a cultivated groundnut (*Arachis hypogaea* L.) collection consisting of 104 accessions (farmer collections, Ugandan breeding lines, ICRISAT materials and landraces from Mozambique) was used to estimate genetic diversity and structure using 2896 single nucleotide polymorphism (SNP) markers. Genetic diversity was analysed using three measures of genetic diversity namely polymorphic information content (PIC), heterozygosity (H) and inbreeding coefficient (f). Genetic differentiation between population pairs were evaluated using Reynold's genetic distance and F_{ST} values. Clustering based on neighbour joining analysis, principal coordinate, as well as the Bayesian model clustering implemented in STRUCTURE were used. Results indicated that 50% of 2896 SNPs were polymorphic with a mean PIC of 0.15 for all populations combined. The least and highest polymorphism was observed in Mozambican landraces (PIC = 0.05) and ICRISAT accessions (PIC = 0.21), respectively. Genotypes were grouped into three major clusters using an unrooted tree. Analysis of molecular variance (AMOVA) showed that maximum diversity was partitioned between and within individual levels but not between populations. The genetic differentiation among the population based on F_{ST} values was small (0.04) due to inbreeding and low genetic diversity of the collection despite the high rate of allelic exchange among the populations. The principal component analysis grouped genotypes into three broad groups, each comprising all the populations in the current collection across the two axes with 27.4% cumulative variation. Results of population structure indicated that maximum Δk was at $K=3$, suggesting three gene clusters in the gene pools of each population. Overall, the groundnut accessions were categorized into three major groups that prominently reflected subspecies, botanical varieties and pedigree. The results clearly demonstrated the existence of low genetic diversity in the current groundnut collection. There is, therefore, a need to improve it through introductions, transformation and genome editing approaches. In addition, more efficiency can be achieved using genomic selection for varietal improvement of complex traits.

4.1 Introduction

Groundnut is an important oilseed crop grown extensively in the semi-arid and subtropical regions of the world by resource-poor farmers to produce edible oil and for human and animal consumption. However, production of this crop is highly constrained by both abiotic and biotic stresses leading to low seed yields (Reddy, 2003). Cultivar improvement through controlled hybridisation based on phenotypic differentiation has been the focus of breeding. Nonetheless, given the complex behaviour of desired traits, this approach is associated with technical difficulties encountered in making major advances. Therefore, the use of molecular breeding approaches has been found to be complementary, but requires pre-requisite conditions, such as availability of genetic variation in the germplasm, critical mass of molecular markers, genetic maps and suitable phenotyping approaches (Pandey et al., 2012).

Genetic diversity assessment is very useful for understanding the genetic variation of a germplasm collection (Varshney et al., 2009). It provides a rational basis for selection and enables understanding of genetic relationship at a fine scale. Besides, it also provides measures of genetic deviation between and genetic diversity within the major genetic clusters that comprise crop germplasm. Among other methods, DNA-based techniques are most suitable for genetic diversity assessment, and for evolutionary and conservation studies for germplasm accessions.

In groundnut, the genetic bottlenecks caused by spontaneous hybridization, polyploidisation, and reproductive isolation from wild relatives have largely affected the development of optimum genetic and genomic resources for molecular breeding (Varshney et al., 2013). Nonetheless, large scale genomic resources through genome sequencing of the ancestors of peanut *A. duranensis* and *A. ipaensis*, has opened the way for several genetic studies, including molecular diversity, genetic mapping and the utilisation of modern breeding strategies (Pandey et al., 2012; Varshney et al., 2013; Ozias-Akins, 2013; Bertoli et al., 2016; Clevenger et al., 2017).

In the last decade, SSR markers have been favoured for genetic mapping in groundnut (Gautami et al., 2012; Qin et al., 2012; Sujay et al., 2012; Shirasawa et al., 2013; Huang et al., 2015). However, polymorphic SSR markers are limited in number, time consuming, and expensive to assay. Therefore, the use of high-throughput markers, like those based on single nucleotide polymorphisms (SNPs), is needed for an efficient application of genomics data for marker assisted breeding, quantitative trait locus (QTL) mapping, and genomic selection. Although SNP arrays have been used in wild relatives of groundnut (Nagy et al., 2012; Bertoli et al., 2014), their development to assay the tetraploid ($2n = x = 40$) cultivated groundnut (*A. hypogaea*) has lagged behind other polyploids including oats (Tinker et al., 2014), wheat (Wang et al., 2014), and strawberry (Bassil et al., 2015). However, recent progress in sequencing has enabled timely detection of large numbers of SNPs at a much lower cost.

More recently, an innovative approach known as genotyping-by-sequencing (GBS) has been developed to perform simultaneous SNP discovery and genotyping (Elshire et al., 2011). This approach is a united one-step procedure of SNP discovery and genotyping and constitutes a rapid, high throughput and cost-effective tool for a genome-wide analysis of genetic diversity, especially for non-model species and germplasm sets. These features make GBS advantageous for genetic diversity studies in plants with informative sets of markers (Peterson et al., 2014).

Among the several processes advanced to cut down genome complexity, DArT-Seq (diversity arrays technology sequencing) method has brought a significant influence through the intelligent selection of the genome fraction corresponding predominantly to active genes. Classic DArTs (diversity arrays technology) markers have been substituted by DArT-Seq markers based on genotyping by sequencing. DArT-Seq and SNP (single nucleotide polymorphism) markers based on GBS technology have been successfully applied for linkage mapping, QTL identification in bi-parental mapping population, genome wide association studies (GWAS), and genetic diversity studies in many other crops (Brinez et al., 2012; Grzebelus et al. 2014;), as well as marker-assisted genomic selection. Given the shortcomings of conventional breeding for groundnut improvement, there is a need to apply molecular tools for groundnut breeding in Uganda. However, genetic diversity and population structure of the Ugandan groundnut materials as revealed by SNP markers has not been reported. Availability of this data would enable groundnut breeders to utilise molecular breeding tools to develop varieties with better expression of the most desired traits. Therefore, the proposed study seeks to uncover underlying genetic diversity and population structure in the Ugandan groundnut collection using SNP markers.

4.2 Materials and methods

4.2.1 Genotypes

A total of 104 groundnut genotypes were used in this study (Appendix 4.1). These materials were selected from landraces, local accessions, introductions and improved varieties/breeding lines released from the National Semi-Arid Resources Research Institute (NaSARRI). Of the 104 genotypes; 16 genotypes originated from ICRISAT-Malawi (ICRISAT genotypes), 36 from the Department of Groundnut Improvement gene-bank at NaSARRI (Ug-breeding lines), 35 from farmers in Hoima, Masindi, Lira, Dokolo, Amuria, Soroti and Kumi districts of Uganda (Farmer cultivars), and 17 were sourced from Mozambique (Mozambican landraces). The genotypes were selected based on preliminary evaluations (Kakeeto, unpublished) and literature surveys of similar studies conducted elsewhere. Genotypes from farmers were collected during visits to the districts and directly requesting farmers to provide cultivars that were local and referred to by their local names during the participatory

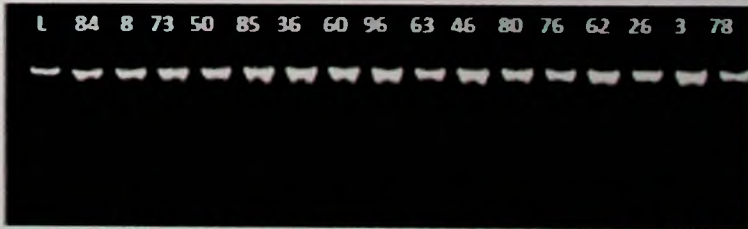
rural appraisal activity. Thus, the germplasm collected from farmers constituted both improved cultivars and landraces.

4.2.2 Genotypic characterisation

Total genomic DNA was isolated from young leaves (two-week-old seedlings) (Plate 1A) of these genotypes using the Zymo research leaf and seed extraction kit (<https://www.zymoresearch.com/quick-dna-plant-seed-miniprep-kit>). DNA quantity for all samples was estimated by spectrophotometry (Nano-drop® 1000-Thermo Scientific, USA) and confirmed on 0.8% agarose gels (Plate 1B) against 50uL ladder and DNA was then diluted to 30ng/μL before shipment for DArT-Seq genotyping.



Plate 1A: Groundnut seedlings at two weeks after planting



0.8% agarose, 5.7Volts/cm, 45 min, λ = 50ng/μl
Plate 1B: Gel image showing DNA bands for the groundnut samples

4.2.3 Genotyping and marker analysis

4.2.3.1 Genotyping by sequencing (GBS analysis)

Genotyping by sequencing of the 104 groundnut accessions was performed using a whole genome profiling service for SNP and DArT-Seq markers. 50 µl of the 30 ng/µl was sent to Diversity Arrays Technology (<http://www.diversityarrays.com/>) centre for SNP and DArT-Seq analysis following procedures as described by Jaccoud et al. (2001).

4.2.3.2 Quality control

SNPs were filtered and converted to Hap map format using a custom Perl script incorporating the criteria for: Missing individual (mind) greater than 0.15; missing loci (geno) greater than 0.5 using a filtration method implemented in the PLINK software (Purcell et al., 2007) v1.09 under Linux environment. Filtering for individuals with missing data was set at a threshold of > 0.15, as result only one individual or sample was removed leaving 103 samples and 2986 variants or SNPs for further Quality Control Processes (Figure 4.1). Filtering for loci with missing genotypic data was set at a threshold of > 0.5, based on this threshold, 40 variants were to be removed because they lacked genotypic data (Figure 4.2). However, given the low number of SNPs, these SNPs were not removed. As a result, 103 samples and 2986 variants or SNPs were maintained for further analysis.

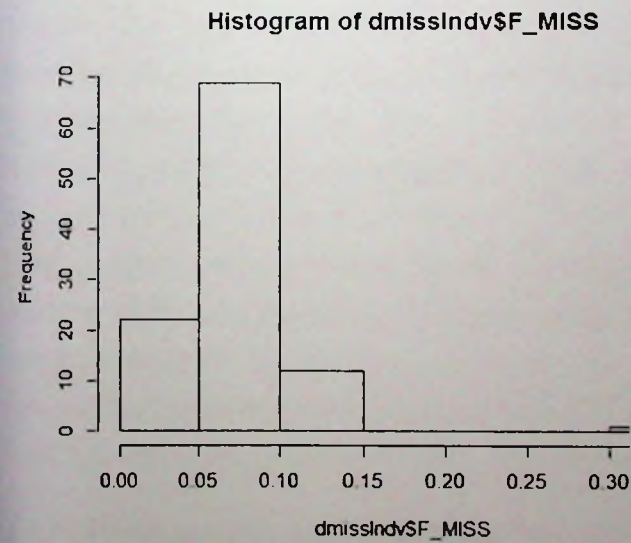


Figure 4.1 Histogram for missing individuals

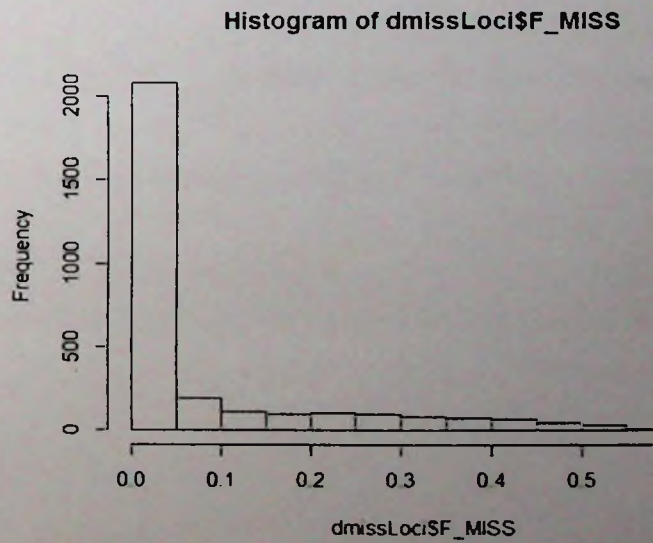


Figure 4.2 Histogram for missing loci

4.3 Data analysis

4.3.1 Population genetic diversity and differentiation

The SNP data in the form of bases were numerically coded as follows: A = 1, C = 2, G = 3, and T = 4 using excel software. Missing data was coded as 9 as suggested by the Power Marker software (Liu and Muse, 2005). Power marker software was used to calculate polymorphic information content (PICs), major allele frequency (MAF), genetic diversity (GD) and inbreeding coefficient (f). These parameters were compared pairwise for the germplasm based on user assigned groupings. Polymorphism information content (PIC) was calculated using the method of Botstein et al. (1980) as below;

$$PIC = 1 - \sum_{i=1}^k p_i^2 - \sum_{i=1}^{k-1} \sum_{j=i+1}^k 2p_i^2 p_j^2$$

Where, p_i and p_j are the frequencies of alleles i and j , respectively.

4.3.2 Analysis of molecular variance (AMOVA)

AMOVA was used to test whether the classification of groundnuts genotypes according to the user assigned populations proposed at the initiation of the study could be supported by genetic data, the partition of genetic variation among different groundnut populations using Arlequin ver. 3.5.1.2 (Excoffier and Lischer, 2005). The same software was also used to estimate observed heterozygosity (H_o), expected heterozygosity (H_e) or gene diversity and effective allele migration rate per generation N_m (Slatkin, 1995). The same package was also used to estimate F_{ST} (Weir and Cockerham, 1984) pair-wise genetic distances between population using genetic distances as deviations from a group mean position and squared deviations as variances. To test the null hypothesis of no population structure within and between the groups, the F_{ST} values were compared on a pairwise basis to determine the level of genetic differentiation at user grouping. Based on the F_{ST} values, differentiation between the populations was classified as little (0.00 – 0.05), moderate (0.05 - 0.15), great (0.15 - 0.25) and very great (> 0.25) (Wright, 1965:cited in Manyasa et al., 2015).

4.3.3 Phylogenetic and population structure analysis

To investigate the genetic relationships between populations using allele frequency differences between populations, the principal components analysis (PCA) was carried out with PLINK software in Linux environment and ggplot2 package implemented in R software v.3.3 (Girke and Riverside, 2011). Additionally, the UPGMA based clustering analysis was conducted on the genetic data using TASSEL software v.5 (Bradbury et al., 2007).

To complement the PCA and cluster analysis, the genetic structure of the groundnut genotypes was determined using the admixture model with correlated allele frequencies based on the Monte Carlo Markov Chain (MCMC) algorithm implemented in STRUCTURE 2.3.3 software (Pritchard et al., 2000; Falush et al., 2003). The admixture model assumed that the genome of each individual resulted from the mixture of K ancestral populations. The estimated proportions of each individual's genotype originating from each of the K ancestral populations (q) was calculated for K ranging from 1 to 10 with three runs for each K value. For each run, a burn-in period of 20,000 and MCMC replications of 5000 was used. The optimum K value was calculated using STRUCTURE HARVESTER, an online available programme (<http://taylor0.biology.ucla.edu>) which computed the log likelihood of the data [LnP(D)] in the STRUCTURE output and adhoc statistic Δk based on the rate of change in LnP(D) between successive K and also computed the final population structure (Evanno et al., 2005).

4.4 Results

4.4.1 Population genetic diversity and SNP Polymorphism

The results of genetic diversity analysis are presented in Table 4.1. A total of 2986 SNP markers were generated by DArTs sequencing. Out of 2986 SNPs revealed, 50% were polymorphic with a mean PIC of 0.15 for all populations combined. Under the Uganda breeding lines, 1359 out of the 2986 SNPs were polymorphic with a mean PIC of 0.14, 1387 out of 2986 were polymorphic with a mean PIC of 0.19 for farmer cultivar materials, 985 out of 2986 were polymorphic with an average PIC of 0.05 for materials originating from Mozambique and 1410 out of 2986 were polymorphic with a mean PIC of 0.21 for ICRISAT genotypes. The average gene diversity for the 103 groundnut genotypes was 0.17 with a range from 0.15 (Mozambique) to 0.19 (ICRISAT). The expected heterozygosity, H_e , varied from 0.24 in Ugandan breeding lines to 0.30 in Mozambican landraces with a mean of 0.27 for the whole collection. Similarly, the observed heterozygosity (H_o) ranged from 0.21 for Ugandan breeding lines and ICRISAT genotypes to 0.29 in Mozambican landraces with a mean of 0.23. The expected heterozygosity was higher than the observed heterozygosity.

Table 4.1 Genetic variability within groundnut populations in the Ugandan collection

Populations	MAF	Ho	He	GD	PIC	f	Monomorphic loci (%)	Polymorphic loci (%)
Ugandan breeding lines	0.90	0.21	0.24	0.16	0.12	0.14	1087 (36.6)	1359 (45.7)
Mozambican landraces	0.90	0.29	0.30	0.15	0.11	0.05	1634 (55.0)	985 (33.2)
Farmer cultivars	0.88	0.20	0.25	0.18	0.13	0.19	1005 (33.8)	1387 (46.7)
ICRISAT genotypes	0.88	0.21	0.27	0.19	0.14	0.21	1015 (34.2)	1410 (47.5)
Mean	0.89	0.23	0.27	0.17	0.13	0.15	1185 (48.0)	1285 (50.9)

MAF= Major allele frequency; Ho = Observed heterozygosity; He = Expected heterozygosity; GD = Gene diversity, PIC = Polymorphic information content, f = Inbreeding coefficient

4.4.2 Genetic differentiation and structure

The analysis of molecular variance (AMOVA) performed among the four user-assigned populations from this study revealed a variation of 3.6%, 15.4%, and about 81% being as a result of differentiation among populations, among individuals within population and within individuals, respectively, of the entire collection (Table 4.2).

Table 4.2 Analysis of molecular variance (AMOVA) design and results based on SNP data (Averaged over 2986 loci)

Source of Variation	Sum of squares	Variance components	Percentage variation
Among populations	1973.57	8.73	3.57
Among individuals within populations	24380.49	37.76	15.43
Within individuals	199944.50	198.20	81.00
Total	46298.56	244.68	

The overall F_{ST} value among the groundnut populations was 0.036 (Table 4.3). Pairwise estimates of F_{ST} among the user assigned population ranged from 0.002 to 0.062. The lowest differentiation was between farmer cultivars and ICRISAT materials. On the other hand, the highest differentiation was between Uganda breeding lines and Mozambican landraces. Using the Reynold's method, the genetic distance within the groundnut genotypes ranged from 0.002 to 0.064 (Table 4.4). The lowest genetic distance was observed between ICRISAT genotypes and farmer cultivars and the highest distance was observed between Mozambican landraces and Ugandan breeding lines, agreeing with F_{ST} based method of comparison. The Uganda breeding lines showed relatively higher level of genetic differentiation (F_{ST} = 0.02019 to 0.06237; Reynold's genetic distance = 0.02040 to 0.06440) from other populations in this study.

The pairwise effective rate of migration or gene flow among the study materials is presented in Table 4.5. Gene flow among the study population ranged from 0.002 to 0.067. The lowest exchange of genes was shown to occur between farmer cultivars and ICRISAT materials, while the highest exchange occurs between Ugandan breeding lines and Mozambican landraces. These results agree with genetic differentiation results.

Table 4.3 Average Fixation-Statistics over all loci

Fixation Indices	Value
Inbreeding (F_{IS})	0.16001
Genetic differentiation (F_{ST})	0.03567
Total inbreeding (F_{IT})	0.18997
Allele migration rate (Nm)	0.13405

Table 4.4 Populations differentiation: Pairwise F_{ST} (below diagonal) and Reynolds' (above diagonal) genetic distance

Populations	Ugandan breeding line	Farmer cultivar	Mozambique	ICRISAT
Ugandan breeding line	0.000	0.020	0.064	0.032
Farmer cultivars	0.020	0.000	0.047	0.002
Mozambican landraces	0.062	0.046	0.000	0.036
ICRISAT genotypes	0.032	0.002	0.035	0.000

Table 4.5 Effective rate of migration among the study groundnut populations: Based on Slatkin (1995) linearized F_{ST} derivation

Populations	Ugandan breeding line	Farmer cultivar	Mozambique
Farmer cultivars	0.021	0.000	
Mozambican landraces	0.067	0.048	0.000
ICRISAT genotypes	0.033	0.002	0.036

4.4.2.1 Principal component analysis

The results of the principal component analysis (PCA) are presented in Figure 4.3A and 4.3B. A biplot of the first three axes accounted for 32.4 % of variation. The results also indicated a clear separation of genotypes across the axes reflecting three clusters. The membership of these clusters included all the four populations under study for the 2-dimensional graph. Of the three clusters under the 2-dimensional graph, cluster I had the highest allocation of genotypes, followed by cluster II and least by cluster III. However, in the 3-dimensional graph (Figure 4.3B), like the 2-dimensional plot (figure 4.3 A), the genotypes/taxa were grouped roughly into 3 groups. Indeed, the 3-dimensional graph had a better differentiation of taxa or populations than the 2-dimensional graph. It was interesting to note that the Mozambican landraces (red) had a unique cluster whereas the farmer cultivar, ICRISAT genotypes and Ugandan breeding lines formed yet another cluster. Finally, the third cluster was comprised of only Ugandan breeding lines

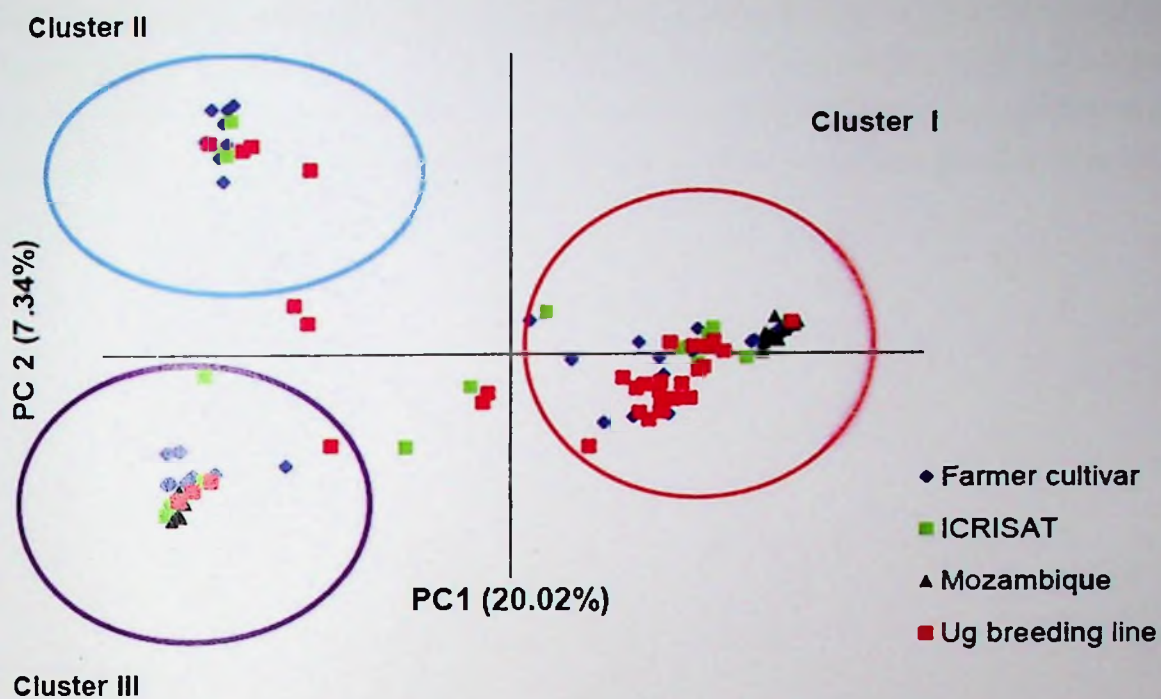


Figure 4.3 A Principal component analysis 2-dimensional graph for the groundnut populations.

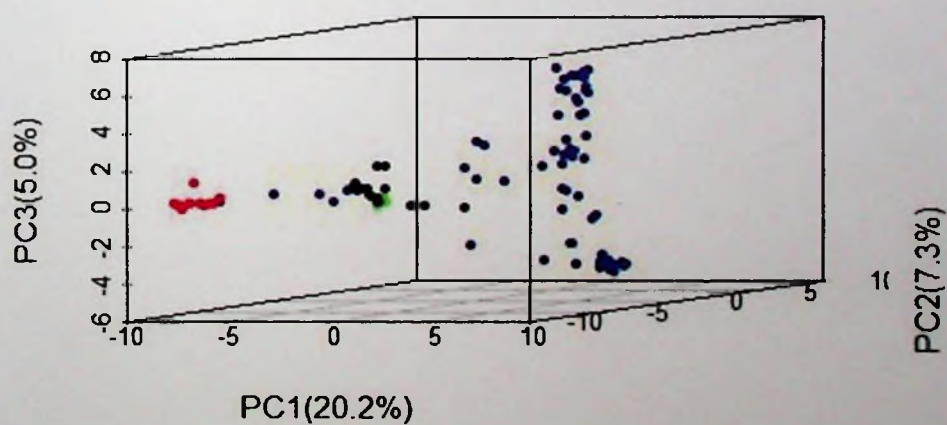


Figure 4.3 B Principal component analysis 3-dimensional graph for the groundnut populations (Blue = Ugandan breeding lines, Black = Farmer cultivar, green = ICRISAT genotypes, and red = Mozambican landraces)

4.4.2.2 Population structure analysis

A graphical representation of structure analysis is presented in Figure 4.4, Figure 4.5, and Figure 4.6. STRUCTURE analysis was run for a range of K (number of fixed subgroups or cluster) from 1 to 10 on the entire set of groundnut accessions. The estimated log probability of the data [LnP(K)] for each K plateaued at K = 3. The maximum K-value was also reached at K = 3 suggesting three distinct groups.

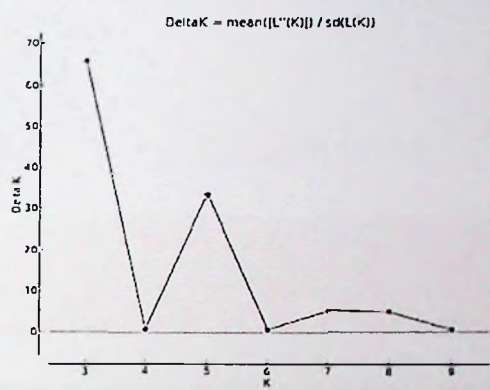


Figure 4.4 Delta K values as inferred by STRUCTURE

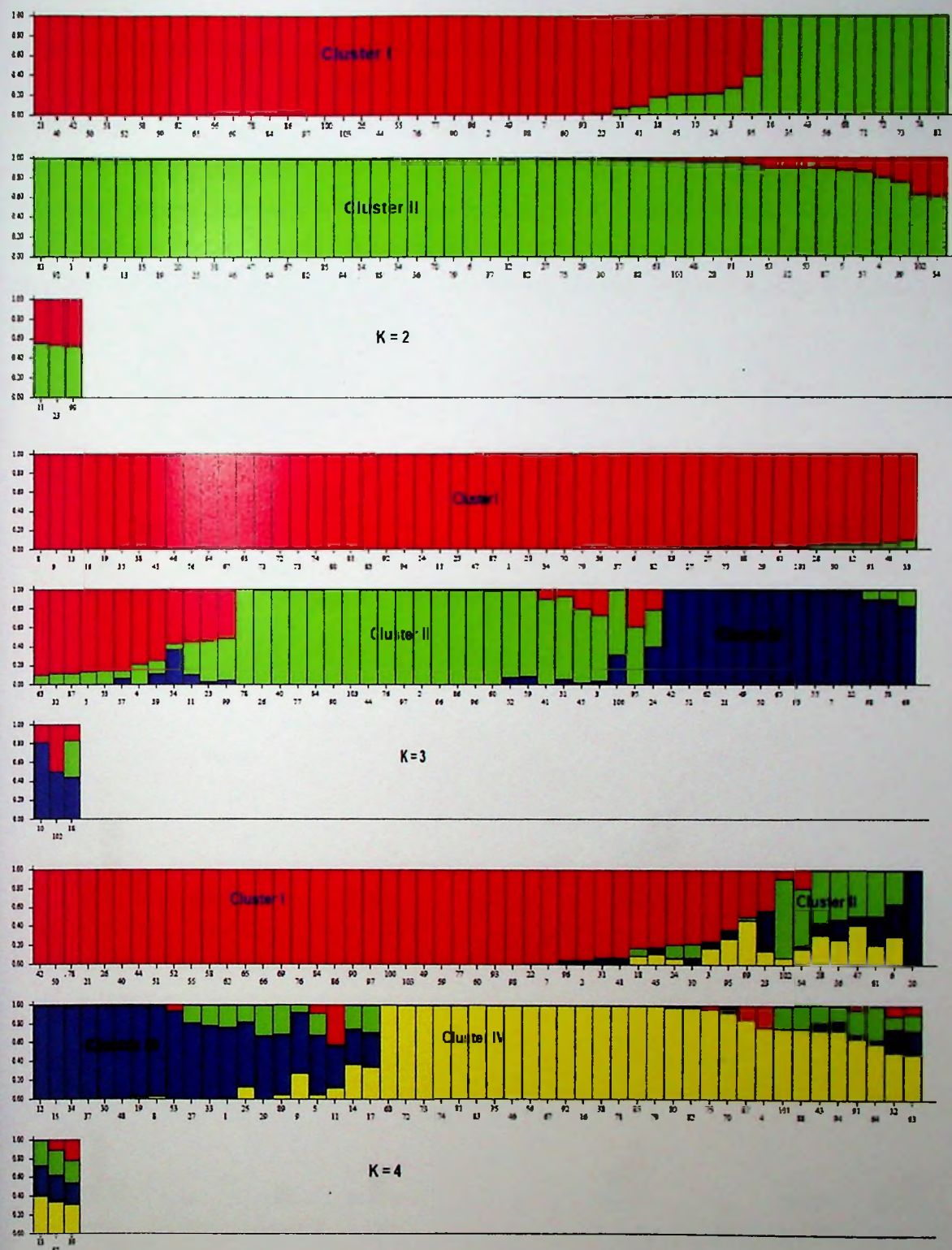


Figure 4.5 Model based clustering of SNP data (from K=2 to K=4) for Ugandan groundnut collection

All the four user populations in the collection were represented in each of the three clusters based on Evanno clustering (Figure 4.5). At $K = 2$, cluster I (red) had 34 genotypes, cluster II (green) had 55 genotypes and 14 admixture genotypes; when $K = 3$, cluster I (red) had 62 genotypes, cluster II (green) had 20 and cluster III (blue) had 13 and 8 admixtures, respectively. When $K = 4$, Cluster I (red) had 36 genotype, cluster II (green) had 1 genotype, cluster III (blue), had 10 genotypes, cluster IV (red) had 36 genotypes and 38 admixtures. The level of admixtures increased with movement away from the appropriate K . Figure 4.6 shows the proportions of genotypes by botanical variety (left) and sub species (right) at from $K = 2$ to $K = 4$.

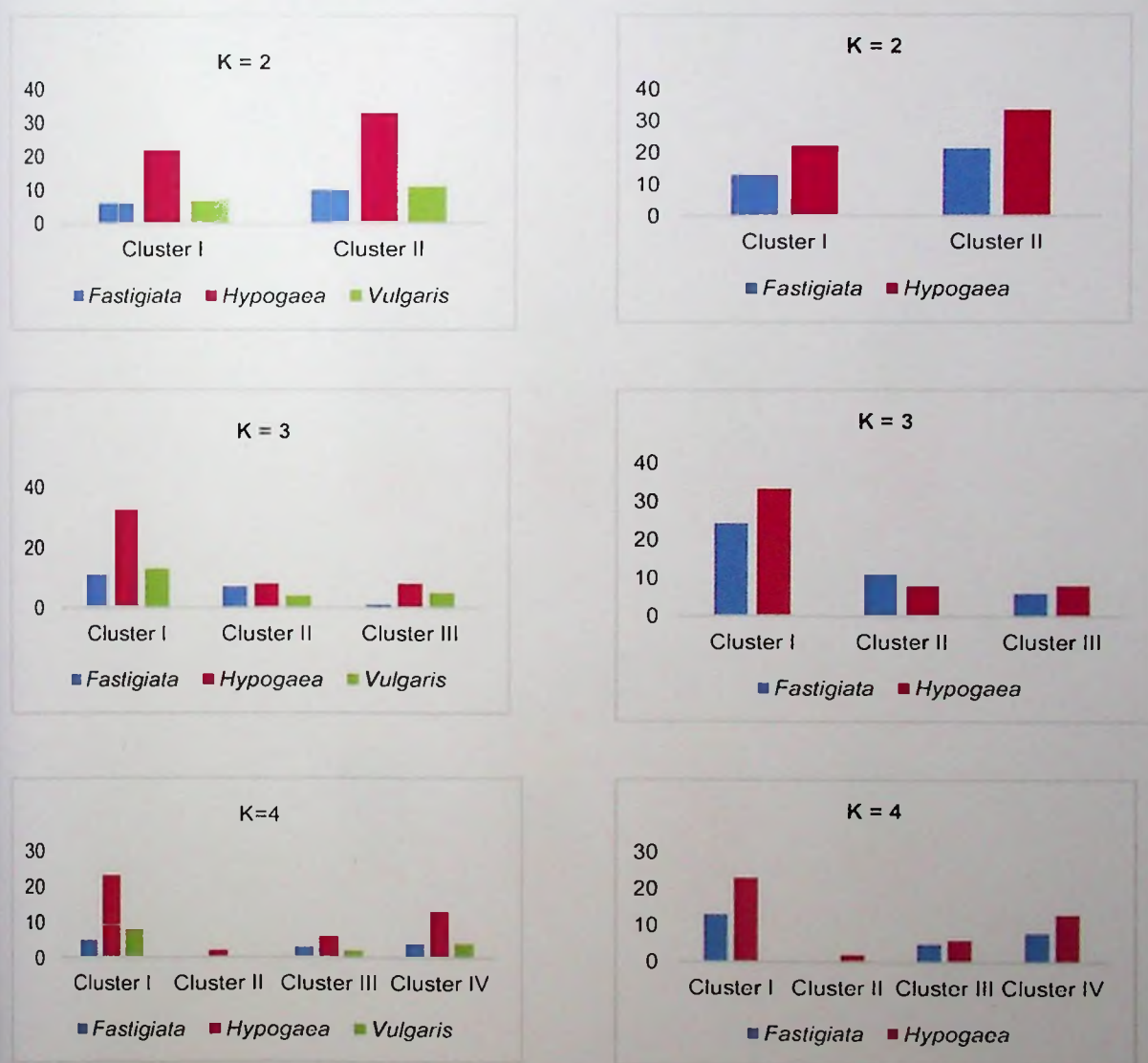


Figure 4.6 Proportion of genotypes allocated by botanical variety (left) and subspecies (right) as inferred by structure (from $K=2$ to $K=4$)

Figure 4.7 shows the allocation of gene clusters in each genepool or user assigned population. At $K=3$, it was observed that the Mozambique population was represented by only two gene clusters compared to the rest which had the three clusters.

