THE UNIVERSITY OF YAOUNDE I
UNIVERSITE DE YAOUNDE I

FACULTY OF SCIENCE
FACULTE DES SCIENCES

DEPARTMENT OF PLANT BIOLOGY

DEPARTEMENT DE BIOLOGIE ET DE PHYSIOLOGIE VEGETALES

Breeding system of *Dacryodes edulis* (G. Don.) H. J. Lam: implications for cultivars development, selective breeding, and conservation of genetic resources

"THESIS"

"Submitted for the Fulfilment of the Degree of Doctor of Philosophy/PhD in Plant Biology"

Option: Botany and Ecology

By

MAKUETI Joséphine Thérèse

Matricule: 90Q378
MSc. Botany and Ecology

Under the supervision of:

NKONGMENECK Bernard-Aloys

Professor

University of Yaoundé I

TCHOUNDJEU Zacharie

PhD

Regional Coordinator World Agroforestry Centre
(ICRAF-West and Central Africa)

Academic year 2013/2014

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ACADEMIC PROTOCOL LIST

Year 2013/2014

(By Department and Grade)

UPDATE: 22 January 2015

ADMINISTRATION

DEAN : BILONG Paul, Professor
VICE-DEAN / DPSAA : NJOPWOUO Daniel, Professor
VICE-DEAN / DSSE : DONGO Etienne, Professor
VICE-DEAN / DRC : OWONO OWONO Luc Calvin, M.C. (Associate Professor)
Chief Division Academic Affairs, Education and Research: ABOSSOLO Monique, Senior Lecturer
Chief Division Administration and Finance: NDOYE FOE Marie C. F., Senior Lecturer

1- DEPARTMENT OF BIOCHEMISTRY (BC) (40)			
N°	NAMES AND FIRST NAMES	GRADE	OBSERVATIONS
1.	MOUNDIPA FEWOU Paul	Professor	Head of Department
2.	OBEN Julius ENYONG	Professor	On site
3.	BENG née NINTCHOM PENLAP V.	M.C. (Associate Professor)	On site
4.	FEKAM BOYOM Fabrice	M.C. (Associate Professor)	On site
5.	FOKOU Elie	M.C. (Associate Professor)	On site
6.	KANSCI Germain	M.C. (Associate Professor)	On site
7.	MBACHAM Wilfried	M.C. (Associate Professor)	On site
8.	MINKA Samuel	M.C. (Associate Professor)	On site
9.	ACHU Merci BIH	C.C. (Senior Lecturer)	On site
10.	ATOGHO Barbara Mma	C.C. (Senior Lecturer)	On site
11.	BELINGA née NDOYE FOE Marie C. Florentine	C.C. (Senior Lecturer)	Head DAF / FS
12.	BIGOGA JUDE	C.C. (Senior Lecturer)	On site
13.	BIYITI BI ESSAM née AKAM ADA L. F.	C.C. (Senior Lecturer)	I.G. MIN. Research
14.	BOUDJEKO Thaddée	C.C. (Senior Lecturer)	On site
15.	DEMMANO Gustave	C.C. (Senior Lecturer)	On site
16.	DJOKAM TAMO Rosine	C.C. (Senior Lecturer)	On site
17.	EFFA ONOMO Pierre	C.C. (Senior Lecturer)	On site
18.	EVEHE BEBANDOUE Marie –Solange	C.C. (Senior Lecturer)	On site
19.	MOFOR née TEUGWA Clautilde	C.C. (Senior Lecturer)	CE SEP MIN. Higher Ed.
20.	NGONDI Judith Laure	C.C. (Senior Lecturer)	On site
21.	NGUEFACK Julienne	C.C. (Senior Lecturer)	On site
22.	NJAYOU Frédéric Nico	C.C. (Senior Lecturer)	On site
23.	TCHANA KOUATCHOUA Angèle	C.C. (Senior Lecturer)	On site
24.	WAKAM née NANA Louise	C.C. (Senior Lecturer)	On site
25.	BEBEE FADIMATOU	ASS. (Assistant Lecturer)	On site

26.	BEBOY EDZENGUELE Sara Nathalie	ASS. (Assistant Lecturer)	On site
27.	DAKOLE DABOY Charles	ASS. (Assistant Lecturer)	On site
28.	DJUIDJE NGOUNOUE Marcelline	ASS. (Assistant Lecturer)	On site
29.	DJUIKWO NKONGA Ruth Viviane	ASS. (Assistant Lecturer)	On site
30.	DONGMO LEKAGNE Joseph Blaise	ASS. (Assistant Lecturer)	On site
31.	EWANE Cécile Anne	ASS. (Assistant Lecturer)	On site
32.	KOTUE KAPTUE Charles	ASS. (Assistant Lecturer)	On site
33.	FONKOUA Martin	ASS. (Assistant Lecturer)	On site
34.	LUNGA Paul KAILAH	ASS. (Assistant Lecturer)	On site
35.	MANANGA Marlyse Joséphine	ASS. (Assistant Lecturer)	On site
36.	MBONG ANGIE MOUGANDE Mary Ann	ASS. (Assistant Lecturer)	On site
37.	MBOUCHE FANMOE Marcelline Joëlle	ASS. (Assistant Lecturer)	On site
38.	PACHANGOU NSANGOU Sylvain	ASS. (Assistant Lecturer)	On site
39.	Palmer MASUMBE NETONGO	ASS. (Assistant Lecturer)	On site
40.	TIENTCHEU DJOKAM Léopold	ASS. (Assistant Lecturer)	On site

2- DEPARTMENT OF ANIMAL BIOLOGY (B.P.A.) (47)

N°	NAMES AND FIRST NAMES	GRADE	OBSERVATIONS
1.	BILONG BILONG Charles Félix	Professor	Head of Department
2.	DIMO Théophile	Professor	On site
3.	FOMENA Abraham	Professor	On site
4.	KAMTCHOUING Pierre	Professor	On site
5.	MIMPFOUNDI REMY	Professor	On site
6.	NGASSAM Pierre	Professor	On site
7.	NJIOKOU Flobert	Professor	On site
8.	DJIETO Lordon Champlain	M.C. (Associate Professor)	On site
9.	KAMGANG René	M.C. (Associate Professor)	C.S. MIN. Research
10.	NJAMEN Dieudonné	M.C. (Associate Professor)	On site
11.	NOLA Moïse	M.C. (Associate Professor)	On site
12.	TAN Paul	M.C. (Associate Professor)	On site
13.	TCHUEM TCHUENTE Louis	M.C. (Associate Professor)	Progr. Coord. Health Min.
14.	AJEAGAH Gidéon AGHAINDOUM	C.C. (Senior Lecturer)	On site
15.	ALENE Désirée Chantal	C.C. (Senior Lecturer)	On site
16.	BAPFUBUSA Benoît Alain	C.C. (Senior Lecturer)	On site
17.	BELLET EDIMO Oscar Roger	C.C. (Senior Lecturer)	On site
18.	DZEUFIET DJOMENI Paul Désiré	C.C. (Senior Lecturer)	On site
19.	ESSOMBA née NTSAMA MBALLA	C.C. (Senior Lecturer)	Health Min.
20.	FOTO MENBOHAN Samuel	C.C. (Senior Lecturer)	CT2 Min. Energy
21.	JATSA MEGAPTCHE Hermine	C.C. (Senior Lecturer)	On site
22.	KEKEUNOU Sévilor	C.C. (Senior Lecturer)	On site
23.	MEGNEKOU Rosette	C.C. (Senior Lecturer)	On site
24.	MONY NTONE Ruth	C.C. (Senior Lecturer)	On site
25.	NGUEGUIM TSOFACK Florence	C.C. (Senior Lecturer)	On site
26.	TOMBI Jeannette	C.C. (Senior Lecturer)	On site
27.	ZEBAZE TOGOUET Serge Hubert	C.C. (Senior Lecturer)	On site
28.	ATSAMO Albert Donatien	ASS. (Assistant Lecturer)	On site
29.	BILANDA Danielle Claude	ASS. (Assistant Lecturer)	On site
30.	Djiogue Sefirin	ASS. (Assistant Lecturer)	On site
31.	ETEME ENAMA Serge	ASS. (Assistant Lecturer)	On site
32.	GOUNOUE KAMKUMO Raceline	ASS. (Assistant Lecturer)	On site

33.	KANDELA KAVAYE Antoine	ASS. (Assistant Lecturer)	On site
34.	KOGA MANG'Dobara	ASS. (Assistant Lecturer)	On site
35.	LEKEUFACK FOLEFACK Guy Benoît	ASS. (Assistant Lecturer)	On site
36.	MAHOB Raymond Joseph	ASS. (Assistant Lecturer)	On site
37.	MBENOUN MASSE Paul Serge	ASS. (Assistant Lecturer)	On site
38.	MOUNGANG NGAMENI Luciane	ASS. (Assistant Lecturer)	On site
39.	MUH Bernice FIEN	ASS. (Assistant Lecturer)	On site
40.	MVEYO NDANKEU Yves Patrick	ASS. (Assistant Lecturer)	On site
41.	NDASSA AROUNA	ASS. (Assistant Lecturer)	On site
42.	NGOUATEU KENFACK Omer BEBE	ASS. (Assistant Lecturer)	On site
43.	NGUEMBOCK	ASS. (Assistant Lecturer)	On site
44.	NJUA Clarisse YAFI	ASS. (Assistant Lecturer)	On site
45.	OBI OBEN Esther	ASS. (Assistant Lecturer)	On site
46.	TADU Zéphirin	ASS. (Assistant Lecturer)	On site
47.	YEDE	ASS. (Assistant Lecturer)	On site

3- DEPARTMENT OF PLANT BIOLOGY (B.P.V.) (26)

N°	NAMES AND FIRST NAMES	GRADE	OBSERVATIONS
1.	NKONGMENECK Bernard Aloys.	Professor	On site
2.	YOUMBI Emmanuel	Professor	Head of Department
3.	AMBANG Zachée	M.C. (Associate Professor)	On site
4.	BELL Joseph Martin	M.C. (Associate Professor)	On site
5.	DJOCGOUE Pierre François	M.C. (Associate Professor)	On site
6.	MOSSEBO Dominique Claude	M.C. (Associate Professor)	On site
7.	ZAPFACK Louis	M.C. (Associate Professor)	On site
8.	ANGONI Hyacinthe	C.C. (Senior Lecturer)	On site
9.	BIYE Elvire Hortense	C.C. (Senior Lecturer)	On site
10.	ESSONO OBOUGOU Germain Gabriel	C.C. (Senior Lecturer)	On site
11.	KENGNE NOUMSI Ives Magloire	C.C. (Senior Lecturer)	On site
12.	MBARGA BINDZI Marie Alain.	C.C. (Senior Lecturer)	CEA Min. Higher Ed.
13.	MBOLO Marie.	C.C. (Senior Lecturer)	On site
14.	NDONGO BEKOLO	C.C. (Senior Lecturer)	CE / Min. Research
15.	NGODO MELINGUI Jean Baptiste	C.C. (Senior Lecturer)	On site
16.	NGOUO Lucas Vincent	C.C. (Senior Lecturer)	On site
17.	NSOM ZAMO Annie Claude ép. Pial	C.C. (Senior Lecturer)	National Expert /UNESCO
18.	TSOATA Esaïe	C.C. (Senior Lecturer)	On site
19.	DJEUANI Astride Carole	ASS. (Assistant Lecturer)	On site
20.	MAFFO MAFFO Nicole Liliane	ASS. (Assistant Lecturer)	On site
21.	MALLA Armand William	ASS. (Assistant Lecturer)	On site
22.	NGALLE Hermine BILLE	ASS. (Assistant Lecturer)	On site
23.	NGONKEU MAGAPTCHE Eddy Léonard	ASS. (Assistant Lecturer)	On site
24.	NNANGA MEBENGA Ruth Laure	ASS. (Assistant Lecturer)	On site
25.	NOUKEU KOUAKAM Armelle	ASS. (Assistant Lecturer)	On site
26.	TONFACK Libert Brice	ASS. (Assistant Lecturer)	On site

4- DEPARTMENT OF INORGANIC CHEMISTRY (C.I.) (34)			
N°	NAMES AND FIRST NAMES	GRADE	OBSERVATIONS
1.	NEMBA Robert	Professor	On site
2.	NGAMENI Emmanuel	Professor	Director Min. Higher Ed.
3.	NJOPWOUO Daniel	Professor	Vice-Dean / DPSAA
4.	AGWARA ONDOH Moïse	M.C. (Associate Professor)	Gen. Insp .MINPMEA
5.	AVOM Jérôme	M.C. (Associate Professor)	Director IAI Gabon
6.	BABALE née DJAM DOUDOU	M.C. (Associate Professor)	Staff at P.R.
7.	DJOUFAC WOUMFO Emmanuel	M.C. (Associate Professor)	On site
8.	ELIMBI Antoine	M.C. (Associate Professor)	On site
9.	GHOGOMU Paul MINGO	M.C. (Associate Professor)	Director PM's Office
10.	KETCHA MBADCAM Joseph	M.C. (Associate Professor)	Head of Department
11.	LAMINSI Samuel	M.C. (Associate Professor)	On site
12.	MELO née CHINJE Uphie F.	M.C. (Associate Professor)	Director Mipromalo
13.	NANSEU Charles Péguy	M.C. (Associate Professor)	On site
14.	NENWA Justin	M.C. (Associate Professor)	On site
15.	NDIFON Peter TEKE	M.C. (Associate Professor)	IS1 Min. Research
16.	NGOMO Horace MANGA	M.C. (Associate Professor)	S.G. Min. Higher Ed.
17.	YOUNANG Elie	M.C. (Associate Professor)	On site
18.	BAIZOUMI ZOUA	C.C. (Senior Lecturer)	Head Unit MINTOUR
19.	EMADACK Alphonse	C.C. (Senior Lecturer)	On site
20.	GWET Simon – Pierre	C.C. (Senior Lecturer)	On site
21.	KEUMEGNE MBOUGUEM J.Claude	C.C. (Senior Lecturer)	On site
22.	KONG SAKEO	C.C. (Senior Lecturer)	Senior Staff P. M.
23.	NDIKONTAR Maurice KOR	C.C. (Senior Lecturer)	Vice-Dean/Ubda
24.	NJIOMOU Chantale épse DJANGANG	C.C. (Senior Lecturer)	On site
25.	NJOYA Dayirou	C.C. (Senior Lecturer)	On site
26.	SIGNING Pierre	C.C. (Senior Lecturer)	On site
27.	ACAYANKA Elie	ASS. (Assistant Lecturer)	On site
28.	BELIBI BELIBI Placide Désiré	ASS. (Assistant Lecturer)	On site
29.	CHEUMANI YONA Arnaud	ASS. (Assistant Lecturer)	On site
30.	KAMGANG YOUBI Georges	ASS. (Assistant Lecturer)	On site
31.	NDI Julius NSAMI	ASS. (Assistant Lecturer)	On site
32.	NYAMEN Linda Dyorisse	ASS. (Assistant Lecturer)	On site
33.	PABOUDAM GBAMBIE Awaou	ASS. (Assistant Lecturer)	On site
34.	TCHAKOUTE KOUAMO Hervé	ASS. (Assistant Lecturer)	On site

5- DEPARTMENT OF ORGANIC CHEMISTRY (C.O.) (37)			
N°	NAMES AND FIRST NAMES	GRADE	OBSERVATIONS
1.	DONGO Etienne	Professor	On site
2.	FON KIMBU Samuel	Professor	On site
3.	GHOGOMU TIH ROBERT RALPH	Professor	On site
4.	MBAFOR Joseph	Professor	On site
5.	NGADJUI TCHALEU B.	Professor	Head of Dept FMBS
6.	NGOUELA Silvère Augustin	Professor	On site
7.	NKENGFACK Augustin Ephraïm	Professor	Head of Department
8.	NYASSE Barthélemy	Professor	Head Unit Min. Higher Ed.

9.	PEGNYEMB Dieudonné Emmanuel	Professor	Head Unit Min. Higher Ed.
10	TSAMO Etienne	Professor	On site
11	WANDJI Jean	Professor	On site
12	FOLEFOC Gabriel NGOSONG	M.C. (Associate Professor)	Vice-Dean/UB
13	KAPNANG Henriette	M.C. (Associate Professor)	On site
14	KOUAM Jacques	M.C. (Associate Professor)	On site
15	NOUNGOUE TCHAMO Diderot	M.C. (Associate Professor)	On site
16	TCHOUANKEU Jean-Claude	M.C. (Associate Professor)	Chief Service Rect. UYI
17	YANKEP Emmanuel	M.C. (Associate Professor)	On site
18	Alex de Théodore ATCHADE	C.C. (Senior Lecturer)	On site
19	BISSECK Paulette	C.C. (Senior Lecturer)	On site
20	EYONG Kenneth OBEN	C.C. (Senior Lecturer)	On site
21	KEUMEDJIO Félix	C.C. (Senior Lecturer)	On site
22	KEUMOGNE Marguerite	C.C. (Senior Lecturer)	On site
23	MBAZOA née DJAMA Céline	C.C. (Senior Lecturer)	On site
24	MKOUNGA Pierre	C.C. (Senior Lecturer)	On site
25	NGO MBING Joséphine	C.C. (Senior Lecturer)	On site
26	NGONO BIKOBO Dominique Serge	C.C. (Senior Lecturer)	On site
27	TABOPDA KUATE Turibio	C.C. (Senior Lecturer)	On site
28	TAGATSING FOTSING Maurice	C.C. (Senior Lecturer)	On site
29	TIH née NGO BILONG E. Anastasie	C.C. (Senior Lecturer)	On site
30	ZONDENDEGOUMBA Ernestine	C.C. (Senior Lecturer)	On site
31	AMBASSA Pantaleon	ASS. (Assistant Lecturer)	On site
32	FOTSO WABO Ghislain	ASS. (Assistant Lecturer)	On site
33	KAMTO Eutrophe Ledoux	ASS. (Assistant Lecturer)	On site
34	NGINTEDO Dominique	ASS. (Assistant Lecturer)	On site
35	NGOMO Orléans	ASS. (Assistant Lecturer)	On site
36	NOTE LOUGBOT Olivier	ASS. (Assistant Lecturer)	On site
37	OUAHOUO WACHE Blandine Marlyse	ASS. (Assistant Lecturer)	On site