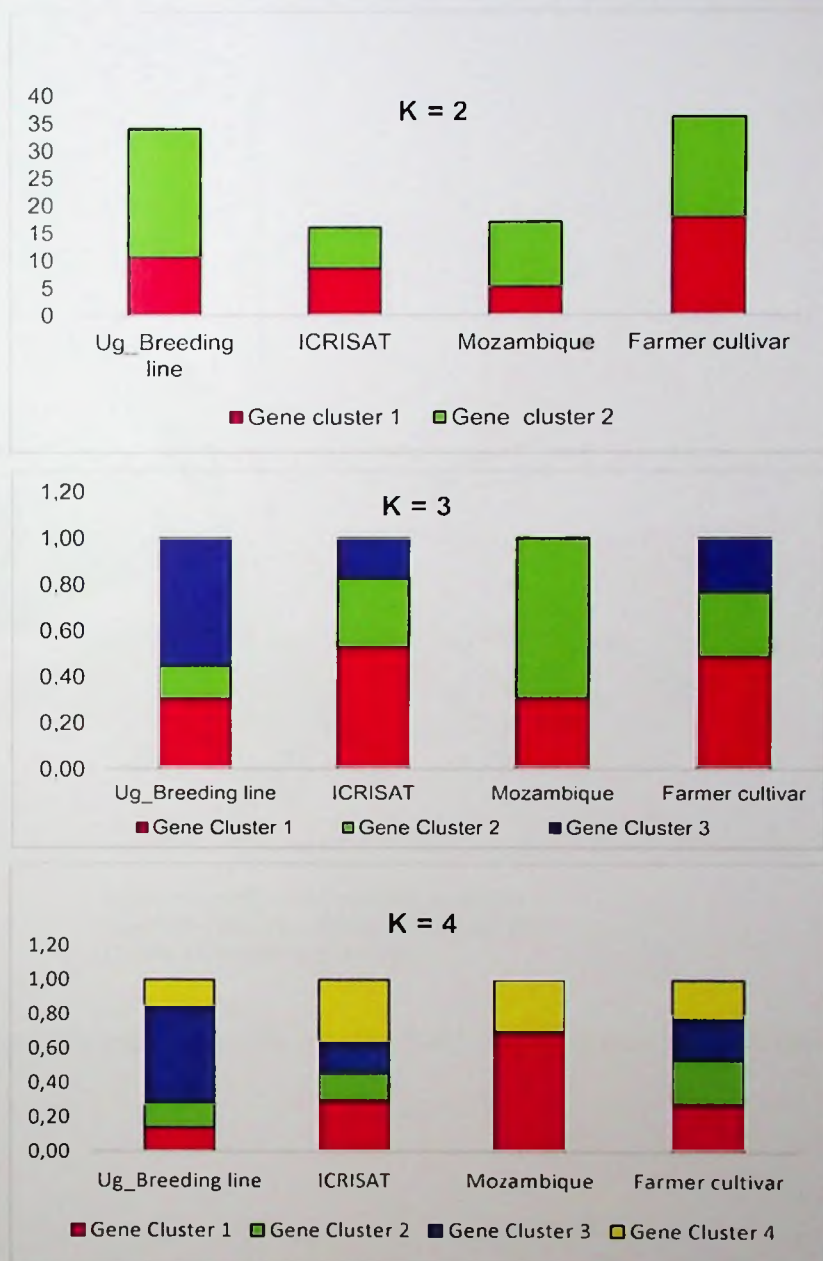


Figure 4.7 Bayesian clustering analysis with allocation of gene clusters in $K=2$; $K=3$; and $K=4$ for each population in the Ugandan groundnut collection

4.4.2.3 Phylogenetic tree

The dendrogram (Figure 4.8) based on neighbour joining algorithm showed three major cluster (indicated by red, green and blue colours). Cluster I comprised mainly of subspecies *fastigiata* while cluster II subspecies *hypogaea* and cluster III only comprised of two genotypes, Subspecies *fastigiata* was further divided into botanical varieties bot. var. *vulgaris* and bot. var. *fastigiata*.

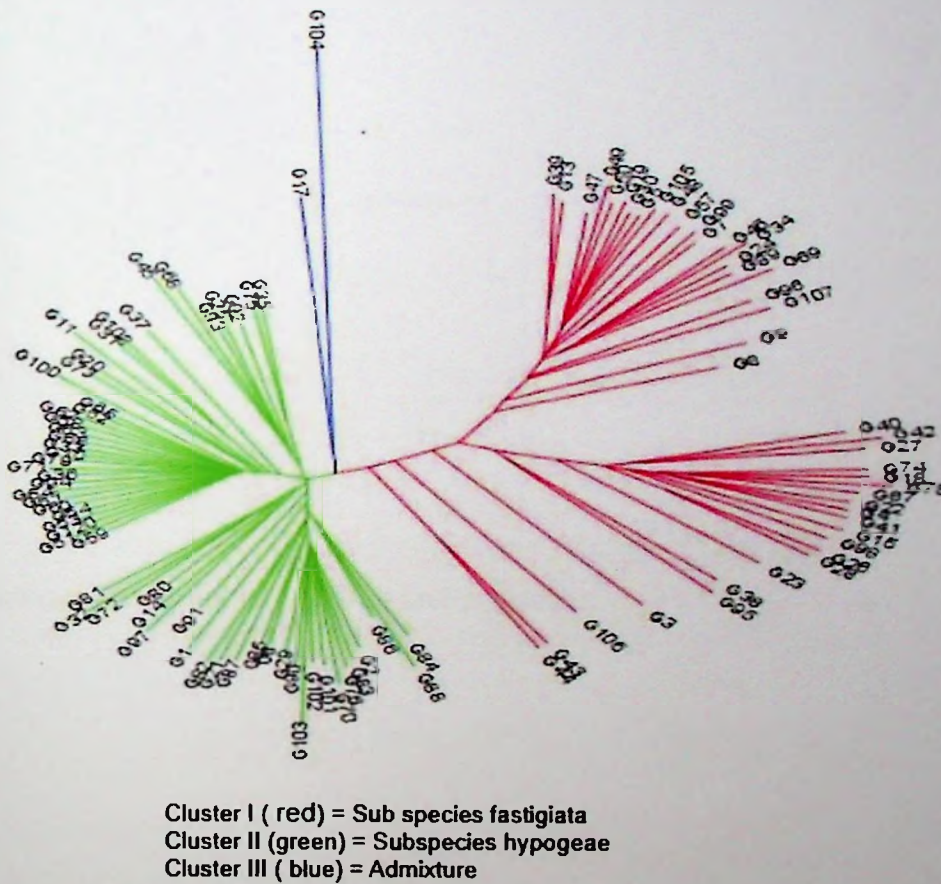


Figure 4.8 Neighbour Joining tree constructed for SNP data based on inferred groups (red, green and blue)

4.4.2.4 Network tree

The network tree based on the F_{ST} values is presented in Figure 4.9. Farmer cultivars and ICRISAT genotypes were positioned on the edge of the tree while Mozambican landraces and Ugandan breeding lines were linked on the network tree by long arms. Of the four populations, the Mozambican landraces had the longest arm from the edge of the network tree.

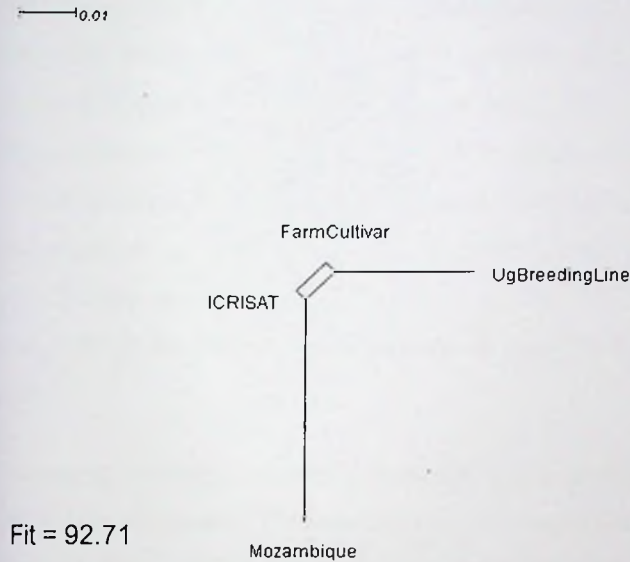


Figure 4.9 Phylogenetic network tree based on F_{ST} values

4.5 Discussions and conclusion

Information on available genetic resources, their geographical locations, and an understanding of their relationships can be used to gain insight into population divergence. A comprehensive knowledge about genetic diversity of groundnut from various eco-geographical regions is expected to contribute to the maintenance and usage of groundnut germplasm, and support the breeding programmes. This study called 2986 SNP for downstream analysis. Given the variable quality control parameters and thresholds from various studies, this number of SNP is almost equivalent to that obtained by other studies (Zhou et al., 2014, and Chopra et al., 2015; Pandey et al., 2017). The comparative number of SNPs obtained in the current study after quality assessment shows the utility of the SNP in studying groundnut populations. It also indicates a high level of genetic diversity despite the weak population differentiation among the user assigned populations of groundnut used in this study. Similar observations were made by Chopra et al. (2016). However, these results were in contrast to previous reports of either absence or presence of low molecular variability (Kochert et al., 1996; Burrow et al., 2009).

The overall average value of polymorphic loci or polymorphism as revealed by the 2986 SNP markers was low to moderate. This result is in contrast to earlier studies that found polymorphism to be in the range of 70% - 81% in the tetraploid genomes of groundnut (Khera et al., 2013; Pandey et al., 2017). Mean major allele frequency, heterozygosity (H_e and H_o) and PIC values were found to be 0.89, 0.265, 0.227 and 0.13, respectively. This result agrees with that of Pandey et al. (2017). PIC in this collection was low and can be attributed to the tetraploid genome (genome complexity and presence of multiple gene copies) as well as presence of homeologous-SNPs (between A- and B-genome) which causes "noise" during genotyping analysis. A similar observation was made by Khera et al. (2013) and Chopra et al. (2015). A higher H_e relative to H_o obtained in the current study agrees with the higher major allele frequencies observed which may result from allelic exchange within the collection. However, the allele migration did not cause a higher level of fixation as would be expected but, instead, reduced it resulting in a depressed inbreeding coefficient (F_{IS}). This maybe because similar alleles are exchanged and as a result, they cause no change in the allelic state which implies low genetic basis of the groundnut collection.

Genetic distances based on neighbour joining clustering and PCA revealed no distinct differentiation among the user assigned populations of groundnut genotypes used in this study. The three major genetic groupings observed were made up of a mix of accession from all the assigned groups. The basis of clustering was subspecies and botanical varieties. Cluster I, Cluster II and cluster III contained accessions from subspecies *hypogaea* and subspecies *fastigiata*, and both subspecies, respectively. During cluster analysis, some genotypes of subspecies *fastigiata* and *hypogaea* overlapped between cluster I and cluster II forming cluster III; this is understandable as during the course of evolution,

there has been considerable inter-crossing among the subspecies *fastigiata* and *hypogaea*. A similar observation was made by Khera et al. (2013).

This undefined clustering based on population was also supported by the AMOVA results, where a higher variability was detected among individuals within a population and within individuals in a population than among populations. The variation among populations within collection was low, suggesting that the populations may not be reproductively isolated. A high within individual variation observed in this study may also be attributed to the tetraploid genome (genome complexity and presence of multiple gene copies) as well as presence of homeologous-SNPs (between A- and B-genome) which causes "noise" during genotyping analysis. A similar observation was made by Khera et al. (2013) and Chopra et al. (2015).

The differentiation of the genotypes based on the overall F_{ST} value among the groundnut populations was considered small. This result supports those seen from AMOVA. In addition, both pairwise F_{ST} and Reynolds' genetic differentiation methods revealed the highest estimates and were observed between Ugandan breeding lines and Mozambican landraces. This was in agreement with the fact that genetic distance increases as geographical distance increases, and this is true considering the distance between Uganda and Mozambique. On the other hand, the smallest differentiation was between ICRISAT genotypes and farmer cultivars. The results of the F_{ST} differentiation were in agreement with those of network tree analysis. In the interpretation of the network tree, the positioning of farmer cultivars and ICRISAT materials at the edges of the network tree implies that these populations exchange genes. This was not expected as these materials are geographically isolated. However, this may be due to frequent use of germplasm introductions from ICRISAT Malawi to make modern varieties by Ugandan groundnut breeding programme. This contributed to the lack of differentiation between ICRISAT and farmer cultivars. In addition, the Ugandan breeding programme is merited to have improved gene diversity in the collection as evidenced from higher differentiation of the breeding lines from the rest of the populations.

At the population structure level, three clusters were observed based on Evanno method as well as by clustering based on dissimilarity. The clustering was based on subspecies, botanical varieties and pedigree. Moreover, there was a limited proportion of admixtures at the estimated K sub-populations. The genetic structures of population in groundnut have previously been reported in several studies (Burrow et al., 2009; Belamkar et al., 2011; Wang et al., 2011; Chopra et al., 2016). In addition, it was noted that the three clusters were present in all the four user assigned populations, except Mozambican landraces perhaps because of sampling bias against this population. This observation is further reinforced from interpretation of the network tree by the positioning of the Mozambican lines far from the edge of the network graphs. The low number of admixture corroborates cluster analysis results, differentiating the sub-species of cultivated groundnut. However, a high level of population

admixture was expected because of the high level of gene flow per generation observed in this study. Moreover, all the current groundnut populations are formed from continuous interbreeding of several populations in recent times. Furthermore, the positioning at the edges and short length edges of the network graphs by groundnut populations supports the notion of high gene exchange of the populations used in this study. An earlier study indicated that, during the evolution of subspecies *fastigiata* and *hypogaea* of the *A. hypogaea* (cultivated tetraploid), selective genomic regions remained conserved and these are presumed to have genes responsible for maintaining subspecies-specific features of groundnut (Pandey et al., 2017; Chopra et al., 2016).

This is the first report of a DArT-Seq analysis for groundnut accessions from Uganda. The results illustrated here, though not conclusive based on samples and SNPs coverage, present an advantageous starting point for future groundnut genomics research in Uganda. The low genetic diversity observed in this study could be improved by considering the addition of germplasm from other geographical regions, and exploring other options such as transformation and genome editing. In addition, genetic relationships could be used for the selection of parents for inclusion in the breeding program, if no pedigree data available. The information generated here could also be used to facilitate classification, proper maintenance, conservation and utilization of these valuable resources and to design breeding programs adapted to local needs. Genomic data generated in this study could be developed and utilised for genomic selection.

Genomic selection as an advanced breeding tool holds great potential for plant breeding, but depends on a large number of molecular markers and having a relatively well-balanced genome-wide coverage. The rapid advancement in sequencing and genotyping technologies, the development of SNP and DArT-Seq arrays, even for polyploidy crops, and the reduction in cost is important information for breeding programmes. One of the most promising approaches for trait improvement is the introduction of novel alleles. As a first step, allele mining approaches should be performed through multi-location field experiments with diverse environments and germplasm to identify the linked markers for genetic dissection of complex traits. Therefore, in order to address the narrow genetic diversity within cultivated groundnut through the exploitation of primary, secondary and tertiary gene pools, an extensive assembly of a well-characterized genetic resource alongside well-developed genomic resources is needed. Groundnut breeders especially in Africa will, therefore, need to modernize their breeding tools in order to reduce the current tedious varietal development process.

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Appendix 4.1: Groundnut germplasm used for molecular genetic diversity analysis.

Entry	Accession name/number	Assigned population	Market type	Botanical variety
G1	ICG 90704	ICRISAT	Virginia	hypogaea
G2	Igola	Farmer cultivar	Virginia	hypogaea
G3	ICG14705	ICRISAT	Spanish	vulgaris
G4	Lukumusala	Farmer cultivar	Valencia	fastigiata
G5	ICG 12988	ICRISAT	Spanish	vulgaris
G6	Serenut 11	Ug_breeding line	Virginia	hypogaea
G7	Two seeded KJ	Farmer cultivar	Spanish	vulgaris
G8	S6T	Ug_breeding line	Spanish	vulgaris
G9	Etesot	Farmer cultivar	Virginia	hypogaea
G10	J11	ICRISAT	Spanish	vulgaris
G11	ICGV-SM 02501	Ug_breeding line	Spanish	vulgaris
G12	JL 24	ICRISAT	Valencia	fastigiata
G13	BT_variegated	Farmer cultivar	Virginia	hypogaea
G14	Red beauty	Farmer cultivar	Valencia	fastigiata
G15	BJ	Farmer cultivar	Valencia	fastigiata
G16	Ug 33	Farmer cultivar	Valencia	fastigiata
G17	ICG 12991	ICRISAT	Spanish	vulgaris
G18	ICG 9418	ICRISAT	Spanish	vulgaris
G19	S9T	Ug_breeding line	Virginia	hypogaea
G20	Gambia	Farmer cultivar	Valencia	fastigiata
G21	ICGV-SM 93541	Ug_breeding line	Valencia	fastigiata
G22	Erudu red	Farmer cultivar	Spanish	vulgaris
G23	ICGV-SM 05701	Ug_breeding line	Virginia	hypogaea
G24	Erudu tan	Farmer cultivar	Spanish	vulgaris
G25	ICGV-SM 95526	Ug_breeding line	Valencia	fastigiata
G26	ICG-6766	ICRISAT	Valencia	fastigiata
G27	S3R	Ug_breeding line	Virginia	hypogaea
G28	S4T	Ug_breeding line	Spanish	vulgaris
G29	ICG 7243	ICRISAT	Virginia	hypogaea
G30	S1R	Ug_breeding line	Virginia	hypogaea
G31	Ug 17	Farmer cultivar	Virginia	hypogaea
G32	Oluk-oluk-arema	Farmer cultivar	Spanish	vulgaris
G33	S5R	Ug_breeding line	Virginia	hypogaea
G34	S5R	Ug_breeding line	Virginia	hypogaea
G35	Magooro DT	Farmer cultivar	Virginia	hypogaea
G36	Tifton 8	ICRISAT	Virginia	hypogaea
G37	ICG 07508	Ug_breeding line	Virginia	hypogaea
G38	ICGVSM 03590	Ug_breeding line	Virginia	hypogaea
G39	ICGV-SM 95731	Ug_breeding line	Valencia	fastigiata
G40	ICG 10890	ICRISAT	Valencia	fastigiata
G41	VAL R2	Ug_breeding line	Valencia	fastigiata
G42	ICGV-SM 86715 X S2 R	Ug_breeding line	Virginia	hypogaea
G43	ICGV-SM 86715 X S2 T	Ug_breeding line	Virginia	hypogaea
G44	Ug 20 1	Farmer cultivar	Valencia	fastigiata

Appendix 4.1: Continued.

Entry	Accession number/name	Assigned population	Market type	Botanical variety
G45	Ug 58	Farmer cultivar	Spanish	vulgaris
G46	Moz 1 (Nac-1)	Mozambican landrace	Spanish	vulgaris
G47	Moz 2 (Nac_3)	Mozambican landrace	Spanish	vulgaris
G48	Moz 3 (Nac_4)	Mozambican landrace	Spanish	vulgaris
G49	Moz 4 (Nac_5)	Mozambican landrace	Spanish	vulgaris
G50	Moz 5 (Mon_1)	Mozambican landrace	Virginia	hypogaea
G51	Moz 6 (Mon_2)	Mozambican landrace	Virginia	hypogaea
G52	Moz 7 (Mon_4)	Mozambican landrace	Virginia	hypogaea
G53	Moz 8 (Bal_1)	Mozambican landrace	Virginia	hypogaea
G54	Moz 11 (Bal_6)	Mozambican landrace	Virginia	hypogaea
G55	Moz 12 (Namo_1)	Mozambican landrace	Virginia	hypogaea
G56	Moz 13 (Namo_2)	Mozambican landrace	Virginia	hypogaea
G57	Moz 14 (Met_1)	Mozambican landrace	Virginia	hypogaea
G58	Moz 15 (Met_2)	Mozambican landrace	Virginia	hypogaea
G59	Moz 16 (Cua)	Mozambican landrace	Virginia	hypogaea
G60	Moz 17 (Nip_2)	Mozambican landrace	Virginia	hypogaea
G61	Moz 18 (Nip_4)	Mozambican landrace	Virginia	hypogaea
G62	Ug 22 (Ebaya)	Farmer cultivar	Virginia	hypogaea
G63	Ug 57 (Good roast)	Farmer cultivar	Virginia	hypogaea
G64	Ug 60	Farmer cultivar	Valencia	fastigiata
G65	Ug 20_2 (Early flower)	Farmer cultivar	Spanish	vulgaris
G66	Ug 2 (Early flowering)	Farmer cultivar	Spanish	vulgaris
G67	Ug 12	Farmer cultivar	Virginia	hypogaea
G68	Ug 25	Farmer cultivar	Virginia	hypogaea
G69	Ug 27	Farmer cultivar	Virginia	hypogaea
G70	Ug 34	Farmer cultivar	Valencia	fastigiata
G71	Ug 44	Farmer cultivar	Spanish	vulgaris
G72	Ug 47	Farmer cultivar	Virginia	hypogaea
G73	Ug 51	Farmer cultivar	Valencia	fastigiata
G74	Ug 54	Farmer cultivar	Valencia	fastigiata
G75	Ug 46	Farmer cultivar	Virginia	hypogaea
G76	ICGV-SM 01731	Ug_breeding line	Virginia	hypogaea
G77	ICGV-SM 08503	Ug_breeding line	Virginia	hypogaea
G78	S7T	Ug_breeding line	Virginia	hypogaea
G79	S2T	Ug_breeding line	Virginia	hypogaea
G80	S12	Ug_breeding line	Virginia	hypogaea
G81	S13	Ug_breeding line	Virginia	hypogaea
G82	S14	Ug_breeding line	Virginia	hypogaea
G83	S10	Ug_breeding line	Virginia	hypogaea
G84	S 8R	Ug_breeding line	Virginia	hypogaea
G85	Alur-arema (Ug 31)	Farmer cultivar	Spanish	vulgaris
G86	SGV 1 (07002)	Ug_breeding line	Virginia	hypogaea
G87	SGV 2 (0080)	Ug_breeding line	Virginia	hypogaea

Appendix 4.1: Continued

Entry	Accession number/name	Assigned population	Market type	Botanical variety
G88	SGV 3 (0029)	Ug_breeding line	Virginia	hypogaea
G89	SGV 4 (1004)	Ug_breeding line	Virginia	hypogaea
G90	Ug 49	Farmer cultivar	Virginia	hypogaea
G91	ICGVSM 07533	Ug_breeding line	Valencia	hypogaea
G92	ICGVSM 03530	Ug_breeding line	Spanish	vulgaris
G93	Ug 41(variegated)	Farmer cultivar	Virginia	hypogaea
G94	Ug 10	Farmer cultivar	Spanish	vulgaris
G95	Ug 19	Farmer cultivar	Valencia	fastigiata
G96	Moz 19 (Bal_7)	Mozambican landrace	Virginia	hypogaea
G97	SGV 07002	Ug_breeding line	Virginia	hypogaea
G98	SGV 0023	Ug_breeding line	Virginia	hypogaea
G99	SGV 0049	Ug_breeding line	Virginia	hypogaea
G100	ICG 11337	ICRISAT	Virginia	hypogaea
G101	TMV2	ICRISAT	Spanish	vulgaris
G102	ICG 86388	ICRISAT	Virginia	hypogaea
G103	ICG 476	ICRISAT	Spanish	vulgaris
G104	ICG 7234	ICRISAT	Virginia	hypogaea

G1-G103 = groundnut genotypes; Ug_breeding line = Ugandan breeding line; Mozambique = Mozambican landrace; Farmer = farmer cultivar; ICRISAT = ICRISAT accession

CHAPTER 5 Gene action governing the inheritance of drought tolerance traits in groundnuts (*Arachis hypogaea* L.)

Abstract

Groundnut production in rain-fed areas is reduced by drought stress, which severely affects pod yield and other growth parameters. The objectives of this study were to; i) determine the combining ability and gene action governing the inheritance of drought tolerance traits, ii) assess the relationship between drought and agronomic traits, and iii) determine the associations among drought tolerance traits. Thirty parental lines with known reaction to drought stress and other biotic stresses, were crossed in a North Carolina design II in three sets. The 30 parents and resulting 75 F₂ progenies were grown in a split plot arrangement using an alpha lattice design, with two replications in an open field and in a rain-out shelter for two cropping seasons. The results revealed that under drought stress, the general combining ability effects due to female parents (GCA_f) were significant for SPAD chlorophyll meter reading at 100 DAP (SCMR₂), harvest index (HI) and drought tolerance index based on biomass [DTI(BIO)], while the GCA effects due to male parents (GCA_m) were not significant, except for SCMR₂. The specific combining ability (SCA) effects were only significant for SCMR at 100 DAP and the drought tolerance index based on pod yield [DTI(PY)]. However, under non-drought stress, the GCA_f effects were significant for SCMR₁, SCMR₂, pod yield (PY), biomass (BIO) and HI, while the GCA_m effects were significant for SCMR₁, SCMR₂, BIO and HI. Moreover, the SCA effects were significant for SCMR₁, PY and BIO. Among the parents, S5R, JL 24, S10T, BJ, S11T and ICG 10890 were the best general combiners for all the traits studied across the water regimes. Both under drought stress and non-drought environment, the best combiners varied among parents and traits. Genotypes KJ and Gambia (locally adapted varieties) were good general combiners for drought tolerance traits and pod yield. Under drought stress environment, the general predictability ratio (GPR) values were above 0.50 for SCMR₁ and HI (0.55) and non-drought stress for SCMR₁(0.59), SCMR₂ (0.59) and HI (0.56), indicating the predominance of additive gene effects (fixable variation). The rest of the traits had low values below 0.50 showing the importance of the non-additive gene effects in controlling the drought tolerance traits. Therefore, in order to harness both additive and non-additive genes, selection needs to be delayed until a later generation. Alternatively, the F₂ segregants can be inter-mated followed by recurrent selection and pedigree breeding. Under drought and non-drought conditions, the SCMR was correlated with the number of pods and pod yield. Significant associations between drought and non-drought environments were found for SCMR, harvest index, pod yield, number of pods, leaf length, and leaf width implying that these traits could be selected under non-drought stress environments.

5.1 Introduction

Groundnut (*Arachis hypogaea* L.) is an important legume crop in Uganda. The production of groundnut is constrained by several factors including biotic and abiotic stresses. Although groundnut is generally a drought tolerant crop, drought is increasingly becoming an important abiotic stress. Combined with biotic stresses such as groundnut rosette virus disease (GRVD), yield losses can reach 100%. Drought mitigation measures are available but are out of reach for most small holder farmers, who are the major producers of this crop. Instead, farmers rely upon traditional methods that are less effective in dealing with drought such as early planting. Improvement of drought tolerance has been the main goal in several crops, especially in rain fed areas where drought is a major constraint limiting productivity and quality. Terminal drought occurring during the seed filling phase of peanut (Boote, 1982) has been associated with decreased pod yield and increased pre-harvest aflatoxin contamination (Ndunguru et al., 1995). Breeding groundnut varieties with drought tolerance is seen as a plausible solution for reducing aflatoxin contamination induced by terminal drought (Holbrook et al., 2000; 2008; 2009; Girdthai et al., 2010;). In addition, a combination of multiple traits, for instance yield improvement and tolerance to drought, or low soil fertility, are requisites for adaptability to a range of groundnut production agroecologies (Hillocks et al., 2006). Furthermore, such attributes ought to be combined with others such as seed size, seed colour, suitable taste and good cooking qualities to make the variety appealing to small holder farmers.

Breeding progress for drought tolerance in groundnut has been slow due to large and uncontrollable genotype $\times$ environment ($G \times E$) interactions. Breeding approaches using physiological traits that have high heritability values and low $G \times E$ interactions can improve the selection efficiency for superior drought tolerant genotypes through indirect selection. Putative selection criteria that could be used for indirect selection to increase drought tolerance in groundnut include improvement of soil water extraction capability, and improvements in water use efficiency (WUE), or both (Wright and Nageswara Rao, 1994; Hebbar et al., 1994). However, WUE is not easy to measure in large segregating breeding populations. Wright et al. (1988, 1994) have found WUE to be negatively correlated with specific leaf area (SLA) over wide ranges of varieties and environments. The SLA, which is negatively related to leaf thickness and photosynthetic capacity, can be measured easily and inexpensively. Nageswara Rao et al. (2001) and Upadhyaya (2005) found a significant negative correlation between SLA and the SPAD chlorophyll meter reading (SCMR), and suggested that the chlorophyll meter could be used as a rapid and reliable tool to identify groundnut genotypes with low SLA and hence high water use efficiency. The harvest index (HI), an important trait that provides a measure of total biomass, actually partitioned into pod yield, was found to be correlated with SLA and SCMR under both well-watered and long-term drought conditions (Songsri et al., 2008). An efficient utilization of germplasm for improvement of drought tolerance traits requires understanding of the

gene action, available tolerance genes and genetic relationships involved in resistance as pre-requisites to achieve a desirable drought tolerance breeding objective.

Genetic variability for drought tolerance exists in groundnut (Sharma and Varshney, 1995; Upadhyaya et al., 2005; Nigam and Aruna, 2008; Songsri et al., 2008; 2009, 2013). A few experiments have shown that drought tolerance traits in groundnut are governed by both additive and non-additive genetic systems. John et al. (2012) reported predominance of non-additive gene action for HI, days to 50% flowering, stomatal conductance and water use efficiency. On the contrary, additive gene action was reported for SLA (Suriharn et al., 2005; Lal et al., 2005), HI (Nigam et al., 2001) and SCMR (Upadhyaya et al., 2011). Therefore, evidence for the quantitative nature of inheritance of drought tolerance traits under terminal drought conditions is small and contradictory. The objectives of this study were to; i) estimate the gene action and combining ability for drought tolerance traits, ii) determine relationships among drought tolerance traits, iii) determine association between drought tolerance traits and agronomic traits under terminal drought conditions, in order to predict indirect responses to selection for drought tolerance.

5.2 Materials and methods

5.2.1 Study sites and genotypes

The trials were conducted over two seasons, in 2017A and 2017B at the National Semi-Arid Resources Research Institute (NaSARRI), located 27 km west of Soroti town in eastern Uganda. The site lies at an altitude of 1146 m with a moderate temperature range (16-24 °C). The area receives a bimodal rainfall running from October/November to April/May. The peak rainfall months are October and May for the two rainfall seasons, respectively.

Thirty groundnut lines, comprising of 10 drought-tolerant (D), 17 droughts susceptible (S) and 3 local/adapted/conventional (C) lines, were selected for the genetic studies (Table 5.1). Drought tolerant lines were selected based on previous work (Coffelt et al., 1985; Nigam et al., 2005; Reddy et al., 2008) and evaluations by the National Groundnut Breeding Programme. The drought susceptible set was selected based on resistance to groundnut rosette disease, leaf spot diseases under humid conditions and seed size. "Conventional" lines were mainly selected for wide adaptation from previous studies.

Table 5.1 Characteristics and type of reaction to drought of the different parental lines used for the North Carolina Design II in sets mating design.

No.	Parent	Source	Botanical Classification	Seed colour	Drought tolerance
1	ICG 9418	ICRISAT	Spanish	Pink	D
2	ICG 12988	ICRISAT	Spanish	Tan	D
3	ICG 10890	ICRISAT	Valencia	Red	D
4	ICG 6766	ICRISAT	Valencia	Tan	D
5	Tifton 8	ICRISAT	Virginia	Tan	D
6	ICG 7243	ICRISAT	Virginia	Tan	D
7	Serenut 4T	SGV	Spanish	Tan	S
8	Serenut 6T	SGV	Spanish	Tan	S
9	Red beauty	FARMER	Valencia	Red	S
10	Gambia	FARMER	Valencia	White	C
11	Serenut 5R	SGV	Virginia	Red	D
12	Serenut1R	SGV	Virginia	Red	D
13	ICG 12991	ICRISAT	Spanish	Tan	S
14	ICG 14705	ICRISAT	Spanish	Tan	S
15	Aboutalanta	FARMER	Valencia	Tan	S
16	ICGV-SM 05701	ICRISAT	Virginia	Tan	S
17	ICGV-SM 93541	ICRISAT	Valencia	Red	S
18	Igola	FARMER	Virginia	Tan	C
19	Oluk-oluk-arema	FARMER	Spanish	Red	C
20	ICGV-SM 95731	ICRISAT	Valencia	Tan	S
21	ICGV-SM 02501	ICRISAT	Spanish	Pink	S
22	ICGV-SM 95526	ICRISAT	Valencia	Red	S
23	ICGV-SM 03590	ICRISAT	Virginia	Pink	S
24	J11	ICRISAT	Spanish	Tan	S
25	Kayunga (BJ)	FARMER	Valencia	Purplish red	S
26	Masindi (KJ)	FARMER	Spanish	Red	S
27	JL 24	ICRISAT	Valencia	Tan	S
28	Magoro DT	FARMER	Virginia	Tan	S
29	Serenut 10R	SGV	Virginia	Red	D
30	Serenut 11	SGV	Virginia	Tan	D

C = conventional line; D = Drought tolerant line; S = drought susceptible lines (with or without resistance to groundnut diseases under humid conditions, SGV = Serere groundnut variety.

5.2.2 Hybridisation using a North Carolina Design II sets mating scheme

Thirty groundnut lines were used as parents in North Carolina II (Comstock and Robinson, 1948; Hallauer et al., 2010) mating scheme in three sets. The sets were constituted equally according to the three botanical varieties: Spanish, Valencia and Virginia, with each set consisting of 10 groundnut lines. From each of these sets, five lines were used as females and the other five as males. Crosses were made in both the field and glass house following the method of Norden (1980) in the 2015B and

2016A cropping seasons. Emasculations were done in the afternoons between 2:00 – 6:00 p.m. followed by pollination the next day between 6:30 – 9:00 a.m. Each emasculated flower was marked with a single thread and once pollinated another thread was added. In addition, non-hybrid flowers were removed from the female parents to encourage further flowering. The F_1 seeds were planted and their seeds harvested in bulk for each cross. The F_2 were developed from the seed of F_1 by selfing. Parents and F_2 progenies were used in the genetic studies.

5.2.3 Evaluation of parents and F_2 families

Seventy-five F_2 families from the three sets and the 30 parents, constituting 105 treatments (entries) were evaluated for drought tolerance and selected agronomic traits in two seasons. Trials were planted in stressed and non-stress plots. Line-source sprinkler irrigation was used for the non-stressed (Y_1) experiment, while hand watering was used for the stressed (Y_0) experiments. The water stressed trial was planted in a rain-out shelter on strips of 0.5 m width, and the non-stress trial was planted in the field. Therefore, irrigation control was the basis of the difference between the field trials and rain-out shelter trials. For both the field trials and rain-out shelter, the F_2 families and parent seeds were sown in four rows of 0.5 m and two rows of 0.5 m plots, respectively, with an inter –and intra-row distance of 30 and 10 cm, respectively, for each genotype in split plots, whereby whole plots and subplots were stress treatments and genotypes, respectively. The genotypes were arranged in 3 x 10 and 5 x 15 alpha lattice designs with two replications. Seeds were directly sown at a rate of 2-3 seeds per hill and later thinned to one seedling per hill and all other recommended agronomic practices were applied.

Irrigation scheduling was adapted from Hamidou et al. (2013) with a few modifications. All the trials were irrigated at regular intervals of 7- 8 days up to 40 days after emergence. Thereafter, the rainout shelter trials were exposed to intermittent stress until maturity to simulate the water stress period 40-75 days after emergency (DAE) corresponding to peg and pod formation, and the pod development phase of the crop. The drought stress was imposed by irrigating the trial based on wilting status of the drought stressed plots and estimated evapotranspiration in the non-drought stress plots. The decision to irrigate the non-water-stressed plots only, was based on the estimated evapotranspiration, while the decision to irrigate all trials (both stressed and non-stressed) based on a leaf wilting assessment of the water stressed plots, whereby the irrigation was supplied once the wilting score of this trial reached a value of 3. The scoring of wilting symptoms was recorded early afternoon as follows: Score 1 = no symptoms of wilting on most plants in a plot, score 2 = 1-20% of plants in a plot have wilted leaves, 3 = 21-50% of plants in a plot show wilting but none has reached permanent wilting, 4 = 51 -70 % of plants in a plot show wilting with partial signs of permanent wilting, 5 = 70-100 % of plants in the plot show signs of permanent wilting. Dry-down assessment under controlled imposition of water stress shows a score of 3 is reached when the transpiration of the water stressed

plants is about 40–50 % of the transpiration of the non-water stressed plants, indicative of a substantial stress, yet not too severe (Bhatnagar-Mathur et al., 2007; Ratnakumar et al., 2009).

5.2.4 Data collection

Data were collected on plot basis for days to emergence, days from sowing to first flower, days to 50% flowering (days from emergence to the stage when 50% plants have begun flowering), leaf width, leaf length and plant height. Additionally, yield data were also recorded from the middle rows excluding plants at the end of rows for each of the germplasm collection to record data on the following traits; pod yield per plant (g), kernel yield per plant (g), 100-kernel weight (g), and shelling percentage. The data were also used to compute harvest index (HI) and total biomass data (Hy).

All plants were clipped at the soil surface, the roots and pods were dug up and pods were then detached, bulked together and weighed to get pod and haulm weight and were converted into pod yield (Py) and haulm yield (Hy), respectively. The above ground parts were weighed and converted into Hy, and all were expressed in g/m². These were then used to determine the total biomass ($Bt = Hy + Py \times 1.65$), and the pod weight was multiplied with a correction factor of 1.65 (Duncan et al., 1978) to adjust for the differences in the energy requirement for producing pod dry matter compared with vegetative part. Pods and the haulms were sundried for two weeks. The HI was determined as a ratio of adjusted pod weight to total biomass ($HI = 1.65 \times Py / Bt$). The drought tolerance index (DTI), as suggested by Nautiyal et al. (2002), was calculated for biomass [DTI (BIO)] and pod yield [DTI (PY)] as the ratio of each parameter under stressed treatments (to that under non-drought stress condition). In addition to the yield and agronomic characterisation, the physiological traits for drought were recorded.

The second fully expanded leaf from the apex (from 10 randomly selected plants of each genotype in each replication) was identified in the morning (08:00–09:30 am) at 80 and 100 DAS. These leaves were detached from the chosen plants and sent to the laboratory in zipped polythene bags for recording of the SCMR. The SCMR was measured using a Minolta SPAD chlorophyll meter (Minolta Corp., Ramsey, NJ, USA) following the procedure described by Nageswara Rao et al. (2001).

5.2.5 Data analysis

The data collected were subjected to analysis of variance (ANOVA) using Genstat version 14 (Payne et al., 2011). The ANOVA was performed for each trait in each season following a split plot design procedure (Gomez and Gomez, 1984). Because water regime $\times$ genotype interaction was significant, each water regime was analysed separately using REML procedure in Genstat. Homogeneity of variance was tested for all characters and a combined analysis of variance of two seasons data was performed. The combined analysis of variance was conducted for parents and crosses, respectively.

In addition, Pearson's correlation analysis was conducted using Genstat software to determine degree of association of traits under each water regime.

The genetic analysis of North Carolina design II pooled over environments (seasons) was performed using the PROC GLM procedure of SAS (SAS Institute, 2011). Genotypes were considered a fixed factor, while environments, season and replications were considered random factors. Variance components were estimated by restricted maximum likelihood, the default method. Duncan test at 5% significance level was used to compare the differences among means for each factor. Gene action controlling drought tolerance and combining ability were determined (Table 5.2). Data were analysed across environments (seasons) following the linear model below;

$$Y_{ijkq} = \mu + r_k + f_i + m_j + (fm)_{ij} + E_q + (Ef)_{iq} + (Em)_{jq} + (Efm)_{ijq} + e_{ijkq}$$

Where;

- Y_{ijkq} is the observed value of the progeny of the i^{th} female crossed with j^{th} male in the k^{th} replication and q^{th} season
- μ = overall population mean
- $r_k(E)$ = the replication effect within q^{th} season
- f_i = general combining ability (GCA) of the female
- m_j = general combining ability of the male
- $(fm)_{ij}$ = specific combining ability (SCA) of the i^{th} X j^{th} cross
- E_q = average effect of the q^{th} season
- $(Ef)_{iq}$ = interaction effect between the q^{th} season and the GCA of female
- $(Em)_{jq}$ = interaction effect between the q^{th} season and the GCA of male nested
- $(Efm)_{ijq}$ = interaction effect between the q^{th} season and the SCA of i^{th} X j^{th} cross
- e_{ijkq} = random error

Table 5.2 Format of analysis of variance of North Carolina design II repeated over seasons

Source	df	Mean square	Expected mean square (EMS) (variance components)
Environment (E)	e-1a		
Sets (S)	s-1		
S x E	(e-1)(s-1)		
Replication/S	es(r-1)		
Female/S	s(f-1)	MSf	$\sigma^2 + r\sigma^2_{fme} + r\sigma^2_{me} + re\sigma^2_{fm} + rem\sigma^2_f$
Male/S	s(m-1)	MSm	$\sigma^2 + r\sigma^2_{fme} + r\sigma^2_{me} + re\sigma^2_{fm} + re\sigma^2_m$
Female x male/S	s(f-1)(m-1)	MSfm	$\sigma^2 + r\sigma^2_{fme} + re\sigma^2_{fm}$
Female/S x E	s(f-1)(e-1)		$\sigma^2 + r\sigma^2_{fme} + r\sigma^2_{fe}$
Male/S x E	s(m-1)(e-1)		$\sigma^2 + r\sigma^2_{fme} + r\sigma^2_{me}$
Female x male/S x E	s(f-1)(m-1)(e-1)		$\sigma^2 + r\sigma^2_{fme}$
Pooled error	es(r-1)(mf-1)	MSe	σ^2
Total	esrmf-1		

^a e, s, r, m, df, and f refer to the number of environments, sets with in an environment, replications, males, and females, degrees of freedom, respectively; σ^2_m =male variance, σ^2 =random error variance, r= number of replication, σ^2_{fm} female x male variance, e= number of environments, σ^2_{fme} = environment x female x male variance, σ^2_{me} = environment x male (set) variance (Hallauer et al., 2010).

Significance of estimates of variance due to GCA and SCA was tested using F- values at $P \leq 0.01$, and $P \leq 0.05$ levels while significance of estimates of GCA and SCA was tested using their respective standard errors. Other genetic and statistical parameters where determined as follows;

- $GCA_{Parent\ x} = \text{observed mean}_{parentx} - \text{trial mean}$
- $SCA_{Cross\ fm} = \text{observed cross mean}_{fm} - \text{trial mean} + GCA_f + GCA_m$
- Standard error of the male parent GCA = square root $[MSE / (r \times f \times \text{sites})]$ where MSE = error mean square of the experiment; r = number of replications; f = number of females; sites = number of sites
- Standard error of female parent GCA = square root $[MSE / (r \times m \times \text{sites})]$ where MSE = error mean square of experiment; r = number of replications; m = number of males; sites = number of sites
- Standard error of SCA female x male = square root $[MSE / (r \times \text{sites})]$ where MSE = error mean square of the experiment; r = number of replications; sites = number of sites
- Significance of GCAs using t- test; $t = (GCA / \text{Standard error})$; Significance of SCA using t -test; $t = SCA / \text{Standard error}$; We therefore infer for both GCA and SCA that; if t value is 2 and above: GCA/ SCA effect is significant at 5%, and if the value of t is 3 and above: GCA/SCA effect is considered significant at 1%.
- Relative importance ratio (Baker, 1978) = $2GCA / 2GCA + SCA$ (all values greater than 0.5 imply additive gene effects while all values below 0.5 are considered non-additive gene effects).

- Maternal effects were estimated from inference made about $F_{\text{calculated}} < F_{\text{critical}}$ value at $F_{m, f}$ degrees of freedom at $P \leq 0.05$; $F_{\text{calculated}} = \text{GCAf/GCAm}$. If $F_{\text{cal}} < F_{\text{critical}}$, we do not reject null hypothesis that $\text{GCAf} = \text{GCAm}$, and therefore maternal effects are not significant at 5%

5.3 Results

5.3.1 Evaluation of parents and F₂ families

The results of the assessment of the genotypic variation among the groundnut genotypes are presented in Tables 5.3 to 5.10. The REML combined analysis showed large and significant differences among parents for SCMR1, leaf length to width ratio, POD, leaf length, leaf width, HI, days to 50% flowering and DTI (BIO) ($P \leq 0.05$ to $P \leq 0.001$) under drought stress (Table 5.3). Significant differences between seasons for days to 50% flowering, SCMR1 and SCMR2 were also observed (Table 5.3). Differences among the interaction effects of genotype x season (G x S) for DTI-BIO and days to 50% flowering were significant ($P \leq 0.05$ to $P \leq 0.001$) (Table 5.3). The SCMR1, DTI (BIO) and the HI had average values of 44.0, 1.1, and 0.4, respectively (Table 5.4), while pod yield and biomass averaged 137.6 and 330.3g/m², respectively, under drought stress (Table 5.4).

Similarly, under non-drought stress, the combined analysis of variance showed large and significant differences among parents for all traits under study ($P \leq 0.05$ to $P \leq 0.001$) (Table 5.4). Seasonal effects were significant ($P \leq 0.05$) only for plant height (Table 5.4). Differences among interaction effects of genotypes x season (G x S) for leaf length to width ratio and plant height were significant ($P \leq 0.05$ to $P \leq 0.001$) (Table 5.4). The SCMR1, SCMR2, BIO, PY and HI had average values of 36.7, 32.7, 338.5 g/m², 108.0 g/m², and 0.4, respectively (Table 5.5). Pod yield and biomass had average yields of 108.4 g/m² and 338.5 g/m², respectively, under non-drought stress (Table 5.5).

Table 5.3 Wald's statistics for drought tolerance traits and agronomic traits among groundnut parental lines evaluated under drought stress and non-drought stress across two seasons in eastern Uganda

SOV	DF	SCMR1	SCMR2	POD	HI	Days	LL	Ratio	Width	DTI-BIO	PH	PY
Drought Stress												
Genotype (G)	29	48.54 *	15.66	76.45 **	2.26 **	56.33 *	77.82 ***	1.17 **	78.35 ***	92.31 ***		
Season (S)	1	14.02 ***	12.12 ***	1.81	52.3	121.2 ***	2.44	63.24	0.58	2.15		
G x S	28	20.66	12.39	31.69	26.4	58.73 *	23.43 *	20.16	36.17	77.58 ***		
Non-drought stress												
Genotypes (G)	28	113.4 ***	65.04 **	72.12 **	24 *	560.8	44.45 *	70.64 ***	51.04 *		234.2 ***	50.69 *
Season (S)	1	1.26	3.48	0	0	0.25 ***	0.09	0.16	0.13		7.05 **	0.03
G x S	28	34.34	36.27	40.04	25.7 *	71 **	29.24	14.77	40.44		61.07 **	23.59

SOV = source of variation; DF = degrees of freedom; G = genotypes; S = season; *** = significant at $P \leq 0.001$; ** = significant at $P \leq 0.01$ and * = significant at $P \leq 0.05$; DTI-BIO = drought tolerance index based on biomass, HI=harvest index; LL=leaf length; Ratio = leaf length/width ratio; PH = plant height; PY = pod yield; BIO=biomass; width=leaf width; Days = days to 50% flowering; DTI-PY= drought tolerance index based on pod yield; SCMR1 and SCMR2 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAS; PY = pod yield; plant height

Table 5.4 Means for REML combined analysis of drought tolerance traits and selected physiological and agronomic traits for groundnut parents evaluated under drought stress averaged over seasons 2017A and 2017B.

Genotype	SCMR1	SCMR2	Days	LL (cm)	LW (cm)	PH (cm)	LL/LW	PY (g/m ²)	BIO (g/m ²)	DTI(PY)	DTI(BIO)	HI
S4T	42.8	42.2	35.2	5.1	2.7	37.1	1.9	156.2	300.0	1.6	1.1	0.5
S6T	43.5	37.5	34.8	5.5	2.9	34.6	1.9	139.6	290.0	1.1	0.8	0.5
ICG12991	40.7	40.4	34.3	6.0	3.0	32.2	2.0	135.4	238.0	2.3	1.4	0.6
J11	42.9	40.8	34.0	5.4	2.8	41.1	1.9	170.4	415.4	1.3	0.9	0.4
KJ	40.5	38.0	35.3	5.5	2.7	45.1	2.1	121.5	315.1	1.1	1.3	0.4
ICG9418	40.0	40.3	35.5	5.8	3.4	34.8	1.7	154.2	332.0	1.7	1.1	0.5
ICG12988	42.7	42.0	36.3	5.6	2.9	39.0	2.0	162.5	314.0	2.4	1.1	0.5
ICG14705	43.5	39.8	33.5	4.7	3.0	35.0	1.6	136.2	408.6	1.0	1.0	0.3
AREMA	46.0	36.9	34.0	5.0	2.7	31.6	1.9	131.3	221.5	1.3	0.9	0.6
ICGVSM5201	47.2	40.8	33.3	6.1	3.5	35.8	1.8	106.2	282.8	0.6	0.6	0.4
S5R	49.4	37.5	32.8	4.6	2.5	30.0	1.8	138.3	309.9	0.6	0.6	0.4
SIR	50.4	49.5	34.3	4.6	2.3	31.0	2.0	81.8	171.6	1.1	0.4	0.4
IGOLA	46.7	43.4	35.0	4.7	2.8	34.1	1.6	143.9	503.1	1.5	1.5	0.3
S11T	43.9	38.9	31.8	5.2	2.7	34.8	2.0	154.0	358.9	1.5	0.8	0.4
DT-MAGORO	43.8	37.2	32.3	4.7	2.8	34.3	1.7	137.0	475.9	1.6	1.5	0.3
TIFTON 8	47.4	41.1	34.8	5.3	2.5	37.0	2.1	127.9	428.0	1.6	1.4	0.3
ICG7243	49.5	42.8	35.5	4.3	2.3	26.1	1.9	41.3	180.1	0.4	0.6	0.2
ICG5701	43.4	38.4	31.8	4.1	2.4	28.2	1.7	107.4	274.2	0.6	0.5	0.4
S10T	47.0	45.5	33.0	4.9	2.5	32.5	2.0	121.5	369.5	1.1	1.2	0.4
ICGVSM0390	43.2	43.2	31.5	5.2	3.0	32.6	1.7	127.1	305.1	1.3	0.9	0.4
RED BEAUTY	43.3	41.1	34.0	5.5	2.8	45.6	2.0	177.1	312.3	2.1	1.1	0.6
GAMBIA	44.5	44.4	33.0	6.0	3.2	39.6	1.9	160.4	344.3	1.6	1.2	0.5
ICGVSM93541	42.0	39.6	33.8	4.9	2.5	38.1	2.0	120.8	332.2	1.8	1.5	0.4
BJ	42.1	39.6	35.3	7.3	3.4	45.5	2.1	156.2	385.5	1.7	1.5	0.4
JL24	42.6	38.9	32.8	5.3	2.9	36.5	1.8	100.0	274.3	1.3	1.2	0.4
ICG10890	39.6	41.1	33.5	5.4	2.7	36.0	2.0	160.4	299.0	2.1	1.5	0.5
ICG6766	43.7	38.0	36.5	5.1	2.5	43.8	2.0	177.1	347.2	2.4	1.2	0.5
SALLA	44.8	38.6	37.0	5.8	2.9	34.5	2.0	150.0	372.8	2.4	1.1	0.4
ICGVSM95731	42.9	39.5	33.0	5.9	2.8	41.3	2.1	133.3	350.6	1.5	1.9	0.4
ICGVSM95526	40.3	38.6	32.3	5.5	2.7	45.4	2.1	200.0	397.3	3.2	1.7	0.5
Mean	44.0	40.5	34.0	5.3	2.8	36.4	1.9	137.6	330.3	1.5	1.1	0.4
S.e.d Av.	6.6	11.0	3.1	1.2	0.6	13.1	0.3	78.2	169.0	0.8	0.4	0.2
S.e.d Max.	8.2	12.7	3.8	1.3	0.7	15.2	0.3	90.4	196.3	1.0		0.3
S.e.d Min.	4.4	7.3	2.0	0.8	0.4	8.5	0.2	52.5	111.6	0.8		0.1

S.e.d = standard error of difference between means; LL= leaf length; LW = leaf width; SCMR1 and SCMR2 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAS; PY = pod yield; BIO = biomass yield.

Table 5.5 Means for REML combined analysis of drought tolerance traits and selected physiological and agronomic traits for groundnut parents evaluated under non- drought stress averaged over seasons 2017A and 2017B.

Genotype	SCMR1	SCMR2	Days	LL (cm)	LW (cm)	LL-LW	PH (cm)	PY (g/m ²)	BIO (g/m ²)	HI
S4T	32.3	27.9	28.5	5.1	2.6	2.0	31.8	127.5	374.8	0.3
S6T	39.8	32.8	28.5	5.0	2.5	2.1	32.5	130.7	371.8	0.4
ICG12991	34.5	29.3	28.0	5.9	2.6	2.3	35.8	59.4	195.8	0.3
J11	36.8	27.8	29.0	5.4	2.5	2.2	45.3	152.6	476.3	0.3
KJ	30.7	25.8	28.0	5.4	2.9	1.9	23.4	98.7	254.0	0.4
ICG9418	29.5	26.5	32.0	4.2	2.1	2.0	16.9	111.1	338.9	0.4
ICG12988	37.4	33.6	28.5	5.4	2.4	2.3	24.8	64.8	303.8	0.2
ICG14705	37.8	35.3	28.5	5.4	2.5	2.2	32.0	151.8	438.3	0.4
AREMA	35.9	32.8	28.3	4.2	1.9	2.2	31.7	75.7	268.8	0.3
ICGVSM5201	37.1	31.6	28.8	4.8	2.3	2.1	33.9	203.8	536.9	0.4
S5R	43.7	35.9	28.3	4.0	2.1	1.9	22.8	235.5	556.8	0.4
S1R	41.2	36.4	29.8	4.8	1.9	2.5	21.2	85.8	403.2	0.2
IGOLA	34.9	35.0	28.8	5.0	2.3	2.1	27.7	103.5	387.9	0.3
S11T	42.0	40.5	32.0	4.1	2.0	2.0	26.9	111.8	430.9	0.3
DT-MAGORO	36.9	36.1	32.5	4.6	2.2	2.1	31.3	98.2	360.7	0.3
TIFTON 8	44.0	35.6	32.3	4.7	1.7	2.7	24.6	78.5	307.6	0.3
ICG7243	38.4	33.0	34.0	4.5	2.1	2.1	16.3	117.2	314.5	0.4
ICG5701	38.5	34.9	33.5	3.7	1.9	1.9	21.4	179.4	568.6	0.3
S10T	43.9	38.0	34.0	3.9	1.8	2.1	23.4	125.4	347.3	0.4
ICGVSM0390	33.0	36.6	29.0	4.3	2.2	2.1	26.7	103.1	348.2	0.3
RED BEAUTY	36.5	34.4	27.0	4.6	2.1	2.2	30.9	86.9	272.1	0.3
GAMBIA	33.6	30.6	28.3	5.0	2.3	2.2	21.7	106.4	284.2	0.4
ICGVSM93541	29.7	32.3	28.3	4.4	2.0	2.2	23.3	71.8	231.2	0.3
BJ	38.7	30.0	29.5	5.5	2.4	2.3	17.1	86.1	245.8	0.4
JL24	32.2	32.9	29.5	4.4	2.3	1.9	18.3	70.2	239.2	0.3
ICG10890	37.4	27.0	28.0	4.5	2.4	2.0	14.1	85.8	225.3	0.4
ICG6766	34.4	29.3	28.3	4.9	2.2	2.2	22.8	93.8	302.0	0.3
SALLA	37.4	30.8	28.0	4.6	2.1	2.2	26.8	80.5	330.3	0.3
ICGVSM95731	32.5	35.0	28.3	4.4	1.9	2.3	17.2	90.6	201.6	0.5
ICGVSM95526	39.6	32.6	28.3	5.1	2.3	2.2	19.3	65.4	239.0	0.3
Mean	36.7	32.7	29.5	4.7	2.2	2.1	25.4	108.4	338.5	0.3
S.e.d Av.	4.2	7.2	1.4	1.3	0.6	0.3	7.1	59.7	131.0	0.1
S.e.d Max.	6.5	8.4	1.6	1.7	0.7	0.4	8.2	69.3	152.8	0.2
S.e.d Min.	2.9	4.9	0.9	0.8	0.4	0.2	4.7	39.4	84.9	0.1

S.e.d = Standard error of difference between means; LL= leaf length; LW = leaf width; SCMR1 and SCMR2 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAS; PY = pod yield; BIO = biomass yield; HI = harvest index

REML combined analysis of variance showed large and significant differences among F_2 families for all traits except SCMR2, biomass and pod yield ($P \leq 0.05$ to $P \leq 0.001$) under drought stress (Table 5.6). Significant differences in season for all traits except leaf width were also observed (Table 5.6). Differences among interaction effects of genotypes x season (G x S) were only significant for SCMR1 ($P \leq 0.001$) (Table 5.6). Similarly, under non-drought stress, combined analysis of variance showed large and significant differences among F_2 families for all traits except leaf length ($P \leq 0.05$ to $P \leq 0.001$) (Table 5.6). Seasonal effects were significant for plant height, POD, and BIO ($P \leq 0.05$ to $P \leq 0.01$) (Table 5.6). Differences among interaction effects of genotypes x season (G x S) were significant for days to 50% flowering, plant height and harvest index ($P \leq 0.05$ to $P \leq 0.001$) (Table 5.6).

Under drought stress, SCMR1, DTI (BIO), HI, DTI(PY), BIO and POD had average values of 45.5, 1.30, 0.5, 1.4, 273.3 g/plot and 55, respectively (Table 5.7). Pod yield and biomass had average values of 110.2 g/m² and 273.3 g/m², respectively, under drought stress (Table 5.7).

Under non-drought stress, SCMR1, SCMR2, BIO, HI and POD had average values of 35.4, 31.7, 275.5 g/m², 0.4, 55, respectively (Table 5.8). Pod yield and biomass had average yields of 112.0 and 275.5 g/m², respectively (Table 5.8)

Table 5.6 Wald's statistics for drought tolerance traits and selected agronomic traits among groundnut F₂ families evaluated under drought stress and non-drought stress across two seasons in eastern Uganda

SOV	DF	SCMR1	SCMR2	POD	PY	BIO	LL
Drought stress							
Season (S)	1	29.7 ***	80.1 ***	10 **	90.8 ***	72 ***	9.2 **
Genotype (G)	74	372.1 ***	89.1	139.7 ***	41.1	30.6	313.2 ***
G X S	73	145.7 ***	58.9	58.2	60.1	65	85.4
Non-drought stress							
Season (S)	1	1.5	2.1	7.6 *	0.6	0.5 **	
Genotype (G)	74	132.3 ***	194.5 **	193.1 ***	166.1 ***	212.2 ***	
G X S	73	59.3	93.7	71.9	85.4	77	

Table 5.6: Continued.

SOV	DF	HI	Days	PH	Ratio	Width	DTI-BIO	DTI-PY
Drought stress								
Season (S)	1	11.3 ***	44.3 ***	36 ***	8.5 **	1	107.6 **	102 ***
Genotype (G)	74	142.4 ***	205.5 ***	131.1 ***	104.7 *	245.9 ***	9.4 **	18.5 *
G X S	73	56.7	69.7	53.9	53.5	81	90.9	75.1
Non-drought stress								
Season (S)	1	0.9	0.8	3.4 *	9.8	17.5 ***		
Genotype (G)	74	115.3 ***	375.3 ***	556 ***	176.5 **	200.9 ***		
G X S	73	71.1 ***	127.9 **	137	140.2	73.8		

SOV = source of variation; DF = degrees of freedom; G = genotypes; S = season; *** = significant at $P \leq 0.001$; ** = significant at $P \leq 0.01$ and * = significant at $P \leq 0.05$; DTI-BIO = drought tolerance index based on biomass, HI = harvest index; LL = leaf length; Ratio = leaf length-width ratio; PH = plant height (cm); PY = pod yield; BIO = biomass; width = leaf width; Days = days to 50% flowering; POD = number pods; DTI-PY = drought tolerance index based on pod yield; SCMR1 and SCMR2 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAS

Table 5.7 Means for REML combined analysis of drought tolerance traits and selected physiological and agronomic traits for F₂ families evaluated under drought stress averaged over seasons 2017A and 2017B

Genotype	SCMR1	SCMR2	Days	Leaf length (cm)	Leaf width (cm)	Leaf length-width	Plant height (cm)	PY (g/m ²)	BIO (g/m ²)	DTI(PY)	DTI(BIO)	HI
S4T	40.2	42.8	34.8	5.8	3.0	2.0	37.8	198.1	456.3	3.7	1.8	0.5
S4T	46.7	39.6	35.3	6.3	3.2	2.0	38.5	144.3	308.3	1.5	1.1	0.5
S4T	40.9	36.8	31.8	5.3	2.6	2.0	30.7	85.2	189.1	1.2	3.2	0.5
S4T	51.0	41.6	29.5	4.4	2.5	1.8	26.5	80.4	533.5	0.8	0.7	0.3
S4T	43.9	38.9	30.8	5.4	3.1	1.7	37.8	147.4	293.0	2.0	1.8	0.5
S6T	46.8	44.1	34.0	5.8	2.8	2.1	36.9	112.0	220.3	1.9	1.1	0.5
S6T	46.5	36.2	31.5	6.0	3.0	2.0	41.2	130.1	281.5	1.5	1.2	0.5
S6T	43.8	44.5	32.0	5.4	2.8	1.9	35.1	112.9	242.2	1.0	1.4	0.5
S6T	44.4	40.8	30.0	5.5	2.8	2.0	36.3	132.3	326.5	1.2	1.2	0.4
S6T	42.3	37.3	31.3	5.5	2.9	1.9	38.2	121.2	251.2	1.5	1.9	0.5
ICG12991	42.6	40.7	33.3	5.8	3.2	1.8	30.6	81.5	210.7	0.7	0.6	0.4
ICG12991	52.4	44.6	31.0	5.3	3.0	1.8	33.1	121.3	259.3	1.6	0.7	0.5
ICG12991	41.1	44.2	33.3	5.8	2.9	2.0	37.6	403.4	567.9	7.1	3.3	0.6
ICG12991	42.9	40.5	33.0	5.9	3.0	2.0	53.1	118.4	333.5	1.0	1.1	0.4
ICG12991	41.1	37.7	31.5	4.5	2.7	1.7	34.5	99.8	224.5	2.0	2.1	0.4
J11	39.6	38.4	32.8	5.6	2.9	1.9	33.6	119.2	255.6	1.6	1.0	0.5
J11	48.5	39.1	32.3	5.4	2.8	2.0	37.2	132.9	271.4	1.2	1.1	0.5
J11	43.6	39.2	31.8	5.1	2.8	1.9	25.6	83.4	170.6	1.2	1.9	0.5
J11	46.8	43.0	32.5	5.1	2.8	1.9	30.7	126.0	293.5	1.1	1.2	0.4
J11	39.9	41.5	32.3	5.0	3.0	1.7	26.3	120.8	260.7	1.3	1.6	0.5
KJ	45.1	37.5	31.5	5.2	2.8	1.9	27.1	81.9	177.1	1.1	1.2	0.5
KJ	48.0	42.7	33.0	6.2	3.2	2.0	34.7	126.8	325.0	2.2	1.2	0.5
KJ	37.1	37.4	33.0	5.4	2.8	1.9	31.1	*	229.2	1.3	1.7	0.5
KJ	43.8	41.8	30.3	4.8	2.5	2.0	38.1	92.7	273.2	1.1	0.9	0.4
KJ	42.5	39.1	31.0	5.3	3.0	1.8	33.8	61.1	561.3	4.6	4.1	0.6

Table 5.7: Continued.

	Genotype	SCMR1	SCMR21	Days	Leaf length (cm)	Leaf width (cm)	Leaf length-width	Plant height (cm)	PY (g/m ²)	BIO (g/m ²)	DTI(PY)	DTI(BIO)	HI
S5R	X	49.0	46.5	32.5	4.2	2.1	2.0	30.4	84.3	253.6	0.3	0.4	0.3
S5R	X	52.3	49.7	40.5	4.0	2.1	2.0	19.8	90.2	178.2	0.8	1.1	0.4
S5R	X	48.8	44.7	33.5	3.6	2.3	1.6	18.5	94.0	165.9	0.4	0.4	0.2
S5R	X	45.5	40.0	38.3	5.5	3.2	1.7	35.3	66.5	253.0	1.5	1.5	0.5
S5R	X								121.2				
SIR	X	47.6	52.7	33.8	4.0	2.3	1.7	20.2	130.8	211.8	0.7	0.6	0.5
SIR	X	56.8	49.8	37.3	4.8	2.5	2.0	22.1	96.3	148.9	2.7	0.4	0.4
SIR	X	47.5	42.8	38.5	4.4	2.5	1.9	30.1	111.0	244.9	0.5	0.6	0.3
SIR	X	44.3	45.7	34.8	4.5	2.5	1.9	27.2	95.1	228.9	0.6	1.0	0.4
SIR	X	44.8	44.8	38.3	5.2	2.6	2.0	28.0	97.0	330.2	0.6	0.8	0.3
IGOLA	X	50.5	47.2	34.0	4.5	2.5	1.8	25.6	66.5	182.7	0.7	0.6	0.4
IGOLA	X	52.0	52.9	33.0	4.1	2.2	1.9	25.2	121.2	435.8	0.9	1.2	0.3
IGOLA	X	42.1	44.8	36.5	4.4	2.4	1.8	28.7	130.8	433.4	1.4	1.0	0.3
IGOLA	X		48.5	34.7	4.9	2.5	2.0	22.9	96.3	206.5	0.7	0.9	0.4
IGOLA	X	38.6	39.5	40.0	5.1	2.7	1.9	27.5	111.0	391.0	2.2	1.5	0.3
S11T	X	50.2	50.1	37.3	4.2	2.3	1.8	20.0	95.1	287.6	0.7	0.8	0.3
S11T	X	51.5	40.8	38.8	4.6	2.3	2.0	25.6	97.0	284.3	0.8	0.7	0.3
S11T	X	45.9	33.3	43.0	4.5	2.4	1.9	30.0	74.6	273.0	0.7	0.9	0.3
S11T	X	37.8	44.1	34.5	4.2	2.3	1.8	21.3	88.0	225.7	0.5	0.5	0.4
S11T	X	40.2	44.5	40.8	5.0	2.9	1.8	33.1	90.2	293.4	1.3	1.6	0.3
MAGORO-DT	X	50.9	37.7	33.8	4.9	2.7	1.8	26.4	118.1	333.1	1.1	1.1	0.4
MAGORO-DT	X	47.3	43.1	32.8	5.1	2.7	1.9	31.1	116.0	292.3	1.0	0.8	0.4
MAGORO-DT	X	49.9	47.2	35.0	4.7	2.5	1.8	22.1	80.8	234.2	0.6	0.7	0.4
MAGORO-DT	X	44.0	48.1	36.3	5.0	2.5	2.0	24.6	97.2	303.8	0.6	0.7	0.3
MAGORO-DT	X	47.2	36.5	33.0	5.1	2.8	1.8	26.3	83.1	293.5	1.6	0.9	0.3

Table 5.7: Continued.

	Genotype	SCMR1	SCMR21	Days	Leaf length (cm)	Leaf width (cm)	Leaf length-width	Plant height (cm)	PY (g/m ²)	BIO (g/m ²)	DTI(PY)	DTI(BIO)	HI
RB	X	47.0	37.9	29.3	4.7	2.5	1.9	30.6	111.4	233.0	1.5	1.1	0.5
RB	X	46.2	40.0	30.8	5.6	2.7	2.1	32.5	102.6	199.9	1.7	0.9	0.6
RB	X	45.9	42.5	31.5	4.9	2.5	1.9	30.6	86.2	195.6	1.0	1.1	0.4
RB	X	48.2	43.2	32.8	6.8	3.4	2.0	29.9	62.1	246.6	0.5	0.9	0.2
RB	X	40.3	37.5	32.8	6.0	3.3	1.8	33.5	115.5	274.2	1.1	0.9	0.4
GAMBIA	X	49.5	36.0	30.3	5.0	2.6	2.0	31.0	89.9	217.4	1.1	1.3	0.4
GAMBIA	X	42.8	35.6	29.5	5.2	3.3	1.7	41.8	139.4	315.0	2.1	1.1	0.4
GAMBIA	X	44.0	38.5	32.0	5.2	2.5	2.1	28.5	98.6	218.7	1.6	1.5	0.5
GAMBIA	X	43.8	44.4	33.0	7.1	3.4	2.1	29.6	110.6	269.0	1.1	1.4	0.4
GAMBIA	X	47.1	43.4	32.8	5.9	3.2	1.9	28.9	93.7	230.8	0.8	1.0	0.4
GAMBIA	X	51.6	48.2	33.8	4.8	2.5	1.9	34.1	85.1	196.8	1.0	1.0	0.4
ICGVS93541	X	44.1	41.8	30.3	5.0	2.6	1.9	24.4	55.4	154.5	0.7	1.2	0.4
ICGVS93541	X	47.3	38.3	34.0	6.3	3.2	2.0	29.3	77.1	198.2	0.6	1.5	0.4
ICGVS93541	X	47.3	41.6	32.3	5.2	2.8	1.9	65.0	107.4	263.4	1.2	1.5	1.2
ICGVS93541	X	43.5	42.1	31.0	5.9	2.8	2.1	38.0	155.8	332.6	1.4	1.0	0.5
ICGVS93541	X	44.0	41.3	32.3	5.3	3.0	1.8	30.0	125.1	268.5	1.9	3.3	0.5
BJ	X	43.9	40.4	31.8	5.5	2.8	1.9	32.4	104.8	248.2	1.3	1.1	0.4
BJ	X	43.9	43.9	33.6	7.4	3.5	2.1	38.3	154.2	403.1	1.6	1.4	0.4
BJ	X	38.6	33.9	32.0	5.9	3.2	1.9	34.5	112.5	242.9	1.3	1.0	0.5
JL24	X	44.8	38.2	30.3	6.0	2.8	2.1	43.2	122.5	312.2	1.8	1.5	0.4
JL24	X	42.6	39.7	30.5	5.0	2.7	1.9	30.7	134.4	271.1	1.0	0.9	0.5
JL24	X	47.8	39.6	32.3	4.8	2.6	1.8	22.9	130.8	239.7	1.7	1.7	0.8
JL24	X	47.3	47.7	32.8	6.6	3.3	2.0	26.8	82.6	229.7	1.0	1.0	0.9
JL24	X	46.4	41.9	32.3	5.1	3.6	1.5	28.6	126.0	264.9	2.1	2.1	1.0
Mean		45.5	42.0	33.4	5.2	2.8	1.9	31.7	110.2	273.3	1.4	1.3	0.5
S.e.d ave.		5.7	11.6	5.5	1.1	0.6	0.3	14.2	182.2	264.2	1.8	1.1	0.2
S.e.d Max.		7.1	14.5	6.9	1.3	0.7	0.4	17.6	224.6	325.8	2.5	1.5	0.2
S.e.d Min.		3.5	7.2	3.4	0.7	0.4	0.2	8.5	111.4	161.3	1.7	1.1	0.1

S.e.d = standard error of differences between means; SCMR1 and SCMR2 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAS, PY = pod yield, BIO = biomass and HI = harvest index

Table 5.8 Means for REML combined analysis of drought tolerance traits and selected physiological and agronomic traits for groundnut parents evaluated under non-drought stress averaged over seasons 2017A and 2017B

	Genotype	SCMR1	SCMR2	Days	Leaf length (cm)	Leaf width (cm)	leaf length-width	Plant height (cm)	PY (g/m ²)	BIO (g/m ²)	HI
S4T	X	34.0	26.9	28.0	5.2	2.3	2.3	31.5	65.5	220.2	0.3
S4T	X	34.7	28.6	28.8	4.7	2.4	1.9	33.3	101.1	287.0	0.4
S4T	X	32.8	35.0	27.8	5.3	2.4	2.2	35.1	104.4	246.8	0.4
S4T	X	34.5	29.5	26.5	4.3	2.1	2.1	43.5	105.6	342.2	0.3
S4T	X	32.7	30.1	27.3	3.6	1.9	1.9	23.8	90.3	163.8	0.6
S6T	X	31.8	33.3	28.8	4.8	2.1	2.3	32.4	61.5	235.0	0.3
S6T	X	35.9	34.1	28.3	4.3	2.0	2.1	30.1	92.3	256.1	0.4
S6T	X	31.5	32.6	27.3	5.2	2.4	2.2	35.4	113.0	248.9	0.6
S6T	X	35.9	32.3	25.5	4.9	2.2	2.2	54.6	110.6	280.2	0.4
S6T	X	34.2	27.1	28.8	3.9	1.8	2.2	31.3	84.5	182.6	0.6
ICG12991	X	34.0	32.9	28.0	4.5	2.0	2.2	37.3	123.6	347.2	0.4
ICG12991	X	40.5	35.2	27.8	5.3	2.4	2.2	44.5	85.0	372.3	0.3
ICG12991	X	32.9	33.6	29.5	5.2	2.2	2.3	32.0	91.6	208.6	0.5
ICG12991	X	34.2	34.2	27.3	4.0	1.9	2.1	38.3	118.0	270.1	0.4
ICG12991	X	29.1	27.4	28.0	3.4	1.7	2.1	21.6	53.2	142.3	0.4
J11	X	34.8	32.3	27.5	5.3	2.2	2.4	32.3	71.4	240.4	0.3
J11	X	33.2	34.7	28.5	4.9	2.1	2.3	37.3	118.8	248.1	0.5
J11	X	37.2	32.5	29.5	5.0	2.4	2.1	35.9	85.1	173.5	0.7
J11	X	35.3	32.4	27.5	4.9	2.3	2.1	43.6	111.0	286.5	0.4
J11	X	32.0	28.0	28.5	4.0	2.0	2.0	21.8	102.7	164.5	0.7
KJ	X	32.3	29.6	27.3	5.0	2.3	2.2	26.9	87.6	185.1	0.5
KJ	X	36.1	27.0	29.5	4.2	2.1	2.1	37.6	75.5	281.5	0.3
KJ	X	36.3	31.4	28.0	5.0	2.2	2.3	34.7	94.5	214.1	0.6
KJ	X	34.6	32.0	27.5	4.3	2.2	2.0	44.8	102.3	294.1	0.4
KJ	X	31.4	26.7	29.0	4.7	2.2	2.2	33.9	78.2	206.3	0.4

Table 5.8: Continued.