6- DEPARTMENT OF COMPUTER SCIENCE (C.S.) (26)			
N°	NAMES AND FIRST NAMES	GRADE	OBSERVATIONS
1.	TCHUENTE Maurice	Professor	PCA UB
2.	ATSA ETOUNDI Roger	M.C. (Associate Professor)	Chief Division MINFOPRA
3.	FOTSO Pauline Laure	M.C. (Associate Professor)	Vice-Rector Uds
4.	FOUDA NDJODO Marcel	M.C. (Associate Professor)	IA4 Min.H. Ed./Head Dpt ENS
5.	NDOUNDAM René	M.C. (Associate Professor)	On site
6.	CHEDOM FOTSO Donatien	C.C. (Senior Lecturer)	On site
7.	LOUKA Basile	C.C. (Senior Lecturer)	Head of Department
8.	MELATAGIA YONTA Paulin	C.C. (Senior Lecturer)	On site
9.	TINDO Gilbert	C.C. (Senior Lecturer)	On site
10	TSOPZE Norbert	C.C. (Senior Lecturer)	On site
11	WAKU KOUAMOU Jules	C.C. (Senior Lecturer)	On site
12	ABESSOLO ALO'O Gislain	ASS. (Assistant Lecturer)	On site
13	BAYEM Jacques Narcisse	ASS. (Assistant Lecturer)	On site
14	DJOUWE MEFFEJA Merline Flore	ASS. (Assistant Lecturer)	On site
15	EBELE Serge	ASS. (Assistant Lecturer)	On site
16	HAMZA Adamou	ASS. (Assistant Lecturer)	On site
17	KAMDEM KENGNE Christiane	ASS. (Assistant Lecturer)	On site
18	KAMGUEU Patrick Olivier	ASS. (Assistant Lecturer)	On site

19	KENFACK DONGMO Clauvice Viliane	ASS. (Assistant Lecturer)	On site
20	KOMGUEM Rodrigue	ASS. (Assistant Lecturer)	On site
21	KOUOKAM KOUOKAM Etienne A.	ASS. (Assistant Lecturer)	On site
22	MEYEMDOU Nadège Sylvianne	ASS. (Assistant Lecturer)	On site
23	MONTHE DJIADEU Valery Martial	ASS. (Assistant Lecturer)	On site
24	MOTO MPONG Serge Alain	ASS. (Assistant Lecturer)	On site
25	OMEKONG AZANZI Fidel	ASS. (Assistant Lecturer)	On site
26	TAPAMO KENFACK Hyppolite	ASS. (Assistant Lecturer)	On site

7- DEPARTMENT OF MATHEMATICS (MA) (39)

N°	NAMES AND FIRST NAMES	GRADE	OBSERVATIONS
1.	BEKOLLE David	Professor	Vice-Rector UN
2.	BITJONG NDOMBOL	Professor	DIPD UY II
3.	DOSSA COSSY Marcel	Professor	On site
4.	NGUETSENG Gabriel	Professor	Chief CUTI UYI
5.	NOUTCHEGUEME Norbert	Professor	On site
6.	TONGA Marcel	M.C. (Associate Professor)	On site
7.	WAMON François	M.C. (Associate Professor)	Head of Department
8.	AYISSI Raoult Domingo	C.C. (Senior Lecturer)	On site
9.	BINZOULI Etienne Jean-Jacques	C.C. (Senior Lecturer)	On site
10.	EMVUDU WONO Yves S.	C.C. (Senior Lecturer)	Head Unit Min.Higher Ed.
11.	FOMEKONG Christophe	C.C. (Senior Lecturer)	On site
12.	KIANPI Maurice	C.C. (Senior Lecturer)	On site
13.	KIKI Maxime Armand	C.C. (Senior Lecturer)	On site
14.	MBAKOP Guy Merlin	C.C. (Senior Lecturer)	On site
15.	MBANG Joseph	C.C. (Senior Lecturer)	On site
16.	MBIANDA Gilbert	C.C. (Senior Lecturer)	On site
17.	MEWOLI Boulchard	C.C. (Senior Lecturer)	On site
18.	NDAKBO Victor	C.C. (Senior Lecturer)	On site
19.	NGUIMTSA Charles	C.C. (Senior Lecturer)	On site
20.	NKUIMI JUGNIA Célestin	C.C. (Senior Lecturer)	On site
21.	NOUNDJEU Pierre	C.C. (Senior Lecturer)	On site
22.	TCHANGANG Roger Duclos	C.C. (Senior Lecturer)	On site
23.	TCHAPNDA NJABO Sophonie Blaise	C.C. (Senior Lecturer)	On site
24.	TCHOUNDJA Edgar Landry	C.C. (Senior Lecturer)	On site
25.	TIAYA TSAGUE N. Anne- Marie	C.C. (Senior Lecturer)	On site
26.	ZAME Alfred	C.C. (Senior Lecturer)	On site
27.	AGHOUKENG JIOFACK Jean Gérard	ASS. (Assistant Lecturer)	On site
28.	CHENDJOU Gilbert	ASS. (Assistant Lecturer)	On site
29.	DJIADEU NGAHA Michel	ASS. (Assistant Lecturer)	On site
30.	MBEHOU Mohamed	ASS. (Assistant Lecturer)	On site
31.	MBIAKOP Hilaire George	ASS. (Assistant Lecturer)	On site
32.	MENGUE MENGUE David Joe	ASS. (Assistant Lecturer)	On site
33.	NGUEFACK Bertrand	ASS. (Assistant Lecturer)	On site
34.	NKONLACK Socgnia Virginie	ASS. (Assistant Lecturer)	On site
35.	NIMPA PEFOUKEU Romain	ASS. (Assistant Lecturer)	On site
36.	POLA DOUNDOU Emmanuel	ASS. (Assistant Lecturer)	On site
37.	TAKAM SOH Patrice	ASS. (Assistant Lecturer)	On site
38.	TANG AHANDA Barnabé	ASS. (Assistant Lecturer)	Chief Serv. MINPLADAT
39.	TETSADJIO TCHILEPECK Mesmin Erick	ASS. (Assistant Lecturer)	On site

8- DEPARTMENT OF MICROBIOLOGY (MB) (12))			
N°	NAMES AND FIRST NAMES	GRADE	OBSERVATIONS
1.	ETOA François-Xavier	Professor	Head of Department, CT/ PM
2.	ESSIA NGANG Jean Justin	M.C. (Associate Professor)	On site
3.	NWAGA Dieudonné M.	M.C. (Associate Professor)	On site
4.	BODA Maurice	C.C. (Senior Lecturer)	On site
5.	BOYOMO ONANA	C.C. (Senior Lecturer)	On site
6.	ENO Anna Arey	C.C. (Senior Lecturer)	On site
7.	NYEGUE Maximilienne Ascension	C.C. (Senior Lecturer)	On site
8.	RIWOM Sara Honorine	C.C. (Senior Lecturer)	On site
9.	SADO KAMDEM Sylvain Leroy	C.C. (Senior Lecturer)	On site
10.	BOUGNOM Blaise Pascal	ASS. (Assistant Lecturer)	On site
11.	NJIKI BIKOÏ Jacky	ASS. (Assistant Lecturer)	On site
12.	TCHIKOUA Roger	ASS. (Assistant Lecturer)	On site

9- DEPARTMENT OF PHYSICS (PH) (39)			
N°	NAMES AND FIRST NAMES	GRADE	OBSERVATIONS
1.	KOFANE Timoléon Crépin	Professor	Head of Department
2.	NJOMO Donatien	Professor	On site
3.	WOAFO Paul	Professor	On site
4.	ESSIMBI ZOBO Bernard	M.C. (Associate Professor)	On site
5.	NDJAKA Jean Marie Bienvenu	M.C. (Associate Professor)	On site
6.	NOUAYOU Robert	M.C. (Associate Professor)	On site
7.	OUMAROU BOUBA	M.C. (Associate Professor)	Rector UY II
8.	PEMHA Elkana	M.C. (Associate Professor)	On site
9.	TABOD Charles TABOD	M.C. (Associate Professor)	Dean/Ubda
10.	TCHAWOUA Clément	M.C. (Associate Professor)	On site
11.	ZEKENG Serge Sylvain	M.C. (Associate Professor)	On site
12.	BEN- BOLIE Germain Hubert	C.C. (Senior Lecturer)	On site
13.	BIYA MOTTO Frédéric	C.C. (Senior Lecturer)	Manager MEKIM Dam
14.	DJUIDJE KENMOE Gemaine épse	C.C. (Senior Lecturer)	On site
15.	ALOYEM KAZE	C.C. (Senior Lecturer)	On site
16.	EKOBENA FOUDA Henri Paul	C.C. (Senior Lecturer)	Head of Dept UN
17.	FEWO Serge Ibraïd	C.C. (Senior Lecturer)	On site
18.	FOUEDJIO David	C.C. (Senior Lecturer)	On site
19.	HONA Jacques	C.C. (Senior Lecturer)	On site
20.	MBANE BIOUELE	C.C. (Senior Lecturer)	On site
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22.	NJANDJOCK NOUCK Philippe	C.C. (Senior Lecturer)	Chief Serv. MIN, Research
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3.	BITOM Dieudonné Lucien	Professor	Dean / UN
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7.	MVONDO ONDOA Joseph	M.C. (Associate Professor)	On site
8.	NDAM NGOUPAYOU Jules-Remy	M.C. (Associate Professor)	On site
9.	NDJIGUI Paul-Désiré	M.C. (Associate Professor)	On site
10.	NGOS III Simon	M.C. (Associate Professor)	D.A.A.C./UM
11.	NKOUMBOU Charles	M.C. (Associate Professor)	On site
12.	TEMDJIM Robert	M.C. (Associate Professor)	On site
13.	ABOSSOLO née ANGUE Monique	C.C. (Senior Lecturer)	Chief DAASR
14.	BEKOA Etienne	C.C. (Senior Lecturer)	On site
15.	BISSO Dieudonné	C.C. (Senior Lecturer)	Projet Manager Memve'ele Dam
16.	EKOMANE Emile	C.C. (Senior Lecturer)	On site
17.	ESSONO Jean	C.C. (Senior Lecturer)	C.E.A. MINIMDT
18.	GHOGOMU Richard TANWI	C.C. (Senior Lecturer)	On site
19.	LAMILEN BILLA Daniel	C.C. (Senior Lecturer)	On site
20.	LIENOU Gaston	C.C. (Senior Lecturer)	On site
21.	MINYEM Dieudonné	C.C. (Senior Lecturer)	On site
22.	MOUAFO Lucas	C.C. (Senior Lecturer)	On site
23.	MOUNDI Amidou	C.C. (Senior Lecturer)	Inspector1 MINIMDT
24.	NGO BIDJECK Louise Marie	C.C. (Senior Lecturer)	On site
25.	NGUEUTCHOUA Gabriel	C.C. (Senior Lecturer)	On site
26.	NJILAH Isaac KONFOR	C.C. (Senior Lecturer)	On site
27.	NJOM Bernard de Lattre	C.C. (Senior Lecturer)	On site
28.	NYECK Bruno	C.C. (Senior Lecturer)	On site
29.	ONANA Vincent	C.C. (Senior Lecturer)	C. S. MINIMDT
30.	TCHAKOUNTE Jacqueline ép. NUMBEM	C.C. (Senior Lecturer)	On site
31.	TCHOUANKOUE Jean-Pierre	C.C. (Senior Lecturer)	On site
32.	YENE ATANGANA Joseph Q.	C.C. (Senior Lecturer)	Chief Div. MINFOF
33.	ANABA ONANA Achille Basile	ASS. (Assistant Lecturer)	On site
34.	GANNO Sylvestre	ASS. (Assistant Lecturer)	On site
35.	MBIDA YEM	ASS. (Assistant Lecturer)	On site
36.	METANG Victor	ASS. (Assistant Lecturer)	On site
37.	NGO BELNOUN Rose Noël	ASS. (Assistant Lecturer)	On site
38.	NOMO NEGUE Emmanuel	ASS. (Assistant Lecturer)	On site
39.	TCHAPTCHET TCHATO De Pesquidoux I	ASS. (Assistant Lecturer)	On site

40.	TEHNA Nathanaël	ASS. (Assistant Lecturer)	On site
41.	TEMGA Jean Pierre	ASS. (Assistant Lecturer)	On site
42.	ZO'O ZAME Philemon	ASS. (Assistant Lecturer)	On site

ALLOTMENT OF LECTURERS IN THE FACULTY OF SCIENCE ACCORDING TO DEPARTMENTS

Department	Nomber of lecturers				
	Pr	**MC**	**CC**	**ASS**	**Total**
BC	2 (0)	6 (1)	16 (11)	16 (7)	**40 (20)**
BPA	7 (0)	6 (0)	14 (7)	20 (5)	**47 (13)**
BPV	2 (0)	6 (0)	11 (3)	8 (5)	**26 (8)**
C.I.	3 (0)	14 (2)	9 (1)	8 (2)	**34 (5)**
C.O.	11 (0)	6 (1)	13 (6)	7 (1)	**37 (8)**
IN	1 (0)	4 (1)	6 (0)	15 (4)	**26 (5)**
MA	5 (0)	2 (0)	19 (1)	13 (1)	**39 (2)**
MB	1 (0)	2 (0)	6 (3)	3 (0)	**12 (3)**
PH	3 (0)	8 (0)	19 (3)	9 (1)	**39 (4)**
ST	3 (0)	10 (1)	20 (3)	10 (1)	**42 (5)**
Total	**38 (0)**	**64 (6)**	**133 (38)**	**109 (28)**	***343 (72)***

IN TOTAL: 344 (71) with

- PROFESSORS 38 (0)
- ASSOCIATE PROFESSORS 64 (6)
- SENIOR LECTURERS 133 (38)
- ASSISTANT LECTURERS 109 (28)

( ) = Number of women

The Dean of the Faculty of Sciences

Pr. BILONG Paul

SUMMARY

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DEDICATION

To my children:

Ivan Rouvier Kueti;
Christian Yannick Dassi Dassi;
Manuel Dassi Kueti, and
Joyce Grâce Dassi Mbeukou

To all of you, my gratitude and my appreciation acquired forever.

ACKNOWLEDGEMENTS

I would like to thank everyone who has help during the preparation of this thesis for all his or her support and encouragement.

My special appreciation and indebtedness go to my promoter, Dr. Zac Tchoundjeu, Principal Scientist (Tree Domestication) and Regional Coordinator of ICRAF, West and Central Africa Regional Program for the unenviable task of initiating me into tree domestication of indigenous fruit (concepts and practice) and for his invaluable guidance and support, and for taking the time to listen to my never-ending doubts. He also acted as an excellent advisor and mentor.

I am very grateful to my co-promoters: Pr. Bernard-Aloys Nkongmeneck, of the Department of Plant Biology at the University of Yaoundé I, for undertaking the task of supervising this research project and for full support during this research; a special thanks to Dr. Antoine Kalinganire, Senior Scientist (Tree improvement) and Coordinator of ICRAF/Sahel Node, for his invaluable guidance, his mentoring and invaluable support throughout this work.

I am indebted to late Pr. Amougou Akoa, Head of the Department of Plant Biology at the University of Yaoundé I for sharing his broad experience on plant biology.

I owe sincere thanks to Pr. Louis Zapfack, Senior Lecturer at the University of Yaoundé I for his advice and constructive suggestions which have improved this work.

Also acknowledged are all my lecturers from the University of Yaoundé I, Department of Plant Biology, especially Prs. Emmanuel Youmbi, Joseph Martin Bell, Dieudonné Nwaga, Claude Dominique Mossebo, Zachée Ambang, Pierre François Djocgoue; then Drs. Mbarga Bindzi, Marie Mbolo, Ives Noumsi, and Boyomo Onana.

I am thankful to Dr. Ebenezer Asaah, Senior Scientist (Tree improvement) and Representative Country of ICRAF Sierra Leone for helping in experiment design and data analysis.

I am grateful to Dr. Ann Degrande, Dr. Divine Foundjem Tita, Edith Souop, Landry Tankam, Charlie Mbosso, Alain Tsobeng, Lyliane Kani, Edith Nella Keguep, Bertin Anselme

Takoutsing, Mireille Feudjio Tsague, Jean Marie Tchouala and Frederick Nkeumoe for their assistance and technical support. I also thank all drivers of ICRAF Cameroon.

I want to express my sincere gratitude to Mr. Julius Atia Isseli, Communicator at ICRAF for his advice and constructive suggestions which have improved this work.

I am deeply grateful to those individuals who gave up their time to take care of my experiments in the field trial during controlled pollination and stock plants in the nurseries in Mbalmayo, Minkoa-Meyos and Nkolbison. The results would not have been as substantial and accurate without their help and commitment: Norbert Biakaiy, Amadou Mbouombouo, Gustave Ebengue, Gaspard Baba and Modeste Ndzana among others.

I wish to express my sincere gratitude to Dr. Avana Tientcheu Marie-Louise and Pr. Mapongmetsem Pierre Marie who reviewed part of this document and for their experienced advice.

Also acknowledged are Mr. Lazare Kouodiekong for assisting in data analysis and Mrs. Precilla Ngaunkam for assisting in drawing the maps.

I would like to express my sincere gratitude to Mr. Aurelien Onana Nkodo for his support and encouragement.

I am thankful to Mr. Martin Mindjos and Moise Akoa Zang for their advice, encouragements and support.

Also, I owe innumerable thanks to family members in particular:

my parents, and especially my father, Edouard Kueti, for his endless support and the assurance that I could do it;

my brothers and sisters and their respective families who were always there for me when nothing seemed to work out particularly: Jeanne and Albert Djeukeng, David and Ernestine Djeugo, Joseph and Odile Tiogning, Dorothée and Gaston Donfack, Généviève Kenfack Tedem, Blandine and Victor Keubou. A special thank you for your parental love, support and prayers;

my nephews and nieces especially Lauraine Tiogning Kueti, Debeauvoir Donfack, Glwadis Tiogning Nanfah, Franck Cabrel Nguekeng and Ornella Marguerite Nkeubou for their love despite the fact I have not also been around to cheer them up.

I acknowledge the moral support and advice tendered to me by Mr. & Mrs Ide Nintedem, Marcelle Meye, Solange Nzolang, Justin Ndjongue, Dr. René Jiofack, Dr. Barbara Tiedeu Atogho, Dr. Hermann Taedoung, Joseph Bertin Tanguedje, Ghislaine Dongmo, Thérèse Dibackto, Brigitte Zoléko, Berthe Dongmo and Yolande Bomba, for their friendship, kind support and their invaluable contribution to this project.

I owe sincere thanks to Mr. Sygnola Tsafack, Martin Asen, Patrick Tabougue, Engelbert Atiojio, and Alain Rostand Letche who were always helpful and kind throughout before and during the preparation of this thesis.

Finally, I wish to acknowledge the support and assistance from the World Agroforestry Centre, also known as International Centre for Research in Agroforestry (ICRAF) for the provision of funds and facilities in conducting research that led to the results presented in this thesis.

LIST OF ABBREVIATIONS/ACRONYMES

AFTPs:	Agro Forestry Tree Products
AG:	Gibberellic Acid
ANOVA:	Analysis of Variance
BUM:	Boumnyebel
BSO:	Breeding Seed Orchard
CK	Cytokinin
CSO:	Clonal Seed Orchards
DNA:	Deoxyribo Nucleic Acid
DRC:	Democratic Republic of Congo
FAO:	Food and Agriculture Organization
IAA:	Indole Acetic Acid
IBA:	Indole-3-Butyric Acid
ICRAF:	International Centre for Research in Agroforestry and Forestry
KEK:	Kekem
Leu:	Leucine
Lys:	Lysine
MAK:	Makenene
MDGs:	Millennium Development Goal
NGOs	Non-Governmental Organizations
PCA	Principal Component Analysis
RAPD:	Random Amplified Polymorphic DNA
RNA:	Ribonucleic Acid
SD:	Standard deviation
SE:	Standard Error
SSA:	Sub-Sahara Africa
SSO:	Seedling Seed Orchard
Thr:	Threonine
UNAIDS:	United Nations Program on HIV/AIDS
UN:	United Nations

WAD: Week After seedlings Decapitation

WAS: Week After seed Sowing

WCFSD: World Commission on Forests and Sustainable Development

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ABSTRACT

Growing food insecurity, increasing poverty and deteriorating environmental conditions are the main scourges that profoundly affect rural populations in the tropics. To help solve these problems, the World Agroforestry Centre, former International Centre for Research in Agroforestry (ICRAF) encourages integrated and improved management of natural resources through the promotion of agroforestry systems.

Nonetheless, success in breeding for higher yield of indigenous fruit trees is still constrained by the lack of availability of improved germplasm. Improvement of indigenous fruit tree cultivars is drawing great attention from breeders. *Dacryodes edulis* (G.Don) H. J. Lam (Burseraceae) commonly known as African plum is an andromonoic and oleaginous fruit tree species, endemic to the Gulf of Guinea. It is currently under domestication and widely commercialized in West and Central Africa. In efforts to enhance the species' genetic conservation and utilization, it was identified as one of the top ten agroforestry tree species for future crop diversification in West and Central Africa. Despite the advantages of vegetative propagation techniques which are hastening sexual maturity and giving an exact replicate of the desired mother-tree characters, it is feared that it could severely narrow the genetic diversity and increase inbreeding within the species at farm level ultimately leading to a decline in future production. However, controlled cross-pollination can help to combine a number of desired fruit characters in one tree and increase inter-tree variability between selected superior genotypes so called "plus trees". By so doing, the species' genetic basis could be better conserved.

Our goal in this research was to beef up *Dacryodes edulis* tree breeding and genetic resources' preservation initiated by ICRAF throughout a tree improvement program, especially through cross-controlled pollinations and vegetative propagating techniques being developed in Cameroon. Specifically, we addressed the following questions: (1) Does African plum fruiting efficiency depend on the parents' provenance and the type of flower which produced the pollen used for fertilization? (2) Do controlled cross-pollination increases quality of the quantitative fruit traits of well-known African plum accessions? Which Cameroonin African plum's ecological provenance possesses best fruits traits for selection through controlled cross-pollination? (3) Do seedlings obtained through controlled cross-pollination of African plum behaviors in the nursery depend on the provenance and the crossing to which they belong? In this perspective, controlled hand cross-pollinations were performed on 25 accessions of *D. edulis*, using a nested mating design. Conventional methods (ANOVA, MANOVA, Ascending Hierarchical Classification and Principal Component Analysis) were used for data analysis. Output data tested were especially size and weight of fruits and more precisely pulp weight or thickness, which is the principal trait of commercial importance.

The pollination experiments were performed during three flowering seasons between January 2010 and March 2012 at two localities, Minkoa-Meyos and Mbalmayo in the Centre region of Cameroon. The experimental design included provenance as a fixed factor, treatment as within-subject (i.e. repeated measures) fixed factor and plant individual as a random factor (subject). Although controlled pollination did not increase fruit size in the studied species as compared to other fruit trees such as avocado and citrus specie, fruit set and fruiting were greatly improved. This technique may help to reduce the phenomenon of fruit drop very current in *D. edulis*. In addition, six best combinations mainly characterized by high fruit-setting rate and fruiting index (>70% and >50% respectively) and a low fruit-dropping rate (<20%) were identified. Variation in fruiting index that

determines fruit yield of the studied species was highly correlated with the combined action of factors studied ((i) provenance of the male parent: Boumnyebel (BUM29), Makenene (MAK33) and Kekem (KEK02); (ii) type of flower (male or hermaphrodite) which produced pollen used for hand fertilization and (iii) female parent status. In order to improve yield, it was also noticed that it is necessary to control fruit load by exploring ways of reducing fruit set during flowering.

Phenotypic variation in the traits of 1604 fruits and seeds were characterized within and between trees, and between provenances. Ascending hierarchical classification (cluster analysis) performed showed that variability in relation between fruit and pulp weight confirms the moderate differences between clusters and may have been driven by both ecological and genetic variation. For the fulfilment of cultivar development, the perceived qualitative variation (in pulp oil content and pulp taste) may be genetically determined and should not be neglected during the characterization of F_2 and F_3 hybrids (further research). Nevertheless, between provenances variation was found to be relatively high, particularly for fruit length, fruit width, fruit weight, pulp weight and thickness. The results suggest that fruit weight is a good predictor of pulp yield, although its predicting power differed among clusters. This study has helped develop a mathematical model for the choice of fruit and pulp size by breeders for *D. edulis* breeding.

Additionally, control-pollinated seedlings obtained from the present study were considered as improved planting material and submitted to early decapitation test. Such approach may produce young seedlings with multiples branches onto which cuttings could be obtained. This approach may also help to characterize African plum control-pollinated seedlings in an attempt to select improved raw-material for the on-going plant breeding program. Thus, early branching induction by the removal of the apex or the uppermost node of 108 selected F_1 hybrids in the net-house produced seedlings with early multiple branches (synchronous branching). This architecture may contribute to yield improvement and also facilitate farmers' handling experiments. In fact, "apical dominance" effect was negative. There was no significant difference from one sprouted seedling to another, regardless of seedling trait targeted and the parent provenance. F_1 hybrids were settled on-station as progeny trials for the on-going breeding program. They will be carefully monitored until the first fruit production during which qualitative agro-morphological parameters such as pulp oil content, taste and color of the mesocarp and epicarp of the fruit, will be evaluated and compared to those of parents or selected mother trees (evaluation of the genetic gain in F_2 and F_3 generations). F_2 hybrids will be established within agro-ecological zones around the country as clonal or progeny trials in the fulfilment of cultivars development.

This study has depicted number options for the genetic improvement of *D. edulis*. In fact, the results of the overall study show that hand pollination can help to combine a number of desired fruit characters of one tree and increase the inter-tree variability between plus-trees, without narrowing its genetic base. Coupled with vegetative propagation techniques (layering and leafy stem cuttings) being developed for *D. edulis* breeding, controlled hand pollination can enhance the genetic resources' conservation of African plum leading to new varieties or cultivars development for the enrichment of African plum plantations with high-quality planting stock.

Key words: African plum, breeding program, controlled pollination, decapitation test, gene bank, germplasm, progeny trial.

RÉSUMÉ

L'insécurité alimentaire grandissante, la pauvreté croissante et la dégradation des conditions environnementales sont les principaux fléaux qui affectent profondément les populations rurales. Pour contribuer à la résolution de ces problèmes, le Centre International pour la Recherche en Agroforesterie (ICRAF) encourage la gestion intégrée des ressources naturelles, à travers la promotion des systèmes agroforestiers.

Malheureusement, l'amélioration du rendement des arbres fruitiers indigènes est encore entravée par le manque de disponibilité du matériel génétique amélioré. Parmi les espèces retenues pour la domestication au Cameroun, *Dacryodes edulis* (G.Don) H. J. Lam communément appelé safoutier est une *Burseracée* andromonoique fruitière, endémique du golfe de Guinée, mais largement cultivée en Afrique Centrale et de l'Ouest. Elle y occupe une place de choix compte tenu de son importance tant du point de vue nutritionnel, économique, agroforestier qu'environnemental. Malgré les avantages des techniques d'amélioration génétique développées pour l'espèce étudiée en l'occurrence la propagation par voie végétative via le marcottage et le bouturage qui ont l'avantage de réduire le temps mis pour la première fructification, et de reproduire exactement les caractères maternels désirés; il semble que ces techniques aient tendance à réduire la base génétique de l'espèce et entrainer ainsi une faible productivité de l'espèce. Dès lors, la pollinisation croisée contrôlée peut permettre de combiner un certain nombre de caractères de fruits souhaités d'un arbre et d'augmenter ainsi la variabilité entre les arbres ou entre génotypes supérieurs sélectionnés appelés "arbres supérieurs". Ce faisant, la base génétique de l'espèce pourrait être mieux conservée.

L'objectif de la présente étude était de renforcer l'amélioration génétique de *D. edulis* initiée par l'ICRAF à travers un programme d'amélioration et assurer la préservation des ressources génétiques de cette espèce, en particulier par la technique de pollinisation croisée contrôlée manuelle, couplée aux techniques de multiplication végétative en cours de développement au Cameroun. Plus spécifiquement, les questions suivantes ont été abordées: (1) La capacité fruitière du safoutier dépend-t-elle de la provenance des parents et du type de fleur ayant produit le pollen utilisé pour la fécondation ? (2) La pollinisation contrôlée manuelle augmente-t-elle la qualité des caractères de fruits issus des accessions dites supérieures de l'espèce étudiée ? Quelles provenances de *D. edulis* au Cameroon possèdent les meilleures qualités de fruits pour la sélection ? (3) Le comportement en pépinière des plants obtenus par pollinisation croisée contrôlée dépend-t-il de la provenance de l'accession ciblée ou du croisement effectué ? Dans cette perspective, des pollinisations croisées ont été effectuées sur 25 accessions de *D. edulis* par la méthode de croisements imbriqués. Des méthodes classiques d'analyse (ANOVA, MANOVA, Classification Ascendante Hiérarchique, Analyse en Composantes Principales) ont été utilisées pour l'analyse des données, notamment la taille et le poids des fruits, et plus précisément le poids de la pulpe, qui est le caractère principal de l'importance commerciale de l'espèce.

Les expériences de pollinisation contrôlées ont été réalisées durant trois saisons fruitières, entre Janvier 2010 et Mars 2012 dans deux localités à savoir Minkoa-Meyos et Mbalmayo dans la région du Centre du Cameroun. Au terme de cette étude, six meilleures combinaisons caractérisées principalement par des taux de nouaison et de fructification élevés (> 70% et > 50%) et un faible taux de chute de fruits après nouaison (< 20%) ont été identifiées. Ces combinaisons constituent pour cette étude des candidats potentiels pour la poursuite de l'amélioration génétique de cette espèce. La variation de l'indice de fructification qui détermine le rendement en fruits de l'espèce étudiée est fortement corrélée à l'action combinée des facteurs étudiés en l'occurrence (i) la provenance du parent mâle : Boumnyebel (BUM29), Makenene (MAK33) et Kekem (KEK02), (ii) le type de fleur (mâle ou hermaphrodite) qui a produit le

pollen utilisé pour la pollinisation manuelle et (iii) le statut du parent femelle. Afin d'améliorer le rendement, il a également été constaté qu'il est nécessaire de contrôler la charge pondérale en fruits de chaque arbre femelle, en explorant les moyens de réduire la nouaison pendant la floraison.

La variation phénotypique des caractères de 1604 fruits et graines a été caractérisée à l'intérieur et entre les arbres et les provenances. À partir de la classification ascendante hiérarchique réalisée pour étudier les accessions sélectionnées, il a été observé que la variabilité entre les fruits et le poids de la pulpe confirme les différences modérées entre les croisements. Cette variation peut avoir été induite à la fois par la variation écologique et génétique. Pour le développement des cultivars, la variation qualitative perçue (teneur en huile et le goût de la pulpe) peut être déterminée génétiquement et ne doit pas être négligée lors de la caractérisation des hybrides F_2 et F_3 (recherche future). Néanmoins, la variation entre les provenances s'est avérée être relativement élevée, en particulier pour la longueur, la largeur et le poids du fruit, ainsi que pour le poids et l'épaisseur de la pulpe. Les résultats suggèrent que le poids des fruits est un bon indicateur du rendement de la pulpe, bien que ce pouvoir de prédiction diffère selon les croisements. Cette étude a permis de développer un modèle mathématique pour le choix des fruits et de l'épaisseur de la pulpe de *D. edulis* pour un programme d'amélioration génétique.

Les plants issus de la pollinisation contrôlée obtenus de la présente étude ont été considérés comme du matériel végétal amélioré et soumis au test de suppression du méristème apical (induction de la réitération précoce). Ainsi, 108 hybrides F_1 ont été sélectionnés en serre au début de l'induction de la réitération par la suppression de l'apex, en vue de produire des jeunes plants à multiples branches à partir desquels des boutures pourront être prélevées. Cette architecture peut contribuer à augmenter le rendement de l'arbre et même favoriser sa gestion par le paysan. Il n'y pas eu de différence significative entre les caractères étudiés, d'un plant réitéré à un autre, indépendamment de la provenance considérée. L'effet de « dominance apicale » a été négatif, ce qui a contribué à la production des jeunes plants à multiples branches. Tous les hybrides F_1 ont été installés sous forme de test de descendances en station pour la poursuite du programme d'amélioration. Ils seront suivis jusqu'à la première production de fruits au cours de laquelle les paramètres agro-morphologiques qualitatifs tels que la teneur en huile et le goût de la pulpe, la couleur du mésocarpe et de l'épicarpe du fruit, seront évalués et comparés à ceux des parents dits « supérieurs » (évaluation du gain génétique des générations F_2 et F_3). Les hybrides obtenus en F_2 seront plantés sous forme d'essai clonal ou de test de descendances sur différents sites ou zones agro-écologiques du pays où pousse naturellement l'espèce dans une perspective de création des cultivars.

La présente étude a relevé quelques options envisageables pour l'amélioration génétique du safoutier. En effet, les résultats de la présente étude témoignent que la propagation par voie sexuée (pollinisation croisée manuelle) permettrait de combiner certains caractères désirés sur un arbre et surtout d'augmenter l'inter-variabilité entre les arbres tout en conservant sa base génétique. Cette technique, couplée aux techniques de propagation par voie végétative (marcottage et bouturage) déjà bien développées pour la domestication à large échelle de cette espèce, viendrait consolider et renforcer l'une des visions des chercheurs qui est celle de la conservation génétique des ressources de l'espèce étudiée par la création des cultivars qui serviront à l'enrichissement des plantations de safoutier avec du matériel végétal amélioré de haute qualité.

Mots clés : Safoutier, programme d'amélioration, pollinisation controlée, test de decapitation, banque de gènes, germplasm, test de descendance.

PHD THESIS OUTLINE

The research work reported in this thesis focused on one priority indigenous fruit trees species in West and Central Africa (*Dacryodes edulis* (G.Don) H. J. Lam (Burseraceae)). This study is divided in four chapters. The first chaper is an introduction to the study which covers the background of the work in terms of current trends in natural resources degradation and the need to adapt current agricultural practices to produce more crops. It ends with the thesis problem statement, and the main objectives of the research conducted within the framework of this thesis.

The second chapter reviews the need for agroforestry and the domestication of indigenous fruit trees to promote food, income and employment, and the environmental services is also discussed. This review includes information related to plant breeding, germplasm and morphological characterization, seed orchard and mechanism for shoot branching. This chapter also deals with the review information on the socio-economic values, botany, reproductive biology, habitat, distribution, medicinal and silvicultural values and constraints to the production of *D. edulis*. The chapter ends with the research needs of *D. edulis*.

The core of the thesis, which is the practical and experimental work on *D. edulis* is made of two chapters (3 and 4). Chapter three focuses on material and methods used for the study. Chapter four deals with the results and discussion of the output data obtained throughout the thesis. Then the chapter ends with general discussions on *D. edulis* methodological approach to breeding (controlled pollination, fruits characterization and the decapitation test investigation), follows by a general conclusion, recommendations and suggestions for further research work on *D. edulis*.

CHAPTER I. INTRODUCTION

1.1-Background

The exploitation of natural resources has always constituted an important source of revenue for many households and communities in the developing countries. In the other hand, the degradation of these natural ecosystems due to demographic pressure, urbanization, mineral exploitation and unsustainability harvesting of both timber and non-timber forest products contribute to accelerate deforestation (World Bank, 2006; Tchoundjeu *et al*., 1998). Immediate consequences are lack of availability of wild fruits, medicinal plants and other plant and animal products. This exposes the most vulnerable segment of the communities, the aged, the poor, women and children, to malnutrition and reduced income, as traditionally their livelihoods partly depend on forest products (FAO, 2005; Ingram *et al.*, 2010). According to The World Resources (2005), almost half the world's population lives on less than $2 per day, more than a billion live on $1 or less. Nevertheless, a landmark meeting of the International Union of Forest Research Organizations in 1992 revealed how far Africa lagged behind in the area of tree domestication relative to Asia and the Pacific (Leakey and Newton, 1994). This information triggered a large increase in the amount of tree research being carried out in Africa (Leakey *et al.,* 2005a).

In Sub-Sahara Africa (SSA), Congo Basin forests which are ranked second after the Amazon as global biodiversity hotspot among major tropical wilderness areas (Mbolo, 2002; Hoare, 2007; McIntyre *et al*., 2009) are one of top priorities areas (De Wasseige *et al*., 2012). Moreover, in SSA, the deforestation rate is 1.7 % annually. Africa is the least forested tropical continent with only 21.4 % forest cover as a percent of land area in 2004 (FAO, 2007; Megevand *et al*., 2013), in comparison to South America, which has 47.7 % of its land in forests (McIntyre *et al.*, 2009). Furthermore, nearly 1 billion people live in chronic hunger (Bruinsma, 2009). Most of these are directly or indirectly dependent on agriculture. Growth in population is expected to result in even greater pressure on the smallholder agricultural sector, with the largest increases expected in areas of high food insecurity and dependence on agriculture, particularly in South Asia and Sub-Saharan Africa (Schmidhuber and Tubiello, 2007).

In Central Africa, about sixty-five million people live in or near these forests (Tchatat and Ndoye, 2006). The main staple foods in this area are cassava (*Manihot esculenta*), maize (*Zea mays*), plantain (*Musa paradisiaca*) and banana (*Musa sapientum*). More precisely in Cameroon, about 17 % of the population still live on less than $1 per day in rural areas, 50 % on less than $2 per day in peri-urban areas, and 40 % are under the national poverty line in urban areas (UNDP, 2008). According to the FAO (2011), between 2000 and 2010 the annual rate of deforestation of Cameroon's forests was estimated to be 1.04%. For food and income, these populations mainly rely on forest and agriculture and the most income generation is limited to few communities' cash crops such as cocoa, coffee and rubber, whose prices are determined internationally. Despite increased export opportunities, the combination of a weak technological environment, and weak price control and regulatory supply mechanisms generally made export crop farmers increasingly uncompetitive and vulnerable. As a result, relatively developed economies in West and Central Africa, like Cameroon, collapsed.