	Genotype	SCMR1	SCMR2	Days	Leaf length (cm)	Leaf width (cm)	leaf length - width	Plant height (cm)	PY (g/m ²)	BIO (g/m ²)	HI
S5R	X	39.3	35.6	27.8	3.8	1.8	2.1	21.7	324.2	536.8	0.6
S5R	X	43.2	36.2	36.8	4.5	2.0	2.4	26.4	82.9	213.6	0.5
S5R	X	32.3	29.5	31.8	3.8	1.9	2.0	23.9	101.5	348.5	0.3
S5R	X	34.2	30.7	30.0	4.2	2.0	2.1	24.7	101.9	274.1	0.5
S5R	X	38.5	36.9	31.5	4.4	2.1	2.1	28.2	155.5	430.5	0.4
SIR	X	42.2	42.1	27.5	3.7	1.8	2.1	22.8	171.2	334.3	0.5
SIR	X	47.8	39.9	32.0	4.1	1.7	2.3	22.4	167.9	443.5	0.3
SIR	X	35.4	34.3	34.5	3.9	1.6	2.4	27.7	174.1	452.9	0.4
SIR	X	44.2	33.8	31.8	3.8	2.0	1.9	26.5	170.4	278.9	0.7
SIR	X	34.0	31.8	32.5	4.4	1.9	2.3	29.8	147.3	419.6	0.4
IGOLA	X	34.8	33.0	32.8	4.4	2.0	2.2	31.2	158.4	288.4	0.6
IGOLA	X	44.3	38.3	29.0	3.9	2.0	1.9	23.2	146.8	403.6	0.4
IGOLA	X	39.3	32.0	32.5	3.7	1.7	2.2	22.5	128.2	343.3	0.4
IGOLA	X	32.3	27.8	34.5	4.0	1.8	2.3	24.2	143.6	300.9	0.5
IGOLA	X	33.2	33.4	33.0	4.0	1.9	2.1	30.5	95.7	278.3	0.3
S11T	X	41.3	36.6	27.5	4.0	1.9	2.1	24.9	162.9	368.3	0.4
S11T	X	44.6	38.2	33.5	3.6	1.6	2.3	15.3	171.2	412.3	0.4
S11T	X	37.2	39.5	33.5	3.7	1.6	2.4	23.2	145.8	322.6	0.5
S11T	X	40.7	35.5	34.2	3.9	1.8	2.1	23.3	217.8	508.3	0.5
S11T	X	39.6	37.8	31.5	4.1	1.9	2.1	26.1	88.7	214.8	0.5
MAGORO-DT	X	36.0	30.2	28.5	4.2	2.0	2.2	24.6	150.1	330.8	0.4
MAGORO-DT	X	36.9	33.0	29.0	3.9	1.8	2.2	15.5	103.1	263.7	0.4
MAGORO-DT	X	34.7	32.3	29.3	3.9	1.9	2.0	27.5	155.1	371.6	0.4
MAGORO-DT	X	32.6	33.9	28.8	4.3	1.8	2.4	24.1	181.9	469.9	0.4
MAGORO-DT	X	31.8	27.8	29.8	4.5	2.2	2.1	36.2	62.3	330.7	0.2

Table 5.8: Continued.

	Genotype	SCMR1	SCMR2	Days	Leaf length (cm)	Leaf width (cm)	leaf length - width	Plant height (cm)	PY (g/m ²)	BIO (g/m ²)	HI
RB	X	32.3	26.0	27.5	3.2	1.5	2.1	26.5	80.8	240.7	0.3
RB	X	33.3	24.0	27.5	4.3	2.1	2.1	30.4	96.7	216.3	0.4
RB	X	30.6	25.9	29.0	3.3	1.6	2.2	25.1	93.2	260.3	0.4
RB	X	35.4	31.3	29.3	5.0	2.1	2.4	21.7	119.5	337.3	0.4
RB	X	30.5	25.6	27.5	4.0	2.1	1.9	22.1	108.2	307.8	0.4
GAMBIA	X	56.2	31.0	26.8	4.2	1.8	2.3	30.5	96.1	222.2	0.4
GAMBIA	X	27.6	34.4	27.5	4.6	2.1	2.2	35.1	72.4	274.6	0.3
GAMBIA	X	33.7	26.8	27.0	3.4	1.5	2.3	22.3	80.6	167.7	0.5
GAMBIA	X	34.7	33.0	31.3	4.7	2.0	2.3	19.7	100.8	182.1	0.6
GAMBIA	X	32.1	27.5	28.5	3.6	1.9	1.9	20.3	120.9	262.6	0.5
ICGVSM93541	X	33.6	30.7	27.5	2.9	1.3	2.3	17.8	125.5	170.4	0.7
ICGVSM93541	X	29.1	28.2	28.1	3.4	1.8	1.9	20.8	87.8	150.2	0.7
ICGVSM93541	X	30.9	29.8	27.8	3.7	1.6	2.3	25.4	114.6	176.3	0.8
ICGVSM93541	X	44.7	45.2	34.6	4.5	1.8	2.4	14.2	95.6	148.9	0.8
ICGVSM93541	X	30.8	27.8	29.5	4.2	2.0	2.2	22.6	49.9	172.8	0.3
BJ	X	33.7	26.2	28.5	3.8	1.7	2.3	31.3	115.6	259.3	0.5
BJ	X	31.9	28.7	27.3	4.0	1.8	2.2	23.7	80.6	161.2	0.7
BJ	X	31.8	30.7	27.5	3.9	1.8	2.2	26.0	87.5	247.4	0.4
BJ	X	33.4	26.7	29.0	4.3	2.1	2.1	27.4	98.6	244.2	0.5
BJ	X	32.1	27.3	29.0	4.2	1.9	2.2	31.1	96.8	284.0	0.3
JL24	X	31.0	27.5	24.8	3.0	1.3	25.8	25.8	75.3	217.0	0.4
JL24	X	35.2	31.2	27.5	3.6	1.8	20.8	20.8	117.8	275.7	0.5
JL24	X	36.4	31.2	27.8	3.6	1.8	32.3	32.3	82.9	226.6	0.4
JL24	X	33.9	33.2	29.8	4.4	1.9	22.8	22.8	94.7	222.1	0.4
JL24	X	34.3	30.4	28.0	4.4	2.1	22.5	22.5	71.0	193.9	0.4
Mean		35.4	31.7	29.2	4.2	1.9	3.7	28.2	112.0	275.5	0.4
S.e.d ave.		11.3	7.9	2.4	0.7	0.3	0.2	6.1	72.4	135.0	0.3
S.e.d Max.		13.8	9.7	3.5	1.0	0.5	0.3	8.7	79.0	147.4	0.4
S.e.d Min.		6.9	4.9	1.5	0.4	0.3	0.1	3.8	45.4	83.8	0.2

S.e.d = Standard error of difference between means; SCMR1 and SCMR2 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAS; PY = pod yield; BIO = biomass.

5.3.2 Gene action controlling the drought tolerance traits under drought stress

The analyses of variance of SCMR1, SCMR2, pod yield, biomass and harvest index combined across environments (seasons) and sets is presented in Table 5.9 and Table 5.12. Under drought stress (Table 5.9), the mean squares due to general combining ability (GCA) and specific combining ability (SCA) were not significant, except for SCMR1, HI and DTI (BIO). The parents and the F_2 families, differed significantly in their GCA and SCA, respectively. In addition, the GCAf x environments and the SCA x environments interactions were only significant for SCMR2, but the GCAm x environment interaction was not significant for all the traits. Interactions of environments with the genetic components were not significant for most of the traits.

The sets were significantly different ($P \leq 0.01$) for all traits except BIO. In general, both GCA and SCA effects were relevant in the genetic control of drought tolerance traits. This is also reflected in the relative importance ratios ranging from 0.22 to 0.63 (Table 5.9). With the exception of SCMR1, all other traits showed predominance of non-additive gene action. However, across sets, the relative importance of these traits varied depending on traits as well as the set. In set 1, SCMR1, and DTI (BIO) showed additive gene control, and, SCMR2, PY, BIO, and HI revealed non-additive genetic control. In set 2, only HI had additive gene effects. Gene effects under set 3 were predominantly non-additive except for HI.

Maternal effects were present for most of the traits with the exception of PY and BIO. Under drought stress, maternal effects were only significant for SCMR1 at 80 DAP (Table 5.9). However, across sets (Table 5.12), the ratios GCAf: GCAm indicated the presence of maternal effects, although the significance of these ratios varied with traits and sets. In set 1, only SCMR1, and DTI (BIO) had significant ($P \leq 0.05$) maternal influences. In set 2, maternal effects were not significant for all traits except HI. Similarly, in set 3 only HI showed significant cytoplasmic influence.

Table 5.9 Summary mean squares and significant tests of combining ability effects for SCMR1, SCMR2, PY, BIO, DTI (PY), DTI (BIO), and HI of groundnut lines evaluated under drought stress for two seasons 2017A and 2017B in eastern Uganda

Source of Variation	DF	SCMR1	SCMR2	PY	BIO	HI	DTI(PY)	DTI(BIO)
T	2	166.2 ***	498.9 ***	67333.7 **	60944.0	0.30 ***	0.83 ***	0.47 ***
C	1	348.5 ***	4213.0 ***	151593.0 ***	438574.6 ***	0.12 ***	0.60 ***	0.30 **
R(LOC)	2	29.6	13.6	60199.6 **	71799.4	0.19 ***	0.21 **	0.08
W(SET)	12	177.9	62.3 ***	6819.9	13169.3	0.05 ***	0.05	0.07 *
B(SET)	12	33.5	43.2 **	8153.1	30746.1	0.01	0.04	0.03
W*MALE(SET)	48	30.9	55.4 ****	13352.4	26939.4	0.01	0.05 *	0.03
C*SET	2	31.4	120.4	18397.2	34570.3	0.00	0.12 *	0.14 *
C*FEM(SET)	12	22.9	50.9	7271.6	11950.5	0.02	0.02	0.04
C*MALE(SET)	12	32.2	21.1 **	7102.3	13213.7	0.00	0.05	0.01
C*FEM*MALE(SET)	47	28.5	45.8 ***	11853.3	27658.6	0.01	0.04	0.03
Residual Error	150	13.5	52.9	12195.8	26832.4	0.01	0.03	0.03
CA/(2GCA+SCA)		0.63	0.32	0.22	0.29	0.55	0.29	0.44
Contribution of GCAf (%)		31.2	5.9	4.1	3.9	19.0	6.2	13.9
Contribution of GCAm (%)		5.9	4.1	4.1	9.0	0.5	5.1	5.2
Maternal effects (P≤0.05)		*						

SCMR1 and SCMR2 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAP; Significance levels: *p≤0.05; ** p≤0.01; ***p≤0.001; ns=non-significant; LOC = Season; PY = pod yield; BIO = biomass yield; DTI (PY)= drought tolerance index based on pod yield; DTI (BIO) = drought tolerance index based on biomass; LOC=Season; GCAf = general combining ability due to female; GCAm = general combining ability due to male; SCA = specific combining ability; Relative importance = 2GCA/2GCA+SCA (Baker, 1978).

5.3.3 Association of drought tolerance traits with agronomic traits under drought stress environment

Results of correlation between drought tolerance traits and agronomic traits under drought stress are presented in Table 5.10. Both SCMR1 and SCMR2 were highly significant and negatively associated with PY ($r = -0.26$, -0.25 , respectively) and POD ($r = -0.24$, -0.31 , respectively). BIO was highly significant and positively correlated to PY ($r = 0.76$), POD ($r = 0.46$), LL ($r = 0.21$) and LW ($r = 0.17$). Similarly, DTI (BIO) was highly significant and positively associated with POD ($r = 0.43$), PY ($r = 0.46$), LL ($r = 0.22$) and LW ($r = 0.21$). The DTI (PY) was negatively associated with days to 50% flowering ($r = -0.18$, $P \leq 0.05$) but highly significant and positively associated with POD ($r = 0.57$), PY ($r = 0.63$), LL ($r = 0.36$) and LW ($r = 0.37$, $P \leq 0.01$). The HI was highly significant and negatively associated with days to 50% flowering ($r = -0.23$) but positively associated with POD ($r = 0.29$), PY ($r = 0.45$), LL ($r = 0.20$) and LW ($r = 0.20$).

5.3.4 Association among drought tolerance traits under drought stress environment

Results of association among drought tolerance traits under drought stress are presented in Table 5.10. Under drought stress, a significant, but low association of SCMR1 and SCMR 2 with all other

drought tolerance traits was observed (Table 5.10). Both SCMR1 and SCMR2 were negatively correlated with the other drought tolerance traits, while BIO was significant and positively associated with DTI (PY) ($r = 0.55$, $P \leq 0.001$), DTI (BIO) ($r = 0.44$, $P \leq 0.001$) LL ($r = 0.21$, $P \leq 0.001$), and LW ($r = 0.17$, $P \leq 0.01$). The HI was negatively associated with SCMR1 ($r = -0.18$, $P \leq 0.01$), SCMR2 ($r = -0.20$, $P \leq 0.001$) and positively associated with DTI(PY) ($r = 0.42$, $P \leq 0.001$) and DTI (BIO) ($r = 0.16$, $P \leq 0.05$), LL ($r = 0.20$, $P \leq 0.01$) and LW ($r = 0.20$, $P \leq 0.001$).

Drought tolerance indices based on pod yield (DTI (PY) and biomass accumulation (DTI (BIO) were also evaluated for association with other drought tolerance traits. DTI (PY) was highly significant and negatively associated with both SCMR1 ($r = -0.26$) and SCMR2 ($r = -0.38$), but positively associated with BIO ($r = 0.55$), (DTI (BIO) ($r = 0.66$), LL ($r = 0.36$) and LW ($r = 0.37$). DTI (BIO) was negatively associated with SCMR1 ($r = -0.27$, $P \leq 0.001$), SCMR2 ($r = -0.25$, $P \leq 0.001$), but positively correlated with BIO ($r = 0.44$, $P \leq 0.001$) and DTI (PY) ($r = 0.66$, $P \leq 0.001$), HI ($r = 0.16$, $P \leq 0.05$), LL ($r = 0.22$, $P \leq 0.001$), and LW ($r = 0.21$, $P \leq 0.001$).

Table 5.10 Pearson's correlation coefficients for association of drought tolerance traits and agronomic traits among 75 F₂ families of groundnut evaluated under drought stress across two seasons in eastern Uganda

	SCMR1	SCMR2	Days	POD	PY	BIO	DTI(PY)	DTI(BIO)	HI	LL	LW	LL/LW
SCMR1	-											
SCMR2	0.29 ***	-										
Days	0.16 **	0.22 ***	-									
POD	-0.24 ***	-0.30 ***	-0.09	-								
PY	-0.26 ***	-0.25 ***	-0.11	0.37 ***	-							
BIO	-0.20 ***	-0.32 ***	-0.06	0.46 ***	0.76 ***	-						
DTI(PY)	-0.26 ***	-0.38 ***	-0.18 *	0.57 ***	0.63 ***	0.55 ***	-					
DTI(BIO)	-0.27 ***	-0.25 ***	-0.10	0.43 ***	0.46 ***	0.44 ***	0.66 ***	-				
HI	-0.18 **	-0.20 ***	-0.23 ***	0.29 ***	0.45 ***	0.03 ***	0.42 ***	0.16 *	-			
LL	-0.25 ***	-0.28 ***	-0.16 *	0.30 ***	0.21 ***	0.21 ***	0.36 ***	0.22 ***	0.2 **	-		
LW	-0.28 ***	-0.27 ***	-0.12 *	0.26 ***	0.19 **	0.17 **	0.37 ***	0.21 ***	0.2 ***	0.73 ***	-	
LL/LW	-0.01	-0.07	-0.07	0.11	0.06	0.08	0.05	0.06	0	0.46 ***	-0.25 ***	-

SCMR1 and SCMR2 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAP; Significance levels: *p≤0.05; ** p≤0.01; ***p≤0.001; Days = days to 50% flowering; LL = leaf length (cm); LW = leaf width (cm); LL/LW = leaf length to width ratio; PY = pod yield (g/m²); BIO = total biomass (g/m²); HI = Harvest index; POD = number of pods/m²; DTI(PY) = drought tolerance index based on pod yield; DTI(BIO) = drought tolerance index based on biomass yield

5.3.5 Gene action controlling the drought tolerance traits under non-drought stress

Under non-drought stress environment (Table 5.11), the mean squares due to GCA and SCA were significant ($P \leq 0.05$) for SCMR1, SCMR2, PY, BIO, HI and POD. In addition, the GCAf x environments and of SCA x environments interactions were not significant for all traits. Similarly, the GCAm x environment interaction was not significant for all the traits. The interactions of environments with the genetic components were all not significant for most of the traits.

The sets were significantly different ($P \leq 0.01$) for all traits, except HI. In general, both the GCA and SCA effects were relevant in the control of drought tolerance traits. This is also reflected in the relative importance ratios ranging from 30.4 to 58.9 (Table 5.11). With the exception of PY, BIO, and POD, all other traits showed predominance of additive gene effects. However, across sets, relative importance of additive and non-additive gene control varied depending on the traits. In set 1, SCMR2, BIO, and HI showed additive genetic control, and SCMR1, POD and PY revealed non-additive gene control. In set 2, all traits showed non-additive gene action, except SCMR1 and SCMR2. The SCMR2, BIO and HI showed additive gene action in set 3.

Although this study revealed evidence of maternal effects on some traits, these effects were not significant (Table 5.11)

Table 5.11 Summary mean squares and significant tests of combining ability effects for SCMR1, SCMR2, PY, BIO, POD, and HI of groundnut lines evaluated for two seasons 2017A and 2017B under non-drought stress in eastern Uganda

Source	DF	SCMR1	SCMR2	PY	BIO	HI	POD
SET	2	638.9 ***	552.5 ***	99158.2 ***	515351.9 ***	0.06	19996.5 ***
LOC	1	11.2	37.2	2451.5	2869.3	0.04	3549.4 **
Rep(LOC)	2	41.2 *	21.8	6348.6 *	24.5	0.09	679.9
FEM(SET)	12	101.2 ***	76.6 ***	7728.5 ***	20022.0 **	0.12 **	755.4
MALE(SET)	12	54.2 ***	84.0 ***	1750.4	15810.3 *	0.10 **	826.5
FEM*MALE(SET)	48	27.1 *	28.0	4399.2 ***	18385.5 ***	0.04	906.1 **
LOC*SET	2	60.7 *	35.4	12715.8 **	95181.0 ***	0.04	146.6
LOC*FEM(SET)	12	16.0	21.9	1196.7	9700.4	0.04	664.4
LOC*MALE(SET)	12	23.0	31.7	1220.3	5215.1	0.05	515.8
LOC*FEM*MALE(SET)	48	20.1	31.5	2710.0	9386.2	0.04	490.7
Pooled Error	150	17.4	23.7	2046.2	7790.3	0.04	530.1
GCA(GCA+SCA)		0.6	0.6	0.4	0.3	0.56	0.3
Contribution of GCAf (%)		19.5	13.5	12.8	7.6	17.6	6.2
Contribution of GCAm (%)		10.4	14.8	2.9	6.0	15.2	6.8
Sign. Maternal effects ($P \leq 0.05$)							

SCMR1 and SCMR2 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAP; Significance levels: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; POD = number of pods; PY = pod yield; BIO = biomass yield; HI = harvest index; LOC = Season; GCAf = general combining ability due to female; GCAm = general combining ability due to male; SCA = specific combining ability; Relative importance = $2GCA/2GCA+SCA$ (Baker, 1978).

However, across sets (Table 5.12), the GCAf by GCAm ratios indicated the presence of maternal effects, although the significance of these ratios varied with traits and sets. In set 1, only SCMR1, PY and BIO had significant ($P \leq 0.05$) maternal influences. In sets, 2 and 3, maternal effects were not significant for all traits (Table 5.12)

5.3.6 Association of drought tolerance traits with agronomic traits under non-drought stress environment

Results of correlation coefficients between drought tolerance and agronomic traits under non-drought stress are presented in Table 5.13. Under non-drought stress, SCMR1 was highly significant and positively associated with PY ($r = 0.20$) and POD ($r = 0.24$). Similarly, SCMR2 was positively associated with PY ($r = 0.18$, $P \leq 0.01$) and POD ($r = 0.24$, $P \leq 0.05$). Biomass accumulation (BIO) was positively associated with SCMR1 ($r = 0.21$, $P \leq 0.001$), SCMR2 ($r = 0.18$, $P \leq 0.01$), PY ($r = 0.67$, $P \leq 0.01$) and POD ($r = 0.50$, $P \leq 0.001$). Harvest index was positively associated with POD ($r = 0.16$, $P \leq 0.01$) and PY ($r = 0.32$, $P \leq 0.01$).

5.3.7 Association among drought tolerance traits under non-drought stress environment

The results of the correlation coefficients among drought tolerance traits under non-drought stress are presented in Table 5.13. The SCMR1 was positively associated with SCMR2 ($r = 0.26$, $P \leq 0.001$), days to 50% flowering ($r = 0.13$, $P \leq 0.05$) and BIO ($r = 0.21$, $P \leq 0.001$). The SCMR2 was positively associated with BIO ($r = 0.18$, $P \leq 0.01$) and LL-LW ratio ($r = 0.13$, $P \leq 0.05$). BIO was positively associated with SCMR1 ($r = 0.21$, $P \leq 0.001$), SCMR2 ($r = 0.18$, $P \leq 0.001$), days to 50% flowering ($r = 0.27$, $P \leq 0.01$) and HI ($r = -0.36$, $P \leq 0.001$). The LL was highly significant and positively associated with plant height ($r = 0.47$; $P \leq 0.001$) and LW ($r = 0.48$; $P \leq 0.001$). The LW was highly significant and positively associated with plant height ($r = 0.48$), and LL ($r = 0.86$). LL/LW ratio was positively associated with SCMR2 ($r = 0.13$, $P \leq 0.05$), LL ($r = 0.20$, $P \leq 0.001$) and negatively associated with LW ($r = -0.32$, $P \leq 0.001$).

Table 5.12 Mean squares and relative importance for SCMR1, SCMR2, PY, BIO, DTI(PY), DTI(BIO) and HI of groundnut lines evaluated under drought and non-drought stress conditions for two seasons in eastern Uganda

Source	df	Drought stress					Non-drought stress						
		SCMR1	SCMR2	PY	BIO	DTI (PY)	DTI (BIO)	HI	SCMR1	SCMR2	PY	BIO	HI
		SET 1											
GCAf	4	710.11	73.32	77896.43	98548.56	0.39	0.73	0.24	199.75	314.52	10911.10	208964.96	0.67
GCAm	4	28.69	41.56	66668.16	136765.70	0.08	0.04	0.06	6.78	160.91	1081.23	23473.27	0.22
SCAmf	16	538.50	527.81	579741.50	928103.20	1.11	0.58	0.13	296.47	293.68	21453.40	111756.20	0.57
2GCA		738.80	114.88	144564.60	235314.30	0.47	0.76	0.30	206.53	475.43	11992.30	232438.23	0.89
2GCA +SCA		1277.30	642.68	724306.10	1163417.00	1.58	1.34	0.42	503.00	769.11	33445.70	344194.44	1.46
R.I = (2GCA/2GCA+SCA)		0.58	0.18	0.20	0.20	0.30	0.57	0.70	0.41	0.62	0.36	0.68	0.61
Significance of maternal effects (p ≤ 0.05)													
SET2													
GCAf	4	1289.39	535.53	3756.50	21189.71	0.15	0.13	0.20	797.72	254.24	79491.60	20148.79	0.36
GCAm	4	288.69	372.77	11250.47	150092.40	0.19	0.12	0.02	560.74	484.64	18585.60	41759.60	0.12
SCAmf	16	528.18	1406.30	29670.73	254800.70	0.83	0.55	0.17	579.71	537.41	160840.00	655559.77	0.52
2GCA		1578.08	908.30	15006.98	171282.10	0.34	0.25	0.22	1358.50	738.88	98077.20	61908.39	0.47
2GCA +SCA		2106.26	2314.60	44677.71	426082.90	1.17	0.80	0.38	1938.20	1276.30	258917.00	717468.15	1.00
R.I = (2GCA/2GCA+SCA)		0.75	0.39	0.34	0.40	0.29	0.31	0.57	0.70	0.58	0.38	0.09	0.48
Significance of maternal effects (p ≤ 0.05)													
SET 3													
GCAf	4	136.92	147.50	2031.63	44613.92	0.04	0.03	0.13	204.30	339.34	2339.68	11149.66	0.36
GCAm	4	86.35	121.34	20016.43	75579.75	0.20	0.18	0.03	77.30	371.20	1337.91	124491.30	0.86
SCAmf	16	418.83	724.83	26288.25	105343.80	0.66	0.39	0.23	408.70	510.97	28870.90	115187.93	0.95
2GCA		223.27	268.84	22048.05	120193.70	0.24	0.22	0.15	281.59	710.54	3677.59	135640.96	1.22
2GCA +SCA		642.10	993.67	48336.30	225537.50	0.90	0.60	0.38	690.30	1221.50	32548.50	250828.89	2.17
R.I = (2GCA/2GCA+SCA)		0.35	0.27	0.46	0.53	0.26	0.36	0.40	0.41	0.58	0.11	0.54	0.56
Significance of maternal effects (p ≤0.05)													

SCMR1 and SCMR2 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAS, R.I = relative importance, PY = pod yield; BIO = biomass; DTI(PY) = drought tolerance index based on pod yield; DTI(BIO) = drought tolerance index based on biomass yield; and HI = harvest index, *, ** = significant at $P \leq 0.05$ and $P \leq 0.01$; GCAf = general combining ability due to female; GCAm = general combining ability due to male; SCA = specific combining ability

Table 5.13 Pair-wise correlation coefficients showing association of drought tolerance traits and agronomic traits 75 F₂ family groundnut lines tested under non-drought stress for two seasons in eastern Uganda

	SCMR1	SCMR2	Days	POD	PY	BIO	HI	PH	LL	LW	LL/LW
SCMR1	-										
SCMR2	0.26 ***	-									
Days	0.13 *	0.22 *	-								
POD	0.24 ***	0.24 *	0.19 **	-							
PY	0.20 ***	0.18 **	0.20 **	0.60 ***	-						
BIO	0.21 ***	0.18 **	0.27 **	0.50 ***	0.67 **	-					
HI	0.01	0.06	-0.08	0.16 **	0.32 **	-0.36 ***	-				
PH	-0.07	-0.16 **	-0.25 ***	-0.10	-0.15 *	0.00	-0.16 **	-			
LL	-0.01	0.03	-0.02	-0.06	-0.07	-0.01	-0.05	0.47 ***	-		
LW	0.01	-0.03	-0.10	-0.05	-0.09	-0.02	-0.05	0.48 ***	0.86 ***	-	
LL/LW	-0.05	0.13 *	0.21 ***	-0.01	0.06	0.03	0.01	-0.07	0.20 ***	-0.32 ***	-

SCMR1 and SCMR2 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAS; Significance levels: *p≤0.05; ** p≤0.01; ***p≤0.001; Days = days to 50% flowering; LL = leaf length(cm); LW = leaf width(cm); PH = plant height (cm); POD = number of pods/m²; LL/LW = leaf length to width ratio; PY = pod Yield (g/m²); BIO = total biomass (g/m²); HI = harvest index

5.3.8 General combining ability effects

Estimates of the GCA effects for the 30 parents are shown in Table 5.14 and Table 5.15. The parents S5R, JL 24, S10T, BJ, S11T and ICG 10890 were good general combiners for most of the traits.

Under drought stress environment (Table 5.14) the parents which had high GCA effects for the traits under study included ICG12991 (SCMR1, HI, DTI (BIO), POD and PY), KJ (SCMR2, PY, DTI(PY), DTI (BIO), POD and HI), and J11 (BIO) among female parents, and ICGVSM2501 (PY, DTI(PY), DTI(BIO), POD, SCMR1, SCMR2 and HI) and ICG 9418 (BIO, DTI (PY), DTI(BIO) and POD) among male parents in set 1. SIR (HI, DTI(PY)), S5R (HI, POD), IGOLA (BIO), Magoro-DT (SCMR2 and DTI(BIO)) and S11T (SCMR1, PY, POD and HI) were the best combiners among female parents in set 2 while ICGVSM05701 (SCMR1, DTI(PY), DTI(BIO), POD, PY and BIO) and ICGVSM3590 (PY, POD, DTI(PY), DTI(BIO) and BIO) were good combiners among male parents in the same set. For Set 3, the best female combiners included GAMBIA (DTI(PY), DTI (BIO), SCMR1, PY and HI), RB (POD, SCMR2 and PY), ICGVSM93541 (HI) and BJ (SCMR1, DTI(BIO) and BIO), while SALLA (SCMR1 and DTI(BIO)), ICGVSM 95731(SCMR1, PY, POD, BIO, DTI(PY), DTI(BIO) and BIO) and ICGVSM 95526 (PY, POD, DTI(PY) and HI) were best combiners among male parents in the same set.

Under non-drought stress environment (Table 5.15), the parents which had high GCA for the traits under study included KJ (SCMR1, SCMR2), J11 (PY, POD and BIO), and ICG 12991(HI) among female parents and ICG 14705 (PY and BIO), Oluk-Oluk (POD, PY and HI) among male parents in set 1. S5R (POD, PY, BIO, and HI), Magoro_DT (SCMR1 and SCMR2) and S11T (SCMR1 and HI) were best combiners among female parents in set 2, while ICG 7243 (POD and BIO), S10T (PY, POD, BIO and HI) were good combiners among male parents in the same set. For Set 3, the best female combiners include JL 24 (SCMR1, SCMR2 and BIO), ICG 10890 (SCMR2 and PY), Gambia (SCMR1) and BJ (PY, POD and HI) while ICG 6766 (POD, SCMR), and SALLA (HI) were best combiners among male parents in the same set. The genotypes S4T in Set 1; Tifton 8, Magoro DT in set 2; and ICGVSM 93541 in set 3 are associated with undesired GCA effect for both drought resistance and yield traits under drought stress environment, while genotypes S4T, ICGVSM2501 in set 1; Tifton 8 in set 2; Red beauty, and ICGVSM 93541 were poor general combiners for all traits investigated under non-drought environment.

Table 5.14 Estimates of general combining ability (GCA) effects and mean performance for SCMR1, SCMR2, PY, BIO, HI, DTI (PY), DTI(BIO), and POD for 75 F₂ groundnut families evaluated under drought stress across two seasons in eastern Uganda

Parents			SCA					
	SCMR1	SCMR2	PY	BIO	HI	DTI(PY)	DTI(BIO)	POD
SET 1								
Female								
S4T	-0.30	0.07	-6.63	-9.40	0.00	0.00	-0.01	2.22
S6T	1.09	0.01	-1.12	-2.82	0.01	0.01	-0.02	-1.62
ICG 12991	-0.70	0.01	4.44	-5.14	0.01	0.00	0.02	0.71
J11	0.43	0.28	-7.47	12.92	-0.02	-0.03	-0.02	-2.62
KJ	-0.50	-0.38	10.79	4.45	0.01	0.02	0.03	1.30
Male								
ICG 9418	0.12	-0.12	-3.50	13.61	-0.01	0.00	0.00	0.95
ICG 12988	0.18	0.05	-5.18	-9.01	0.00	0.00	0.00	0.25
ICG 14705	0.00	0.28	5.62	4.70	-0.01	0.00	0.00	-1.52
Oluk-Oluk	-0.10	-0.04	-6.49	-12.50	0.00	-0.01	0.00	0.04
ICGVSM2501	-0.20	-0.18	9.54	3.20	0.01	0.01	0.01	0.29
SE	0.90	0.80	38.10	51.30	0.02	0.60	0.30	5.34
SET2								
Female								
S5R	1.56	*	0.96	-0.06	-2.02	0.01	-0.01	1.46
S1R	2.15	*	1.07	0.93	1.65	0.00	0.01	0.61
IGOLA	0.86	-0.10	-1.70	2.85	-0.01	-0.01	-0.01	-1.30
S11T	-2.30	0.56	3.90	-2.74	0.02	0.00	0.00	0.04
MAGORO-DT	-2.30	-2.48	-3.07	0.26	-0.03	0.01	0.02	-0.81
Male								
TIFTON 8	-1.10	-1.70	-6.64	-22.18	-0.01	-0.01	-0.01	-2.87
ICG 7243	1.20	1.04	-0.93	-6.78	0.01	0.00	-0.01	-0.05
ICGVSM 05701	-1.70	0.89	3.93	18.21	0.00	0.01	0.01	0.90
S10T	0.43	-0.11	0.27	3.05	0.00	-0.01	0.00	-0.25
ICGVSM 3590	1.12	-0.12	3.38	7.70	0.00	0.01	0.01	2.27
SE	1.00	1.00	8.70	28.90	0.00	0.20	0.10	5.69
SET3								
Female								
Red Beauty	1.82	**	-0.10	1.71	2.11	0.00	0.00	1.28
Gambia	-1.20		-0.17	0.63	-2.80	0.01	0.00	-1.04
ICGVSM 93541	1.44		-0.08	-1.64	-7.47	0.01	0.00	0.04
BJ	-3.00		0.66	-0.91	9.31	-0.02	0.01	-2.77
JL 24			-0.31	0.22	-1.15	0.00	0.01	2.49
Male								
ICG 10890	1.38	**	-0.17	-2.63	-5.02	0.00	-0.01	-0.65
ICG 6766	1.36	**	-0.33	0.35	0.81	0.00	0.00	-0.17
SALLA	-2.70		0.49	-5.93	-10.52	0.00	-0.02	-2.52
ICGVSM 95731	-1.50		-0.14	5.72	12.57	0.00	0.02	0.01
ICGVSM 95526	1.45	**	0.14	2.50	2.16	0.01	0.01	-0.01
SE	0.52		1.02	9.83	19.24	0.03	0.18	0.20

*, ** = significant at $P \leq 0.05$ and $P \leq 0.01$; S.E = standard error; SCMR1 and SCMR2 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAS; PY = pod yield (g/m^2); BIO = biomass (g/m^2); HI = harvest index; POD = number of pods/ m^2 ; DTI (PY) = drought tolerance index based on pod yield; DTI(BIO) = drought tolerance index based biomass, and GCA = general combining ability.

Table 5.15 Estimates of general combining ability (GCA) effects and mean performance for SCMR1, SCMR2, POD, PY, BIO, and HI for 75 F₂ groundnut families evaluated under non-drought stress across seasons in eastern Uganda.

Parents	SCA					
	SCMR1	SCMR2	POD	PY	BIO	HI
SET1						
Female						
S4T	-0.17	-0.05	-0.24	-2.80	0.42	-0.02
S6T	0.50	0.19	1.11	0.36	11.28	-0.02
ICG 12991	0.02	0.46	-1.18	1.16	-6.38	0.03 **
J11	0.21	0.23	2.6	4.10	12.68	-0.01
KJ	-0.50	-0.83	-2.28	-2.82	-18.00	0.02 **
Male						
ICG 9418	-0.08	-0.29	-2.13	0.07	2.02	-0.01
ICG 12988	-0.05	0.17	2.00	-0.18	-0.83	0.00
ICG 14705	0.01	0.37	-0.18	0.29	6.05	-0.01
Oluk-Oluk	0.11	0.20	0.90	1.18	-5.32	0.02 *
ICGVSM2501	0.02	-0.46	-0.59	-1.37	-1.92	0.00
SE	1.25	1	4.25	7.50	19.44	0.01
SET2						
Female						
S5R	0.18	0.28	1.62	11.26	3.53	0.02
S1R	1.36	0.66	0.28	-3.49	-2.57	-0.01
IGOLA	-0.57	-0.21	0.12	-1.85	2.54	-0.01
S11T	-0.33	-0.51	-0.67	3.69	2.21	0.02
MAGORO-DT	-0.64	-0.22	-1.36	-9.61	-5.71	-0.02
Male						
TIFTON 8	-0.11	-0.16	-2.48	1.22	0.77	0.00
ICG 7243	0.68	0.50	3.38	4.45	7.06	0.00
ICGVSM 05701	-0.33	-0.37	-0.7	-3.45	-8.67	0.00
S10T	0.66	0.79	0.07	2.24	1.92	0.01
ICGVSM 3590	-0.90	-0.75	-0.28	-4.46	-1.07	-0.02
SE	2	1.23	6.03	13.54	19.84	0.04
SET3						
Female						
Red Beauty	-0.15	-0.33	0.21	1.03	-0.74	0.00
Gambia	-0.35	-0.09	-1.17	-0.87	-2.31	0.01
ICGVSM 93541	-0.07	-0.17	-0.05	-0.69	-2.3	0.00
BJ	0.83	1.04	2.34	1.83	0.52	0.02
JL 24	-0.26	-0.46	-1.33	-1.29	4.84	-0.03
Male						
ICG 10890	-0.14	-0.75	0.55	1.29	11.9	-0.02
ICG 6766	-0.28	0.24	0.70	-0.10	-0.76	0.00
SALLA	0.25	0.65	-1.14	0.04	-15.28	0.04
ICGVSM 95731	-0.13	-0.41	-0.76	0.32	3.59	0.00
ICGVSM 95526	0.30	0.28	0.65	-1.55	0.55	-0.02
SE	1.46	1.02	5.03	6.83	18.37	0.05

*, ** = significant at $P \leq 0.05$ and $P \leq 0.01$; S.E = standard error; SCMR1 and SCMR2 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAS; PY = pod yield (g/m²); BIO = biomass yield (g/m²); POD = number of pods/m²; and HI = harvest index, and GCA = general combining ability.

5.3.9 Specific combining ability effects for the crosses

Under drought stress environment (Table 5.16), the following crosses had high significant SCA effects for various traits; S4T x ICGVSM5201, S6 x ICG 9418 for SCMR1, POD. Families from the cross S6T x Oluk_Oluk had high SCA effects for PY and POD. Crosses S6T x ICG 14705 and KJ x ICGVSM 2501, and ICG 12991 x ICGVSM5201 and KJ x ICGVSM2501 had high SCA effects for BIO and HI, in set 1. Cross SIR x ICGVSM3590 had high SCA effect for SCMR1, but crosses, S11T x S10T and S11T x ICGVSM3590 had high SCA effects for BIO, and crosses S1R x ICGVSM 3590 and S5R x 3590 ICGVSM had high SCA effects for SCMR1 and SCMR2 in set 2. For set 3, cross GAMBIA x ICGVSM95526 had significant SCA effects for PY and BIO, while crosses GAMBIA x ICG 6766 and BJ x ICG 10890 had high SCA effects for BIO.

Under non-drought stress environment (Table 5.17), crosses with high SCA effects included; S6T x ICG 14705 for SCMR1, SCMR2, and BIO, S4T x ICG 14705 for POD, PY and BIO, S4T x ICGVSM2501 and KJ x ICG 9418 for all other traits except HI in set 1. In set 2, crosses, MAGORO-DT x Tifton 8, S11T x S10T had moderate SCA effects for POD, and SCMR1. For set 3, cross JL24 x ICG 6766 had high SCA effects for PY, POD and BIO. Cross BJ x ICG 10890 had high SCA effects for SCMR2, POD, PY and BIO. Cross GAMBIA x ICGVSM95526 had high SCA effects for PY, BIO and HI. Cross BJ x SALLA had high SCA effect for SCMR1 and SCMR2.

Table 5.16 Estimates of specific combining ability effects (SCA) and mean performance for SCMR1, SCMR2, POD, PY, BIO, HI, DTI (PY) and DTI(BIO) of F₂ groundnut families evaluated under drought stress across two seasons in eastern Uganda

Genotype (Cross)		SCA					DTI(PY)		DTI(BIO)	
		SCMR1	SCMR2	POD	PY	BIO	HI			
		SET 1								
S4T	X	ICG 9418	-0.80	7.77	-4.18	-8.37	0.00	0.06	0.03	
S4T	X	ICG 12988	0.80	-1.04	-4.93	-1.81	-0.02	0.02	0.01	
S4T	X	ICG 14705	-0.10	-4.40	10.12	19.35	0.01	-0.06	-0.04	
S4T	X	ICG Oluk-luk-A	-0.70	1.49	-3.81	4.02	-0.03	0.02	0.00	
S4T	X	ICGVSM2501	0.80	-3.82	2.79	-13.20	0.04	-0.04	0.00	
S6T	X	ICG 9418	-0.60	-2.15	1.56	-2.53	0.01	-0.01	0.01	
S6T	X	ICG 12988	-0.70	-2.07	-0.38	-7.40	0.00	0.00	0.01	
S6T	X	ICG 14705	1.00	-1.44	-2.68	14.77	-0.01	0.00	-0.02	
S6T	X	ICG Oluk-luk-A	0.10	0.64	4.89	-4.89	0.01	-0.01	0.00	
S6T	X	ICGVSM2501	0.10	5.02	-3.39	0.05	-0.01	0.02	0.00	
ICG12991	X	ICG 9418	-0.20	-2.47	1.60	5.08	-0.03	-0.03	-0.01	
ICG12991	X	ICG 12988	0.40	0.98	4.00	8.45	0.00	-0.02	-0.02	
ICG 12991	X	ICG 14705	0.00	3.74	-1.83	-8.49	0.00	0.06	0.05	
ICG12991	X	ICG Oluk-luk-A	-0.10	0.49	-0.56	1.00	-0.01	0.00	-0.01	
ICG12991	X	ICGVSM2501	-0.90	1.88	0.55	0.85	0.01	-0.01	-0.02	
J11	X	ICG 9418	1.20	-5.40	-1.04	9.88	-0.01	-0.02	-0.02	
J11	X	ICG 12988	-0.50	3.05	0.46	-2.76	0.01	0.01	0.01	
J11	X	ICG 14705	-0.70	2.57	1.83	-12.18	0.02	0.00	0.01	
J11	X	ICG Oluk-luk-A	0.40	0.64	-0.81	3.29	-0.02	0.02	0.02	
J11	X	ICGVSM2501	-0.30	-0.86	-0.43	1.78	0.00	-0.01	-0.02	
KJ	X	ICG 9418	-0.70	2.57	1.83	-12.18	0.02	0.00	0.01	
KJ	X	ICG 12988	-0.10	-0.92	0.85	3.51	0.01	-0.01	-0.01	
KJ	X	ICG 14705	-0.20	-0.47	-7.44	-13.45	-0.02	0.00	0.00	
KJ	X	ICG Oluk-luk-A	-0.40	1.35	4.06	3.47	0.02	-0.02	-0.01	
KJ	X	ICGVSM2501	0.30	-2.21	0.48	10.52	-0.03	0.04	0.03	
		SE	1.90	12.00	85.28	114.60	0.05	1.26	0.72	

Table 5.16: Continued.

Genotype (Cross)		SCA							
		SCMR1	SCMR2	POD	PY	BIO	HI	DTI(PY)	DTI(BIO)
SET 2									
S5R	X	TIFTON 8	0.90	1.62	1.26	31.50	40.49	0.02	-0.02
S5R	X	ICG7243	-1.70	0.42	2.57	-10.00	-16.41	-0.01	0.01
S5R	X	ICGVSM05701	1.90	-0.79	-6.40	-5.30	-12.16	0.01	-0.02
S5R	X	S10T	-0.30	0.93	1.45	-9.85	-2.77	-0.03	0.01
S5R	X	ICGVSM3590	-0.80	-2.17	1.11	-6.35	-9.15	0.00	0.03
S1R	X	TIFTON 8	1.20	2.32	-1.40	-14.08	-34.21	0.02	0.03
S1R	X	ICG7243	0.00	-0.41	-1.90	3.92	16.98	-0.02	-0.03
S1R	X	ICGVSM05701	1.70	0.52	1.33	6.56	22.74	-0.01	0.01
S1R	X	S10T	-0.60	-1.50	-0.10	6.96	14.33	-0.01	-0.02
S1R	X	ICGVSM3590	-2.30	-0.93	2.04	-3.36	-19.85	0.01	0.00
IGOLA	X	TIFTON 8	1.60	2.24	-1.30	-11.08	-5.59	-0.03	-0.02
IGOLA	X	ICG7243	-1.00	-0.99	0.07	3.83	14.23	-0.01	0.00
IGOLA	X	ICGVSM05701	0.50	-0.32	1.12	0.26	2.56	0.00	0.01
IGOLA	X	S10T	-0.70	-2.21	1.27	-1.01	-13.20	0.02	0.01
IGOLA	X	ICGVSM3590	-0.40	1.29	-1.10	8.00	2.01	0.02	0.00
S11T	X	TIFTON 8	3.90	0.39	5.49	-16.52	-23.84	-0.01	0.03
S11T	X	ICG7243	1.30	-0.92	-1.60	-2.64	-28.94	0.04	0.02
S11T	X	ICGVSM05701	-6.90	-0.13	-1.60	-1.43	-7.70	0.00	0.00
S11T	X	S10T	0.40	-0.18	-2.00	11.43	33.56	-0.02	-0.04
S11T	X	ICGVSM3590	1.30	0.84	-0.30	9.16	26.93	-0.01	-0.02
MAGORO-DT	X	TIFTON 8	-7.50	-6.57	-4.00	10.19	23.15	0.00	
MAGORO-DT	X	ICG7243	1.50	1.90	0.90	4.89	14.15	0.00	-0.01
MAGORO-DT	X	ICGVSM05701	2.80	0.73	5.50	-0.10	-5.44	0.00	0.01
MAGORO-DT	X	S10T	1.10	2.96	-0.70	-7.54	-31.92	0.03	0.03
MAGORO-DT	X	ICGVSM3590	2.10	0.97	-1.70	-7.44	0.06	-0.02	-0.01
		SE	2.26	2.21	12.70	19.47	64.70	0.05	0.28

Table 5.16: Continued.

Genotype (Cross)		SCA								
		SCMR1	SCMR2	POD	PY	BIO	HI	DTI(PY)	DTI(BIO)	
SET 3										
RB	X	ICG 10890	-1.40	-0.49	-0.50	-5.75	-7.20	-0.01	0.03	0.01
RB	X	ICG6766	-0.80	-0.78	-3.60	-0.55	0.83	-0.01	-0.01	0.00
RB	X	SALLA	3.80	1.43	-0.60	6.68	2.41	0.03	-0.01	-0.02
RB	X	ICGVSM95731	0.50	0.54	2.49	3.91	5.75	0.00	-0.01	-0.02
RB	X	ICGVSM95526	-2.10	-0.70	2.22	-4.29	-1.78	-0.01	0.01	0.03
GAMBIA	X	ICG 10890	1.40	0.11	0.99	0.12	-11.73	0.00	0.01	-0.01
GAMBIA	X	ICG6766	0.60	-0.81	4.20	-4.57	15.50	-0.06	0.04	-0.01
GAMBIA	X	SALLA	-	0.54	-4.00	-0.84	-1.06	0.00	-0.02	-0.01
GAMBIA	X	ICGVSM95731	3.70	0.40	0.19	-2.94	-17.20	0.04	0.01	0.05
GAMBIA	X	ICGVSM95526	0.40	-0.25	-1.30	8.23	14.48	0.01	-0.04	-0.02
ICGVSM93541	X	ICG 10890	-1.40	0.65	-1.80	-0.92	-0.75	-0.01	0.00	0.00
ICGVSM93541	X	ICG6766	-1.80	-0.19	0.81	-2.70	-11.23	0.02	0.01	0.01
ICGVSM93541	X	SALLA	3.10	-0.18	1.04	5.67	5.45	0.03	-0.03	0.00
ICGVSM93541	X	ICGVSM95731	1.00	0.10	-2.40	-1.38	4.35	-0.03	-0.01	-0.02
ICGVSM93541	X	ICGVSM95526	-1.00	-0.38	2.40	-0.67	2.17	-0.01	0.02	0.01
BJ	X	ICG 10890	3.70	0.09	0.29	3.13	15.69	-0.01	-0.03	-0.01
BJ	X	ICG6766	2.60	0.54	-1.10	-0.17	-10.46	0.02	0.00	0.01
BJ	X	SALLA	-	-1.78	3.06	-1.60	-4.22	0.01	0.03	0.01
BJ	X	ICGVSM95731	-	0.25	0.13	-1.13	0.73	-0.01	0.02	0.00
BJ	X	ICGVSM95526	3.40	0.90	-2.40	-0.23	-1.74	-0.01	-0.02	-0.01
JL24	X	ICG 10890	-2.30	-0.37	1.02	3.42	3.98	0.03	-0.01	0.00
JL24	X	ICG6766	-0.60	1.25	-0.30	7.98	5.36	0.03	-0.04	-0.01
JL24	X	SALLA	3.50	-0.01	0.59	-9.90	-2.58	-0.06	0.03	0.03
JL24	X	ICGVSM95731	0.20	-1.29	-0.40	1.54	6.37	-0.01	-0.01	-0.01
JL24	X	ICGVSM95526	-0.80	0.42	-0.90	-3.04	-13.13	0.02	0.03	-0.01
		SE	1.20	2.30	10.80	22.00	43.00	0.10	0.40	0.50

*, ** = significant at $P \leq 0.05$ and $P \leq 0.01$; S.E = Standard error; SCMR1 and SCMR2 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAS; PY = pod yield (g/m^2), POD = number of pods/ m^2 ; BIO = biomass (g/m^2) and HI = harvest index; DTI (PY) = drought tolerance index based on pod yield; DTI (BIO) = drought tolerance index based biomass, and SCA = specific combining ability.

Table 5.17 Estimates of specific combining ability effects (SCA) and mean performance for SCMR1, SCMR2, POD, PY, BIO, and HI of groundnut families evaluated under non-drought stress across two seasons in eastern Uganda

Genotype (cross)			SCA					
			SCMR1	SCMR2	POD	PY	BIO	HI
SET1								
S4T	X	ICG 9418	0.23	-0.74	-2.3	-4.18	-8.37	0.00
S4T	X	ICG 12988	-0.34	0.4	-5	-4.93	-1.81	-0.02
S4T	X	ICG 14705	0.15	0.1	5.8	10.12	19.35	0.01
S4T	X	Oluk-luk-A	0.24	0.12	-0.5	-3.81	4.02	-0.03
S4T	X	ICGVSM2501	-0.28	0.11	2.04	2.79	-13.2	0.04
S6T	X	ICG 9418	-0.26	-0.53	4.05	1.56	-2.53	0.01
S6T	X	ICG 12988	0	0.36	-0.1	-0.38	-7.4	0.00
S6T	X	ICG 14705	1.09	0.45	-1.9	-2.68	14.77	-0.01
S6T	X	Oluk-luk-A	-0.81	0.49	0.44	4.89	-4.89	0.01
S6T	X	ICGVSM2501	-0.02	-0.77	-2.5	-3.39	0.05	-0.01
ICG12991	X	ICG 9418	-0.25	0.78	-1	1.6	5.08	-0.03
ICG12991	X	ICG 12988	-0.6	-0.27	2.3	4	8.45	0.00
ICG12991	X	ICG 14705	-0.33	-0.22	0.66	-1.83	-8.49	0.00
ICG12991	X	Oluk-luk-A	-0.02	0.03	0.05	-0.56	1	-0.01
ICG12991	X	ICGVSM2501	0.52	0.05	1.07	0.55	0.85	0.01
J11	X	ICG 9418	-0.01	-0.36	1.4	-1.04	9.88	-0.01
J11	X	ICG 12988	0.29	-0.12	-2.1	0.46	-2.76	0.01
J11	X	ICG 14705	-0.19	0.17	0.16	1.83	-12.2	0.02
J11	X	Oluk-luk-A	0	-0.12	0.06	-0.81	3.29	-0.02
J11	X	ICGVSM2501	-0.09	0.43	0.48	-0.43	1.78	0.00
KJ	X	ICG 9418	-0.19	0.17	0.16	1.83	-12.2	0.02
KJ	X	ICG 12988	0.64	-0.37	4.98	0.85	3.51	0.01
KJ	X	ICG 14705	-0.72	-0.5	-4.7	-7.44	-13.5	-0.02
KJ	X	Oluk-luk-A	-0.08	-0.17	3	4.06	3.47	0.02
KJ	X	ICGVSM2501	-0.13	0.17	-1.1	0.48	10.52	-0.03
		SE	2.8	2.2	9.45	16.76	43.5	0.03
SET 2								
S5R	X	TIFTON 8	0.26	0.19	2.25	31.5	40.49	0.02
S5R	X	ICG7243	0.19	0.17	0.94	-10	-16.4	-0.01
S5R	X	ICGVSM05701	-0.64	-0.26	-4.5	-5.3	-12.2	0.01
S5R	X	S10T	-0.02	-0.52	-2	-9.85	**	-2.77
S5R	X	ICGVSM3590	0.21	-0.58	3.27	-6.35	-9.15	0.00
S1R	X	TIFTON 8	0.12	-0.1	-5.6	-14.1	-34.2	0.02
S1R	X	ICG7243	0.42	0.22	3.17	3.92	16.98	-0.02
S1R	X	ICGVSM05701	0.55	0.67	4.94	6.56	**	22.74
S1R	X	S10T	-0.37	-0.51	0.97	6.96	14.33	-0.01
S1R	X	ICGVSM3590	-0.72	-0.28	-3.5	-3.36	**	-19.9
IGOLA	X	TIFTON 8	-0.75	-0.84	-1.5	-11.1	**	-5.59
IGOLA	X	ICG7243	-0.77	-0.31	-4.4	3.83	14.23	-0.01
IGOLA	X	ICGVSM05701	1.23	-0.02	1.99	0.26	2.56	0.00
IGOLA	X	S10T	-0.35	0.75	1.48	-1.01	-13.2	0.02
IGOLA	X	ICGVSM3590	0.64	0.42	2.41	8	2.01	0.02
S11T	X	TIFTON 8	-0.51	-0.25	-4.6	-16.5	**	-23.8
S11T	X	ICG7243	1.21	-0.14	0.3	-2.64	**	-28.9
S11T	X	ICGVSM05701	-0.92	-0.73	-1.4	-1.43	-7.7	0.00
S11T	X	S10T	0.36	-0.01	0.65	11.43	33.56	-0.02
S11T	X	ICGVSM3590	-0.13	1	5.03	9.16	26.93	-0.01
MAGORO-DT	X	TIFTON 8	0.88	-0.93	9.34	10.19	23.15	0.00
MAGORO-DT	X	ICG7243	-1.05	0.34	0.01	4.89	14.15	0.00
MAGORO-DT	X	ICGVSM05701	-0.22	0.29	-1.1	-0.1	-5.44	0.00
MAGORO-DT	X	S10T	0.38	-0.69	-1.1	-7.54	-31.9	0.03
MAGORO-DT	X	ICGVSM3590	0		-7.2	-7.44	0.06	-0.02
		SE	4.47	2.75	10.3	30.28	44.37	0.10

Table 5.17: Continued.

Genotype (cross)			SCA					
			SCMR1	SCMR2	POD	PY	BIO	HI
SET 3								
RB	X	ICG 10890	0.13	0.17	-2.3	-5.75	-7.2	-0.01
RB	X	ICG6766	-0.02	0.44	-2.6	-0.55	0.83	-0.01
RB	X	SALLA	0.05	-0.03	2.24	6.68	2.41	0.03
RB	X	ICGVSM95731	0.47	-0.1	3.76	3.91	5.75	0.00
RB	X	ICGVSM95526	-0.63	-0.48	-1.1	-4.29	-1.78	-0.01
GAMBIA	X	ICG 10890	0.57	-0.54	1.63	0.12	-11.7	0.00
GAMBIA	X	ICG6766	-0.71	1.05	-2.1	-4.57	15.5	-0.06
GAMBIA	X	SALLA	-0.69	-1.01	0.71	-0.84	-1.06	0.00
GAMBIA	X	ICGVSM95731	0.22	0.27	-2.5	-2.94	-17.2	0.04
GAMBIA	X	ICGVSM95526	0.61	0.22	2.29	8.23	14.48	0.01
ICGVSM93541	X	ICG 10890	-0.37	0.01	-4.2	-0.92	-0.75	-0.01
ICGVSM93541	X	ICG6766	0.54	-0.76	0.89	-2.7	-11.2	0.02
ICGVSM93541	X	SALLA	-0.7	-0.42	0.43	5.67	5.45	0.03
ICGVSM93541	X	ICGVSM95731	-0.1	0.87	1.58	-1.38	4.35	-0.03
ICGVSM93541	X	ICGVSM95526	0.63	0.29	1.25	-0.67	2.17	-0.01
BJ	X	ICG 10890	-0.1	0.13	1.66	3.13	15.69	-0.01
BJ	X	ICG6766	-0.13	-0.44	-0.5	-0.17	-10.5	0.02
BJ	X	SALLA	1.87	2.07	2.5	-1.6	-4.22	0.01
BJ	X	ICGVSM95731	-0.75	-1.35	-2.6	-1.13	0.73	-0.01
BJ	X	ICGVSM95526	-0.89	-0.41	-1.1	-0.23	-1.74	-0.01
JL24	X	ICG 10890	-0.23	0.23	3.17	3.42	3.98	0.03
JL24	X	ICG6766	0.32	-0.29	4.32	7.98	5.36	0.03
JL24	X	SALLA	-0.54	-0.62	-5.9	-9.9	-2.58	-0.06
JL24	X	ICGVSM95731	0.16	0.31	-0.2	1.54	6.37	-0.01
JL24	X	ICGVSM95526	0.28	0.38	-1.4	-3.04	-13.1	0.02
SE			3.26	2.29	11.3	15.27	41.07	0.10

*, ** = significant at $P \leq 0.05$ and $P \leq 0.01$; S.E = Standard error; SCMR1 and SCMR2 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAS; PY = pod yield (g/m²); POD = number of pods/m²; BIO = biomass (g/m²) and HI = harvest index and SCA = specific combining ability;

5.4 Discussion

5.4.1 Genetic variability of yield, biomass, and physiological traits

Genetic variability of traits plays an important role in plant survival, adaptability, and can also be used to predict the genetic gain from selection in breeding programmes. A wide range in values of yield, biomass, and other physiological traits was observed for the 75 groundnut crosses under different water regimes in this study, which confirmed the existence of genetic variability for drought tolerance in groundnut (Sharma and Varshney, 1995; Upadhyaya et al., 2005; Nigam and Aruna, 2008; Songsri et al., 2008; 2009, 2013). This, therefore, provides an opportunity for improvement of these traits in groundnut.

Pod yield and biomass, decreased under terminal drought stress, whereas SCMR increased as was previously reported (Nigam and Aruna, 2008; Songsri et al., 2009; Girdthai et al., 2010). The increase in SCMR has been attributed to an increase in leaf thickness as a result of groundnut genotypes having smaller leaves (Boontang et al., 2009). This result also agrees with that of Pasala and Vadez (2011) who found that genotypes with small leaf canopy are more drought tolerant than those with bigger leaf canopies. Several experiments, including this study have concluded that SCMR is relatively stable and less influenced by environmental conditions. This result agrees with earlier studies (Wright et al., 1996; Songsri et al., 2008, Arunyanark et al., 2009, Janila et al., 2015). Therefore, SCMR can be applied to screen large genotype collections in a large scale breeding programme. In practice, SCMR could be applied during screening of early generations under well water conditions while the empirical selection can take place during advanced generation.

Among drought tolerance traits, the traits, BIO, DTI (PY), DTI (BIO) and HI had the highest correlation with PY. Measurement of HI is more difficult, laborious, and costly than that of PY, DTI (PY), DTI (BIO) and BIO. Of these, DTI (PY) and HI are directly measured from pod yield. The HI was positively associated with the number of pods per plant under both drought and non-drought stress environments. This study found HI to be highly associated with PY compared to DTI (PY). In addition, genetic correlations between SCMR and PY and HI have been found to be low from similar studies (Songsri et al., 2008). However, these traits had a lower $G \times E$ interaction than yield (Wright et al., 1996). Thus, yield improvement by selection of high HI, high number of pods per plant and SCMR is possible instead of selecting for pod yield. The SCMR is an indicator of the photosynthetically active light-transmittance characteristics of the leaf and is positively correlated with chlorophyll content (Akkasaeng et al., 2003), chlorophyll density (Arunyanark et al., 2008), and WUE (Sheshshayee et al., 2006). Nonetheless, the integration of physiological traits (or their surrogates) during selection would be advantageous in selecting genotypes that are efficient water utilizers (SCMR [surrogate

trait]) or good partitioning photosynthates into economic yield (HI) (Nigam et al., 2005; Janila et al., 2015) and a high number of pods per plant (Painadawee et al., 2009, Wunna et al., 2009; Puangbut et al., 2010; and Koolachart et al., 2013). The SPAD chlorophyll meter provides an easy opportunity to integrate a surrogate measure of WUE with PY, in the selection scheme of a drought resistance breeding programme in groundnut.

Significant Interactions between seasons and genotypes were observed for some traits such as pod and biomass yield. Such interactions could cause changes in genotypic performance between seasons as was observed for certain genotypes in the current study. This implies that selection of drought resistant genotypes based on multiple seasons should in addition rely upon a combination of parameters.

5.4.2 Gene action and combining ability effects

The genetic analysis of F_2 families' data showed the importance of both additive and non-additive gene action in controlling drought tolerance traits and pod yield under both drought stress and non-drought stress environments. These results agree with earlier results obtained by John et al. (2012) who found that non-additive gene effects were dominant over the additive gene effects in controlling drought tolerance related traits such as harvest index, SPAD chlorophyll meter readings and days to 50% flowering. In contrast, other experiments by Surihan et al. (2005); Lal et al. (2005) and Upadhyaya et al. (2011) reported predominance of additive gene action for drought tolerance traits such as SLA, HI, and SCMR. The prediction of the success of a cross in a hybridization programme may be based on the *per se* performance of the parents and their respective GCA effects. The parents S5R, JL 24, S10T, BJ, S11T and ICG 10890 had good mean performance for most drought tolerance and yield characters, and were also good general combiners. A high GCA effect is largely attributed to additive gene effects or additive x additive interactions, which correspond to fixable genetic variance. Inclusion of parents with favourable alleles in a breeding programme should assist in an effective improvement of particular traits, thereby enhancing the drought tolerance as well as yield in target environments.

Generally, parents KJ, J11, ICGVSM2501 and ICG 9418 were good combiners among the Spanish botanical variety types (set1). In set 2 (Virginia botanical variety types), ICGVSM05701, CGVSM3590, S10T, ICG 7243, S11T and S5R were the best combiners. Parents BJ, SALLA, Gambia, RB, and ICGVSM 95731 were good combiners among the Valencia botanical variety types (set 3) with high negative GCA for drought tolerance traits (SCMR) and high positive GCA for yield related traits. A few examples of crosses such as S11T x S10T showed good performance across seasons under drought stress environment. These crosses showed high and stable performance.

There were no significant maternal effects for all traits under both watering regimes, except for SCMR1 under drought stress. This observation agrees with that of Lal et al. (2005). However, across sets, maternal effects varied across the two watering regimes and traits. Significant maternal effects imply the influence of maternal parents in the control of the traits and thus highlight importance of selection of parents in breeding for drought improvement. The donor parents identified for specific traits and their importance as female or male can help in further use of these genotypes

5.5 Conclusions

The present study revealed the importance of both additive and the non-additive gene action in conferring drought tolerance as well as pod yield accumulation. In order to harness both additive and non-additive genes, selection needs to be delayed until a later generation. Alternatively, the F2 segregants can be inter-mated, followed by recurrent selection and pedigree breeding. The present data, apart from being a starting point for further investigation of the genetic control of drought tolerance in groundnut, could be useful for the development of an effective breeding programme to develop drought tolerant cultivars. Groundnut lines such as KJ, J11, ICGVSM2501 and ICG 9418 were good combiners among the Spanish botanical variety types (set 1). In set 2 (Virginia botanical variety types), ICGVSM05701, ICGVSM3590, S10T, ICG 7243, S11T and S5R were the best combiners. The parents BJ, SALLA, Gambia, RB, and ICGVSM 95731 and their crosses had good genetic potential for drought tolerance and yield attributes, and were consistent across different water regimes. Such lines should be exploited in groundnut improvement programmes, especially for areas prone to drought occurrence.

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CHAPTER 6 Gene action and inheritance of seed physical quality traits in groundnut (*Arachis hypogaea* L.)

Abstract

The inheritance of several physical seed traits of groundnut (*Arachis hypogaea* L.), particularly the shelling percentage (SP), hundred seed weight (HSW), seed length (SL), seed width (SD) and length to width ratio (SL/SD) were investigated in this study. The objectives were to; i) understand the combining ability and gene action governing physical quality traits, and ii) investigate the relationship among physical traits and between these traits with drought tolerance traits. Thirty groundnut genotypes with varying seed sizes were used as parents and crossed in a North Carolina design II in three sets. The 30 parents and 75 F_2 progenies were grown in a split plot arrangement using an alpha lattice design with two replications in an open field, and in a rain-out shelter for two cropping seasons. The results revealed that under both drought stress and non-drought stress, the effects of general combining ability due to males were not significant for all traits. Under drought stress, the GCA due to females (GCAf) were significant for HSW, SL, SD, and SL/SD under both drought and non-drought stress conditions. Under drought stress, the effects due to specific combining ability (SCA) were not significant for all traits, except for SD. In the non-drought stress environment, the SCA effects differed significantly for HSW, SL, and SD only. Generally, the parents J11, ICGVSM250, S6T, ICG 12988 and ICG 14705 were good combiners among the Spanish botanical variety types, while for the Virginia botanical variety types, S5R and ICG7243 were the best combiners. The parents BJ, SALLA, ICGVSM95526, and ICGVSM95731 were good combiners among the Valencia botanical variety types for all traits studied across the water regimes. Both under drought stress and non-drought environment, the best combiners varied among parents and traits. Under both drought stress and non-drought stress environments, the relative importance ratio values were above 0.50 only for SL/SD, indicating the predominance of additive gene effects (fixable variation). The rest of the traits had values below 0.50 showing the importance of the non-additive effects in controlling the physical quality traits. Therefore, in order to target both additive and non-additive gene effects, the breeding procedures have to be amended by postponing selection to later generations or inter-mating of F_2 segregants followed by recurrent selection and pedigree breeding. Significant maternal effects were revealed for some traits, signifying the role of maternal parent in the regulation of quality traits and thus highlighted the importance of selection of parents in breeding for quality improvement. Seed yield was highly significantly and positively correlated with seed physical quality traits. Such a relationship can be exploited for improving seed yield without compromising seed size. Therefore, the selection of high pod yield potential under no-stress or small reduction in pod yield under drought stress should guarantee high seed size.

6.1 Introduction

Groundnut (*Arachis hypogaea* L.) is an annual legume grown in more than 100 countries around the world for a variety of uses. In Uganda, it is primarily utilized as a source of cheap protein because of its high-energy value, high-protein content, low cholesterol, and presence of some of the essential vitamins and minerals, while in many other countries it is used as a source of edible oil (Hariprasanna et al., 2012). As a source of food and confectionery, the demand for the crop is on the rise for both rural and urban communities (Mugisha et al., 2014). As a result, the crop is gaining importance as a significant food security and household income source contributing to poverty alleviation (Okello et al., 2014). Therefore, breeding for sweet, medium to large seeded groundnuts suited for confectionery purposes should be prioritized. Various physical, sensory, chemical and nutritional factors determine the quality of groundnut seed (Dwivedi and Nigam, 2005). Hence, the development of genotypes with a combination of multiple traits, such as high yielding potential, tolerance to drought and low soil fertility, coupled with appropriate pod and seed characteristics are a requisite for adaptability to a range of groundnut production agro-ecologies and utilisation niches.

In any breeding programme, the existence of variation for traits of economic importance and the precise understanding of genetic composition of the breeding stocks available, and the nature of gene action involved in the expression of the trait to be improved, is the basic requirement of the breeder. Several studies have revealed genetic variation among breeding germplasm and landraces for several quality traits in cultivated groundnut (John et al., 2008; Jean-Baptiste et al., 2012; Kumar et al., 2014; Maurya et al., 2014), and even higher variation in other *Arachis* species (Cherry, 1977). The existence of this variation offers opportunity to breed for grain quality to meet specific market requirements. Studies on the nature of gene action for physical qualities are few and conflicting (Dwivedi et al., 1989; Palmar et al., 2000; Vindhiyavarman, 2000; 2001; Hariprasanna et al., 2008).

Recent studies (Venuprasad et al., 2011) reported predominance of the additive gene action for seed weight, seed length (SL), seed width (SD), and seed length to width ratio (SL/SD). Earlier studies found that the traits governing groundnut grain physical qualities are predominantly controlled by additive genes, although non-additive genes also play a role (Dwivedi et al., 1989; Palmer et al., 2000; Hariprasanna et al., 2008). In addition, significant reciprocal effects for all grain physical traits have been related to the role of the maternal parent and the importance of parental selection in quality breeding (Hariprasanna et al., 2008; Venuprasad et al., 2011). However, other authors have also suggested the predominant role of the non-additive gene action in the control of these traits (Vindhiyavarman, 2000; 2001). Furthermore, recent studies (Lal et al., 2014) have found inter-allelic gene control for physical traits such as shelling percentage (SP), 100-pod weight, hundred seed weight (HSW), sound mature kernels, pod length, SD and SL/SD ratio. Given the conflicting reports regarding the inheritance of the physical grain traits in groundnut, there is a need for further

investigations. In addition, there are also a few studies regarding inheritance of grain quality traits in crosses among sub-interspecific lines and the correlation of grain quality traits with agronomic traits under stress and non-water stress conditions which warrant further investigations. Furthermore, the role of maternal effects in the inheritance of grain quality traits in sub-interspecific lines needs to be investigated using appropriate models. Therefore, the objectives of the current study were to; (i) estimate the relative importance of additive and non-additive gene action in controlling the inheritance of physical traits, (ii) investigate the relationship among physical traits and between these traits with drought tolerance traits, (iii) identifying good general combiners and specific cross combinations for use as donor parents for the improvement of these traits and to suggest breeding strategies for improvement of seed physical quality traits.

6.2 Materials and methods

6.2.1 Study sites and genotypes

The sites description is as given in section 5.2.1

Thirty groundnut lines, composed of ten drought-tolerant (D), 17 droughts susceptible (S) and three locally adapted/conventional (C) lines, were selected for the genetic studies (Table 6.1). Drought tolerant lines were selected based on previous studies (Coffelt et al., 1985; Nigam et al., 2005; Reddy et al., 2008) and evaluations by National Groundnut Breeding Programme. The drought susceptible set was selected based on seed size and resistance to groundnut rosette disease, leaf spot diseases under humid conditions. "Conventional" lines were mainly selected for wide adaptation from previous studies including data from the National Groundnut Breeding Programme.

Table 6.1 Characteristics and seed traits of the different parental lines used for the North Carolina Design II mating design.