Against this background, there is an urgent need to diversify farmers' livelihood options through the development of sustainable poverty reduction and tree crop management strategies, such as tree domestication. Fruit tree domestication can be considered as a linear process from collection of fruits and seeds in natural forests to cultivation of improved trees species in specialized tree production systems such as monocrop plantations (Wiersum, 2008). Hence, efforts to improve the productivity of many species at the base of the diet of many populations (Charrier *et al.*, 2004; Okiror *et al*., 2011) constitute a source of major concern not only for research but also for the political (Leakey, 2012). Therefore, fruits and vegetables from the wild, protected trees and small woodlots of planted trees are crucial not only in providing protein to a generally malnourished people but also in generating cash incomes through trade in areas where few alternative sources of income exist (Janick and Paul, 2008; Glover *et al.*, 2010; Simbo *et al*., 2012). Improved production, uses and management of these wild foods especially fruit trees (domestication) is thought to be profitable to farm-households and the environment (Ayuk, 1997; Ayuk *et al.*, 1999). Consequently, new initiatives in tropical forest tree improvement aiming at developing cultivars of trees with desired fruit, nut and medicinal characteristics (Leakey and Newton, 1994; Franzel *et al.*, 1996, Simons and Leakey, 2004; Leakey and Page, 2006) are underway. Botanically, a fruit is a mature ovary; in this study, the term "fruit" or "fruit crops" refers to cultivated plant species in which some component of the fruit is used by humans (e.g., mature ovary, seed, and additional flower parts attached to the ovary).

The West and Central Africa region of the World Agroforestry Centre (ICRAF) covers a geographical area of 1200 million hectares, covering 21 countries with a population of over 330 million people. The region contains two main agro-ecological zones; the dry Sahelian zone, a semi-arid landscape stretching from Chad to Senegal and the Humid Tropics, spreading along the coast and extending to the central part of Africa (World Agroforestry Centre, 2011). In this region, over 90 % of rural people eat less than half of the FAO's recommended daily protein intake of 60 gms, and rely predominantly on the subsistence production of cereals, plantains and tubers mostly cassava as staple diets (FAO, 2007; Cribb, 2010). Across the region, 125 million (out of a total population of 308 million) people live in extreme poverty, are undernourished and their food deficit expressed in percentage of kilocalorie per person per day ranges between 160-390 kcal/person/day in Central Africa and 210-390 kcal/person/day in West Africa (FAO, 2009; 2010). Consequently, the diets lack essential nutrients (vitamins A and C as well as minerals: calcium, zinc, magnesium and iron). This situation resulted in the malnourishment of many leading to a high rate of infant mortality which is one of the highest in the world (UNAIDS, 2000; FICR-IFPRI, 2012). However, we must remember that agriculture is not the only cause of these statistics; wars and natural disasters also contribute to the misery of many people (Leakey, 2012).

It is worth nothing that from the Millennium Development Goals (MDGs) set by the Cameroonian government, the largest recorded in the international agenda is the eradication of extreme poverty and hunger (Schreckenberg *et al.*, 2006; National Research Council, 2008). One of the urgent actions to address this problem, according to the World Commission on Forests and Sustainable Development (WCFSD), is to provide more extensive support to community-based agroforestry, in order to reduce the exploitation of primary forests for subsistence products. In addition, there is an urgent need to contribute to the provision of ecological resilience and the maintenance of beneficial ecological functions. Thus, scientists, national governments, framers and non-government organizations (NGOs) must be able to break the traditional sectorial divide between "agriculture" and "forestry", and recognize "agroforestry" as farmer-led efforts to meet livelihood needs on a limited land base without categorical distinctions between "perennial" and "annual" components of their enterprise (Van Noordwijk *et al.*, 2003)

Moreover, the International Assessment of Agricultural Science and Technology for Development made a detailed study of the sustainability of agriculture and promoted the concept of multifunctional agriculture for enhanced environmental, social and economic sustainability (The Royal Society, 2009). This poverty-reduction and forest-protection strategy (Fig. 1) could be achieved through the development and cultivation of marketable and under-utilized "new crops" from these forests (Leakey *et al.*, 2005b; Simbo *et al.*, 2012, Leakey and Asaah, 2013).

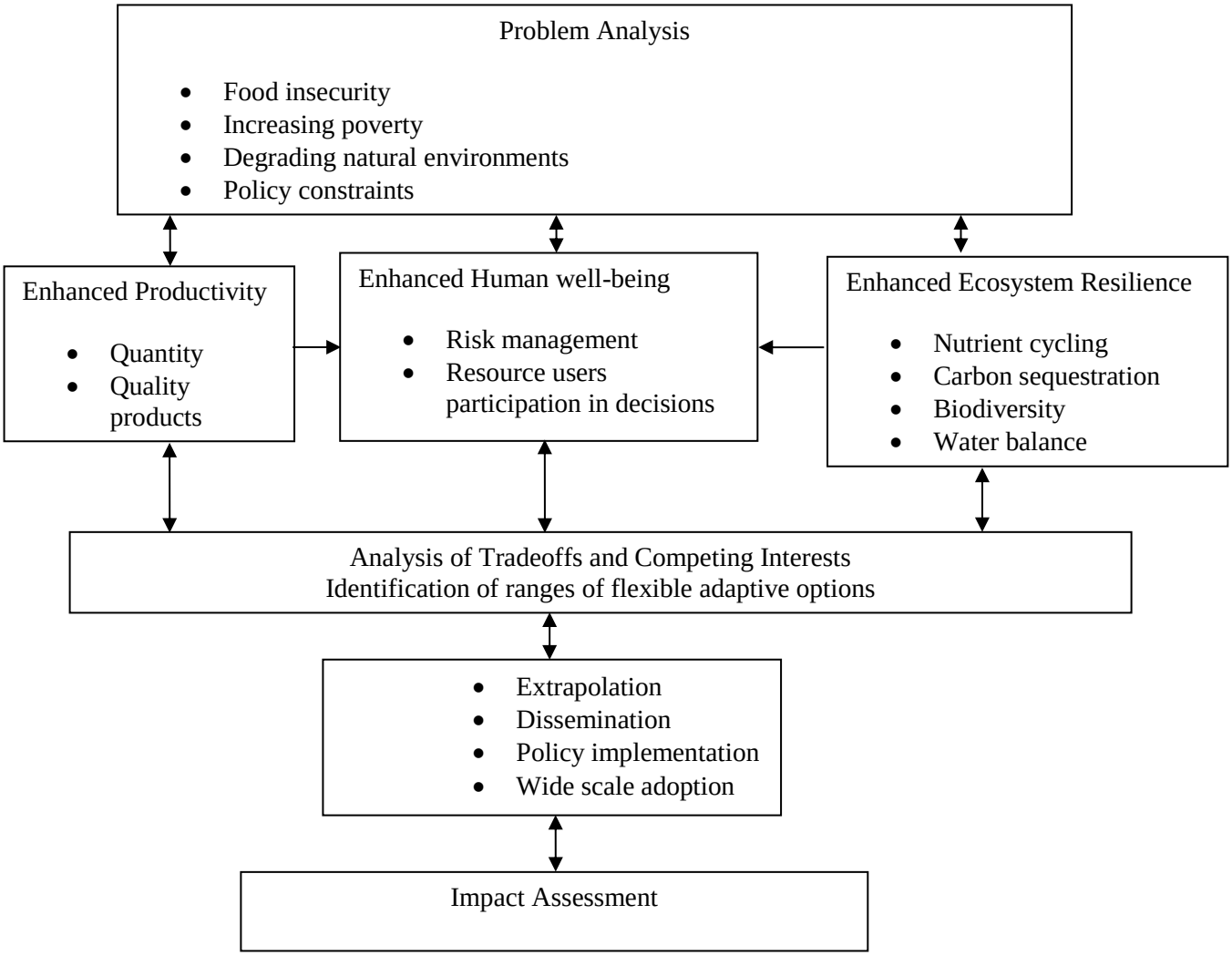


Fig.1. Integrated Natural Resource Management (INRM) approach (Adapted from Izac and Sanchez, 1998.

Therefore, participatory tree domestication, an approach that involves farmers, market traders and consumers in activities such as species prioritization, trait selection, germplasm collection and strain development has been well received (Simons and Leakey, 2004; Tchoundjeu *et al.*, 2006; Dawson *et al*., 2009). These initiatives are now beginning to show positive impact in terms of increased tree planting (Franzel and Scherr, 2002) and increased product quality (Tchoundjeu *et al*., 2004).

For the domestication strategy to be of benefit to the target farm population, it is worthy to note that it should be based on participatory approaches in decision making on both choices of species for domestication and the domestication approach to use (Leakey *et al*., 2003; Tchoundjeu *et al*., 1998). The use of participatory approaches has been observed to be an incentive to farmers adopting tree domestication as farmers see this as an opportunity to raise themselves out of poverty, malnutrition and hunger through enhanced livelihoods, food and nutritional security (Asaah *et al*., 2011b). This sets a solid foundation for participatory processes and ensures that domestication is a *farmer-driven* process with a local market focus in order to also ensure that farmers will be able to sell their products (Scherr, 2004; Tchoundjeu *et al*., 2008; Termote *et al*., 2011). The domestication of trees producing agroforestry tree products (AFTP) will promote food and nutritional security and contribute to achieving the UN Millennium Development Goals. Agroforestry practices developed by ICRAF in order to improve these indigenous fruit trees are mostly based on selection, collection and vegetative propagation through air-layering, cuttings and grafting techniques (Mialoundama *et al.,* 2002; Ofori *et al*., 2008; Dolor *et al.,* 2009; Tchoundjeu *et al.,* 2010a), of selected superior accessions with exceptional characteristics for domestication so called "plus trees".

In this region, ICRAF has implemented a research and development initiative to domesticate and commercialize indigenous fruit trees in nine West and Central African countries mainly: Cameroon, Nigeria, Democratic Republic of Congo (DRC) and Ivory Coast for the Humid Tropics zone; then Mali, Burkina Faso, Senegal, Niger and Sierra Leone for Sahelian zone (Tchoundjeu *et al.,* 2006). The philosophy of the ICRAF's Agroforestry Participatory Tree Domestication Program is to build on the desire of local people to cultivate indigenous fruits and nuts and enhance the ways in which communities promote food and nutritional security, increase household income, create employment and diversify farming systems and the rural economy. In participatory tree domestication, researchers work with communities to select species from their natural habitats and adapt them for cultivation on

farms (Islam *et al*., 2012). The procedure involves the identification, reproduction, adoption and diffusion of high quality and high market germplasm (i.e. seeds, seedlings, cuttings, grafts, etc). In fact, the goal of domesticating these trees is to increase their quality and productivity, and to create opportunities for marketing their products, so empowering smallholder-farming communities to conserve and cultivate them (Akinnifesi *et al.,* 2008; Weber *et al.,* 2009; Kalaba *et al.,* 2010). This is now seen as an important strategy to reduce poverty and hunger and to create employment opportunities in rural areas (Simons and Leakey, 2004; Termote *et al*., 2011).

Although tree domestication includes tree breeding, very little has been done to assess the level of genetic control in traits of interest in the tree species undergoing tree domestication in West and Central Africa. These species include indigenous fruit and nut trees such as *Adansonia digitata, Allanblackia* spp., *Balanites aegyptiaca, Irvingia gabonensis, Dacryodes edulis, Ricinodendron heudelotii, Chrysophyllum albidum, Garcinia kola, Cola* spp, *Annonidium mannii, Tamarindus indica, Vitellaria paradoxa, Ziziphus mauritiana and Detarium microcarpum.*

Others include oil tree species such as *Allanblackia floribunda* and vegetables including *Gnetum africanum*, *Moringa oleifera*; Spice specie such as *Afrostyrax lepidophyllus, Monodora myristica, Fagara heitzii, F. macrophylla,* and medicinal specie, mainly, *Annickia chlorantha, Khaya senegalensis, Pausinystalia johimbe* and *Prunus africna* (Table I).

In the Humid Tropics agro-ecological zone, studies are in progress to develop and fine-tune rooting of leafy stem cuttings and marcotting in these species, and quantitative descriptors of variation in fruits and seeds of *I. gabonensis* have been described by Leakey *et al.,* (2002a). These descriptors have been used to assess phenotypic variation in fruits and seeds of *I. gabonensis* and *D. edulis* in Cameroon and Nigeria (Leakey and Lapido, 1996; Waruhiu, 1999; Atangana *et al.,* 2001; Waruhiu *et al.,* 2004; Anegbeh *et al.,* 2005), and "plus trees" have been selected for domestication (Atangana *et al.,* 2001; 2002). For *D. edulis*, improvement in its breeding stock for cultivation, as well as its cultivation itself, are possible and would further increase the benefits and importance of the species. Additionally, studies on the organoleptic characteristics on *D.edulis* were conducted in Cameroon by Akamba (2000) and Kengni *et al.,* (2001), and in Nigeria by Emuh *et al.,* (2007).

In the Sahelian agro-ecological zone, many studies were undertaken to assess the phenotypic variation in fruits of *Adansonia digitata* (Assogbadjo *et al.*, 2011; De Smedt *et al.*, 2011; Kouyaté *et al.*, 2011; Parkouda *et al.*, 2012); *Tamarindus indica* (Diallo *et al.*, 2008; Fandohan *et al.*, 2011a); *Detarium microcarpum* (Kouyaté (2005; Ky-Dembele *et al.*, 2010a); *Vitellaria paradoxa* (Kelly *et al.*, 2004; Sanou *et al.*, 2006; Ugese *et al*., 2010; Okiror *et al.*, 2011); *Balanites aegyptica* var. *aegyptica* (Abasse *et al.*, 2010; Elfeel, 2010); *Ziziphus mauritiana* (Ouédraogo *et al.*, 2006; Kalinganire and Koné, 2011); *Khaya senegalensis* (Ky-Dembele *et al.*, 2010b) as well as *Blighia sapida* (Ekué *et al.*, 2010).

Table I. List of priority tree species included in tree domestication activities by the World Agroforestry Centre (West and Central Africa region).

Agro-ecological zone	Fruit/nut tree/species	Medicinal Plants	Spices species	Leaves
Humid Tropic Zone	*Dacryodes edulis* *Irvingia gabonensis* *Chrysophyllum albidum* *Anonidium mannii* *Allanblackia flroribunda* *Garcinia kola* *Cola* spp.	*Prunus africana* *Pausynistalia joyimbe* *Annickia chlorantha*	*Monodora myristica* *Afrostyrax lepidophyllus* *Fagara heitzii* *Fagara macrophylla*	*Gnetum africanum* *Moringa oleifera*
Sahelian Zone	*Adansonia digitata* *Balanites aegyptiaca* *Detarium microcarpum* *Tamarindus indica* *Vitellaria paradoxa* *Ziziphus mauritiana* *Blighia sapida*	*Kaya senegalensis*		*Adansonia digitata* *Moringa oleifera*

The importance of the contribution of local fruit trees to reduce the poverty has been recognized (Garrity, 2004; Kalinganire *et al.*, 2008; Pye-Smith, 2010a; Faye *et al.*, 2011; Adjoumani *et al.*, 2012). To diversify and intensify farmers' agroforestry systems, it is necessary to provide a wide range of marketable forest products in order to diversify their sources of income, improve their nutritional base and restore biodiversity. This intensification

can be done through the creation of new cultivars of different local products (Leakey *et al.*, 2003; Leakey and Page, 2006). To address this problem, a certain number of solutions exist including participatory domestication. Domestication of indigenous trees is a multidimensional process that involves identification, production, management and the adoption of the desired germplasm (Simons and Leakey, 2004; Degrande *et al.*, 2007). One of the main constraints for the production of these local species is lack of availability of improved germplasm (Akinnifesi *et al.*, 2007). In addition, germplasm is considered as the material being able to transmit the hereditary traits from one generation to the other, like spores, pollen, tissues or parts of plants, seeds, DNA or RNA (Engels and Visser, 2003; Bacchetta *et al.*,2007; Ferreira *et al.*, 2007).

In this view, it is appropriate to include in the list of exotic fruit trees widely cultivated (Leipzig, 1996), namely mango (*Mangifera indica*), avocado (*Persea americana*), pawpaw (*Carica papaya*) and citrus species (*Citrus* spp), indigenous species with high commercial value, selected according to farmers' preferences and their market potential. This is the case of *D. edulis* or African plum, which has been classified as a second priority species in the sub-region of Central and West Africa, after *I. gabonensis* (Mollet *et al.*, 1995; Franzel *et al.*, 1996).

In Cameroon, ICRAF has undertaken since 1998, a program on improvement and propagation of *Dacryodes edulis* (Tchoundjeu *et al.*, 2006) based on selection, collection and mass multiplication by vegetative propagation techniques well-developed of improved genotypes characterized by exceptional morphological, phenological, organoleptic and pomological fruit traits for domestication (Leakey *et al.*, 2002a; Kengni *et al.*, 2002; Waruhiu *et al.*, 2004; Tchoundjeu *et al.*, 2008). For *D. edulis* for instance, selection pressure by farmers is strong enough in some areas of the country such as the Southern region of Cameroon, where farmers from wild species selected 67 % of African plum trees (Schreckenberg *et al.*, 2006). Because of this empirical selection, unproductive male trees and trees producing fruits with sour taste are systematically eliminated.

The species has been reported to be amenable to vegetative propagation methods like air-layering and stem-cutting (Mialoundama *et al.*, 2002). In addition, the rooting system of vegetative propagate trees of African plum have been reported to be stable (Asaah *et al.*, 2010) and apparently less competitive for below ground resource compare to trees of seed origin (Asaah *et al.*, 2012). *In vitro* culture studies on African plum are not yet implemented

(Youmbi, 1991; Youmbi *et al.,* 1998; Youmbi, 2000). Despite the advantages of vegetative propagation techniques: which are hastening sexual maturity and giving the exact replicate of the desired mother-tree fruit characters, it is feared that they could severely narrow the genetic diversity and increase inbreeding within the species at farm level, ultimately leading to a decline in future production (Hollingsworth *et al.,* 2005; Van Tassel *et al.,* 2010). However, controlled hand cross-pollination may help to combine a number of desired fruit characters in one tree and increase the inter-tree variability between selected superior genotypes so called "plus trees" (Farah *et al.,* 2002).

Success in breeding for yield superiority of indigenous fruit trees is still constrained by the lack of availability of improved germplasm (Akinnifesi *et al.,* 2007). Improvement of indigenous fruit tree cultivars is drawing great attention from breeders (Adjoumani *et al.,* 2012). In some cases, a participatory approach to cultivar development is implemented with success (Leakey *et al.,* 2003). In the fulfilment of cultivars development for priority tree species, two key elements are (i) the identification of "plus trees" in natural populations and (ii) their propagation by vegetative techniques. Prior to "plus trees" identification, quantitative characterization of fruit, nut and kernel variation (Leakey *et al.,* 2005a), variation in nutritive value and other food properties (Leakey *et al.,* 2005b) have to be studied and an understanding of the interactions between different traits for multi-trait selection is needed (Leakey *et al.,* 2004).