No.	Accession name	number/ Source	Botanical Classification	Seed size	Seed colour
1	ICG 9418	ICRISAT	Spanish	Medium -large	Pink
2	ICG 12988	ICRISAT	Spanish	Medium-large	Tan
3	ICG 10890	ICRISAT	Valencia	medium	Red
4	ICG 6766	ICRISAT	Valencia	Small- medium	Tan
5	Tifton 8	ICRISAT	Virginia	large	Tan
6	ICG 7243	ICRISAT	Virginia	medium	Tan
7	Serenut 4T	SGV	Spanish	Small-medium	Tan
8	Serenut 6T	SGV	Spanish	Medium -large	Tan
9	Red beauty	FARMER	Valencia	Small-medium	Red
10	Gambia	FARMER	Valencia	Medium	White
11	Serenut 5R	SGV	Virginia	Medium	Red
12	Serenut1R	SGV	Virginia	large	Red
13	ICG 12991	ICRISAT	Spanish	Small	Tan
14	ICG 14705	ICRISAT	Spanish	Medium to large	Tan
15	Aboutalanta	FARMER	Valencia	Medium	Tan
16	ICGV-SM 05701	ICRISAT	Virginia	Medium-large	Tan
17	ICGV-SM 93541	ICRISAT	Valencia	Medium	Red
18	Igola	FARMER	Virginia	Large	Tan
19	Oluk-oluk-arema	FARMER	Spanish	medium	Red
20	ICGV-SM 95731	ICRISAT	Valencia	small	Tan
21	ICGV-SM 02501	ICRISAT	Spanish	large	Tan
22	ICGV-SM 95526	ICRISAT	Valencia	medium	Red
23	ICGV-SM 03590	ICRISAT	Virginia	medium	Tan
24	J11	ICRISAT	Spanish	Large	Tan
25	Kayunga (BJ)	FARMER	Valencia	Medium-Large	Purplish red
26	Masindi	FARMER	Spanish	Small	Red
27	JL 24	ICRISAT	Valencia	Small - medium	Tan
28	Magoro DT	FARMER	Virginia	Large	Tan
29	Serenut 10R	SGV	Virginia	large	Red
30	Serenut 11	SGV	Virginia	Large	Tan

6.2.2 Hybridisation using a North Carolina Design II mating scheme

Thirty groundnut lines were used as parents in North Carolina II (Comstock and Robinson, 1948; Hallauer et al., 2010) mating scheme in three sets. The sets were constituted equally according to the three botanical varieties: Spanish, Valencia and Virginia, with each set consisting of 10 groundnut lines. From each of these sets, five lines were used as females and the other five as males. Crosses were made in both the field and glass house following the method of Norden (1980), in the 2015B and 2016A cropping seasons. Emasculations were done in the afternoon between 2:00 – 6:00 p.m.

followed by pollination on the next day between 6:30 – 9:00 a.m. Each emasculated flower was marked with a single thread and once pollinated another thread with a tag was added. In addition, non-hybrid flowers were removed from the female parents to encourage further flowering. The F₂ progenies were developed from the seed of F₁ by selfing. The parents and F₂ progenies were used in the genetic studies.

6.2.3 Evaluation of parents and F₂ families

The genotypes, experimental design, seeding rate, irrigation scheduling and agronomic practices were the same as described in section 5.2.3

6.2.4 Data collection

Data for selected agronomic traits such as days to 50% flowering, plant height and yield data were collected as described in section 5.2.5. However, seed size traits (seed length, seed width, ratio of seed length to seed width) were measured according to the method of Lal et al. (2014)

6.2.5 Data analysis

The data collected were subjected to analysis of variance to determine whether the mean squares due to genotypes were significant using Genstat version 14 (Payne et al., 2011). An analysis of variance was performed for each trait in each season following a split plot design (Gomez and Gomez, 1984). Because water regime × genotype interaction was significant, each water regime was analysed separately using REML in Genstat. Homogeneity of variance was tested for all characters and a combined analysis of variance of two seasons data was performed. The REML combined analysis of variance was conducted for parents and crosses, respectively. In addition, Pearson's correlation analysis was conducted using Genstat software to determine degree of association of traits under each water regime.

The genetic analysis of North Carolina design II pooled over environments (seasons) was performed using the PROC GLM procedure of SAS (SAS Institute, 2011). Genotypes were considered as a fixed factor, while environments, (season) and replications were considered random factors. Variance components were estimated by restricted maximum likelihood, the default method. Gene action controlling physical grain traits was determined (Table 6.2). Data were analysed across environments (seasons) for drought stress and non- drought stress, separately, following the linear model below;

$$r_{ijkq} = \mu + r_k + f_i + m_j + (fm)_{ij} + E_q + (Ef)_{iq} + (Em)_{jq} + (Efm)_{ijq} + e_{ijkq}$$

Where;

- Y_{ijkpq} is the observed value of the progeny of the i^{th} female crossed with j^{th} male in the k^{th} replication and q^{th} season
- μ = overall population mean
- $r_k(E)$ = the replication effect within q^{th} season
- f_i = general combining ability (GCA) of the female
- m_j = general combining ability of the male
- $(fm)_{ij}$ = specific combining ability (SCA) of the i^{th} X j^{th} cross
- E_q = average effect of the q^{th} season
- $(Ef)_{iq}$ = interaction effect between the q^{th} season and the GCA of female
- $(Em)_{jq}$ = interaction effect between the q^{th} season and the GCA of male nested
- $(Efm)_{ijq}$ = interaction effect between the q^{th} season and the SCA of i^{th} X j^{th} cross
- e_{ijkq} = random error

Table 6.2 Format of analysis of variance of North Carolina design II repeated over seasons

Source of variation	df	Mean square	Expected mean square (EMS) (variance components)
Environment (E)	$e-1^a$		
Sets (S)	$s-1$		
S x E	$(e-1)(s-1)$		
Replication/S	$es(r-1)$		
Female/S	$s(f-1)$	MS_f	$\sigma^2 + r\sigma_{fme}^2 + r m \sigma_{me}^2 + r e \sigma_{fm}^2 + r e m \sigma_t^2$
Male/S	$s(m-1)$	MS_m	$\sigma^2 + r\sigma_{fme}^2 + r f \sigma_{me}^2 + r e \sigma_{fm}^2 + r e f \sigma_m^2$
Female x male/S	$s(f-1)(m-1)$	MS_{fm}	$\sigma^2 + r \sigma_{fme}^2 + r e \sigma_{fm}^2$
Female/S x E	$s(f-1)(e-1)$		$\sigma^2 + r \sigma_{fme}^2 + r m \sigma_{te}^2$
Male/S x E	$s(m-1)(e-1)$		$\sigma^2 + r \sigma_{fme}^2 + r m \sigma_{me}^2$
Female x male/S x E	$s(f-1)(m-1)(e-1)$		$\sigma^2 + r \sigma_{fme}^2$
Pooled error	$es(r-1)(mf-1)$	MSe	σ^2
Total	$esrmf-1$		

^a e, s, r, m, and f refer to the number of environments, sets with in an environment, replications, males, and females, respectively; σ_m^2 = male variance, σ^2 = random error variance, r = number of replication, σ_{fm}^2 female x male variance, e = number of environments, σ_{fme}^2 = environment x female x male variance, σ_{me}^2 = environment x male (set) variance. Source: Hallauer et al. (2010).

Significance of estimates of variance due to GCA and SCA was tested using F- values at $P \leq 0.01$, and $P \leq 0.05$ levels, while significance of estimates of GCA and SCA effects was tested using their respective standard errors. Other genetic and statistical parameters were determined as follows;

- $GCA_{Parent\ x} = \text{observed mean}_{parent\ x} - \text{trial mean}$
- $SCA_{Cross\ fm} = \text{observed cross mean}_{fm} - \text{trial mean} + GCA_f + GCA_m$
- Standard error of the male parent GCA = square root $(MSE/r \times f \times \text{sites})$ where MSE = error mean square of the experiment; r = number of replications; f = number of females; sites = number of sites
- Standard error of female parent GCA = square root $(MSE/r \times m \times \text{sites})$ where MSE = error mean square of experiment; r = number of replications; m = number of males; sites = number of sites
- Standard error of SCA female x male = square root $(MSE/r \times \text{sites})$ where MSE = error mean square of the experiment; r = number of replications; sites = number of sites
- Significance of GCAs using t- test; $t = (GCA/\text{Standard error})$; Significance of SCA using t -test; $t = SCA/\text{Standard error}$; We therefore infer for both GCA and SCA that; if t value is 2 and above: GCA/ SCA effect is significant at 5%, and if the value of t is 3 and above: GCA/SCA effect is considered significant at 1%.
- Relative importance ratio (Baker, 1978) = $2GCA / (2GCA + SCA)$ (all values greater than 0.5 imply additive gene effects while all values below 0.5 are considered non-additive gene effects)
- Maternal effects were estimated from inference made about $F_{\text{calculated}} < F_{\text{critical}}$ value at $F_{m, f}$ degrees of freedom at $P \leq 0.05$; $F_{\text{calculated}} = GCA_f/GCA_m$. If $F_{\text{cal}} < F_{\text{critical}}$, we do not reject null hypothesis that $GCA_f = GCA_m$, and therefore maternal effects are not significant at 5%

6.3 Results

6.3.1 Evaluation of parents and F₂ families

The results of the assessment of genotypic variation among groundnut genotypes (parents and crosses) are presented in Tables 6.3 to 6.10. The combined analysis of variance showed large and significant differences among parents for POD, PY, SL/SD and SL ($P \leq 0.01$ to $P \leq 0.001$) under drought stress (Table 6.3). Significant differences in season for KY and SP were observed (Table 6.3). Differences among interaction effects of season x genotype (G x S) were not significant ($P > 0.05$) for all traits (Table 6.3). POD, PY, SL/SD and the SL had average values of 69 pods/m², 144 g/m², 1.58 and 1.25 cm average values, respectively (Table 6.4).

Similarly, under non-drought stress, the combined analysis of variance showed large and significant differences among parents for POD, PY, SL and SL/SD ($P \leq 0.05$ to $P \leq 0.001$) (Table 6.3). The differences in season were only significant ($P \leq 0.05$) for SP and KY (Table 6.3). Differences among interaction effects of season x genotype (G x S) were not significant ($P > 0.05$) for all physical quality

traits (Table 6.3). The POD, PY, SL, and SL/SD had average values of 54 pods/m², 70.4 g/m², 1.0 cm and 0.6, respectively (Table 6.5).

Table 6.3 Wald's statistics for physical quality traits and agronomic traits among groundnut parental lines evaluated under drought stress and non-drought stress across two seasons in eastern Uganda

SOV	DF	SCMR1	PY	KY	POD	HI	Days	SP	SL	SD	SL/SD	PH
Drought stress												
Genotype (G)	29	48.54 *	74.95 ***	47.14	76.45 **	2.26 *	56.33 *	47.36 *	98.25 **	31.9 **	366	
Season (S)	1	14.02 ***	1.8	5.18 *	1.81	52.27	121.15 ***	5.06	0.34 ***	0.09	2.9	
G x S	28	20.66	27.54	27.35	31.69	26.42	58.73 *	25.09	25.18	34.4	32.7	
Non-drought stress												
Genotype (G)	29	113.4 ***	86.1 **	32.23	72.12 **	24.0 **	560.8 *	105.6	56.18 ***	69.4	31.5 ***	234.2 ***
Season (S)	1	1.3	0.0	3.55 *	0	0.0	0.3	6.21 *	10.88	1.7	0.1	7.1 **
G x S	28	34.3	18.0	27.65	40.04	25.7 *	71.0 **	31.55	28.03	44.7	33.8	61.1 **

SOV = source of variation; DF = degrees of freedom; ***= significant at $P \leq 0.001$; **= significant at $P \leq 0.01$ and *= significant at $P \leq 0.05$; G = genotypes; S = season; PY = pod yield; KY= kernel yield; SD =seed width; Days = days to 50% flowering; SP= shelling percentage; SL = seed length; SD = seed width; SL/SD= seed length-width ratio; HI = harvest index; POD = no. of pods; SCMR1 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 DAS; PH = plant height

Table 6.4 Means for REML combined analysis for drought tolerance traits, selected agronomic and seed physical quality traits of groundnut parents evaluated under drought stress averaged over seasons 2017A and 2017B in eastern Uganda.

Genotype	SCMR1	PY (g/m ²)	KY (g/m ²)	No. of pods/m ²	HSW (g)	Plant height (cm)	Days	SP (%)	SL (cm)	SD (cm)	SL/SD
S4T	42.8	156.7	121.3	96	39.2	37.1	35	75.2	0.98	0.81	1.2
S6T	43.5	139.6	85.3	71	45.8	34.6	35	58.2	1.28	0.8	1.61
ICG12991	40.7	145.4	94.0	85	34.9	32.2	34	59.3	1.01	0.79	1.26
J11	42.9	170.4	112.2	75	55.7	41.1	34	66.3	1.36	0.86	1.58
KJ	40.5	165.0	100.5	92	38	45.1	35	60.9	1.02	0.79	1.3
ICG9418	40.0	158.3	111.8	95	46.1	34.8	36	70.8	1.23	0.82	1.51
ICG12988	42.7	165.8	122.9	104	36	39.0	36	70.4	1.04	0.79	1.31
ICG14705	43.5	138.7	95.3	77	41.9	35.0	34	65.2	1.2	0.8	1.52
AREMA	46.0	131.2	90.6	67	145	31.6	34	67.8	1.07	0.78	1.37
ICGVSM5201	47.2	106.2	69.5	61	38.1	35.8	33	64.2	1.13	0.77	1.48
S5R	49.4	154.0	94.9	80	48.8	30.0	33	62.3	1.49	0.79	1.88
S1R	50.4	87.1	65.3	55	49	31.0	34	78.5	1.12	0.68	1.63
IGOLA	46.7	151.4	85.9	76	46.6	34.1	35	59.3	1.39	0.79	1.75
S11T	43.9	159.3	85.3	63	67.1	34.8	32	60.1	1.51	0.94	1.63
DT-MAGORO	43.8	142.0	94.5	75	54.1	34.3	32	66.0	1.46	0.85	1.72
TIFTON 8	47.4	137.7	81.2	63	64.3	37.0	35	58.4	1.77	0.83	2.13
ICG7243	49.5	54.8	18.5	39	28.3	26.1	36	35.7	0.96	0.56	1.77
ICG5701	43.4	124.4	69.1	63	49.8	28.2	32	55.7	1.41	0.81	1.75
S10T	47.0	128.9	91.0	66	54.2	32.5	33	70.3	1.46	0.81	1.81
ICGVSM0390	43.2	127.1	77.8	60	53.9	32.6	32	61.3	1.3	0.83	1.58
RED BEAUTY	43.3	177.1	114.9	67	42.4	45.6	34	63.1	1.09	0.82	1.33
GAMBIA	44.5	160.4	100.3	59	41.7	39.6	33	61.7	1.16	0.79	1.47
ICGVSM93541	42.0	150.8	83.4	61	45.1	38.1	34	54.1	1.19	0.83	1.44
BJ	42.1	156.2	77.5	31	40.7	45.5	35	52.3	1.62	0.69	2.37
JL24	42.6	124.6	79.1	63	49.1	36.5	33	61.8	1.32	0.81	1.62
ICG10890	39.6	160.4	109.5	86	42.2	36.0	34	68.7	1.04	0.82	1.26
ICG6766	43.7	177.1	106.8	67	42.8	43.8	36	62.5	1.21	0.82	1.48
SALLA	44.8	150.0	85.7	57	44.7	34.5	37	55.8	1.29	0.81	1.6
ICGVSM95731	42.9	133.3	68.1	43	44.8	41.3	33	49.4	1.16	0.82	1.41
ICGVSM95526	40.3	200.0	118.8	71	45.6	45.4	32	60.6	1.27	0.82	1.55
Mean	44.0	144.5	90.4	68.9	49.2	36.4	34	61.9	1.25	0.8	1.58
S.e.d Av.	6.6	46.0	33.3	20.5	35.8	13.1	3.1	12.1	0.22	0.12	0.14
S.e.d Max.	8.2	46.6	33.4	28.5	35.9	15.2	3.8	17.0	0.22	0.12	0.2
S.e.d Min.	4.4	45.6	33.0	20.0	35.4	8.5	2	11.8	0.22	0.12	0.14

S.e.d = standard error of difference between means; SCMR = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 days after sowing; Days = days to 50% flowering; PY = pod yield; KY=kernel yield; SP = shelling percentage, HSW = hundred seed weight; SL = seed length; SD = seed width; SL/SD = seed length to width ratio.

Table 6.5 Means for REML combined analysis for drought tolerance, selected agronomic and seed physical quality traits of groundnut parents evaluated under non-drought stress averaged over two seasons 2017A and 2017B in eastern Uganda

Genotype	SCMR1	PY (g/m ²)	KY (g/m ²)	No. of pods/m ²	HSW (g)	Plant height (cm)	Days	SP (%)	SL (cm)	SD (cm)	SL/SD
S4T	32.3	77.3	47.9	65	26.0	31.8	29	65.1	0.67	0.61	1.12
S6T	39.8	79.2	42.3	63	34.9	32.5	29	53.4	1.57	0.66	0.45
ICG12991	34.5	52.5	36.0	30	23.5	35.8	28	70.0	0.9	0.47	0.56
J11	36.8	100.9	37.9	75	35.5	45.3	29	36.9	1.29	0.66	0.53
KJ	30.7	71.0	48.7	25	24.7	23.4	28	68.1	0.9	0.59	0.7
ICG9418	29.5	72.0	49.2	50	25.0	16.9	32	67.7	0.66	0.38	0.58
ICG12988	37.4	60.0	39.3	34	18.2	24.8	29	68.2	0.97	0.57	0.59
ICG14705	37.8	92.0	32.5	85	23.0	32	29	34.6	1.1	0.58	0.56
AREMA	35.9	52.3	45.0	89	25.4	31.7	28	71.6	1.04	0.61	0.61
ICGVSM5201	37.1	123.5	33.9	87	25.7	33.9	29	26.2	1.01	0.49	0.54
S5R	43.7	112.8	51.7	84	31.3	22.8	28	48.3	1.36	0.65	0.51
SIR	41.2	68.8	41.3	37	24.2	21.2	30	60.4	0.95	0.52	0.55
IGOLA	34.9	66.8	27.3	56	28.8	27.7	29	42.5	1.1	0.55	0.5
S11T	42	69.7	41.1	96	36.8	26.9	32	58.4	1.33	0.7	0.53
DT-MAGORO	36.9	59.5	16.3	57	27.5	31.3	33	24.7	1.28	0.66	0.54
TIFTON 8	44	59.3	45.7	22	26.6	24.6	32	77.2	1.05	0.55	1.06
ICG7243	38.4	71.0	42.0	54	28.2	16.3	34	62.1	0.75	-	0.76
ICG5701	38.5	108.8	40.6	109	29.0	21.4	34	35.2	1.46	0.64	0.46
S10T	43.9	76.0	26.0	72	32.0	23.4	34	35.2	1.45	0.51	0.4
ICGVSM0390	33	65.7	52.8	53	32.6	26.7	29	79.5	1.2	0.52	0.47
RED BEAUTY	36.5	59.1	47.7	37	20.4	30.9	27	82.4	0.91	0.5	0.59
GAMBIA	33.6	64.5	33.9	49	26.9	21.7	28	56.6	0.82	0.48	0.59
ICGVSM93541	29.7	54.1	43.2	29	26.9	23.3	28	73.9	0.9	0.39	0.44
BJ	38.7	55.2	41.1	31	28.1	17.1	30	77.6	0.86	0.34	0.4
JL24	32.2	52.9	40.2	36	26.4	18.3	30	77.1	1.03	0.45	0.47
ICG10890	37.4	60.2	43.0	43	28.7	14.1	28	71.7	0.94	0.51	0.56
ICG6766	34.4	68.3	36.1	38	31.7	22.8	28	57.1	0.92	0.56	0.66
SALLA	37.4	57.9	37.5	22	30.1	26.8	28	64.3	0.98	0.54	0.56
ICGVSM95731	32.5	54.9	40.7	41	30.0	17.2	28	75.5	0.75	-	-
ICGVSM95526	39.6	44.5	32.5	40	29.4	19.3	28	75.0	1.16	0.46	0.42
Mean	36.68	70.4	39.8	53.6	27.9	25.4	29.5	59.9	1.04	0.54	0.58
S.e.d Av.	4.2	22.4	15.0	29.9	6.64	7.10	1.4	17.8	0.34	0.12	0.32
S.e.d Max.	6.5	22.4	15.0	30.0	6.64	8.20	1.6	21.7	0.34	0.12	0.38
S.e.d Min.	2.9	22.4	15.0	29.5	6.64	4.70	0.9	17.7	0.33	0.11	0.31

S.e.d = standard error of difference between means; SCMR = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 days after sowing; Days = days to 50% flowering; PY = pod yield; KY=kernel yield; SP = shelling percentage, HSD = hundred seed weight; SL = seed length; SD = seed width; SL/SD = seed length-width ratio.

The combined REML analysis of variance showed large and significant differences among F₂ families for all traits, except PY and SP under drought stress ($P \leq 0.05$ to $P \leq 0.001$) (Table 6.6). Significant differences in season for all traits except KY and SL were observed ($P \leq 0.05$ to $P \leq 0.001$) (Table 6.6). Differences among interaction effects of genotype x season (G x S) were not significant for all traits

($P > 0.05$) (Table 6.6). The SCMR, KY, POD, HSW, SL, SD, SL/SD, and HI had average scores of 45.5, 67.1 g/m², 55 pods /m², 44.3g, 1.15 cm, 0.77cm, 1.55, and 0.48, respectively (Table 6.7).

Similarly, under non-drought stress, the combined analysis of variance showed large and significant differences among F₂ families for all traits ($P \leq 0.05$ to $P \leq 0.001$) (Table 6.6). The differences in season were significant for HSW, SP, POD, and SL/SD ($P \leq 0.01$ to $P \leq 0.01$) (Table 6.6). Differences among interaction effects of genotype x season (G x S) were significant only for SD ($P \leq 0.001$) (Table 6.6). The SCMR1, HSW, SP, POD and SL/SD, SL, SD, and HI had mean traits scores of 35.4, 31.6 g, 43.01 %, 55.4 pods/m², 1.53, 0.97 cm, 0.66 cm and 0.44, respectively (Table 6.8).

Table 6.6 Wald's statistics for physical quality traits and agronomic traits among groundnut F2 families evaluated under drought stress across two seasons in eastern Uganda

SOV	DF	SCMR1	PY	KY	POD	HSD	Days
Drought stress							
Genotype (G)	74	372.1 ***	93.5	117.6 ***	136.6 ***	107.1 **	205.5 ***
Season (S)	1	29.7 ***	33.8 ***	0.6	13.1 ***	8.3 **	44.3 ***
G X S	73	145.7 ***	59.9	43.4	58.2	71.3	69.7
Non-drought stress							
Genotype (G)	74	132.3	273 ***	238 ***	192.5 ***	246.7 ***	375.3
Season (S)	1	1.5 ***	1.3	3.5	6.7 **	5.1 *	0.8 ***
G X S	73	59.3	82.4	86.8	71.4	77.2	127.9 **

Table 6.6: Continued.

SOV	DF	PH	SP	SL	SD	SL-SD	HI
Drought stress							
Genotype (G)	74	131.1 ***	81.1	106 **	149.3 ***	235.6 ***	11.3 ***
Season (S)	1	36 ***	88.1 ***	0.9	3.9 *	12.6 ***	142.4 ***
G X S	73	53.9	46.9	37.7	56.8	49.8	56.7
Non-drought stress							
Genotype (G)	74	556 *	131 ***	309.5 ***	227.5 ***	155.6 ***	0.9
Season (S)	1	3.4 ***	6.49 *	0.9	2.3	6.6 *	115.3 ***
G X S	73	137.4	63.9	82.4	131.8 ***	58.3	71.1 ***

SOV = source of variation; DF = degrees of freedom; *** = significant at $P \leq 0.001$; ** = significant at $P \leq 0.01$ and * = significant at $P \leq 0.05$; G = genotypes; S = season; PY = pod yield; KY = kernel yield; width = leaf width; Days = days to 50% flowering; HSW = hundred seed weight; SP = shelling percentage; SL = seed length; SD = seed width; SL-SD = seed length-width ratio; HI = harvest index; POD = no. of pods; PH = plant height; SCMR1 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 and 100 DAS.

Table 6.7 Means for REML combined analysis for drought tolerance, selected agronomic and seed physical quality traits of groundnut F2 families evaluated under drought stress averaged over seasons 2017A and 2017B in eastern Uganda

	Genotype	SCMR1	PY (g/m ²)	KY (gm ²)	No. of pods/m ²	HSW (g)	Plant height (cm)	Days	SP (%)	SL (cm)	SD (cm)	SL/SD	HI
S4T	X	ICG 9418	40.2	126.9	112	39.5	37.8	35	78.2	1.06	0.83	1.28	0.45
S4T	X	ICG 12988	46.7	78.5	57	53.9	38.5	35	55.5	1.13	0.86	1.30	0.47
S4T	X	ICG 14705	40.9	63.5	65	36.1	30.7	32	70.8	0.86	0.80	1.08	0.47
S4T	X	Oluk-luk-A	51.0	53.6	40	39.9	26.5	30	65.9	1.02	0.82	1.25	0.28
S4T	X	ICGVSM2501	43.9	108.5	86	44.4	37.8	31	73.7	1.21	0.81	1.49	0.49
S6T	X	ICG 9418	46.8	83.0	74	38.0	36.9	34	73.8	1.08	0.79	1.38	0.51
S6T	X	ICG 12988	46.5	88.5	54	59.3	41.2	32	70.2	1.34	0.90	1.49	0.46
S6T	X	ICG 14705	43.8	84.5	76	38.8	35.1	32	72.6	1.17	0.77	1.52	0.47
S6T	X	Oluk-luk-A	44.4	97.5	71	49.4	36.3	30	55.6	1.35	0.85	1.59	0.38
S6T	X	ICGVSM2501	42.3	91.8	71	41.0	38.2	31	71.7	0.95	0.80	1.17	0.48
ICG12991	X	ICG 9418	42.6	60.9	53	35.5	30.6	33	67.7	1.03	0.78	1.33	0.38
ICG12991	X	ICG 12988	52.4	82.8	50	64.8	33.1	31	69.5	1.39	0.93	1.50	0.47
ICG12991	X	ICG 14705	41.1	89.0	80	38.5	37.6	33	54.8	0.89	0.81	1.09	0.55
ICG12991	X	Oluk-luk-A	42.9	82.6	62	52.1	53.1	33	68.3	1.35	0.86	1.57	0.36
ICG12991	X	ICGVSM2501	41.1	72.1	65	38.8	34.5	32	71.1	1.14	0.78	1.46	0.44
J11	X	ICG 9418	39.6	84.1	83	38.2	33.6	33	68.9	1.10	0.78	1.42	0.46
J11	X	ICG 12988	48.5	87.0	64	59.8	37.2	32	65.9	1.40	0.88	1.59	0.49
J11	X	ICG 14705	43.6	59.5	55	33.9	25.6	32	67.7	0.85	0.79	1.06	0.50
J11	X	Oluk-luk-A	46.8	81.1	60	52.5	30.7	33	61.9	1.16	0.86	1.35	0.43
J11	X	ICGVSM2501	39.9	87.4	79	38.9	26.3	32	70.8	1.13	0.78	1.45	0.47
KJ	X	ICG 9418	45.1	51.4	63	34.7	27.1	32	57.1	0.87	0.77	1.11	0.47
KJ	X	ICG 12988	48.0	102.7	83	51.9	34.7	33	63.3	1.40	0.82	1.71	0.50
KJ	X	ICG 14705	37.1	86.7	80	34.6	31.1	33	72.5	0.78	0.76	1.03	0.51
KJ	X	Oluk-luk-A	43.8	73.1	55	45.1	38.1	30	66.6	1.25	0.79	1.59	0.39
KJ	X	ICGVSM2501	42.5	83.8	66	35.4	33.8	31	57.6	0.87	0.78	1.12	0.62

Table 6.7: Continued.

Genotype	SCMR1	PY (g/m ²)	KY (g/m ²)	No. of pods/m ²	HSW (g)	Plant height (cm)	Days	SP (%)	SL (cm)	SD (cm)	SL/SD	HI
S5R	49.0	79.0	62.1	48	45.8	30.4	33	82.0	1.30	0.94	1.56	0.31
S5R	52.3	65.5	43.4	34	48.9	19.8	41	71.5	1.23	0.77	1.62	0.36
S5R	48.8	43.1	25.1	22	41.2	18.5	34	58.2	1.14	0.60	1.94	0.23
S5R	45.5	126.8	90.0	59	68.3	35.3	38	68.9	1.44	0.88	1.63	0.52
S5R	-	-	13.8	-	20.3	-	-	-	0.47	0.37	-	-
S1R	47.6	92.7	63.1	64	40.9	20.2	34	71.1	1.25	0.75	1.66	0.48
S1R	56.8	60.0	51.3	43	47.7	22.1	37	77.3	1.32	0.72	1.88	0.40
S1R	47.5	84.3	54.9	43	54.0	30.1	39	67.9	1.50	0.78	1.93	0.33
S1R	44.3	90.2	59.0	42	64.7	27.2	35	63.6	1.49	0.91	1.66	0.39
S1R	44.8	94.0	61.8	49	53.8	28.0	38	66.1	1.35	0.84	1.62	0.30
IGOLA	50.5	66.5	45.5	32	54.1	25.6	34	66.7	1.43	0.82	1.75	0.39
IGOLA	52.0	124.9	68.0	60	46.9	25.2	33	71.6	1.29	0.77	1.69	0.29
IGOLA	42.1	130.4	64.9	51	62.5	28.7	37	67.6	1.50	0.85	1.78	0.33
IGOLA	-	96.1	31.5	39	30.8	22.9	35	64.6	0.76	0.45	1.61	0.44
IGOLA	38.6	123.6	84.3	71	46.4	27.5	40	62.3	1.12	0.78	1.43	0.27
S11T	50.2	95.1	56.3	59	40.0	20.0	37	63.1	1.21	0.78	1.55	0.34
S11T	51.5	99.1	63.8	50	50.1	25.6	39	69.3	1.31	0.77	1.69	0.32
S11T	45.9	74.6	49.8	47	49.4	30.0	43	66.0	1.16	0.82	1.41	0.31
S11T	37.8	88.0	53.4	40	41.5	21.3	35	50.5	1.09	0.61	1.70	0.39
S11T	40.2	90.4	48.8	42	38.1	33.1	41	61.3	1.10	0.58	1.87	0.29
MAGORO-DT	50.9	118.1	76.2	68	47.1	26.4	34	65.5	1.12	0.67	2.04	0.37
MAGORO-DT	47.3	117.1	78.5	68	56.8	31.1	33	65.7	1.41	0.82	1.72	0.39
MAGORO-DT	49.9	83.1	55.0	48	46.8	22.1	35	64.1	1.40	0.78	1.80	0.35
MAGORO-DT	44.0	97.2	66.9	57	55.4	24.6	36	66.0	1.43	0.82	1.74	0.34
MAGORO-DT	47.2	83.1	45.8	47	42.8	26.3	33	58.6	1.12	0.76	1.51	0.28

Table 6.7: Continued.

	Genotype	SCMR1	PY (g/m ²)	KY (gm ²)	No. of pods/m ²	HSW (g)	Plant height (cm)	Days	SP (%)	SL (cm)	SD (cm)	SL/SD	HI
RB	X	ICG 10890	47.0	111.4	73.0	50	40.6	30.6	68.9	1.00	0.79	1.29	0.48
RB	X	ICG6766	46.2	102.6	58.7	46	37.1	32.5	64.8	1.09	0.82	1.33	0.59
RB	X	SALLA	45.9	87.3	60.0	39	41.0	30.6	71.1	1.09	0.82	1.32	0.43
RB	X	ICGVSM95731	48.2	62.1	37.0	37	37.1	29.9	98.8	1.32	0.66	2.11	0.24
RB	X	ICGVSM95526	40.3	119.6	79.8	61	47.5	33.5	67.3	1.31	0.77	1.70	0.37
GAMBIA	X	ICG 10890	49.5	89.9	56.6	39	35.3	31.0	61.6	0.88	0.78	1.12	0.42
GAMBIA	X	ICG6766	42.8	139.4	94.8	61	41.3	41.8	65.5	1.17	0.79	1.48	0.44
GAMBIA	X	SALLA	44.0	98.6	67.7	52	41.6	28.5	72.0	1.16	0.83	1.40	0.46
GAMBIA	X	ICGVSM95731	43.8	110.6	29.6	33	30.1	29.6	37.5	1.74	0.65	2.66	0.39
GAMBIA	X	ICGVSM95526	47.1	93.4	77.7	57	47.4	28.9	69.9	1.30	0.79	1.65	0.37
ICGVSM93541	X	ICG 10890	51.6	85.1	54.8	42	35.4	34.1	67.0	1.10	0.77	1.43	0.44
ICGVSM93541	X	ICG6766	-	53.5	18.5	16	17.7	24.4	58.0	0.35	0.54	1.08	0.40
ICGVSM93541	X	SALLA	47.3	77.1	68.4	43	36.4	29.3	198.7	1.15	0.77	1.50	0.39
ICGVSM93541	X	ICGVSM95731	-	105.3	25.1	38	20.4	64.0	47.7	0.83	0.52	2.51	1.53
ICGVSM93541	X	ICGVSM95526	47.3	88.4	55.5	51	39.0	65.0	64.1	0.96	0.76	1.28	0.41
BJ	X	ICG 10890	43.5	155.8	91.0	69	39.9	38.0	61.3	1.17	0.82	1.43	0.48
BJ	X	ICG6766	44.0	125.1	80.5	51	39.6	30.0	64.5	1.14	0.79	1.43	0.45
BJ	X	SALLA	43.9	104.8	66.4	45	133.7	32.4	65.5	1.12	0.82	1.37	0.42
BJ	X	ICGVSM95731	-	153.8	33.1	41	22.1	38.3	48.6	0.90	0.34	2.70	0.38
BJ	X	ICGVSM95526	38.6	112.8	82.5	62	45.9	34.5	74.3	1.17	0.83	1.41	0.46
JL24	X	ICG 10890	44.8	142.5	84.0	72	37.9	43.2	60.6	1.15	0.85	1.39	0.40
JL24	X	ICG6766	42.6	136.2	60.0	48	35.9	30.7	55.4	1.11	0.76	1.46	0.50
JL24	X	SALLA	47.8	130.8	89.0	67	43.1	22.9	69.1	0.99	0.81	1.21	1.70
JL24	X	ICGVSM95731	47.3	82.6	26.0	37	33.2	26.8	36.3	1.65	0.63	2.63	1.01
JL24	X	ICGVSM95526	46.4	126.0	86.8	64	51.5	28.6	68.5	1.10	0.83	1.33	2.10
Mean			45.5	115.6	67.1	55.4	44.3	31.7	67.3	1.15	0.77	1.55	0.48
S.e.d ave.			5.7	119.9	35.2	24.6	24.1	14.2	40.6	0.37	0.16	0.38	0.19
S.e.d Max.			7.1	161.2	35.4	33.8	24.1	17.6	54.8	0.38	0.23	0.51	0.23
S.e.d Min.			3.5	111.8	34.6	23.1	24.0	8.5	38.6	0.36	0.16	0.33	0.11

S.e.d = standard error of difference between means; SCMR = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 days after sowing; Days = days to 50% flowering; PY = pod yield; KY = kernel yield; SP = shelling percentage; HSW = hundred seed weight; SL = seed length; SD = seed width; SL/SD = seed length to width ratio; HI = harvest index

Table 6.8 Means for REML combined analysis for drought tolerance, selected agronomic and seed physical quality traits of groundnut parents evaluated under non-drought stress averaged over seasons 2017A and 2017B

	Genotype	SCMR1	PY (g/m ²)	KY (g/m ²)	No. of pods	HSW (g)	Plant height (cm)	Days	SP (%)	SL (cm)	SD (cm)	SL/SD	HI
S4T	X	ICG 9418	34.0	65.5	14.4	29	22.4	31.5	28	21.0	0.81	1.28	0.29
S4T	X	ICG 12988	34.7	101.1	32.8	60	32.5	33.3	29	32.7	1.18	1.77	0.35
S4T	X	ICG 14705	32.8	104.4	19.9	30	23.2	35.1	28	17.7	0.77	1.43	0.40
S4T	X	Oluk-luk-A	34.5	105.6	30.2	55	29.3	43.5	27	27.5	1.17	1.76	0.31
S4T	X	ICGVSM2501	32.7	90.3	16.0	21	25.0	23.8	27	18.7	1.00	1.75	0.58
S6T	X	ICG 9418	31.8	61.5	12.9	34	18.5	32.4	29	21.4	0.91	1.54	0.27
S6T	X	ICG 12988	35.9	92.3	38.9	59	29.9	30.1	28	44.7	0.86	1.29	0.37
S6T	X	ICG 14705	31.5	113.0	25.9	60	24.4	35.4	27	22.7	0.88	1.40	0.56
S6T	X	Oluk-luk-A	35.9	110.6	36.7	58	36.5	54.6	26	32.5	1.17	1.71	0.43
S6T	X	ICGVSM2501	34.2	84.5	39.8	66	29.4	31.3	29	53.6	0.63	1.12	0.56
ICG12991	X	ICG 9418	34.0	123.6	40.6	69	29.0	37.3	28	33.4	1.00	1.50	0.36
ICG12991	X	ICG 12988	40.5	85.0	23.8	44	31.3	44.5	28	27.3	1.11	1.63	0.28
ICG12991	X	ICG 14705	32.9	91.6	18.7	45	20.0	32.0	30	20.9	0.84	1.37	0.50
ICG12991	X	Oluk-luk-A	34.2	118.0	44.9	58	33.8	38.3	27	46.7	1.19	1.83	0.44
ICG12991	X	ICGVSM2501	29.1	59.9	26.6	19	27.7	21.6	28	41.0	1.03	1.67	0.38
J11	X	ICG 9418	34.8	71.4	18.7	48	16.5	32.3	28	25.8	0.73	1.47	0.30
J11	X	ICG 12988	33.2	118.8	37.4	57	30.7	37.3	29	31.8	1.04	1.49	0.48
J11	X	ICG 14705	37.2	85.6	31.7	34	23.9	35.9	30	44.7	0.86	1.43	0.69
J11	X	Oluk-luk-A	35.3	111.0	31.5	62	28.3	43.6	28	27.9	1.17	1.76	0.40
J11	X	ICGVSM2501	32.0	102.7	31.1	54	26.7	21.8	29	29.7	0.79	1.42	0.69
KJ	X	ICG 9418	32.3	92.8	35.5	52	32.6	26.9	27	41.2	0.89	1.28	0.50
KJ	X	ICG 12988	36.1	75.5	21.2	40	25.5	37.6	30	30.1	1.16	1.68	0.29
KJ	X	ICG 14705	36.3	94.5	42.2	45	18.3	34.7	28	45.9	0.86	1.36	0.55
KJ	X	Oluk-luk-A	34.6	102.3	36.7	58	31.5	44.8	28	35.9	1.20	1.74	0.36
KJ	X	ICGVSM2501	31.4	79.8	33.8	32	21.4	33.9	29	47.2	0.89	1.55	0.37

Table 6.8: Continued.