Studies on African plum conducted especially in Nigeria (Anegbeh *et al.,* 2005) and Cameroon (Leakey *et al.,* 2002a; Waruhiu *et al.,* 2004) have revealed considerable phenotypic and genotypic variation and allowed selection of superior trees based on fruit and pulp weight, fruit width, pulp taste and pulp color.

1.2. Problem statement

Domestication of indigenous fruit trees has received far less attention than that of annual crop plants (Leakey and van Damme, 2014). In the wild, most tree species reach reproductive maturity after a long period of juvenility and even then, sexual reproduction appears sporadically, often in a mode of mating. Hence, improvement for tree production encounters a number of difficulties particularly in relation to ageing, slow growth, long juvenile phase, fruit production variability and lack of knowledge on the silviculture of the

species (Lovett and Haq, 2000). This perception has been aggravated by the limited understanding of the natural variability, reproductive biology, propagation and the lack of techniques for adding value and cultivation. Moreover, one of the major constraints in the production of local species is the lack of availability of good quality germplasm (Akinnifesi *et al.*, 2007). Likewise, knowledge of both pollination biology and breeding systems of indigenous fruit trees is essential for successful management and breeding programs. Such information may provide insights into the vulnerability of a species.

Recent research showed that the best ways for *D. edulis* mass propagation are leafy stem cuttings (95%) as compared to air-layering (80%) and grafting (12%). Unfortunately, in order to produce a great number of improved cuttings and/or marcots to satisfy farmers' needs, these techniques required a great number of improved trees to be submitted to high pruning. Despite the advantages of these vegetative propagation techniques, which lead to hastening sexual maturity (early fruiting), exact replication of the desired mother-tree traits or characters, easy reproduction of species whose seeds are difficult to collect and conservation of values species, it is feared that they could severely narrow the genetic diversity and increase inbreeding within the species at farm level ultimately leading to a decline in future production (Hollingsworth *et al.*, 2005; Duminil *et al.*, 2009; Van Tassel *et al.*, 2010). Inbreeding depression is the process by which self-or related-matings lead to homozygosity, the loss of heterozygote superiority and the 'exposure' of deleterious mutations (Boshier 2000; Lowe *et al*., 2005). Inbreeding depression reduces individual fitness and raises the possibilities of population and/or species extinction (Charlesworth and Charlesworth, 1987; Hansson and Westerberg, 2002; Reed and Frankham, 2003); indeed, the negative effects of inbreeding in trees are well documented and include embryo abortion, limited fruit set, reduced overall seed yield and lower germination rates for remaining seed.

Furthermore, selfed or inbred progeny can suffer from lower seedling vigor and poor growth form, and end up being less productive when they reach maturity (Stacy, 2001). Several authors have suggested, however, that genetic diversity levels may be relatively low within on-farm material, as a result of bottlenecks caused by collection of a limited number of maternal parents and widely varying sampling practices during propagation (Weber *et al.*, 1997; Kindt and Lengkeek, 1999; Hyten *et al.*, 2006; Olsen and Gross, 2008; Mariette *et al.*, 2010).

For the on-going breeding program initiated on *Dacryodes edulis* by ICRAF since 1998, most of the trees on farms are old and do not produce adequate fruits. Therefore, there is a need on enhanced production for the species. The options are either to rehabilitate old *D. edulis* trees to increase yields on farm or to replace the old trees with improved planting materials with shorter juvenile phase to first fruit production, and that will yield quality fruits of desired traits. All these, require that appropriate technologies and policies (Foundjem, 2013) are developed that could complement current domestication efforts on *D. edulis* and encourage the use of improved planting materials (derived from vegetative propagation methods) for any new plantings of the species. Furthermore, genetic resources' preservation in the species under domestication in West and Central Africa has been restricted to the establishment of vegetatively propagation gene banks in West and Central Africa countries, little work has been done in breeding. To date, this important fruit tree has been subjected to little genetic improvement due mostly to the lack of understanding of his pollination biology, breeding systems, genetic parameters and the infrastructure needed for genetic improvement. This information is vital for an efficient breeding strategy and prediction of genetic gains.

One of the ways to address the further improved planting materials is breeding through controlled hand cross-pollination. In fact, as cross-pollination is beneficial for fruit set (Brevis, 2005), this technique may help to combine a number of desired fruit characters in one tree and increase the inter-tree variability between selected superior genotypes so called "plus trees" onto which vegetative propagation could be undertaken for further mass multiplication and cultivar development. By so doing, the species' genetic basis could be better managed and conserved (Bretell *et al.,* 2004).

1.3. Research questions

This study will seek to answer the following questions:

- Does African plum fruiting efficiency depend on the parent provenance and the sex (male or hermaphrodite) of flowers that produced the pollen used for fertilization?
- Do controlled cross-pollination increases quality of the quantitative fruit traits of well-known African plum accessions? Which African plum's geographical provenance possesses best fruits traits for selection through controlled cross-pollination?

- Do seedlings obtained through controlled cross-pollination of African plum behaviors in the nursery depend on the provenance and the crossing to which they belong?

1.4. Hypotheses

- Control-pollinated fruits' quality and quantity within different provenances, from the "plus trees" are influenced by the parent provenance and the sex of flowers which produced pollen used for fertilization;
- F_1 hybrids from controlled pollination can be characterized and seedlings can be produced in the nursery for further seed orchards and clonal trial establishment;
- Decapitation of some young seedlings can produce early branching planting materials, which could be submitted to high pruning in order to produce a great number of improved cuttings;
- New cultivars could be produced through progeny trials establishment for further vegetative propagation of improved planting material through air-laying and leafy stem cuttings.

1.5. Objectives of the study

The main objective of this study is to beef up *Dacryodes edulis* tree breeding and genetic resources' preservation initiated by ICRAF throughout a tree improvement program, especially through hand cross-controlled pollinations and vegetative propagating techniques being developed in Cameroon. Specific objectives are three-fold:

- ❖ to develop methods for assessing controlled hand cross-pollination of *Dacryodes edulis* well-known accessions (plus trees);
- ❖ to characterize control-pollinated African plum fruits, produce F_1 seedlings in nurseries and establish seed and/or clonal orchards for further breeding improvement leading to the expression of the genetic gain in F_2 and F_3 generations (cultivar development);

- to assess the decapitation test in *Dacryodes edulis* control-pollinated seedlings and establish the relationship between branching habit, harvest index and yield improvement.

CHAPTER II. LITERATURE REVIEW

2.1. Agroforestry and tree domestication concepts

2.1.1 Agroforestry

2.1.1.1. Concept and terminology

Agroforestry is a relatively new subject for scientific study but a traditional practice with a long history in many parts of the tropics (Nair, 1989). Agroforestry has been further defined as the set of land use practices which involve the deliberate combination of woody perennials and herbaceous crops and/or animals on the same land management unit, in some form of spatial arrangement or temporal sequence, such that there are significant ecological and economic interactions between woody and non-woody components (Sinclair *et al.*, 1994). A new definition of agroforestry has been proposed: "A dynamic, ecologically-based natural resource management system that, through the integration of trees in farms and in the landscape, diversifies and sustains smallholder production for increased social, economic and environmental benefits for land users at all levels" (Leakey, 1996). By synthesizing the different definitions used by ICRAF, Huxley and Van Houten (1997) believe that the agroforestry land use is the deliberate combination or alternation cultivation of woody and non-woody (sometimes animals) in order to generate multiple products and services. These systems are increasingly recognized as important options for smallholder livelihoods, with neutral-to-positive environmental impacts (Leakey, 2010). Additionally, as pointed out by Termote *et al.,* (2011), agroforestry provides unique outputs not often provided by other systems which include:

(i) provision of indigenous products from underutilized species for food and markets to generate income and enhance nutritional/health status;

(ii) restoration of integrated agro-ecosystems of diverse plant species with the potential of developing into natural woodlands and forests and;

(iii) maintain linkages with human cultures through the availability of traditional foods and other products important to local people.

2.1.1.2. Advantages of agroforestry practices

The cultivation of high-value trees on-farm represents an opportunity of contributing to household food security as well as generating income (Simons and Weber, 2000; Weber *et al.,* 2001; Russel and Franzel, 2004; Kalinganire *et al.,* 2008; Tchoundjeu *et al.,* 2010b). Agroforestry practices are widespread in the tropics and used by more than 1.2 billion people (FAO, 2005). Many studies shown that agroforestry can deliver a wide range of benefits for the livelihoods of millions of people in developing countries (Leakey *et al.,* 2003; Tchoundjeu *et al.,* 2006; Glover *et al.,* 2010; Pye-Smith, 2010a). The area under agroforestry worldwide has not been exactly determined, but is estimated that over one billion hectares (46 %) of farmland have more than 10 % tree cover, thus concerning about 30 % of all rural people worldwide (Zomer *et al.,* 2009).

Compare to other sustainable forest management systems, in agroforestry systems, different species fulfil diverse functions as providing food, medicine, fodder, timber and income generation from the sales of surplus food stuffs energy, cash crop products and extracted agroforestry tree products (AFTPs) such as fruits, nuts, leaves, bark, etc. to billions of farmers. This constitutes an advantage of optimizing the trade-offs between farmers' private benefits and those of the global environment (Shackleton *et al.,* 2003; Mbile *et al*., 2005; Schrenkeberg *et al.,* 2006). An important ecological basis for yield advantages through the intimate integration of trees with agricultural crops in agroforestry is that the combined system will utilize environmental resources more efficiently than monocultures through niches differentiation in space and time (O'Neil *et al.,* 2001; Roshetko, 2013). Another potential benefit of agroforestry is the diversification of species grown on-farm (Simons and Weber, 2000).

For undomesticated trees with potential for exploitation, the best place for conservation is cultivation (Simmonds, 1987), but agroforestry may involve a reduction in genetic diversity, when compared with the natural vegetation it may replace (Kindt and Lengkeek, 1999; Hollingsworth *et al.,* 2005; Duminil *et al.,* 2009). Agroforestry is a delivery mechanism of multifunctional agriculture (Leakey, 2010) as the latter allows to and actually does better address the issues of: (i) restoration of soil fertility; (ii) rehabilitation of degraded land; (iii) restoration of above and belowground biodiversity; (iv) sequestration of carbon (Atiojio *et al*., 2014) and (v) protection of soils and watersheds. Overall, agroforestry practices could roll back deforestation and soil depletion, as well as increase, stabilize and

diversify farmers' income, and improve health care in rural areas through domestication of high-value trees and/or plants (fruit, culinary, timber, medicinal, fodder, etc.).

2.1.2. Tree domestication

2.1.2.1. Concept and terminology

The process of "domestication" which has been applied so successfully to agricultural and horticultural crops (Leakey and Newton, 1994; Tchoundjeu *et al.,* 1999) is a result of management, selection and cultivation of useful forest species by indigenous people for subsistence purposes and it is as old as that of human kind's use of forest ecosystems. In other words, it is a process that includes a wide range of activities - exploration and collection of natural populations, evaluation and selection of suitable species and provenances, breeding to develop superior cultivars, development of propagation techniques, multiplication and dissemination of germplasm, development of management techniques, utilization and tree product marketing, and development and dissemination of relevant technical information (Leakey and Newton 1992; Luukkanen 1998) cited by Apiah (2003).

Efforts are necessary to domesticate a large number of tree species producing agroforestry tree products (AFTPs) collected in the wild. It is a matter of avoiding serious erosion of genetic diversity, extinction and overuse of indigenous plants, on the one hand, while ensuring their availability and quality assurance on the other (Trouche, 2001; Fok and Bachelier, 2004; Emshwiller, 2006; Duminil *et al.*, 2009; Van Taseel *et al.*, 2010).

The interest in the domestication of trees is growing both:

(i) in Latin America (Weber, 2001; Hollingsworth *et al.,* 2005; Rochon *et al.,* 2007; Dawson *et al.*, 2008; Ugarta Guerra, 2010);

(ii) South-East Asia (Singh *et al.,* 1997; Singh, 2001; Dani *et al.*, 2009) and

(iii) in several regions of tropical Africa (Maghembe *et al.,* 1998; Lovett and Haq, 2000; Muchugi-Mwangi, 2001; Leakey *et al.,* 2002b; Thiong'o *et al.*, 2002; Nwase *et al.*, 2006; Kadzere *et al.,* 2006; Mng'omba, 2007; Mujaju et Chakauya, 2008 and Sotelo Montes *et al.*, 2010).

Plant domestication is an evolutionary process operating under the influence of human activities (Harlan, 1992: Emshwiller, 2006; Gross and Olsen, 2010). Over time, artificial selection causes cultivated populations to diverge morphologically and genetically from their wild progenitors (Zohary and Hoppf, 2000; Pickersgill, 2007; Gunn *et al.,* 2010). Domestication of plants began with agricultural crops around 10,000 years ago, when humans began the deliberate selection of desired variants in cereals, cucurbits and pulses (Shull, 1909; Duvick, 2001; Gepts, 2002; 2004; 2006; Baenziger *et al.,* 2006; Chalapathy *et al.,* 2009; Gross and Olsen, 2010; Miller and Gross, 2011).

The domestication of tree species is a "dynamic process which develops from deciding which species to domesticate and proceeds through background socio-economic studies, the collection of germplasm, genetic selection and improvement, to the integration of domesticated species in land use systems" (Leakey and Newton, 1994a; Leakey and Jeanicke, 1995). A modified definition was proposed as "Domesticating agroforestry trees involves accelerated and human-induced evolution to bring species into wider cultivation through a farmer-driven or market-led process". This is an iterative procedure involving the identification, production, management and adoption of desirable germplasm (Howe *et al.,* 2003; Lyle, 2006; Marcano *et al.,* 2007; Ross-Ibarra *et al.,* 2008). Domestication can occur at any point along the continuum from the wild to the genetically transformed state. Farmers domesticate trees by bringing the min to cultivation, adapting them to their needs and environmental conditions by deliberately or inadvertently selecting for certain characteristics and applying particular management strategies (Leakey, 2012). Domestication of AFTPs trees in agroforestry systems is a multifaceted process in which a progressively closer interaction between the tree resource and people takes place (Degrande *et al.,* 2007; Tchoundjeu *et al.,* 2008).

2.1.2.2. Domestication process

Domestication is an on-going process in which genetic and cultivation improvement are continuously refined (Van Tassel *et al.,* 2010; Miller and Gross, 2011). Two principal pathways are generally distinguished in the domestication strategy for most agroforestry species in smallholder farming systems in the tropics. These include:

- Phase 1: domestication is implemented on farm by farmers, who bring trees into cultivation themselves (Leakey *et al*., 2004) or through genetic improvement program

on research stations (Leakey and Simons, 1998). Increasingly, scientific approaches are also being introduced into on-farm domestication through the application of participatory approaches to tree improvement;

- Phase 2: here, researchers mentor and advise farmers, and sometimes implement and monitor joint on-farm research. Among the advantages of the use of participatory approaches are the benefits of building on tradition and culture while promoting rapid adoption by growers to enhance livelihood and environmental benefits (Tchoundjeu *et al*., 2006; 2008). The bottom-line is that both domestication pathways should strive to meet traditional as well as emerging market opportunities for the species (Leakey and van Damme, 2014).

For the domestication strategy (Fig. 2) to be of benefit to the target farm population, it should be based on participatory approaches in decision making on both choices of species for domestication and the domestication approach to use (Tchoundjeu *et al.,* 1998; Franzel *et al.,* 1996; Leakey *et al.*, 2003). The use of participatory approaches has been observed to be an incentive to farmers adopting tree domestication as farmers see this as an opportunity to raise themselves out of poverty, malnutrition and hunger through enhanced livelihoods, food and nutritional security (Asaah *et al.*, 2011a). This sets a solid foundation for participatory processes and ensures that domestication is a farmer-driven process with a local market focus in order to also ensure that farmers will be able to sell their products (Tchoundjeu *et al.*, 2006; 2008; Sahara *et al.*, 2011; Degrande *et al.*, 2012).

Wiersum (1996) has identified three stages in the domestication process:

- the change from uncontrolled utilization of the wild trees products to their controlled exploitation;
- the purposeful cultivation of wild trees in either a resource-enriched natural environment or in indigenous agroforestry systems such as forest gardens;
- the cultivation of domesticated trees in either agroforestry systems or commercial tree-crop plantations.

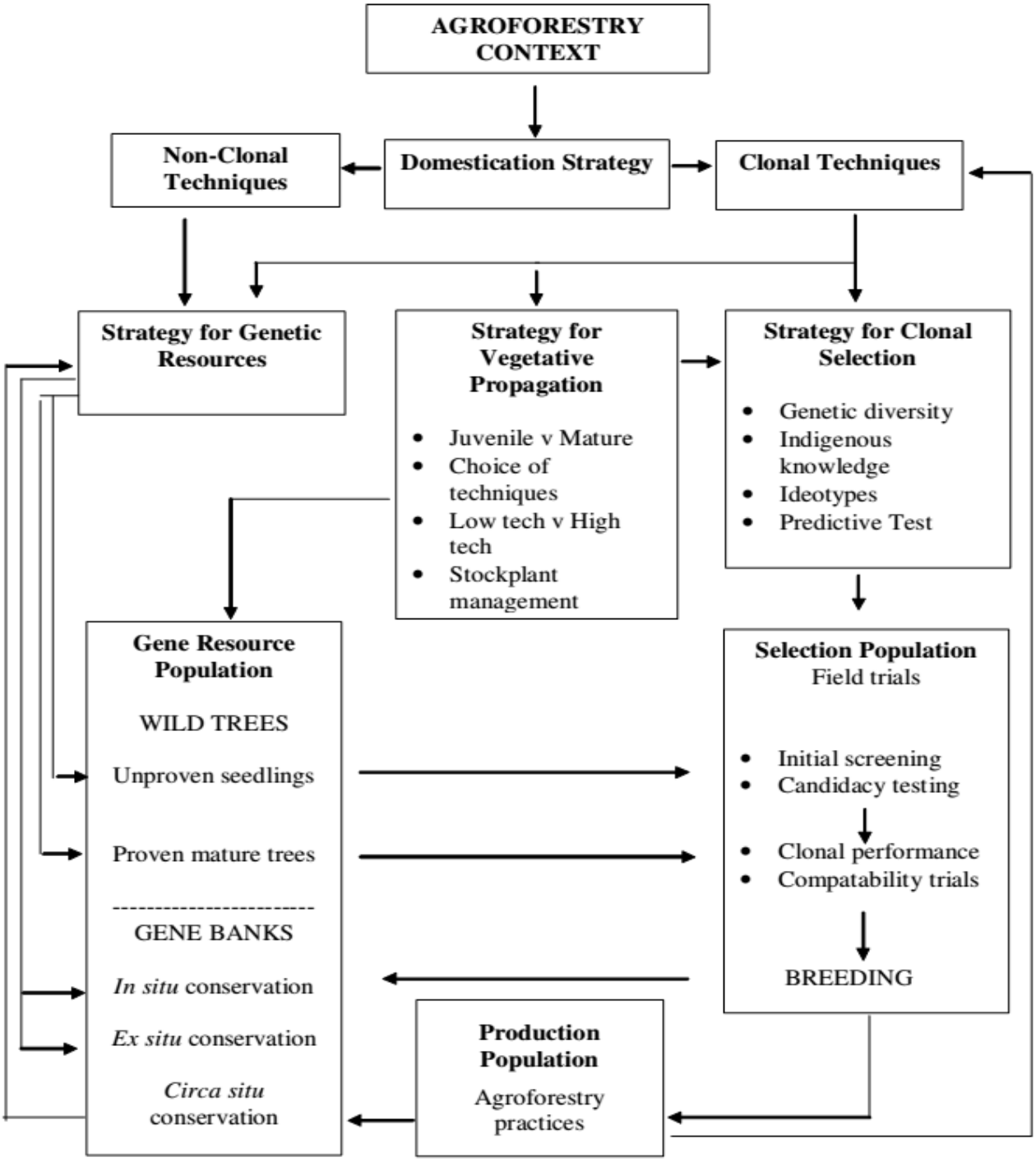


Fig. 2**:** Domestication strategy for agroforestry trees (after Leakey and Akinnifesi, 2008 and White, 1987), adapted from Leakey *et al*. (2009).