	Genotype	SCMR1	PY (g/m ²)	KY (gm ²)	No. of pods	HSW (g)	Plant height (cm)	Days	SP (%)	SL (cm)	SD (cm)	SL/SD	HI
S5R	X	39.3	324.2	114.4	77	41.2	21.7	28	33.3	1.22	0.75	1.81	0.61
S5R	X	43.2	82.9	32.0	41	29.4	26.4	37	39.5	0.96	0.60	1.63	0.49
S5R	X	32.3	101.5	21.9	56	27.3	23.9	32	22.0	1.13	0.73	1.65	0.29
S5R	X	34.2	101.9	39.2	41	28.9	24.7	30	43.7	1.03	0.59	1.73	0.49
S5R	X	38.5	155.5	56.6	94	34.3	28.2	32	38.0	1.20	0.74	1.61	0.35
SIR	X	42.2	171.2	61.6	95	35.9	22.8	28	47.9	1.19	0.69	1.75	0.49
SIR	X	47.8	192.2	92.1	99	37.0	22.4	32	49.7	1.16	0.71	1.64	0.34
SIR	X	35.4	174.1	94.5	68	35.8	27.7	35	53.1	1.14	0.76	1.50	0.40
SIR	X	44.2	170.4	53.6	84	35.6	26.5	32	36.6	1.02	0.57	1.78	0.68
SIR	X	34.0	147.3	48.3	80	31.0	29.8	33	32.6	1.18	0.67	1.77	0.35
IGOLA	X	34.8	158.4	52.1	57	34.3	31.2	33	38.1	1.11	0.65	1.70	0.56
IGOLA	X	44.3	151.5	71.3	90	43.0	23.2	29	50.2	1.24	0.69	1.81	0.38
IGOLA	X	39.3	128.2	42.3	77	35.4	22.5	33	35.1	1.09	0.70	1.53	0.39
IGOLA	X	32.3	143.6	75.7	61	37.6	24.2	34	54.7	0.99	0.71	1.39	0.50
IGOLA	X	33.2	104.4	46.0	59	39.5	30.5	33	46.7	1.22	0.76	1.60	0.34
S11T	X	41.3	162.9	53.8	71	34.6	24.9	28	35.1	1.21	0.71	1.71	0.43
S11T	X	44.6	171.2	76.5	77	40.6	15.3	34	46.2	1.18	0.72	1.63	0.40
S11T	X	37.2	154.1	67.7	78	34.9	23.2	34	44.4	1.13	0.79	1.48	0.51
S11T	X	40.7	217.8	95.1	72	41.0	23.3	34	39.3	1.19	0.77	1.53	0.45
S11T	X	39.6	88.7	38.6	62	29.0	26.1	32	49.1	1.11	0.67	1.67	0.52
MAGORO-DT	X	36.0	153.3	66.3	90	40.0	24.6	29	50.4	1.25	0.72	1.74	0.43
MAGORO-DT	X	36.9	103.1	45.8	58	42.8	15.5	29	42.6	1.10	0.69	1.57	0.39
MAGORO-DT	X	34.7	155.1	65.7	81	38.1	27.5	29	44.2	0.83	0.74	1.12	0.42
MAGORO-DT	X	32.6	181.9	82.4	88	47.0	24.1	29	48.9	1.33	0.76	1.74	0.39
MAGORO-DT	X	31.8	67.7	25.9	36	32.8	36.2	30	41.4	1.04	0.68	1.54	0.21

Table 6.8: Continued.

	Genotype	SCMR1	PY (g/m ²)	KY (g/m ²)	No. of pods	HSW (g)	Plant height (cm)	Days	SP (%)	SL (cm)	SD (cm)	SL/SD	HI
RB	X	ICG 10890	32.3	80.8	39.1	41	29.9	26.5	52.7	0.85	0.55	1.56	0.34
RB	X	ICG6766	33.3	108.8	46.1	51	32.6	30.4	42.2	0.78	0.54	1.49	0.42
RB	X	SALLA	30.6	96.1	52.1	32	27.4	25.1	55.9	0.84	0.57	1.47	0.35
RB	X	ICGVSM95731	35.4	119.5	52.5	65	33.7	21.7	43.8	0.59	0.78	0.75	0.43
RB	X	ICGVSM95526	30.5	108.2	61.4	56	37.1	22.1	56.8	0.73	-	-	0.38
GAMBIA	X	ICG 10890	56.2	96.1	36.7	40	31.8	30.5	35.9	1.02	0.67	1.50	0.42
GAMBIA	X	ICG6766	27.6	74.6	35.5	37	30.5	35.1	47.4	1.03	0.70	1.50	0.27
GAMBIA	X	SALLA	33.7	80.6	43.5	53	30.5	22.3	54.5	0.69	0.62	1.13	0.54
GAMBIA	X	ICGVSM95731	34.7	100.8	58.5	57	34.2	19.7	58.3	0.59	0.65	0.92	0.62
GAMBIA	X	ICGVSM95526	32.1	120.9	54.0	62	35.3	20.3	45.2	0.58	-	-	0.48
ICGVSM93541	X	ICG 10890	33.6	128.6	45.3	52	35.2	17.8	43.2	0.67	-	-	0.73
ICGVSM93541	X	ICG6766	29.1	95.0	56.0	40	33.2	20.8	59.5	0.62	-	-	0.67
ICGVSM93541	X	SALLA	30.9	121.6	63.0	44	31.4	25.4	53.6	0.67	0.70	0.95	0.78
ICGVSM93541	X	ICGVSM95731	44.7	95.6	55.7	62	34.5	14.2	58.2	0.66	0.68	0.97	0.75
ICGVSM93541	X	ICGVSM95526	30.8	55.2	39.1	13	31.3	22.6	70.2	1.19	0.67	1.82	0.29
ICGVSM93541	X	ICG 10890	33.7	115.6	70.3	60	34.8	31.3	61.8	0.76	-	-	0.45
BJ	X	ICG6766	31.9	87.6	53.6	29	33.7	23.7	64.9	0.69	0.54	1.29	0.68
BJ	X	SALLA	31.8	87.5	46.7	50	33.5	26.0	56.6	0.91	-	-	0.37
BJ	X	ICGVSM95731	33.4	98.6	52.2	43	33.7	27.4	53.1	0.89	-	-	0.53
BJ	X	ICGVSM95526	32.1	96.8	27.1	38	14.8	31.1	35.6	0.94	0.49	2.53	0.33
JL24	X	ICG 10890	31.0	75.3	53.4	46	30.3	25.8	71.8	0.83	0.57	1.44	0.35
JL24	X	ICG6766	35.2	117.8	61.7	54	31.6	20.8	55.2	0.77	0.67	1.13	0.49
JL24	X	SALLA	36.4	82.9	27.7	54	23.8	32.3	31.3	0.86	0.63	1.38	0.36
JL24	X	ICGVSM95731	33.9	96.1	67.3	55	37.0	22.8	72.4	1.01	0.67	1.46	0.43
JL24	X	ICGVSM95526	34.3	81.9	48.3	39	32.3	22.5	61.9	1.01	0.55	1.86	0.36
Mean			35.4	113.7	46.8	55.4	31.6	28.2	43.0	0.97	0.66	1.53	0.44
S.e.d ave.			11.3	43.7	22.7	23.0	6.9	6.1	19.6	0.19	0.08	0.38	0.32
S.e.d Max.			13.8	43.8	22.7	23.1	6.9	8.7	19.7	0.27	0.11	0.52	0.35
S.e.d Min.			6.9	43.4	22.6	23.0	6.9	3.8	19.3	0.19	0.08	0.36	0.20

S.e.d = standard error of difference between means; SCMR1 = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 days after sowing; Days = days to 50% flowering; PY = pod yield; KY = kernel yield; SP = shelling percentage; HSW = hundred seed weight; SL = seed length; SD = seed width; SL/SD = seed length to width ratio; HI = harvest index.

6.3.2 Gene action controlling the physical quality traits under drought stress

The combined analyses of variance of HSW, SP, SL, SD and SL/SD across environments and sets is presented in Table 6.9 and Table 6.10.

Under drought stress, the mean squares due to general combining ability (GCAf) were significant for HSW, SL, SD, and SL/SD ($P \leq 0.01$ to $P \leq 0.001$) (Table 6.9). However, the mean squares due to specific combining ability (SCA) were not significant except for SD. In addition, the GCAf x environment and of SCA x environments, and the GCAm x environment interaction effects were not significant for all the traits. Interactions of environments with the genetic components were not significant for most of the traits.

The sets were significantly different ($P \leq 0.05$ to $P \leq 0.001$) for all traits, except HSW and SP. In general, both GCA and SCA effects were relevant in the genetic control of physical grain traits. This is also reflected in the relative importance ratios ranging from 0.35 to 0.76 (Table 6.9). With the exception of SL/SD, all other traits showed predominance of non-additive gene effects. However, across the sets, the relative importance of the additive and non-additive gene actions varied depending on the traits. In set 1, HSW, SL and SL/SD showed additive gene action, while POD, SD and KY revealed non-additive gene action. Similarly, in set 3, only SD and SL/SD showed additive gene action. Gene action in set 2 was predominantly non-additive.

Generally, this study revealed the evidence of maternal effects on some traits although the level of significance of these varied. Under drought stress, maternal effects were only significant for the SL/SD ratio (Table 6.9). However, across sets (Table 6.10), just as there was good evidence of maternal effects for most traits as determined by the GCAf by GCAm ratios, the significance of these ratios also varied with the traits and sets. In set 1, all traits showed significant ($P \leq 0.05$) maternal effects except for SP. In set 2, maternal effects were not significant for all traits. In set 3, only the SL/SD ratio had significant cytoplasmic effects.

Table 6.9 Summary mean squares and significant tests of combining ability effects for HSW, SP, SL, SD and SL/SD of groundnut lines evaluated for two seasons under drought stress in eastern Uganda

Source of Variation	DF	HSW	SP	SL	SD	SL/SD
SET	2	1086.231	155.6392	0.507667 *	0.178078 ***	2.865182 ***
LOC	1	4808.003 **	6492.628 *	0.117612	0.110802 *	1.312915 ***
Rep(LOC)	2	30.54253	8780.921 **	0.666358 **	0.004671	1.833395 ***
FEM(SET)	12	1653.573 **	1633.627	0.37693 ***	0.093915 ***	1.476926 ***
MALE(SET)	12	717.3708	850.2899	0.239368	0.024793	0.06866
FEM*MALE(SET)	48	655.7106	1135.071	0.163951	0.037722 *	0.12084
LOC*SET	2	764.6025	1447.294	0.175244	0.034468	0.00581
LOC*FEM(SET)	12	589.2868	877.3396	0.02915	0.020249	0.038874
LOC*MALE(SET)	12	614.1895	933.7742	0.067413	0.024638	0.064208
LOC*FEM*MALE(SET)	47	529.4426	1258.36	0.091202	0.018207	0.139663
Pooled Error	150	585.215	1459.582	0.136587	0.025888	0.117523
R.I = 2GCA/(2GCA+SCA)		0.48	0.35	0.48	0.44	0.76
Contribution of GCAf (%)		18.3	9.4	19.2	21.2	40.6
Contribution of GCAm (%)		7.9	4.9	12.2	5.6	1.9
Maternal effects ($P \leq 0.05$)						*

Significance levels: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; DF = Degrees of freedom; LOC = Season; GCAf = general combining ability due to females, GCAm = general combining ability due to male parents; HSW = hundred seed weight (g), SP = shelling percentage (%); SL = seed length; SD = seed width; SL/SD = seed length to width ratio; 2GCA/(2GCA+SCA) = relative importance ratio (Baker, 1978)

Table 6.10 Summary mean squares, relative importance ratios and significance tests of maternal effects for KY, POD, HSW, SP, SL, SD and SL/SD of groundnut lines evaluated for two seasons under drought stress in eastern Uganda

Source	DF	KY	POD	HSW	SP	SL	SD	SL/SD
SET 1								
GCAf	4	637.47	1325.89	1658.15	113.45	0.56	0.03	0.40
GCAm	4	490.38	266.94	103.11	90.71	0.08	0.01	0.07
SCAmf	16	1438.75	938.72	48.61	187.32	0.06	0.00	0.12
2GCA		4511.40	6371.28	7045.06	816.62	2.55	0.16	1.89
SGCA+SCA		27531.41	21390.74	7822.80	3813.77	3.57	0.19	3.74
R.I = (2GCA/2GCA +SCA)		0.16	0.30	0.90	0.21	0.71	0.84	0.50
GCAf/GCAm		1	5	16	1	7	5	6
Significance of maternal effects ($P \leq 0.05$)			*	*		*	*	*
SET2								
GCAf	4	625.43	381.79	471.65	157.35	0.29	0.05	0.09
GCAm	4	841.88	994.78	239.38	147.13	0.22	0.03	0.07
SCAmf	16	1440.61	608.04	459.46	68.19	0.20	0.09	0.11
2GCA		5869.23	5506.27	2844.11	1217.94	2.06	0.31	0.64
2GCA+SCA		28918.91	15234.91	10195.40	2308.96	5.25	1.73	2.41
R.I = (2GCA/2GCA +SCA)		0.20	0.36	0.28	0.53	0.39	0.18	0.27
GCAf/GCAm		1	0	2	1	1	2	1
Significance of maternal effects ($P \leq 0.05$)								
SET 3								
GCAf	4	6945.46	1181.67	2830.92	4500.62	0.28	0.20	3.92
GCAm	4	2224.62	910.65	1809.62	2300.14	0.42	0.04	0.07
SCAmf	16	827.57	350.63	1459.07	3128.83	0.23	0.02	0.13
2GCA		36680.31	8369.29	18562.16	27203.05	2.79	0.96	15.94
2GCA+SCA		49921.44	13979.45	41907.24	77264.32	6.45	1.33	18.09
R.I = (2GCA/2GCA +SCA)		0.73	0.60	0.44	0.35	0.43	0.72	0.88
GCAf/GCAm		3	1	2	2	1	5	58
Significance of maternal effects ($P \leq 0.05$)								*

GCAf = general combining ability due to females, GCAm = general combining ability due to male parents, DF = degrees of freedom; R.I = relative importance; KY= kernel yield; POD = no. of pods; HSW = hundred seed weight; SP = shelling percentage; SL = seed length; SD = seed diameter; SL/SD = seed length-width ratio; 2GCA/(2GCA+SCA) = relative importance ratio (Baker, 1978)

6.3.3 Association of seed physical traits with drought tolerance traits under drought stress

The results of association analysis among the seed physical and drought tolerance traits under drought stress are presented in Table 6.11. Positive but low associations were found for drought tolerance with seed physical traits. The SCMR1 (SP, HSW, SL, SL/SD), DTI (PY) (HSW and SD), HI (SP, HSW and SD), days to flowering (HSW, SP and SL/SD). Significant but negative associations between the drought tolerance traits and physical traits in groundnut were observed for DTI (PY) (SP:

$r = -0.16$; $P \leq 0.01$; SL: $r = -0.16$, $P \leq 0.01$ and SL/SD: $r = -0.22$, $P \leq 0.001$). The HI was negatively correlated to SP ($r = -0.23$, $P \leq 0.001$), SL ($r = -0.23$; $P \leq 0.001$), and SD ($r = 0.15$; $P \leq 0.01$). Days to 50% flowering was positively associated with most of the physical grain traits, except HSW and SD which were negative and non-significant

Shelling percentage (SP) had non-significant, but negative associations with most of the seed physical traits except, SD. The hundred seed weight (HSW) was positively associated with all traits except SP and SL/SD which were negative and non-significant.

Positive associations were observed among all physical traits with pod yield, except PY and SP ($r = -0.19$, $P \leq 0.001$), PY and SL ($r = -0.18$, $P \leq 0.01$) and PY and SL/SD ($r = -0.21$, $P \leq 0.001$). The KY and SL/SD were negatively associated ($r = -0.21$, $P \leq 0.001$).

Table 6.11 Pearson's correlation coefficients showing association of PY, DTI (PY), SCMR, KY, HSW, PH, Days, SP, SL, SD, SL/SD and HI for 75 F₂ family lines tested under drought stress for two seasons in eastern Uganda

	SCMR	DTI(PY)	HI	Days	PH	PY	KY	SP	HSW	SL	SD	SL/SD
SCMR	-											
DTI(PY)	-0.28 ***	-										
HI	-0.18 **	0.43 ***	-									
Days	0.12 *	-0.19 ***	-0.22 ***	-								
PH	-0.35 ***	0.48 ***	0.20 ***	-0.27 ***	-							
PY	-0.27 ***	0.64 ***	0.44 ***	-0.11 ***	0.35 ***	-						
KY	-0.23 ***	0.57 ***	0.29 ***	-0.04 ***	0.50 ***	0.37 ***	-					
SP	0.02	-0.16 **	-0.23 ***	0.05 ***	-0.04 ***	-0.19 ***	0.19 ***	-				
HSW	0.04	0.01	0.00	-0.01	0.06	0.02	0.12 *	-0.00	-			
SL	0.24 ***	-0.16 **	-0.23 ***	0.18 *	-0.02	-0.18 **	0.00	-0.07	0.17 **	-		
SD	-0.03	0.13 *	0.15 *	-0.04 **	0.19	0.12 *	0.39 ***	0.09	0.29 ***	0.15	-	
SL/SD	0.25 ***	-0.22 ***	-0.29 ***	0.17 *	-0.12 *	-0.21 ***	-0.20 ***	-0.11 ***	-0.01	0.84 ***	-0.37 ***	-

Significance levels: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; SCMR = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 days after sowing; HI = harvest index; Days = days to 50% flowering; PH = plant height (cm); PY = pod yield (g/m²); KY = kernel yield (g/m²); SP = shelling percentage; HSW = hundred seed weight (g); SL (cm) = seed length (cm); SD = seed width (cm); SL/SD = seed length-width ratio; DTI (PY) = drought tolerance index based on pod yield.

6.3.4 Gene action controlling the physical quality traits under non-drought stress

Under non-drought stress environment, the mean squares due to general combining ability (GCAf) were significant ($P \leq 0.05$ to $P \leq 0.001$) for HSW, SL, SD and SL/SD (Table 6.12). The mean squares due to GCAm were not significant for all traits. On the other hand, the mean squares due to SCA differed significantly ($P \leq 0.05$ to $P \leq 0.001$) for HSW, SL, SD and SL/SD. In addition, all interactions, GCAm x environment, GCAf x environment and of SCA x environment were not significant ($P > 0.05$) for all the traits. However, the sets were significantly different ($P \leq 0.001$) for all traits.

In general, both GCA and SCA effects were relevant in the genetic control of physical quality traits. This is also reflected by the relative importance ratios ranging from 0.29 to 0.63 (Table 6.12). With the exception of SL/SD, all other traits showed predominance of non-additive gene effects. However, across sets, the relative importance of additive and non-additive gene control varied depending on the traits. In set 1, similar to results under drought stress, HSW, SL, SD and SL/SD showed additive genetic control. Of the remaining traits, POD and SP revealed non-additive gene action. In set 3, all traits showed predominance of non-additive gene control except SL/SD. Also, similar to results under drought stress, the gene action under set 2 was predominantly non-additive.

This study revealed evidence of maternal effects on some traits although the significance of these varied. Under non-drought stress, maternal effects were only significant for SL/SD ratio (Table 6.12). Across sets (Table 6.13), GCAf by GCAm ratios indicated the presence of maternal effects although the significance of these ratios varied with traits and sets. In set 1, only HSW, SL and SD had significant ($P \leq 0.05$) maternal influences. Just like under drought stress, in set 2, maternal effects were not significant for all traits. Similarly, in set 3, only SL/SD ratio showed significant cytoplasmic influence.

Table 6.12 Summary of mean squares and significant tests of combining ability effects for HSW, SP, SL, SD and SL/SD of groundnut lines evaluated under non-drought stress for two seasons in eastern Uganda

Source	DF	HSW		SP		SL		SD		SL/SD	
SET	2	2284.87 ***		10839.21 ***		2.464 ***		0.180 ***		0.950 ***	
LOC	1	239.16 *		2415.02 **		0.031		0.009		1.189 **	
Rep(LOC)	2	129.67		1.62		0.003		0.018 *		0.349	
FEM(SET)	12	179.84 ***		170.24		0.184 ***		0.024 ***		0.769 ***	
MALE(SET)	12	80.95		482.58		0.048		0.010		0.140	
FEM*MALE(SET)	48	81.58 **		404.99		0.069 **		0.012 **		0.144	
LOC*SET	2	6.40		1575.19 *		0.026		0.003		0.368	
LOC*FEM(SET)	12	50.15		434.50		0.047		0.010		0.160	
LOC*MALE(SET)	12	73.25		135.97		0.029		0.013		0.104	
LOC*FEM*MALE(SET)	48	44.75		297.04		0.044		0.012 *		0.094	
Pooled Error	150	47.49		386.25		0.037		0.006 ***		0.136	
R.I = GCA/(GCA+SCA)		0.44		0.29		0.46		0.43		0.63	
Contribution of GCAf (%)		13.7		2.7		15.3		12.7		30.7	
Contribution of GCAm (%)		6.2		7.7		4.0		5.1		5.6	
Maternal effects ($P \leq 0.05$)										*	

Significance levels: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; DF = Degrees of freedom; LOC = Season; GCAf = general combining ability due to females, GCAm = general combining ability due to male parents; HSW = hundred seed weight (g), SP = shelling percentage; SL = seed length; SD = seed width and SL/SD = seed length-width ratio; 2GCA/(2GCA+SCA) = relative importance ratio (Baker, 1978)

Table 6.13 Summary mean squares, relative importance ratio and significance tests of maternal effects for KY, POD, HSW, SP, SL, SD, and SL/SD of groundnut lines evaluated under non-drought stress for two seasons in eastern Uganda

Source	DF	KY	POD	HSW	SP	SL	SD	SL/SD
SET 1								
GCAf	4	365.69	1169.58	343.67	265.95	0.45	0.04	0.43
GCAm	4	347.62	778.34	34.31	725.59	0.07	0.01	0.12
SCAmf	16	344.66	722.86	73.59	382.53	0.04	0.00	0.09
2GCA		2853.26	7791.69	1511.92	3966.17	2.11	0.18	2.17
2GCA+SCA		8367.81	19357.46	2689.28	10086.61	2.71	0.26	3.54
R.I = (2GCA/2GCA +SCA)		0.34	0.40	0.56	0.39	0.78	0.70	0.61
GCAf/GCAm		1	2	10	0	6	6	4
Significance of maternal effects (P≤0.05)				*		*	*	
SET2								
GCAf	4	2378.74	401.09	109.20	126.90	0.04	0.01	0.20
GCAm	4	1014.63	1453.24	179.14	345.37	0.01	0.01	0.07
SCAmf	16	2393.67	1371.07	75.02	230.65	0.05	0.01	0.06
2GCA		13573.46	7417.29	1153.36	1889.07	0.22	0.09	1.10
2GCA+SCA		51872.13	29354.39	2353.68	5579.48	1.08	0.29	2.03
R.I = (2GCA/2GCA +SCA)		0.26	0.25	0.49	0.34	0.20	0.31	0.54
GCAf/GCAm		2	0	1	0	4	1	3
Significance of maternal effects (P≤0.05)								
SET 3								
GCAf	4	425.15	695.46	86.64	117.87	0.05	0.02	1.70
GCAm	4	94.74	247.90	29.38	376.78	0.06	0.01	0.24
SCAmf	16	641.48	624.47	96.15	601.79	0.12	0.02	0.32
2GCA		2079.54	3773.44	464.10	1978.58	0.46	0.13	7.74
2GCA+SCA		12343.25	13764.95	2002.45	11607.19	2.30	0.38	11.85
R.I = (2GCA/2GCA +SCA)		0.17	0.27	0.23	0.17	0.20	0.34	0.65
GCAf/GCAm		4	3	3	0	1	2	7
Significance of maternal effects (P≤0.05)								*

Significance levels: *p≤0.05; GCAf = general combining ability due to females, GCAm = general combining ability due to male parents, Df = degrees of freedom; R.I = relative importance; KY = kernel yield; POD = number of pods; HSW = hundred seed weight; SP = shelling percentage; SL = seed length; SD = seed width and SL/SD = seed length to width ratio; 2GCA/(2GCA+SCA) = relative importance ratio (Baker, 1978)

6.3.5 Association of seed physical traits with drought tolerance traits under non-drought stress

Results of the association analysis of the seed physical and drought tolerance traits are presented in Table 6.14. The SCMR was significantly and positively associated with most physical traits in groundnut, except, SD, SL, and SL/SD but negatively associated with SP (r = - 0.01). The HI was negatively associated with SL (r = - 0.23, P≤0.001) and SL/SD (- 0.17, P≤ 0.01). Days to 50% flowering were positively associated with most physical traits except, SP.

The physical traits in groundnut were positively associated with each other with a few exceptions, such as SP and SL and HSW and SL/SD, which were negative but non-significant, SP and SL/SD ($r = -0.14$, $P \leq 0.05$), and SD and SL/SD ($r = -0.30$, $P \leq 0.001$).

Positive and significant associations were revealed for all yield traits (PY, KY and POD) and physical traits although a few exceptions were also noted such as KY and SL/SD and POD and SL/SD, which were negative but non-significant.

Table 6.14 Pearson's correlation coefficients showing association of pod yield, SCMR, HI, Days, PH, PY, KY, POD, SP, HSW, SL, SD, SL/SD for 75 F₂ family lines evaluated under non-drought stress for two seasons in eastern Uganda

	SCMR	HI	Days	PH	PY	KY	POD	SP	HSW	SL	SD	SL/SD
SCMR	-											
HI	0.02	-										
Days	0.13	*	-0.07									
PH	-0.09	-0.16	**	-0.28	***							
PY	0.21	***	0.28	***	0.23	***	-0.16	*				
KY	0.17	**	0.21	***	0.14	*	-0.31	***	0.70	***		
POD	0.23	***	0.15	**	0.20	***	-0.09	***	0.65	***	0.57	***
SP	-0.01	0.00	-0.06		-0.17	**	-0.26	***	-0.17	**	0.52	***
HSW	0.19	***	0.05		0.16	*	-0.23	***	0.39	***	0.43	***
SL	0.08	-0.23	***	0.16	**	0.09	0.22	***	0.15	**	0.19	***
SD	0.06	-0.10	0.17	**	-0.04	0.27	***	0.30	***	0.34	***	0.43
SL/SD	0.04	-0.17	**	0.05	0.14	*	0.04	-0.08	-0.14	*	-0.02	0.64
											***	***

Significance levels: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; SCMR = SPAD (Soil plant analysis development) chlorophyll meter reading at 80 days after sowing; HI = harvest index; Days = days to 50% flowering; PH = plant height (cm); PY = pod yield (g/m²); KY = kernel yield (g/m²); POD = no. of pods per m²; SP = shelling percentage; HSW = hundred seed weight (g); SL = seed length (cm); SD = seed width (cm); SL/SD = seed length to width ratio.

6.3.6 General combining ability effects

Estimates of the GCA effects for the 30 parents under drought and non-drought stress are presented in Table 6.15 and Table 6.16. The parents ICG 14705, ICG 7243, and BJ were good general combiners for both yield and physical quality traits.

Under drought stress (Table 6.15) environment, the parents which possessed good GCA effects for the traits included; S6T (KY, HSW, SL, SD and SL/SD) among the female parents, and ICG 14705 (HSW, SP, SD and SL/SD) and ICG 12988 (KY, SL SL/SD) among the male parents in set 1. Parents S5R (POD, and SD), and IGOLA (SL and SL/SD) were the best combiners among the female parents in set 2, while ICG 7243 (HSW, SP, SL, SD, and SL/SD) and ICGVSM 3590 (KY, POD, SL and SL/SD) were good combiners among the male parents in the same set. For Set 3, the best female combiners included ICGVSM 93541 (HSW and SD), and BJ (SL, SD and SL/SD), while ICGVSM 95731 (KY, HSW and SL/SD), and ICGVSM 95526 (POD, SD and SL/SD) were best combiners among the male parents in the same set.

Under non-drought stress (Table 6.16) environment, the parents which possessed good GCA for physical and yield traits under study included J11 (POD, KY, HSW, SL, SD and SL/SD) among the female parents and ICG 14705 (KY, HSW, SL, SD and SL/SD) and ICGVSM2501 (KY, SP, SL and SD) among the male parents in set 1. Parents S5R (KY, POD, SL and SL/SD) and SIR (HSW, SP, and SL/SD) were the best combiners among female parents in set 2, while ICG 7243 (KY, POD, SP and SL/SD), ICGVSM 3590 (HSW, SP and SD) and ICGVSM 05701 (HSW, SP and SD) were good combiners among the male parents in the same set. For Set 3, the best female combiner was BJ (KY, POD, HSW and SP), while SALLA (POD, HSW, and SP), and ICGGVSM 95526 (SP, SL, SD and SL/SD) were the best combiners among the male parents in the same set.

The genotypes KJ and ICGVSM 2501 in Set 1; Magoro DT and Tifton 8 in set 2; and Gambia in set 3 were associated with low GCA effects for physical traits under drought stress environment. Genotypes KJ and Oluk-Oluk in set 1 were poor general combiners for all traits investigated under non-drought environment. Parents KJ, Magoro_DT, Gambia and Oluk-Oluk are popular local groundnut cultivars grown by farmers in western and northern regions of Uganda.

Table 6.15 Estimates of general combining ability (GCA) effects and mean performance for KY, POD, HSW, SP, SL, SL/SD for 75 F₂ groundnut families evaluated under drought stress across two seasons in eastern Uganda.

Parents	GCA						
	KY	POD	HSW	SP	SL	SD	SL/SD
SET 1							
Female							
S4T	-0.29	2.22	-1.66	0.07	-0.02	-0.01	-0.01
S6T	1.36	-1.62	3.54	** 0.01	0.06	0.02	* 0.04
ICG 12991	-1.44	0.71	-1.86	0.01	-0.05	-0.01	-0.05
J11	-1.21	-2.62	1.00	0.28	0.03	0.01	0.03
KJ	1.58	1.30	-1.03	-0.38	-0.01	-0.01	-0.01
Male							
ICG 9418	0.95	0.95	-0.26	-0.12	-0.01	0.00	-0.02
ICG 12988	1.66	0.25	0.38	0.05	0.02	0.00	0.02
ICG 14705	-1.24	-1.52	0.54	0.29	0.01	0.00	0.01
Oluk-Oluk	-0.65	0.04	0.22	-0.04	0.00	0.00	0.00
ICGVSM2501	-0.72	0.29	-0.87	-0.18	-0.02	-0.01	-0.01
SE	6.93	5.34	1.35	3.06	0.06	0.01	0.07
SET 2							
Female							
S5R	1.03	1.46	-0.55	0.96	0.01	0.01	0.02
S1R	1.12	0.61	0.58	1.07	0.02	0.01	0.02
IGOLA	-1.65	-1.30	0.75	-0.10	0.03	0.01	0.03
S11T	0.91	0.04	1.09	0.56	0.00	0.00	0.01
MAGORO-DT	-1.41	-0.81	-1.87	-2.48	-0.05	-0.02	-0.09
Male							
TIFTON 8	-2.41	-2.87	-0.72	-1.70	-0.03	-0.01	-0.07
ICG 7243	0.37	-0.05	1.11	1.04	0.04	0.01	0.03
ICGVSM 05701	0.58	0.90	0.09	0.89	0.00	0.00	0.00
S10T	-0.52	-0.25	-0.99	-0.11	-0.02	-0.01	0.01
ICGVSM 3590	1.99	2.27	0.50	-0.12	0.01	0.01	0.03
SE	7.32	5.69	3.36	2.96	0.09	0.05	0.09
SET 3							
Female							
Red Beauty	2.41	1.28	-0.85	-0.10	-0.01	0.01	-0.07
Gambia	0.06	-1.04	-1.73	-0.17	-0.04	0.00	-0.07
ICGVSM 93541	2.01	0.04	4.48	-0.08	0.00	0.02	-0.06
BJ	-8.02	-2.77	-3.16	0.66	0.04	-0.04	0.23
JL 24	3.55	2.49	1.26	-0.31	0.01	0.01	-0.03
Male							
ICG 10890	-0.14	-0.65	-0.14	-0.17	0.01	0.01	-0.01
ICG 6766	0.76	-0.17	-0.52	-0.33	0.03	0.01	0.02
SALLA	-4.45	-2.52	-2.86	0.49	-0.06	-0.02	-0.02
ICGVSM 95731	2.11	1.22	3.75	-0.14	0.00	-0.01	0.02
ICGVSM 95526	1.72	2.12	-0.23	0.14	0.02	0.01	0.00
SE	6.73	4.81	8.72	14.60	0.10	0.04	0.07

Significance levels: * $p \leq 0.05$; ** $p \leq 0.01$; KY = kernel yield; POD = no. of pods; SP = shelling percentage; HSW = hundred seed weight; SL = seed length; SD = seed width; SL/SD = seed length-width ratio; GCA = general combining ability; SE = standard error.

Table 6.16 Estimates of general combining ability (GCA) effects and mean performance for POD, KY, HSW, SP, SL, SD and SL/SD of 75 F2 groundnut families evaluated under non-drought stress across two seasons in eastern Uganda.

Parents	GCA						
	POD	KY	HSW	SP	SL	SD	SL/SD
SET 1							
Female							
S4T	-0.24	-1.32	-0.73	-1.08	-0.03	0.00	-0.03
S6T	1.11	0.29	0.81	0.11	0.03	0.01	0.01
ICG 12991	-1.18	-0.50	-1.20	-0.62	-0.03	-0.01	-0.03
J11	2.60	1.58	1.28	0.30	0.05	0.01	0.06
KJ	-2.28	-0.05	-0.17	1.29	-0.02	-0.01	-0.01
Male							
ICG 9418	-2.13	-1.75	-0.07	-2.34	0.01	0.00	0.02
ICG 12988	2.00	0.29	0.26	0.52	-0.02	0.00	-0.03
ICG 14705	-0.18	0.31	0.41	0.24	0.02	0.00	0.02
Oluk-Oluk	0.90	0.11	-0.38	-0.22	-0.01	-0.01	0.00
ICGVSM2501	-0.59	1.05	-0.22	1.79	0.01	0.01	0.00
SE	4.23	2.53	1.52	3.48	0.03	0.02	0.05
SET 2							
Female							
S5R	1.62	2.22	0.23	-0.39	0.02	0.00	0.03
S1R	0.29	0.69	0.57	0.79	0.00	-0.01	0.01
IGOLA	0.12	-0.59	-0.50	-0.69	-0.02	0.01	-0.04
S11T	-0.67	2.10	0.44	0.53	0.00	-0.01	0.00
MAGORO-DT	-1.36	-4.42	-0.74	-0.24	0.01	0.00	0.00
Male							
TIFTON 8	-2.48	-1.99	-1.02	-1.80	-0.01	0.00	0.01
ICG 7243	3.38	2.31	-0.31	0.36	0.00	-0.01	0.02
ICGVSM 05701	-0.70	-0.82	0.42	0.61	0.00	0.00	0.00
S10T	0.07	1.39	-0.06	0.08	0.01	0.01	-0.01
ICGVSM 3590	-0.28	-0.89	0.97	0.75	-0.01	0.00	-0.02
SE	6.03	7.55	1.92	4.14	0.05	0.02	0.07
SET 3							
Female							
Red Beauty	0.21	-0.23	0.23	-0.15	0.01	-0.01	-0.07
Gambia	-1.17	0.17	0.57	0.04	-0.01	0.06	**
ICGVSM 93541	-0.05	-0.83	-0.50	-0.83	0.00	0.02	-0.05
BJ	2.34	1.86	0.44	0.87	-0.02	0.04	*
JL 24	-1.33	-0.98	-0.74	0.06	0.02	-0.10	0.15
Male							
ICG 10890	0.55	0.09	0.09	-0.85	-0.01	0.04	*
ICG 6766	0.70	-1.04	0.18	-1.36	-0.01	0.04	*
SALLA	-1.14	0.48	0.34	0.81	-0.01	0.01	-0.04
ICGVSM 95731	-0.76	0.02	-0.42	0.18	0.01	-0.04	-0.17
ICGVSM 95526	0.65	0.45	-0.19	1.21	0.02	0.07	**
SE	5.03	3.61	1.07	5.30	0.04	0.02	0.12

Significance levels: * $p \leq 0.05$; ** $p \leq 0.01$; KY=kernel yield; POD = no. of pods per m², SP = shelling percentage, HSW = hundred seed weight; SL = seed length; SD = seed width; SL/SD = seed length-width ratio; GCA = general combining ability; SE = standard error.

6.3.7 Specific combining ability effects for the crosses

Specific combining ability effects for crosses under drought and non-drought conditions are presented in Table 6.17 and Table 6.18.

Under drought stress (Table 6.17), the following crosses had high SCA effects for various traits; S4T x ICG 9418 and S6T x ICGVSM 2501 had high SCA effects for KY, POD and SD. The cross S6T x ICG 14705 had high SCAs for HSW and SD. The cross 12991 x 12988 had high SCA effect for SL and SL/SD in set 1. In set 2, S11T x Tifton 8 had significant and high SCA effects for all traits under study. The cross S5R x Tifton 8 had high SCA for KY, SP and SD. In set 3, Gambia x ICG 6766 had high SCA effect for KY, POD, HSW, SP. ICGVSM 93541 x SALLA had high SCA for KY, SP, SL and SL/SD. Cross RB x SALLA had high SCA for HSW, SL, SD and SL/SD.

Under non-drought stress (Table 6.18), the crosses with high SCA effects included; S4T x ICG 14705 and S6T x ICG 9418 for POD, KY, SL, SD and SL/SD. Cross S4T x 9418 had high SCA effects for KY, POD, SL and SL/SD in set 1. Cross S11T x ICGVSM 3590 had high SCA effects for POD, HSW, SL, SD and SL/SD. Cross Igola x ICG 7243 had high SCA effects for KY, SP and SD in set 2. In set 3, the cross JL 24 x ICG 10890 had high SCA effects for POD, HSW and SD. Cross JL 24 x ICG 6766 had high SCA effects for POD, KY and HSW. Cross RB x 95731 had high SCA effect for SP, SD and SL/SD, while cross Red beauty x ICGVSM 95731 had high SCA effect for SP, HSW, KY and POD

Table 6.17 Estimates of specific combining ability effects (SCA) and mean performance for KY, POD, HSW, SP, SL, SD, and SL/SD of groundnut F₂ families evaluated under drought stress in three sets across two seasons in eastern Uganda

Genotype (cross)			SCA						
			KY	POD	HSW	SP	SL	SD	SL/SD
SET 1									
S4T	X	ICG 9418	10.46	7.77	0.84	1.52	0.02	0.01	0.01
S4T	X	ICG 12988	-1.22	-1.04	-0.17	0.75	0.00	0.00	0.00
S4T	X	ICG 14705	-3.86	-4.40	-0.95	-0.14	-0.01	-0.01	0.00
S4T	X	ICG Oluk-luk-A	1.36	1.49	0.04	-0.04	0.01	0.00	0.02
S4T	X	ICGVSM2501	-6.74	-3.82	0.25	-2.09	-0.02	0.00	-0.04
S6T	X	ICG 9418	-3.28	-2.15	-0.75	-2.76	-0.04	-0.01	-0.04
S6T	X	ICG 12988	-1.52	-2.07	-0.04	0.83	-0.02	0.00	-0.03
S6T	X	ICG 14705	-0.04	-1.44	1.18	1.28	0.00	0.01	-0.01
S6T	X	ICG Oluk-luk-A	0.43	0.64	0.25	0.20	0.01	0.00	0.01
S6T	X	ICGVSM2501	4.42	5.02	-0.65	0.45	0.04	-0.01	0.06
ICG12991	X	ICG 9418	-4.23	-2.47	0.19	0.35	0.00	0.00	0.00
ICG12991	X	ICG 12988	0.31	0.98	0.23	0.73	0.05	-0.01	0.07
ICG 12991	X	ICG 14705	4.32	3.74	-0.01	-3.09	-0.02	0.00	-0.02
ICG12991	X	ICG Oluk-luk-A	-0.15	0.49	-0.36	0.10	-0.01	0.00	0.00
ICG12991	X	ICGVSM2501	3.23	1.88	0.42	2.06	-0.01	0.00	-0.02
J11	X	ICG 9418	-6.94	-5.40	-1.72	0.15	-0.04	-0.01	-0.04
J11	X	ICG 12988	3.32	3.05	0.03	-2.50	0.01	0.00	0.01
J11	X	ICG 14705	2.50	2.57	0.54	1.29	0.02	0.00	0.02
J11	X	ICG Oluk-luk-A	1.53	0.64	0.96	-0.50	-0.02	0.00	-0.03
J11	X	ICGVSM2501	-0.40	-0.86	0.19	1.57	0.03	0.00	0.04
KJ	X	ICG 9418	2.50	2.57	0.54	1.29	0.02	0.00	0.02
KJ	X	ICG 12988	-0.89	-0.92	-0.05	0.19	-0.04	0.00	-0.06
KJ	X	ICG 14705	-2.92	-0.47	-0.76	0.66	0.01	-0.01	0.02
KJ	X	ICG Oluk-luk-A	0.32	1.35	-0.42	0.39	0.01	0.00	0.02
KJ	X	ICGVSM2501	-0.51	-2.21	-0.21	-1.99	-0.03	0.01	-0.04
SE			15.50	11.93	3.02	6.84	0.13	0.02	0.15
SET 2									
S5R	X	TIFTON 8	2.79	1.26	0.78	4.58	0.04	0.05	0.03
S5R	X	ICG7243	0.24	2.57	-2.28	-0.81	-0.04	-0.02	-0.04
S5R	X	ICGVSM05701	-4.37	-6.39	2.04	-1.45	0.05	0.01	0.01
S5R	X	S10T	-0.55	1.45	-0.41	-1.17	0.00	0.01	-0.05
S5R	X	ICGVSM3590	1.89	1.11	-0.12	-1.15	-0.05	-0.04	0.05
S1R	X	TIFTON 8	-1.99	-1.40	0.43	2.04	0.01	0.01	0.05
S1R	X	ICG7243	-2.81	-1.90	-1.71	-0.24	-0.03	-0.03	0.01
S1R	X	ICGVSM05701	1.18	1.33	-0.89	-0.96	0.00	0.00	-0.01
S1R	X	S10T	1.23	-0.07	0.99	0.08	0.02	0.01	-0.02
S1R	X	ICGVSM3590	2.39	2.04	1.18	-0.93	0.01	0.01	-0.03
IGOLA	X	TIFTON 8	-3.80	-1.34	-1.69	0.83	-0.02	-0.03	0.11
IGOLA	X	ICG7243	0.86	0.07	-0.31	-0.53	0.00	-0.01	0.01
IGOLA	X	ICGVSM05701	3.17	1.12	2.84	-0.57	0.04	0.02	0.00
IGOLA	X	S10T	0.49	1.27	0.65	0.66	-0.03	0.02	-0.10
IGOLA	X	ICGVSM3590	-0.71	-1.13	-1.5	-0.4	0.00	0.00	-0.02
S11T	X	TIFTON 8	9.87	5.49	4.76	3.14	0.08	0.05	0.06
S11T	X	ICG7243	-0.65	-1.64	2.03	-1.27	0.03	0.03	-0.04
S11T	X	ICGVSM05701	-7.74	-1.56	-5.43	0.61	-0.12	-0.07	-0.03
S11T	X	S10T	-1.17	-2.00	-1.67	-2.89	-0.02	-0.02	0.02
S11T	X	ICGVSM3590	-0.31	-0.28	0.31	0.41	0.03	0.02	-0.02
MAGORO-DT	X	TIFTON 8	-6.86	-4.01	-4.28	-	-0.11	-0.07	-
MAGORO-DT	X	ICG7243	2.34	0.90	2.27	2.85	0.04	0.03	0.06
MAGORO-DT	X	ICGVSM05701	7.77	5.50	1.44	2.37	0.03	0.03	0.03
MAGORO-DT	X	S10T	0.01	-0.65	0.44	3.31	0.03	-0.01	0.14
MAGORO-DT	X	ICGVSM3590	-3.26	-1.74	0.13	2.07	0.01	0.02	0.02
SE			16.40	12.73	7.51	6.62	0.20	0.11	0.20

Table 6.17: Continued.

Genotype (cross)			SCA						
			KY	POD	HSW	SP	SL	SD	SL/SD
SET 3									
RB	X	ICG 10890	0.41	-0.45	0.84	-0.09	-0.03	-0.01	0.00
RB	X	ICG6766	-4.57	-3.62	-0.11	1.16	-0.08	-0.01	-0.07
RB	X	SALLA	0.18	-0.64	2.26	-3.88	0.07	0.01	0.04
RB	X	ICGVSM95731	2.66	2.49	-3.23	0.81	0.03	0.01	0.01
RB	X	ICGVSM95526	1.32	2.22	0.25	2	0.00	0.01	0.01
GAMBIA	X	ICG 10890	-0.81	0.99	0.84	-0.46	0.02	0.01	0.01
GAMBIA	X	ICG6766	7.31	4.20	2.27	2.78	0.02	0.01	0.02
GAMBIA	X	SALLA	-6.55	-4.04	-1.29	-5.3	-0.10	-0.03	-0.08
GAMBIA	X	ICGVSM95731	2.40	0.19	-2.43	2.25	0.05	0.02	0.01
GAMBIA	X	ICGVSM95526	-2.35	-1.33	0.62	0.73	0.01	0.00	0.03
ICGVSM93541	X	ICG 10890	-2.43	-1.84	-4.4	-7.39	-0.01	0.00	0.00
ICGVSM93541	X	ICG6766	-1.41	0.81	-3.87	-4.08	-0.02	0.00	-0.01
ICGVSM93541	X	SALLA	3.97	1.04	-2.83	21.2	0.07	0.01	0.06
ICGVSM93541	X	ICGVSM95731	-3.09	-2.40	14.9	-6.01	0.01	0.01	-0.01
ICGVSM93541	X	ICGVSM95526	2.95	2.40	-3.79	-3.72	-0.05	-0.01	-0.04
BJ	X	ICG 10890	1.86	0.29	2.27	9.82	0.00	0.02	-0.09
BJ	X	ICG6766	-0.89	-1.13	0.9	-2.41	0.08	0.02	0.02
BJ	X	SALLA	3.18	3.06	0.82	-6.04	-0.05	0.01	0.01
BJ	X	ICGVSM95731	-1.38	0.13	-5.37	0.26	-0.09	-0.05	0.03
BJ	X	ICGVSM95526	-2.77	-2.35	1.38	-1.62	0.07	0.01	0.03
JL24	X	ICG 10890	0.96	1.02	0.45	-1.88	0.03	-0.01	0.07
JL24	X	ICG6766	-0.44	-0.27	0.81	2.56	0.00	-0.01	0.03
JL24	X	SALLA	-0.79	0.59	1.05	-5.98	0.01	0.01	-0.03
JL24	X	ICGVSM95731	-0.59	-0.41	-3.84	2.69	0.01	0.01	-0.03
JL24	X	ICGVSM95526	0.86	-0.93	1.54	2.61	-0.04	0.00	-0.04
SE			15.04	10.75	19.5	32.64	0.21	0.08	0.16

Significance levels: * $p \leq 0.05$; ** $p \leq 0.01$; KY= kernel yield; POD = No. of pods per m^2 , SP = shelling percentage, HSW = hundred seed weight; SL = seed length; SD = seed width; SL/SD = seed length-width ratio; SCA = specific combining ability; SE = standard error

Table 6.18 Estimates of specific combining ability effects (SCA) and mean performance for POD, KY, HSW, SP, SL, SD, and SL/SD of 75 F₂ groundnut families evaluated under non-drought stress across two seasons in eastern Uganda.

Genotype (Cross)			SCA						
			POD	KY	HSW	SP	SL	SD	SL/SD
SET 1									
S4T	X	ICG 9418	-2.33	-0.75	-0.29	0.46	-0.02	0.01	-0.05
S4T	X	ICG 12988	-5.04	-3.17	-1.58	-2.32	0.03	-0.01	0.06
S4T	X	ICG 14705	5.80	3.74	0.89	0.97	0.02	0.01	0.00
S4T	X	Oluk-luk-A	-0.47	-1.54	-1.45	-0.47	-0.02	-0.02	0.02
S4T	X	ICGVSM2501	2.04	1.72	2.43	1.37	0.00	0.01	-0.03
S6T	X	ICG 9418	4.05	2.25	0.70	2.17	0.02	0.00	0.03
S6T	X	ICG 12988	-0.13	1.72	-0.26	2.32	-0.03	0.00	-0.04
S6T	X	ICG 14705	-1.90	-2.06	-0.09	-1.75	-0.01	0.00	0.00
S6T	X	Oluk-luk-A	0.44	1.55	0.56	-0.15	0.00	0.01	-0.02
S6T	X	ICGVSM2501	-2.46	-3.46	-0.91	-2.59	0.01	0.00	0.03
ICG12991	X	ICG 9418	-1.00	-0.19	0.37	-0.82	-0.02	-0.01	-0.01
ICG12991	X	ICG 12988	2.30	-0.73	0.36	-2.44	0.03	0.01	0.03
ICG12991	X	ICG 14705	0.66	-2.56	-0.89	-2.62	-0.02	0.00	-0.02
ICG12991	X	Oluk-luk-A	0.05	-0.33	-0.17	-0.33	0.00	0.00	-0.01
ICG12991	X	ICGVSM2501	1.07	2.58	-0.70	2.08	0.00	0.00	-0.01
J11	X	ICG 9418	1.40	0.31	-0.59	0.69	-0.01	0.00	-0.02
J11	X	ICG 12988	-2.11	-0.12	0.90	-0.91	0.02	0.01	0.02
J11	X	ICG 14705	0.16	1.91	0.08	2.90	-0.01	-0.01	0.00
J11	X	Oluk-luk-A	0.06	-1.22	-0.52	-1.34	0.01	0.00	0.00
J11	X	ICGVSM2501	0.48	-0.88	0.13	-1.34	0.00	0.00	0.00
KJ	X	ICG 9418	0.16	1.91	0.08	2.90	-0.01	-0.01	0.00
KJ	X	ICG 12988	4.98	2.29	0.59	3.36	-0.04	0.00	-0.07
KJ	X	ICG 14705	-4.72	-1.02	0.01	0.50	0.02	0.01	0.02
KJ	X	Oluk-luk-A	3.00	0.31	0.54	-1.85	-0.01	0.00	-0.02
KJ	X	ICGVSM2501	-1.13	0.04	-0.94	0.49	0.00	-0.01	0.01
SE			9.45	5.65	3.39	7.78	0.07	0.04	0.11

Table 6.18: Continued.

Genotype			SCA						
			POD	KY	HSW	SP	SL	SD	SL/SD
SET 2									
S5R	X	TIFTON 8	2.25	13.17	2.03	-0.10	0.01	0.02	-0.01
S5R	X	ICG7243	0.94	-4.32	-0.03	1.37	0.00	0.00	-0.01
S5R	X	ICGVSM05701	-4.48	-3.56	-1.15	-1.33	-0.02	-0.01	-0.01
S5R	X	S10T	-1.98	-5.35	-0.59	-1.54	-0.01	-0.01	0.00
S5R	X	ICGVSM3590	3.27	0.06	-0.26	1.61	0.02	0.00	0.02
S1R	X	TIFTON 8	-5.56	-5.90	-1.27	0.27	-0.04	-0.02	-0.02
S1R	X	ICG7243	3.17	4.82	-0.08	0.65	0.01	0.01	-0.02
S1R	X	ICGVSM05701	4.94	2.77	0.69	0.53	0.03	0.00	0.04
S1R	X	S10T	0.97	1.85	0.58	0.06	0.00	0.00	0.00
S1R	X	ICGVSM3590	-3.52	-3.54	0.08	-1.51	0.00	0.00	0.00
IGOLA	X	TIFTON 8	-1.46	-7.14	-0.74	-2.64	0.02	0.00	0.04
IGOLA	X	ICG7243	-4.42	6.71	0.69	2.97	0.02	0.01	-0.01
IGOLA	X	ICGVSM05701	1.99	-3.22	-0.14	-1.77	0.01	-0.01	0.02
IGOLA	X	S10T	1.48	0.94	0.21	1.07	0.01	0.00	0.01
IGOLA	X	ICGVSM3590	2.41	2.71	-0.01	0.36	-0.05	0.00	-0.06
S11T	X	TIFTON 8	-4.57	-5.50	-1.26	1.57	-0.02	-0.02	0.01
S11T	X	ICG7243	0.30	-6.21	-0.30	-2.38	-0.03	-0.02	0.02
S11T	X	ICGVSM05701	-1.40	2.45	-0.53	1.90	-0.03	0.01	-0.05
S11T	X	S10T	0.65	5.07	0.81	-1.41	0.01	0.02	-0.02
S11T	X	ICGVSM3590	5.03	4.19	1.28	0.32	0.06	0.02	0.05
MAGORO-DT	X	TIFTON 8	9.34	5.38	1.25	0.91	0.02	0.01	-0.02
MAGORO-DT	X	ICG7243	0.01	-1.01	-0.27	-2.61	0.01	0.00	0.02
MAGORO-DT	X	ICGVSM05701	-1.05	1.56	1.13	0.67	0.02	0.02	-0.01
MAGORO-DT	X	S10T	-1.11	-2.51	-1.02	1.81	-0.02	-0.02	0.01
MAGORO-DT	X	ICGVSM3590	-7.19	-3.42	-1.08	-0.79	-0.02	-0.01	0.00
		SE	13.49	16.87	4.29	9.26	0.12	0.04	0.16

Table 6.18: Continued.

Genotype			SCA						
			POD	KY	HSW	SP	SL	SD	SL/SD
SET 3									
RB	X	ICG 10890	-2.30	-2.55	-0.72	0.76	0.02	0.01	0.10
RB	X	ICG6766	-2.61	-2.03	-0.32	-2.93	0.05	0.03	0.06
RB	X	SALLA	2.24	-1.40	0.36	-3.29	-0.03	-	-
RB	X	ICGVSM95731	3.76	5.30	1.01	2.00	-0.03	-	-
RB	X	ICGVSM95526	-1.09	0.67	-0.33	3.46	-0.02	-0.01	0.07
GAMBIA	X	ICG 10890	1.63	-1.20	-0.02	-2.05	0.01	-0.07	-0.03
GAMBIA	X	ICG6766	-2.09	-2.73	-0.64	-0.26	0.07	-0.03	-0.05
GAMBIA	X	SALLA	0.71	0.87	-0.11	0.60	-0.03	-0.04	0.02
GAMBIA	X	ICGVSM95731	-2.53	0.74	0.76	2.58	-0.03	0.05	0.12
GAMBIA	X	ICGVSM95526	2.29	2.33	0.02	-0.86	-0.02	-0.02	-0.06
ICGVSM93541	X	ICG 10890	-4.15	1.28	-0.57	2.23	0.02	-0.03	0.06
ICGVSM93541	X	ICG6766	0.89	0.28	0.13	2.39	-0.02	-0.02	-0.05
ICGVSM93541	X	SALLA	0.43	3.62	0.17	-0.02	-0.02	0.04	0.03
ICGVSM93541	X	ICGVSM95731	1.58	0.00	1.46	1.37	0.02	-	-
ICGVSM93541	X	ICGVSM95526	1.25	-5.18	-1.20	-5.97	-0.01	-0.03	0.04
BJ	X	ICG 10890	1.66	-1.30	-0.33	-2.48	-0.03	0.01	-0.08
BJ	X	ICG6766	-0.51	1.44	-0.28	1.64	-0.03	-0.02	-0.06
BJ	X	SALLA	2.50	-0.88	-0.37	-0.55	-0.01	0.02	0.08
BJ	X	ICGVSM95731	-2.58	-1.30	0.19	-1.19	0.03	-	-
BJ	X	ICGVSM95526	-1.08	2.05	0.79	2.59	0.04	-0.04	0.10
JL24	X	ICG 10890	3.17	3.77	1.64	1.56	-0.03	0.08	* -0.05
JL24	X	ICG6766	4.32	3.05	1.12	-0.83	-0.07	0.04	0.10
JL24	X	SALLA	-5.88	-2.21	-0.05	3.26	0.09	0.08	* 0.06
JL24	X	ICGVSM95731	-0.23	-4.74	-3.43	-4.76	0.00	0.19	** 0.05
JL24	X	ICGVSM95526	-1.38	0.13	0.73	0.78	0.01	0.10	** -0.15
SE			11.25	8.08	2.39	11.90	0.10	0.04	0.28

Significance levels: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$, KY = kernel yield; POD = No. of pods per m^2 , SP = shelling percentage, HSW = hundred seed weight; SL = seed length; SD = seed width; SL/SD = seed length-width ratio; SCA = specific combining ability; SE = standard error.

6.4 Discussion

6.4.1 Genetic variability of yield and physical-quality traits

Genetic variability of traits is an important requisite for crop improvement, and can also be used to predict the genetic gain from selection in breeding programmes. A wide range in values of yield and physical quality traits of 75 F₂ groundnut crosses under different water regimes in this study confirm the existence of genetic variability for these traits in groundnut (John et al., 2008; Hariprisanna et al., 2008; Jean-Baptiste et al., 2012; Kumar et al., 2014; Maurya et al., 2014). The existence of this variation offers opportunity to breed for improved physical quality traits in groundnut.

Under drought stress, the physical quality traits showed low but positive correlations with drought tolerance traits such as SCMR (SP, HSW, SL, and SL/SD), drought tolerance index based on pod yield [DTI(PY) (HSW and SD)] and harvest index (SP, HSW, and SD). The DTI (PY) was negatively associated with SP, and SL/SD. The harvest index was weakly and negatively associated with SP, SL and SD. Songsri et al. (2008) reported similar results. Yield traits such as pod yield were negatively associated with SP, SL, and SL/SD under drought stress. This result agrees with those of Clavel et al. (2004) and Songsri et al. (2008).

Under non-drought stress, this study found positive and significant associations between yield traits and physical quality traits except, for SL/SD ratio. This finding agrees with studies conducted elsewhere (Roy et al., 2003; Gopal Reddy, 2008). The SCMR was weakly associated with most physical quality traits except, SD. Similarly, harvest index was weak and negatively associated with SL and SL/SD. These results corroborate with those by Songsri et al. (2009) and Girdthai et al. (2010).

This study and those of Gopal Reddy (2008) agree on the weak or negative association of drought tolerant traits with physical quality traits in groundnut. Such weak association points to the possibility of simultaneous improvement of drought tolerance and physical quality traits through enhanced seed yield under stress and non-stress conditions. Such relationship can be exploited for improving seed yield without compromising seed size. Thus, the selection of high pod yield potential under non-drought stress or a small reduction in pod under drought stress should guarantee high seed size.

This study also found the physical traits to be associated with each other regardless of drought stress treatment. This association can be utilised to improve groundnuts for physical quality traits simultaneously. This finding agrees with that of Venuprasad et al. (2011).

6.4.2 Genetic action and combining ability effects

The genetic analysis of F_2 families' data showed the importance of both additive and non-additive gene action in controlling pod yield and physical quality traits in groundnut under both drought stress and non-drought stress environments. This study revealed that under both stress and non-stress environments, there is a predominance of non-additive genetic control for HSD, SL, SD, and additive gene action for SL/SD. This result agrees with findings from several earlier studies (Dwivedi et al., 1989; Palmer et al., 2000; Vindhiyavarman, 2000; 2001; Hariprasanna et al., 2008,). However, the same findings contradict a study by Venuprasad et al. (2011), but also agrees on the gene control for only SL/SD. The authors reported predominance of additive gene action for HSW, SL, SD, and SL/SD.

The prediction of the success of a cross in a hybridization programme may be based on the *per se* performance of the parents and their respective GCA effects. The parents ICG 14705, ICG 7243 and BJ showed good mean performance for most of the physical quality traits and yield characters and were also good general combiners. Generally, the crosses involving parents J11, ICGVSM 250, S6T, ICG 12988 and ICG 14705 were good combiners among the Spanish botanical variety group. In the Virginia botanical variety group, S5R and ICG 7243 were the best combiners. BJ, SALLA, ICGVSM 95526, and ICGVSM 95731 were good combiners among the Valencia botanical variety group, with high GCA for physical quality trait and high GCA for yield related traits, though with exceptions. A few examples of crosses, such as S11T x Tifton 8, showed good performance across seasons and drought stress environment.

Under both drought and non-drought stress conditions, maternal effects were only significant for SL/SD. However, across sets, the maternal effects varied depending on water regime and traits. High and significant SCA effects were observed in crosses involving parents with large pods and seeds. These results highlight the role of maternal parent in the regulation of quality traits and thus the importance of selection of parents in breeding for quality improvement. Earlier (Dwivedi et al., 1989; Vindhiyavarman, 2000; 2001) and recent (Hariprasanna et al., 2008) experiments also showed the maternal influence on physical quality traits of groundnut. Therefore, future hybridizations should have at least one parent with large pods and seeds for obtaining better segregants for physical quality traits improvement.

6.5 Conclusions

The present study revealed the predominance of both additive and the non-additive gene control for physical as well as pod yield traits. This result implies that there is an opportunity to select for physical seed traits in early generation if traits that are under control of additive gene effects are considered. However, in situations where both additive and non-additive genes are observed, the breeding

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CHAPTER 7 General overview

Improvement of drought tolerance traits in groundnut (*Arachis hypogaea* L) is an important breeding objective, especially when targeting rain fed regions where drought is a major constraint limiting productivity and quality. However, the critical limitations including restricted access to germplasm resources, lack of access to phenotyping tools and lack of adequate information on gene action and combining ability has slowed down breeding for drought tolerance in this crop. This research was, therefore, undertaken with a view to generating information that would be useful for not only the enhancement of drought tolerance in this crop, but also for the improvement of other important agronomic traits, including yield and physical seed traits, among others. This chapter summarises the findings of the study based on the set objectives and the implication for breeding.

Farmer perception of drought, other production constraints and production system, their implication for groundnut breeding in Uganda

The major objectives of this study were, to determine how small holder farmers perceived and coped with drought and other constraints to groundnut production and, their production systems for groundnut. The key findings were as follows:

- Groundnut in Uganda is mainly grown for subsistence by small-scale farmers with land holdings of 0.4 ha, on average, under both mono and mixed cropping systems depending on the region. Groundnut and maize, or groundnut and pearl millet were the most popular crops combinations in the intercrop.
- Drought was a major production constraint although its rank among production constraints varied with location and season.
- Local perceptions of drought included hot sunny weather, and poorly distributed and little rainfall. In the eastern Uganda, most farmers (55.7%) perceived drought as warm/hot windy conditions. In the northern Uganda, most farmers (82.5%) perceived drought as little rainfall while in the mid-western Uganda, majority (48.39%) perceived drought as hot sunny weather.
- More than 77% of the farmers surveyed, indicated that the major impact of drought to their farming activity was low yields, which implies that farmers clearly understood the effects and consequences of drought.
- Drought mitigation measures used by farmers included early planting, use of drought tolerant varieties and use of short maturing varieties or simply not grow groundnut in the season associated with drought. Nonetheless, most farmers, irrespective of the region, would like drought tolerance to be bred into their preferred varieties.

Participatory varietal selection criteria for groundnut varieties in selected regions of Uganda

- The results of the farmer evaluation of selected groundnut varieties including the commonly grown or local cultivars using ITKs, revealed significant differences between the parental varieties in mean scores of traits in all districts, except for quality (greenness) of leaves, number of flowers per node, seed size, plant vigour, drought tolerance, oil content and ease of drying, implying that farmers' evaluation was able to uncover genotypic differences between varieties.
- Districts differed in variety ranking scores for most of the traits evaluated demonstrating differences in farmers' priorities, environments and/or genotype x environment interaction effects.
- Variety rankings significantly correlated with different trait scores, as measured by the breeder, in each district.
- Simple selection indices were developed for each district/region, using correlation coefficients as weightings from correlations between variety ranks, as measured by the farmers, and trait scores, as measured by the breeder
- This is the first attempt to formulate a selection index for groundnuts based on farmer preferred traits

Genome wide SNP diversity and population structure in a Ugandan groundnut (*Arachis hypogaea* L.) collection

Molecular diversity analysis of the groundnut collections revealed the following;

- Out of 2986 SNPs used, 50% were polymorphic with a mean PIC of 0.15 for all populations combined implying low allelic diversity in the groundnut collection.
- A high level of genetic relatedness at population level was observed, as individuals from all assigned populations aggregated into three clusters based on dissimilarity analysis under principal component analysis (PCA).
- A high level of genetic differentiation within individuals rather than among populations was observed based on analysis of molecular variance (AMOVA) and cluster analysis
- Based on structure analysis, three gene clusters were observed underlying genepools for the groundnut populations used in this study.

Gene action governing the inheritance of drought tolerance traits in groundnuts (*Arachis hypogaea* L.)

Genetic analysis to determine the nature of gene action controlling the inheritance of drought tolerance traits was conducted and their association with agronomic traits of groundnut was examined. The study revealed that;

- General combining ability (GCA) was more important than specific combining ability (SCA) for SPAD chlorophyll meter readings and harvest index.
- Additive gene action was predominant over non-additive gene action for these traits.
- Non-additive gene control was involved in the inheritance for some drought tolerance traits, including drought tolerance index based on pod [DTI (PY)] and biomass [DTI(BIO)], and biomass (BIO) yield.
- Under drought stress environment, genotypes ICG 12991 and ICGVSM 2501 among Spanish botanical variety; S11T, ICGVSM 05701, S11T and ICGVSM 05701 under Virginia botanical variety; and Gambia and ICGVSM 95731 among Valencia botanical variety had high GCA effects for traits that are important for drought tolerance, that is, SCMR1, pod yield and biomass.
- Under non-drought stress environment, genotypes ICG 12991 among Spanish botanical variety, S10T under Virginia botanical variety and JL 24 among Valencia botanical variety had good GCA effects for traits that are important for drought tolerance, that is, SCMR1, pod yield and biomass. These were also good combiners for pod yield.
- Under drought and non-drought conditions, SCMR was correlated with number of pods and pod yield.
- Significant associations between drought and non-drought environments were found for SCMR, harvest index, pod yield, number of pods, leaf length, and leaf width.

Gene action and inheritance of seed physical quality traits in groundnut (*Arachis hypogaea* L.)

The genetic analysis to determine the nature of gene action controlling the inheritance of physical traits in groundnut was conducted. The study revealed that;

- The expression of the majority of the physical quality traits was regulated by additive gene action, while non-additive gene action also played an equally important role in the control of seed physical traits.
- This study has for the first time reported that genetic control for physical traits also varied between botanical varieties for some traits. Among the Virginia botanical variety types, non-additive gene action was predominant for all physical quality traits regardless of the test environment.

- Significant maternal effects were observed in some traits showing the importance of parental selection in seed physical quality breeding. However, such cytoplasmic influences were not observed within the Virginia types.
- Generally, the crosses involving parents J11, ICGVSM 2501, S6T, ICG 12988 and ICG 14705 were good combiners among the Spanish botanical variety types, while for the Virginia botanical variety, S5R and ICG 7243 were the best combiners. Genotypes BJ, SALLA, ICGVSM 95526, and ICGVSM 95731 were good combiners among the Valencia botanical variety types.
- A low but positive or negative association of the drought tolerance traits with physical quality traits under both drought and non-drought environments was revealed.
- Seed yield was highly significantly and positively correlated with seed physical quality traits. Such a relationship can be exploited for improving seed yield without compromising seed size.

Breeding implications and future research outlook

The participatory rural appraisal studies showed that although drought was an important production constraint among groundnut farmers, adoption of improved drought tolerant varieties by farmers was very low. This observation highlighted the need for breeders to involve farmers in developing new varieties through the use of local varieties, and apply local farmer knowledge in defining the final selection criteria for drought improvement of their preferred groundnut varieties. This would consequently help to capture farmer preferred traits and help in enhancing the adoption of drought tolerant varieties among farmers. However, incorporating local varieties in developing new varieties could present challenges as some traits may be negatively correlated with yield or taste. It was also observed in this study that a significant proportion of farmers did not know of any improved drought tolerant varieties released in Uganda. This reflects the need for breeders to work with extension staff or NGOs involved in seed distribution to promote the use of the released improved drought tolerant varieties, and eventually help in increasing groundnut productivity in Uganda. The results from genetic studies showed that drought tolerance and physical quality traits were associated through yield, and that selection of high pod yield under non-drought stress or small reduction in pod yield under drought stress would guarantee seed size traits. Therefore, by leveraging the observed associations, these two traits could be improved simultaneously. In addition, the genetic studies showed that both additive and non-additive gene effects controlled the expression of these traits. This suggests that progress in increasing the level of drought tolerance and physical traits could be achieved by delaying the selection to advanced generations followed by recurrent and pedigree breeding. The selected parents and families are useful genetic resources for improving drought tolerance and seed physical traits of groundnut. Information from genetic diversity studies could be used to guide future selection of parents to avoid co-ancestry leading to higher diversity in the segregants for improvement of drought tolerance and physical quality related traits. Moreover, complementing the conventional breeding with

molecular tools could lead to faster progress in breeding drought tolerant groundnut varieties with end-user traits through the use of approaches such as marker-assisted genomic selection where possible.

In summary, the present study identified genetically distant genotypes combining high yield, drought tolerance and adequate physical quality traits for developing improved groundnut lines in Uganda. The selected parental lines are important genetic resources to enhance groundnut productivity in the semi-arid regions of Uganda or countries with similar environments in sub-Saharan Africa.