The three domestication stages are associated with specific socio-economic and ecological environment (Mbile *et al.,* 2005). ICRAF's approach for domestication is more participative as farmers are fully involved in the design and implementation of the program. The steps are as follows:

The first participatory approach to domestication step is the selection of priority indigenous fruit tree species based on farmers' preferences and market orientation (Franzel *et al*., 1996; 2008). This is to ensure that the outputs of the domestication process are relevant to farmers' needs and by so doing stimulates their active interest and involvement. This model developed by ICRAF and its partners has been repeated in the semi-arid lowlands of West Africa and in the Peruvian Amazon. Fortunately, almost everywhere in the world where this priority setting has been done, farmers have selected familiar and locally-marketed indigenous fruits and nuts as their top priority (Leakey and Asaah; 2013). This is probably because most traditionally important products are no longer readily available in the wild and are important domestically to rural people because of their cultural and nutritional value.

The second step is the identification of superior or elite trees based on established criteria by users, marketers and market preference (tagging and naming trees for purpose of ownership and property right recognition); for any domestication program, this step is the collection and maintenance of a wide range of genetic diversity. Tree germplasm can be collected for many reasons: because there is a need of planting material for users, for conservation of species endangered by deforestation and for capture of genetic variation of undomesticated species as this is needed for the selection and improvement that are part of domestication (Dawson and Were, 1997). These collections must be conformed to the requirements of the Convention on Biological diversity and the rights of sovereign states and the rural people (Engels and Visser, 2003; Williams *et al.,* 2003; Bacchetta *et al.,* 2007).

The third step in a participatory approach to domestication consist of development and applying efficient vegetative propagation and nursery management techniques for producing quality propagules of on-farm dissemination; After capturing the genetic variation in natural stands through germplasm collection, vegetative propagation (regenerating plants from vegetative parts of a stockplant) can proceed as a part of the domestication process to select for desirable characteristics found in wild tree populations (Tchoundjeu *et al.,* 1997). For outcrossing species with additively controlled genetic traits, in order to mass-produce and

maintain the superior traits of the selected germplasm, the plants have to be propagated vegetatively through grafting, marcotting or rooting of stem cuttings. Vegetative propagation techniques can be used to circumvent problems of poor and erractic seed supply or production. Rooting of stem cuttings is the most common vegetative propagation technique used for commercial forest trees (Tchoundjeu, 1989) and in the domestication of agroforestry tree species (Tchoundjeu *et al.,* 2010a). The development of low technology non-mist propagator for the propagation of tropical trees by stem cuttings (Leakey and Longman, 1988; Leakey *et al.,* 1990) allows the production of large numbers of individual clones (Leakey and Jeanicke, 1995).

The fourth step is the integration of improved germplasms into farming systems; it aimed at empowering local communities, promoting food self-sufficiency, generating income and employment, and enhancing nutritional benefits. By providing knowledge and training, farmers are assisted to develop the right skills to set up tree nurseries and apply simple researched, adapted and adoptable approaches to nursery management, mother tree selection and horticultural techniques of vegetative propagation (rooting of stem cuttings, grafting/budding, marcotting or air-layering). For example, after about 12 years, the number of communities that engaged in this approach under ICRAF's guidance in Cameroon has grown from 2 pilot villages to 485 villages centred on five Rural Resource Centres and involving about 7100 farmers (Asaah *et al*., 2011b; Degrande *et al*., 2013; Takoutsing *et al*., 1013).

The fifth and latest step in a participatory approach to domestication is post-harvest handling, processing and marketing research of fresh and processed products from domesticated species. The domestication of trees for agroforestry approaches to poverty alleviation and environmental rehabilitation in the tropics depends on the expansion of the market demand for non-timber products. Therefore, research on the processing and commercialization of AFTPs are part of domestication strategies of these tree species. In order to provide farmers and AFTPs collectors with valuable alternatives income-generating opportunities from sales of fruit, nut, leave, and medicinal tree products, markets research are underway (Facheux *et al.,* 2006; Leakey and van Damme, 2014).

According to the Convention on Biological Diversity (Williams *et al.*, 2003; Bacchetta *et al.*, 2007), another important element of the village-level participatory domestication strategy is its recognition of the rights of local people to their indigenous knowledge (German *et al.*, 2010) and traditional use of native plant species. Protection of farmers' intellectual property rights is needed to ensure that participatory domestication by local farmers can be recognized as a valuable model of biodiscovery (recognizing and patenting farmers' indigenous best practices) rather than biopiracy by expatriate or local entrepreneurs (Asaah, 2012). Farmers' rights remain at risk of being exploited until global negotiations create an effective means of protecting the intellectual property (Kalaba *et al.*, 2010; Lombard and Leakey, 2010).

2.1.2.3. Advantages and constraint of tree domestication

Domestication results in the spread of the species from their natural range to be introduced elsewhere around (Weber *et al.*, 1997; Leakey and Tomich, 1999). Strategic approaches to domestication can help avoid the potential pitfalls of traditional methods, such as the propagation of materials of insufficient genetic variation, or the use of poor quality or maladapted materials because good sources of adapted germplasm are scarce (Weber *et al.*, 1997). Through agroforestry and the domestication of an increasing number of tree species, it should be possible to make smallholder farming both more biologically diverse and more rewarding economically (Hollingsworth *et al.*, 2005; Faye *et al.*, 2011; Weber *et al.*, 2011). Some tree species have the potential to become high-value cash crops for large numbers of farmers and are capable of producing significant export earnings as inputs for international pharmaceutical or food processing industries (Tchoundjeu *et al.*, 2006). With appropriate selection strategies, farmers can achieve improvements in timber-tree form, fruit quality and other commercially important traits (Leakey *et al.*, 2004; Akinnifesi *et al.*, 2007; 2008; Leakey *et al.*, 2008). The challenge is to determine efficient methods for characterizing variation, and selecting the best genetic material for agroforestry systems (Leakey *et al.*, 2000).

A key constraint to the domestication of agroforestry trees is that they are predominantly out-breeders therefore a constant mating of related/unrelated parents trees of the same species with diverse attributes. This means that gains resulting from crosses of parent trees in any given trait of interest for example size, color, pulp tickness, etc. are on average small because of the wide range of intra-specific variation in the progeny arising from

uncontrolled cross-pollinations. Additionally, the long juvenile phase to fruiting of many tree species (10-20 years), means that breeders have to wait multiple years (sometimes decades) before fruits can be evaluated, selected and cultivated. Fortunately, these problems can be circumvented through clonal multiplication (rooting of stem cuttings, marcotting, grafting etc.) of individual trees of a given species with superior characteristics. In fact, major constraints to tree domestication are lack of quality germplasm, knowledge regarding propagation and management, slow growth rates and policy disincentives (Murdiyarso *et al*., 2002; Foundjem Tita, 2012).

2.2. Germplasm characterization

The conservation and use of plant genetic resources are essential to the continued maintenance and improvement of agricultural and forestry production and thus, to sustainable development and poverty alleviation (Jarvis and Hookin, 2000; Russel and Franzel, 2004; Pye-Smith, 2010b; Glover *et al.*, 2010). The importance of plant genetic resource to global food security as well as to the security of the livelihood of millions of rural families was underlined at the first United Nations Conference on the Human Environment in Stockholm in 1972 (Ngo Mpeck, 2004). It is well known that considerable variation exists within and between populations of tropical trees (Brown and Brubaker, 2000; Diallo, 2002; Peprah *et al.*, 2009). To manage germplasm resources effectively, in terms of exploitation and conservation of biodiversity, knowledge of the genetic diversity present in natural populations is required (Barrett and Kohn, 1991; Brodie *et al.*, 1997; Asaah *et al.*, 2003; Ceccarelli *et al.*, 2003; Roussel, 2005; Moose and Mumm, 2008). Moreover, population genetic variability should be determined in order to formulate an appropriate conservation strategy, as the conserved populations should be representative of the genetic variation in the natural population (Simons *et al.*, 1994; O'Neil *et al.*, 2002; Engels and Visser, 2003; Avana *et al.*, 2004; De la Bandera and Trasevet, 2006; Dawson *et al*., 2009).

There has been little systematic assessment of genetic variability or evaluation of the spatial distribution of diversity within the gene pools of agroforestry tree species (Atangana *et al.*, 2002; Ngo Mpeck *et al.*, 2003; Kelly *et al.*, 2004; Anegbeh *et al.*, 2005; Diallo *et al.*, 2008; Elfeel, 2010; Assogbadjo *et al.*, 2011). Descriptive information about genetic variation between and within species is increasing rapidly using biochemical, cytological and molecular

markers. Nevertheless, how these variations are functionally related to the phenotypic expression of traits is still little known (White and Powell; 1997; Ruotsalainen and Lindgren, 1998; Muluvi *et al.,* 1999; Hughes *et al.,* 2002; Leberg, 2002; Weber *et al.,* 2009).

2.3. Morphological characterization

In any tree improvement program, particularly in the case of indigenous species, an important step is the definition of selection criteria (Franzel *et al.,* 1996; 2008; Fandohan *et al.,* 2011a). Traditionally, genetic resources have been characterized using a combination of morphological traits, particularly agro-morphological characteristics of direct interest to users. These techniques have been used for some fruit tree species such as apple (*Malus sylvestris*; Coart *et al.,* 2003), grape (*Vitis vinifera* subsp. *sylvestris*, Aradhya *et al.,* 2003; Myles *et al.,* 2011), olive (*Olea europea* subsp. *europea* var. *sylvestris*; Lumaret *et al.*, 2004; Baldoni *et al.,* 2006), sweet cherry (*Prunus avium*; Mariette *et al.,* 2010). These techniques have also been used for tropical trees such as *Theobroma cacao* (Lopez-Baez *et al.,* 1998; Crouzillart *et al.,* 2000; Motamayor *et al.,* 2002; 2003; Asare, 2005; Marcano *et al.,* 2007), and coffee (*Coffea* spp; Amidou *et al.,* 2007).

The same techniques have also been used for description of variation for many crops such as: tomato (*Solanum lycopercicum*; Cong *et al.,* 2002; Bay and Lindhout, 2007); maize (Yu *et al.,* 2008); wheat (*Triticum* spp; Jacquard, 2007); rice (*Oryza sativa;* Egerson and Golin, 2003; *Oryza glaberrina*; Li *et al.,* 2011); sorghum (*Sorghum bicolor*; Casa *et al.,* 2005); common bean (*Phaseolus* spp.; Chacon *et al.,* 2005; Kwak and Gepts, 2009; Spataro *et al.,* 2011); soybean (*Glycine max*; Li *et al.,* 2010); bean (*Vicia faba*; Yahuza, 2012); chiles (*Capsicum anuum*; Aguilar *et al.,* 2009), including fleshy roots and other belowground materials such as cassava (Dupitié *et al.,* 2007; Clement *et al.,* 2010), and sweet potato (*Solanum tuberosum*; Scurrah *et al.,* 2008).

Phenotypic characterization studies on *D. edulis* fruit traits (fruit length, width and pulp thickness) (Leakey and Lapido, 1996; Leakey *et al.,* 2002a; Waruhiu *et al.,* 2004) in wild and planted village populations in Cameroon and Nigeria, observed a frequent occurrence (about 80 %) of intraspecific variation in the above-measured fruit traits. The observed tree-to-tree variation in fruit size was 3-to-10-fold (Waruhui *et al*., 2004; Anegbeh *et al*., 2005).

Findings from these studies are not in line with those reported by Okafor (1983), who claims the existence of two varieties, var. *edulis* with large fruits and var. *parvicarpa* with small fruits, there is continuous variation in the fruits and thus there is no indication of any distinct varieties. Furthermore, Youmbi *et al.*, (1989), Ndoye *et al.*, (1997) and Silou (2000) characterized *D. edulis* fruits into size classes for market studies. Interestingly, this variation is greatest at within village level, while variation between villages is modest; suggesting that genetic diversity at species level can be maintained by village level domestication (Leakey *et al.*, 2002a; Waruhiu *et al.*, 2004; Anegbeh *et al.*, 2005). In the same way, cultivar development at village level will also minimize loss of genetic diversity as selected cultivars developed in different villages will all have for example large fruits for *D. edulis* whereas at the same time they will be genetically diverse in all unselected traits, such as pest and disease resistance, etc., especially when wild populations remain present nearby. This could therefore be another advantage of implementing a participatory domestication strategy independently in different villages. Furthermore, this intra-specific variability and the household and market demands for high quality fruits have led most farmers interested in the production of *D. edulis* fruits to engage themselves in the selection of elite trees in their farms (Kengue *et al.*, 2011).

A descriptive study on the variability in the shape and color of *I. gabonensis* fruits was used to assess morphological variations in vegetative and reproductive characteristics of this species (Ladipo *et al.*, 1996). Recently, methods for the quantification of the variation in the fruit, nut and kernel traits have been developed for *I. gabonensis* (Leakey *et al.*, 2000; Atangana *et al.*, 2001). For *Ricinodendron heudelotii*, variations in fruits morphology, seeds number per fruit and seed weight between provenances in southern Cameroon were investigated (Fondoun *et al.*, 1999). The long generation time of most perennial crops also indicates that many of the morphological descriptors can only be assessed at maturity (Weber *et al.*, 2001). Furthermore, most of the vegetative characteristics used as descriptors can only be assessed at maturity and are greatly influenced by the environment (Simons *et al.*, 2000).

Additionally, modern molecular techniques are useful in the development of a more informed strategy for the maintenance of genetic diversity. In fact, molecular and biochemical markers that are not subjected to environmental influences provide an alternative approach for evaluating more precisely the relationship between accessions in crop plants (Duvick, 2001; Singh, 2001; Zhebentyayeva *et al.*, 2003; Sikdar *et al.*, 2010), and trees (Andrade *et al.*, 2009; Dani *et al.*, 2009; Matallana *et al.*, 2009). Within the geographic range of a particular

species they can be used to identify "hotspots" of intraspecific diversity (e.g. Assogbadjo *et al*. (2006), suggested *in* or *ex situ* conservation options for *Adansonia digitata*, and Lowe *et al*. (2000), for *Irvingia* species. Pauku *et al*. (2010), reported in *Barringtonia procera* in Solomon Island that genetic diversity within 5 sampled populations was 87 % whereas between populations was 13 %. This suggests that trees selected for their large kernels are most likely not to be unrelated, so providing opportunities to develop superior cultivars without severely narrowing intraspecific genetic diversity. With a good understanding of intraspecific variation in all traits of importance for selection and improvement to meet different market opportunities, clonal approaches can then be used for improvements in yield and quality traits (Leakey *et al*., 2005ac; Miller and Gross, 2011). Furthermore, hotspots that should, whenever possible, be protected for *in situ* genetic conservation, or be the source of germplasm collections if *ex situ* conservation is required can be identified. Definitely, the development of molecular technologies has resulted in alternative DNA-based procedures that give geneticists powerful new tools to use in the analysis of genes and their effects on phenotypes (Muchugi-Mwangi *et al*., 2008).

2.4. Sexual propagation

Sexual or generative propagation is the regeneration of trees from seeds. This is the method used by most rural farmers to multiply their elite trees. The major inconvenience associated with generative propagation is the bi-parental origin of the offspring, which does not usually allow for the exact copying of a desirable parental trait. For tropical trees, breeding and propagation by seed have usually been the method of multiplication. Seed is the easiest and cheapest method of propagation and is generally considered as the default approach, unless other considerations apply (Rao *et al.,* 2006). Seed is the natural vehicle for gene dispersal and has advantages in *ex situ* gene conservation, being easily manipulated and immediately available for seedling production. Sexual propagation has been successfully used in the process of natural regeneration of several local tree species (Mapongmetsem, 1994; Guedjé, 2002; Avana, 2006). However, a consideration of high importance in deciding practical handling methods is the storage physiological category of the seed: "orthodox" seed can be stored dry and cold, whereas "recalcitrant" seed cannot be dried to low moisture contents without loss of viability and so must be stored moist (ICRAF data, unpublished).

With regard to *D. edulis*, a tree with large fruits may not be homozygous (seed heterozygosis), thus there is a possibility that seeds from such a tree germinate and grow into a plant that produces small fruits (Kengue, 2002). For this species, some seeds do not germinate especially when they are planted a week after harvest (Youmbi *et al.,* 1994a). It is very difficult to conserve seeds for more than 7 days (Kengue, 1990). Other seeds have a long latency period that can reach 3 months (Vivien and Faure, 1996). Such seeds are very vulnerable to disease (fungi) and insect (termite) attack. In addition, generatively propagated trees take long (about 7 years) to bear the first fruits (Kengue, 2002). However, this method allows for the improvement of trees that perform poorly in some traits through cross-fertilization.

In other hand, there are a number of circumstances that may limit or even eliminate the option to propagate trees from seed. Although propagation by seed is the main method of plant multiplication, availability of quality seed is a major constraint affecting planting (Kang, 2001). Problems that prevent the use of seed can be broadly classified as irregular or infrequent flowering and seed unviability and/or dormancy (Mapongmetsem, 1994; Avana, 2006). For some species, seed is produced only at intervals of between 2 and 5 years in any particular location, creating difficulties in acquiring material (Leakey and Newton, 1994). Often the main reason for using seeds is of progenies, which are not true to type. Although sexual reproduction of woody plants has been the dominant theme both evolutionarily and throughout the history of human agriculture, woody plants have evolved a diverse array of vegetative reproductive strategies as well (Tsobeng *et al.,* 2011). Vegetative propagation offers the opportunity rapidly to overcome these limitations, by circumventing the need for sexual reproduction and facilitating the capture of individual genotypes (Leakey *et al.,* 1994).

2.5. Vegetative propagation

Vegetative propagation, as a mean for reproducing selected plants from vegetative organs is not new, but in fact, it goes back not just centuries but millennia (Tchoundjeu *et al.,* 1997). Written records of vegetative propagation of more than 2000 years have been reported. Vegetative propagation is defined as the regeneration of new individuals from vegetative organs such as stems, roots, leaves, buds and even single cells (Jaenicke and Beniest, 2003). For the purpose of producing plants that are true-to-type, the domestication strategy adopted

in agroforestry tree domestication is the clonal propagation approach based on well-known horticultural techniques of vegetative propagation (Leakey, 2004b; Tchoundjeu *et al.,* 1998; 2000) applied in a simple, robust and low-tech manner (Leakey and Longman, 1988; Leakey *et al.,* 1990), so as to be appropriate for implementation in remote areas of tropical countries which lack reliable supplies of running water or electricity but also other basic resources.

The advantage of using clonal propagules outweighs those of seedlings especially when the products are of high nutritional or income value, or when the tree has a long juvenile phase before first fruiting, and when seeds are scarce, difficult to germinate or difficult to store (Tchoundjeu *et al.,* 2006; 2008; Leakey and Akinnifesi, 2008). The resultant uniformity in the eventual crop is advantageous in terms of maximizing quality, matching market specifications and increasing (if this has been a selection criteria) productivity, but it increases the risks of pest and disease problems. Therefore, risk aversion through diversification of initial clonal production population is a crucial component in the domestication strategy adopted. However, through agroforestry, risk aversion can also be achieved by diversification of the agro-ecosystem by introducing other species and food crops in order to improve the overall agro-ecological system functions (Leakey, 2010).

Vegetative propagation techniques can also be very important as part of a tree improvement program because superior genotypes can be efficiently and economically multiplied (Vallejo-Marin *et al.,* 2010). There are number of different forms of vegetative propagation: grafting, budding, marcotting or air-layering, rooting of root and leafy stem cuttings, and also root suckering and tissue culture (Hartman *et al.,* 2002). Several of these techniques have the disadvantages of a low rate of multiplication, a high requirement for skilled labor, or the need for high capital investment (Leakey *et al.,* 1994). Apomixis is a special case of naturally occurring asexual reproduction in which seed is produced that contains an asexual (not zygotic) embryo which arose from mitotic division of maternal cells in flower associated tissues, rather than by fertilization of a maternal egg cell by pollination (Grossniklaus *et al.,*2001; Koltunow et Grossniklaus, 2003; Jacquard, 2007).

2.5.1. Propagation by air-layering techniques or marcotting

Layering involves induction of adventitious roots along a portion of the shoot of an intact plant so that the newly rooted shoot can be subsequently detached and transplanted (Jaenicke, 2006; Tchoundjeu *et al.,* 2010a). Marcotting (or air-layering), is a technique in which an aerial stem is girdled and enclosed in a rooting medium to produce roots on the

upper part of branch while still on the tree (Hartmann *et al.*, 2002). Although an early research on *D. edulis* indicated that it was difficult to propagate by vegetative methods (Phillippe, 1957), this technique has been developed and used successfully for the propagation of *D. edulis* (Mampouya *et al.*, 1994; Kengue and Tchio, 1994). Mialoundama *et al.*, (2002), recommend that *D. edulis* marcots should be set on horizontal branches with diameter above 4 cm. Mbondo (2002), cited by Kengue (2002), reported on the contrary that irregular rooting was observed to characterize marcotted plants derived from horizontal branches of *D. edulis*.

Although there have been few studies to critically evaluate the factors important in marcotting, this technique produces clonal propagules possessing the same characteristics as those of parent plants and are early fruiting (Kengue *et al.*, 1990; Kengue, 2002). Even though this technique presently gives the best results for *D. edulis* (Kengue, 2002), it cannot be used for mass production since it is done on large branches of *D. edulis* (with diameters of up to 4 to 5 cm) leading to high pruning of trees, and a very low rate of multiplication. However, it should be used to capture and replicate the phenotype of a superior individual mother tree of *D. edulis* with desirable fruit characteristics. The resultant marcot can then be planted and managed to resprout copiously providing vegetative growth (shoots) which can then be multiplied by stem cuttings (Mialoundama *et al.*, 2002). Eighty percent success on air layering has been reported for *D. edulis* (Kengue, 1990; Kengue and Tchio, 1994).

2.5.2. Propagation by rooting stem cuttings

Stem cuttings is one of the important means of vegetative propagation which helps in mass multiplication of a species having desired genetic constitution and also to bring out the flowering and fruiting much earlier than from seedlings (Tchoundjeu and Leakey, 1996). Cuttings are portions of stems, roots or leaves that are detached from plants and used to clonally multiply new plants (Hartmann *et al.*, 2002). Man previous researches with a range of factors that influence adventitious root development in leafy stem cuttings. These include genotype, rooting medium, type and concentration of auxins, length of cutting, leaf area, shoot and node position for *Milicia excelsa* (Ofori *et al.*, 1996), *Cordia alliodora* (Oken, 1997); *Khaya ivorensis* and *Lovoa trichilioides* (Tchoundjeu, 1989; Tchoundjeu and Leakey, 2000; Tchoundjeu *et al.*, 2002), *D. edulis* (Mialoundama *et al.*, 2002), *I. gabonensis* (Schiembo *et al.*, 1996), *Irvingia wombolu* (Dolor *et al.*, 2009), *Baillonela toxisperma* (Ngo Mpeck *et al.*, 2007), *Ricinodendron heudelotii* (Schiembo *et al.*, 1997), *Allanblackia*

floribunda (Atangana *et al.,* 2006), *Pausinystalia yohimbe* (Ngo Mpeck *et al.,* 2003b), *Nauclea diderrichii* (Caspa *et al.,* 2009) and/or *Prunus africana* (Tchoundjeu *et al.,* 2002b). Thus, successful propagation of tropical trees by rooting leafy stem cuttings has shown to depend upon many factors (Avana *et al.,* 2000; Tchoundjeu *et al.,* 2006; Tsobeng *et al.,* 2011).

In addition, Mialoundama *et al*., (2002), in a study on the rooting of stem cuttings of *D. edulis*, reported that sawdust is a suitable rooting medium giving the best result (95 % rooting of stem cuttings after 12 weeks) in a low technology, non-mist polythene propagator developed by Leakey *et al*., (1990). In a separate study reported by the same authors, auxin application (IBA, IAA and a mixture of both) did not impact on the rooting ability of either treated or untreated cuttings of *D. edulis.*

2.5.3. Grafting

Grafting is an age-old practice, that involves placing two similar or dissimilar plants organs (stem/stem, stem/root or root/root) from genetically compatible plants in intimate contact, with sufficient pressure and cambial alignment to induce the formation of an anatomically and physiologically functional graft union between the scion and stock (Hartmann *et al.,* 2002). The major advantage, especially for fruit trees is that the graft is in the sexually mature state and so has the ability to flower and fruit while still small trees. Grafting can also be used to preserve elite genetic material, allowing for multiplication via other forms of vegetative propagation or by further grafting (Abbas *et al.,* 2008). Traditionally in horticulture, grafting has been among the most popular, but problems such as graft incompatibility, high labor costs and relatively low rate of multiplication are disadvantages.

Grafting *Dacryodes edulis* trees with scions from adult trees has not produced encouraging results. Some variants of grafting (approach grafting) have produced some success (12-50 %) (Kengue, 2002), but need greater skill just like in rooting of cuttings and marcots (Damesse *et al.,* 2001 cited by Kengue, 2002). Meanwhile and contrarily to *D. edulis*, grafting has proven to be very successful in *Allanblackia* species (Asaah, 2011). Ofori *et al.,* (2008), cited by Asaah *et al*. (2011b) reported grafting success of 80 % using cleft grafting as opposed to 50 % for side veneer grafting on *Allanblackia parviflora*. Similarly, Mng'omba *et al*., (2012) found over 70 % graft success in marula (*Sclerocarya birrea*).

2.5.4. Propagation by culture tissue or *in vitro* propagation

In vitro propagation is the culture of plant cells (callus, cells, protoplast) or organs (stems, roots, embryos) in aseptic culture vessels (like test tubes) under controlled environment and in sterile nutritive growth medium (Jaenicke and Beniest, 2003; Jacquard, 2007). Tissue culture techniques have one or two aims: to vegetatively reproduce plants whilst retaining their genetic identity and conversely, to induce further soma-clonal transgenic variation (Trigiano *et al.,* 1993; Kicherer *et al.,* 2000; Pence *et al.,* 2002). However, the establishment and maintenance of the tissue in an appropriate condition to induce the rapid division and subsequent differentiation of cells limit the capacity for propagation by *in vitro* culture. Moreover, the cost of the equipment is quite high (Muchugi *et al*., 2008).

Three *in vitro* propagation systems have evolved organogenesis, embryogenesis and meristem proliferation or micro-propagation (Jacquard, 2007). In the broad-sense, micropropagation refers to *in vitro* plant regeneration involving the use of a relatively small propagule, referred to as an explant (containing preformed meristems), on an artificial nutrient medium within an aseptic environment. In the more narrow-sense, micropropagation refers specifically to axillary or nodal shoot culture, which is the most common/important type of *in vitro* induction of adventitious organs (shoot and/or root). Through *in vitro* propagation, calli and adventitious roots have been formed from shoot tips and auxiliary buds of young seedlings of *D. edulis* (Youmbi, 1991; Youmbi *et al.,* 1994b; 1998; Youmbi and Benbadis, 2001). Unfortunately, these results are not yet implemented due to the high cost of the technique (sophisticated structures and equipment are required). Studies on *in vitro* regeneration test have also been conducted with success in some fruit trees such as guava (*Psidium guajava* ; Yassen *et al.,* 1995), *Cola* species (Dossa *et al.,* 1994; Fotso *et al.,* 2002), *I. gabonensis* (Omokolo *et al.,* 2004), and *R. heudelotii* (Donfagsiteli, 2002; Omokolo, 2002; Fotso *et al.,* 2007).

2.5.5. Advantages and constraints of vegetative propagation

Despite the genetic gain that can be achieved through vegetative propagation, there are some constraints in the practice of this technique. In fact, Leakey and Newton (1994), Tchoundjeu *et al.* (2006), Leakey and Akinnifesi (2008), associated the following advantages with vegetative propagation:

- when mature adult bud wood is used, early fruiting and fruit set at low height can be achieved;
- higher genetic gains per generation are available compared with a seed orchard/seedling-based tree improvement program;
- conservation of genetic variation (such as hybrids produced by breeding) can be achieved through vegetative multiplication, in the form of clone banks of both 'adult' and 'juvenile' material;
- Non-additive genetic variation may be captured and utilized.

According to the same authors, there are some constraints associated with vegetative propagation that must be taken in consideration when formulating a strategy for propagation of tree species in the case of domestication activities:

- the cost: vegetatively produced plant material can be several times as expensive as seedlings;
- the propagation environment: sophisticated structures and equipment are required, especially for micropropagation;
- labor-intensive: all vegetative propagation methods require more hand labor, which often exceeds 80 % of the total costs (Davies, 1994).

Another concern, which has been raised about asexual propagation is that it will result in a narrowing of the gene pool, which could render a population of a given species more vulnerable to biotic (diseases and pests) or physical stress (Cornelius *et al.*, 2006; Vallejo-Marin *et al.*, 2010; Miller and Gross, 2011). Such an approach would seriously erode the genetic base that exists in most undomesticated species if deliberate attempts are not made to ensure that the full genetic diversity of a species is utilized (Leakey, 1991; Hollingsworth *et al.*, 2005).

2.6. Forest tree breeding and progeny testing

Progeny test aimed at parental ranking is a commonly used method in both animal and plant breeding. In forest tree breeding, progeny testing is often viewed as a fundamental part of the whole procedure (Zobel and Talbert, 1984). It is used to obtain additional genetic gain through roguing seed orchards and establishing seed orchards with the top ranking clones. Progeny testing is also considered essential for advanced generation breeding, because the progenies of the best "plus trees" from the base material for the next generation breeding (forward selection). Ranking parents according to the performance of their progeny (backward selection) is especially important with characters, which have a low heritability (Falconer and Mackey, 1996), as is the case with many important characters in forest tree breeding (Wright, 1976; Cornelius, 1994).

Forest tree breeding aims at solving some specific problem or producing a specially desired product (Zobel and Talbert 1991), by using genetic information to increase performance in certain traits. Forest tree breeders have been aware of the choice between backward selections for a long time; the gain may differ considerably for the different alternatives (Falconer and Mackey, 1996). However, breeders have considered it to be an "either/or" decision, and not realized that they can use different options for different families. The original idea in many tree breeding programs was to use the progeny tests of the phenotypically selected "plus trees" only for parental ranking. The base material for the second generation breeding was to be created by crossing the best ranking "plus trees" (Werner *et al.*, 1981; Ruotsalainen and Lindgren, 1998). This plan has been put into practice for example with Sitka spruce in Britain (Lee, 1993).

However, the question that arises is whether to use the progeny tested "plus trees" or their offspring in long term breeding. Phenotypic selections among the progeny from "plus trees" may actually be a favorable option under certain circumstances (Spanos *et al.*, 1997). Lindgren (1986) stated that, as a general principle, the best progeny tested genotypes should be selected backward and others forward. This is caused by the fact that the best genotypes in most forest tree breeding cases are mated with individuals which can be assumed to have, on the average, a lower breeding value than the best parents themselves (Howe *et al.*, 2003). The differential increase with increasing genetic value of the parent, whereas the within-family selection gain is independent becomes more and more difficult to balance against the difference between increases of the parental values. Thus the gain

achieved by selecting the best individual within the progeny consistently with the breeding value of the parent (Bay and Lindhout, 2007). Therefore, backward selection is the most favorable method for the best-ranked parents. One contribution reason is that selection backwards does not mean the introduction of new genetic relationships but instead keeps the gene mass of the best founders intact. In fact, tree breeding refers to plant material submitted to evolution forces (Simmonds, 1987), and has two main objectives: (1) breeding, and (2) conservation of genetic resources.

2.6.1. Plant Breeding

The term "plant breeding" is often used synonymously with "plant improvement". Hence, breeding is about manipulating plant attributes, structure, and composition, to make them more useful to humans. Plant breeding describes methods for the creation, selection and fixation of superior plant phenotypes in the development of improved cultivars suited to needs of farmers and consumers (Zohary, 2004; Moose and Mumm, 2008). Primary goals of plant breeding with agricultural and horticultural crops have typically aimed at improved yields, nutritional qualities, and others traits of commercial value. The plant breeding paradigm has been enormously successful on global scale, with such examples as the development of hybrid maize (Duvick, 2001), the introduction of wheat (*Triticum aestivum*; Kang *et al.,* 2003, Labbani *et al.,* 2005), rice (Kiviharju *et al.,* 2005) and soybean (Rodrigues *et al.,* 2005), varieties that spawned the Green Revolution (Everson and Golin, 2003), and the recent commercialization of transgenic crops (Mulcachy *et al.,* 1992; James, 2007). These and many other products of plant breeding have contributed to the numerous benefits global society has received from greater sustainable supplies of carbon that may be harvest as food, feed, forests, fiber, and fuel (Stanton *et al.,* 1996; Carron *et al.,* 2007).

Plant breeding has a long history of integrating the latest innovations in biology and genetics to enhance crop improvement. Prehistoric selection for visible phenotypes that facilitated harvest and increased productivity led to the domestication of the first crop varieties (Harlan, 1992) and can be considered the earliest examples of biotechnology. Darwin (1859; 1899) outlined the scientific principles of hybridization and selection, and Mendel defined the fundamental association between genotype and phenotype, discoveries that enabled a scientific approach to plant breeding at the beginning of the 20th century (De Candolle, 1886; Shull, 1909). Despite the immediate recognition among some plant breeders

of the importance of Mendelian genetics, full integration was delayed for nearly 20 years until quantitative genetics reconciled Mendelian principles with the continuous variation observed for most traits considered important by most plant breeders (Paul and Kimmelan, 1988). Subsequently advances in our understanding of plant biology, the analysis and induction of genetic variation, cytogenetics, quantitative genetics, molecular biology, biotechnology, and, most recently, genomics have been successively applied to further increase the scientific base and its application to the plant breeding process (Baenziger *et al.,* 2006; Jauhar, 2006; Varshney *et al.,* 2006; Sikdar *et al.,* 2010).

2.6.1.1. Breeding schemes

Conceptually, plant breeding is simple: cross the best parents, and identify and recover progeny that outperform the parents. In practice, plant breeding is in three step process, wherein populations and germplasm collections with useful genetic variation are created or assembled, individuals with superior phenotypes are identified, and improved cultivars are developed from selected individuals (Zobel and Talbert, 1984):

- the first step is when the breeding goal's is to upgrade and establish elite genotype with trait (s) controlled by one or few loci, thus we can proceed by backcross which is used either to introgress a single gene or gene pyramid for a few genes (Bandel, 2000);
- the second and the third steps are for genetically complex traits, germplasm improvement instead requires reshuffling of the genome to produce new favorable gene combinations in the progeny. The pedigree breeding method produces such novelty via crossing and recombination among superior, yet complementary, parents and selection among segregating progeny for improved performance (Nanson, 2004; 2008);
- the third step which is recurrent selection aims to simultaneously increase the frequencies of favorable alleles at multiple loci in breeding populations through interacting of selected individuals.

2.6.1.2. Genetic improvement and genetic gain concept

Genetic improvement can be defined as process whereby genetic value is improved while joint consideration is given to the genetic diversity of deployed material (Kang, 2001). It includes selection, testing and breeding from the species through the population and family, to the clonal level (Barnes, 1995). As show in figure 3, Li *et al.*, (1999) cited by Kang (2001) stated that, genetic gain in seed orchards (SO) for example can be achieved at different stages from "plus tree" selection through roguing inferior parents and/or crossing superior parents. From this study, "plus tree" selection (which is mass selection) itself gives some extra gain (may be 1-2 %) compared to natural stands, due to the avoidance of relatedness as the "plus trees" are usually selected in different stands.

Generally, one gene (Mendelian traits) or many genes (polygenic traits) influence traits. Polygenic (or quantitative) traits are of utmost importance in tree breeding and are of three types (Hartl, 1988):

- continuous traits for which there is a continuum of phenotypes (e.g., growth rate, weight);
- meristic traits for which the phenotype is expressed in discrete or integral classes (e.g., number of flowers on a petal); when the number of possible phenotypes is large, there is no distinction between a meristic and a continuous trait;
- threshold traits.

Quantitative genetic principles in tree breeding have been particularly powerful as the theoretical basis for both population improvement and methods of selecting and stabilizing desirable genotypes (Namkoong *et al.*, 1966; Hallauer, 2007). An important concept in quantitative genetics and plant breeding is genetic gain (ΔG), which is the predicted change in the mean value of a trait within a population that occurs with selection. Regardless of species, the trait of interest, or the breeding methods employed, ΔG serves as a simple universal expression for expected genetic improvement (Fehr, 1987; Falconer and Mackey, 1996).

Moose and Mumm (2008) in figure 4 described the genetic gain equation and an expansion of its terms to fundamental parameters of quantitative genetics. Though clearly an over simplification of the advanced quantitative genetic principles employed in plant

breeding, the genetic gain equation effectively relates the four core factors that influence breeding progress:

- the degree of phenotypic variation present in the population (represented by its SD, σ_p);
- the probability that a trait phenotype will be transmitted from parent to offspring (heritability, h^2);
- the proportion of the population selected as parents for the next generation (selection intensity, *i*, expressed in units of SD from the mean);
- the length of time necessary to complete a cycle of selection (L). L is not a function of how many generations are required to complete a selection cycle, but also how quickly the generations can be completed and how many generations can be completed per year.

If it is clear that ΔG can be enhanced by increasing σp, h2, or i, and by decreasing L, thus, the genetic gain equation provides a framework for comparing the predicted effectiveness of particular breeding strategies and is often used as a guide to the judicious allocation of resources for achieving breeding objectives.

Within-tree variance allows estimation of repeatability (Falconer and McKay, 1996), which expresses the proportion of the variance of single measurement that is due to permanent differences between individuals, both genetic and environmental. No conclusion about the genetic control of a character can be drawn from studies in wild stands, as trees are of unknown pedigrees. Common gardens are multi-site experiments in which several genetic materials (provenances, families and individuals) are assessed for their performance in traits of interest, to quantify the effects of genotype, environment and genotype x environment interaction.

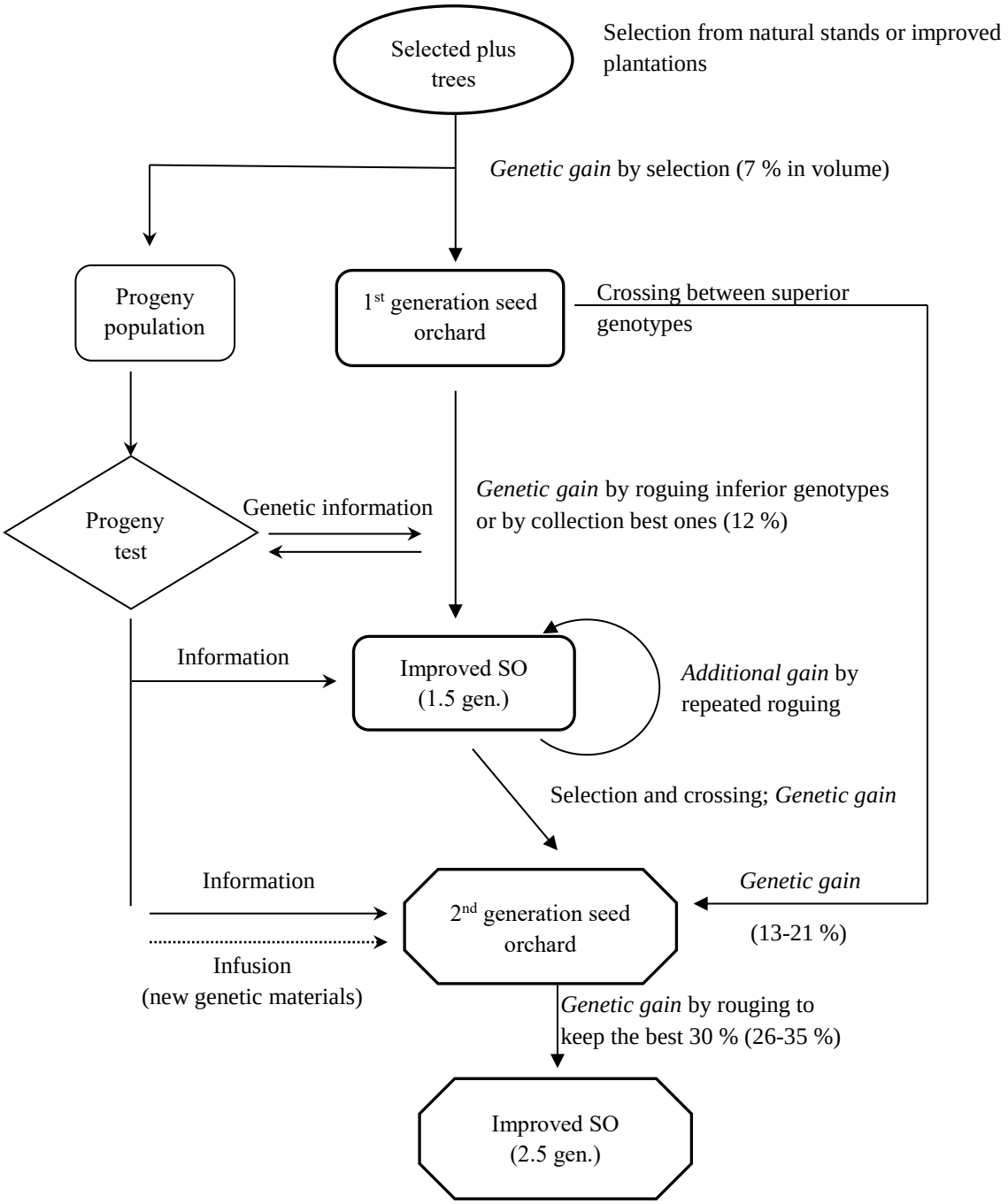


Fig. 3. Flow-charts of the generation of seed orchards. Values for genetic gain are from Li *et al.*, (1999). SO: seed orchard; gen: generation.

Randomization and replication of treatments in each site is essential for such experiments, to estimate heritability values per site and overall, heritability being the ratio of genetic variance to total variance (Zhou, 2005). The heritability of a trait within a population is the proportion of observable differences in a trait between individuals within a population that is due to genetic differences. Heritability thus analyses the relative contributions of differences in genetic and non-genetic (due to environment) factors to the total phenotypic variance in a population. In addition, repeatability refers to the ratio of genetic variance and general environment variance to the phenotypic variance. Clonal repeatability is used when the correlation refers to different plants of the same genotype, usually planted at two different locations (Falconer, 1989).

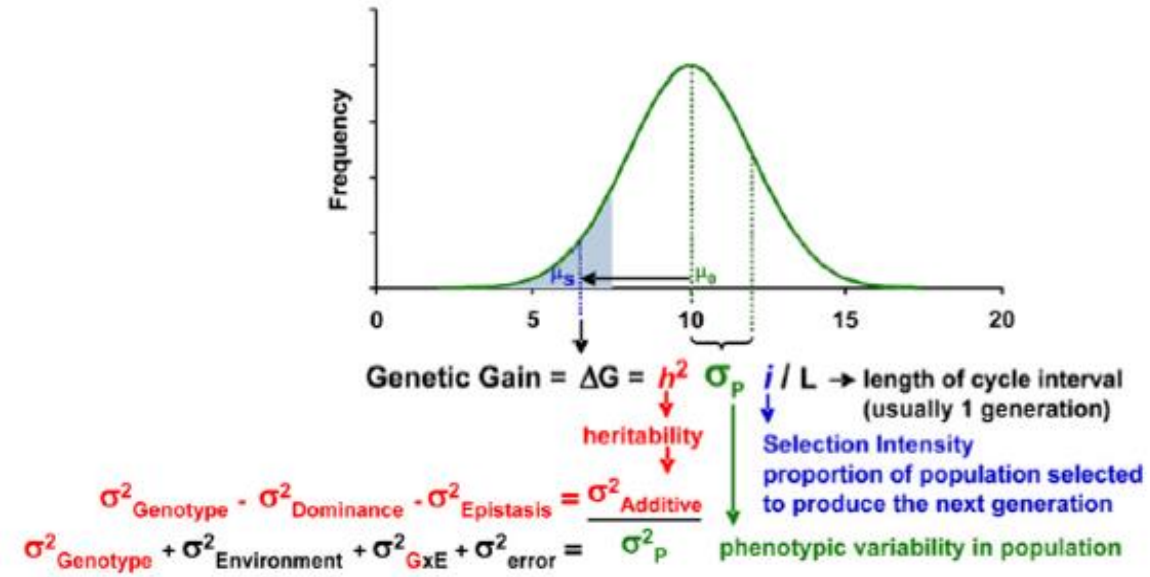


Fig. 4. The genetic gain equation and its component variables. The top portion illustrates an idealized distribution showing the frequency of individuals within a breeding population (*Y* axis) that exhibit various classes of phenotypic values (*X* axis). Mean phenotypic value (μ_0) of the original population (shown as entire area under the normal curve) and mean (μ_s) for the group of selected individuals (shaded in blue) are indicated. Components of variation (σ^2) that contribute to the SD of the phenotypic distribution (σ_P) are indicated below the histogram (Adapted from Moose and Mumm, 2008).

Common gardens allow the partition of phenotypic variance into genetic and environment components using the formula:

$$V_P = V_G + V_E + V_{GxE}$$

Where, V_P, V_G, V_E and V_{GXE} are, respectively, phenotypic, genetic, environmental, and genetic x environmental variances. Genetic variance is the sum of additive (V_A or breeding value: part of the genetic material transmitted from parent to offspring through sexual reproduction) and non-additive (V_{NA}) variances, the latter being divided into dominance (due to interaction of specific alleles at gene locus) and epistatic (due to interactions among gene loci; Zobel and Talbert, 1991). Therefore, the degree of resemblance between relatives, which expresses the extent to which phenotypes are determined by the genes transmitted from the parents, can be obtained as the ratio V_A/V_P (Falconer and Mackay, 1996; Holland and Cervantes-Martinez, 2003) also called narrow-sense heritability (h^2).

The degree of genetic determination, also called broad-sense heritability (H^2), is the ratio V_G/V_P (the whole genetic material is transmitted from parent to offspring: asexual reproduction) also obtained from common gardens (Levi *et al.*, 2001; Zhang *et al.*, 2010). Broad-sense heritability estimates for a component allow separation of variability into additive and non-additive effects. If additive effects exist, and they are correlated with yield, it may be possible to exploit the component for yield improvement. The best breeding method to be used for achieving gains is determined by heritability (Namkoong *et al.*, 1966). High narrow-sense heritability indicates that phenotypic variation provides a good estimate of genetic variation; hence, individual selection is appropriate, whereas low heritability indicates that selection should be done among families (Lindgren, 2002; Howe *et al.*, 2003; Lan, 2011).

In addition, the presence of a significant GXE interaction means that genotypes are responding differently to different environments and indicates that stability analysis may be useful for comparisons among genotypes (Finlay and Wilkinson, 1963). Stability across environments may be a desirable property of a genotype intended for use in a wide range of conditions (Singh and Chaundhary, 1985). A large GXE interaction (relative to the genotype effect) and low broad-sense heritability estimate for a character indicates that progress in yield improvement through direct selection for that character is probably not feasible (Namkoong *et al.*,1966). If this occurs for all yield components then alternative methods for discriminating between genotypes must be found.

2.6.2. Conservation of genetic resources

Deforestation and degradation cause the loss of more than just the bioversity, products and environmental services that forests and trees provide such as carbon sequestration, stabilization of soils, and adaptation to the destructive effects rising temperatures (The World Resources, 2005). Failure to optimize land use means we are squandering an opportunity to improve the livelihoods of more than a billion of the world's poorest people, as well as the national balance sheets of developing countries (FAO, 2013). In accordance with the Convention on Biological Diversity (Painting *et al.,* 1993; Prescott, 1994; Bacchetta *et al.,* 2007), the improvement of indigenous trees valued for their traditionally important fruits offers a flexible means by which, to add poverty reduction and enhanced food security to the global challenges faced today through reducing deforestation and environmental degradation (Leakey, 2001; Agustino *et al.,* 2011).

The main evolutionary factors (mutation, selection, gene flow and genetic drift) shaping the genetic structures of populations are theoretically in equilibrium for each species in wild stands; any significant external influence on one of these factors will disrupt the existing equilibrium, and affect the evolutionary trajectory, hence diminishing the species' adaptive potential of these populations (Stebbins, 1950; Barrett and Kohn, 1991; Mckey *et al.,* 2010). Selecting and breeding a species for a character will certainly increase in the population the frequency of alleles controlling the character of interest, provided this character is under genetic control (Stroup *et al.,* 1993; Stockel, 2006; Srikanta *et al.,* 2009). Applying repeatedly artificial selection (recurrent selection) in each breeding cycle would disrupt the equilibrium between forces driving evolution, and bottlenecks can occur (Nei *et al.,* 1975; Hyten *et al.,* 2006; Olsen and Gross, 2008; Mariette *et al.,* 2010). Therefore, any tree breeding program should develop strategies aimed at preserving whole or majority of source's genetic diversity in the species both at functional and neutral levels during tree improvement (Rüter *et al.,* 1999; Atangana, 2010).

In addition, preserving genetic resources in a species should be based on a detailed inventory of the genetic diversity of that species (FAO, 2013). This inventory is done using common gardens for species undergoing breeding programs. However, these tests are time-consuming, although they are useful in dissecting phenotypic variation. Population genetics is a science that deals with Mendel's laws and other genetic principles as they apply to entire populations of organisms, including the study of the various forces that result in evolutionary

changes in species through time (Hartl and Clark, 2007; Zougab, 2008). Population genetics is essential in conservation, plant breeding, evolutionary biology, ecology, genetics, genomics, natural history, and one of its goals is to understand the evolutionary and biological significance of genetic variation, then recommendations can be made about how to best manage genetic resources (Mulcachy *et al.,* 1992; Gaillard, 2008; Van Tassel *et al.,* 2010). A key element in population genetics is the understanding of genetic diversity, which is the variation in allelic and genotypic composition in a given species (Namkoong *et al.,* 1966; Ruotsalainen and Lindgren, 1998).

2.7. Seed orchard

Seed orchards constitute an important component in most tree improvement programs, and seeds from seeds orchards are superior to stand seeds. A seeds orchard is defined as an area where seeds are mass-produced to obtain the greatest gain, as quickly and inexpensively as possible (Zobel *et al.,* 1958; Wehner *et al.,* 2001). Also, it is defined as plantation of selected clones or progenies which is isolated or managed to avoid or reduce pollination from outside sources, and manage to produce frequent, abundant, and easily harvested crops of seed (Kang, 2001). Clonal propagation techniques have been improving in effectiveness, both biologically and economically, for many years. These may influence the nature of future output systems and modify the present role of seed orchards (Sweet, 1995). In the future, mass propagation techniques, like tissue culture, somatic embryogenesis and artificial seeds, may make it possible to get seeds or plants directly from *in vitro* conditions. In the foreseeable future, however, the role of seeds orchard as a primary system for genetic improvement programs is likely to continue. We can distinguish three types of seed orchards:

- seedling seed orchards (SSO) have a broad genetic base because of the large number of parents involved, but the differential is less than in the vegetative seed orchard;
- the breeding seedling orchard (BSO), a derivative of the SSO, is a flexible strategy that lies somewhere between a SSO and a progeny test (Barnes, 1995). In a BSO, the conventional hierarchy of sequential testing, selection and seed production is combined in a single planting. This may be a cheaper and less complicated way to run a tree improvement;

- the clonal seed orchard (CSO) in which there may be some level of graft incompatibility, but the problem has simply been accepted. On the other hand, grafting is particularly useful for species where flowering is delayed, as grafts retain the physiological age of the parents. Root deformities and low productive output may also be problems in seed orchards established with cuttings or by tissue culture. The possibility of selfing is considerably greater in vegetative orchards, but this can be minimized by keeping ramets of the same clone well separated. Anyway, the decision whether to use clonal, seedling or polycross orchards should be made based on economic and genetic considerations (Sweet, 1995). The choice of seedling versus clonal seed orchards depends primarily on the earliness of flowering of grafted trees and of seedlings, the relative difficulty, cost and speed of establishing grafted trees and seedlings, and selection differential possible with clones and families.

2.8. Mechanisms of shoot branching

All organisms have a finely tuned homeostasis for uniform growth and maintenance, and plants are no exception. The plant body has a hierarchy of organs, tissues, and cells. Basic morphology of vascular plants reflects their evolution as organisms that draw nutrients from below ground and above ground. Three basic organs evolved: roots, stems, and leaves. They are organized into a root system and a shoot system. Roots rely on sugar produced by photosynthesis in the shoot system, and shoots rely on water and minerals absorbed by the root system. Shoot branching has an important role in generating a large variety of diverse plant forms (Shimizu-Sato *et al*., 2009). Many processes have been described in the control of shoot branching. Apical dominance is defined as the control exerted by the shoot tip on the outgrowth of axillary buds, whereas correlative inhibition includes the suppression of growth by other growing buds or shoots (Mazid *et al*., 2011). Likewise, an axillary bud is a structure that has the potential to form a lateral shoot, or branch while an apical bud, or terminal bud, is located near the shoot tip and causes elongation of a young shoot.

Variable hormone production and response are thought to act in perfect balance within a genetically predetermined framework to produce a structure and developmental strategy optimized to the given growth conditions, and yet with the ability to rapidly respond to changes within the environment (Nagarathma *et al*., 2010). Moreover, hormonal response is a

key adaptation that radically alters whole-plant architecture in order to optimize growth and development under diverse environmental conditions. Therefore, simple models for controlling whether buds grow out involve downward-moving signals that come from the shoot tip (apex) and inhibit bud growth (Brewer *et al*., 2013). As stated by Ferguson and Beveridge (2009), the degree of apical dominance varies depending on the plant species. In fact, in many plant species, the intact main shoot apex grows predominantly and axillary bud outgrowth is inhibited. The most studied apical signal is auxin which is produce in young leaves in the tip (Chao *et al*., 2007) of the main shoot and transported basipetally down the stem in a polar manner by active transport in the vascular parenchyma (Ferguson and Beveridge, 2009) (see Fig. 5).

The amount of auxin produced is thought to be proportional to the activity of the shoot tip and provides tissues below the shoot with information about the growth status of the shoot and allows for the decision making about lateral growth (Li and Bangerth, 1999). In addition to the long-standing evidence for the role of auxin in this process, other hormone and non-hormone signals are clearly involved (Morris *et al*., 2005).

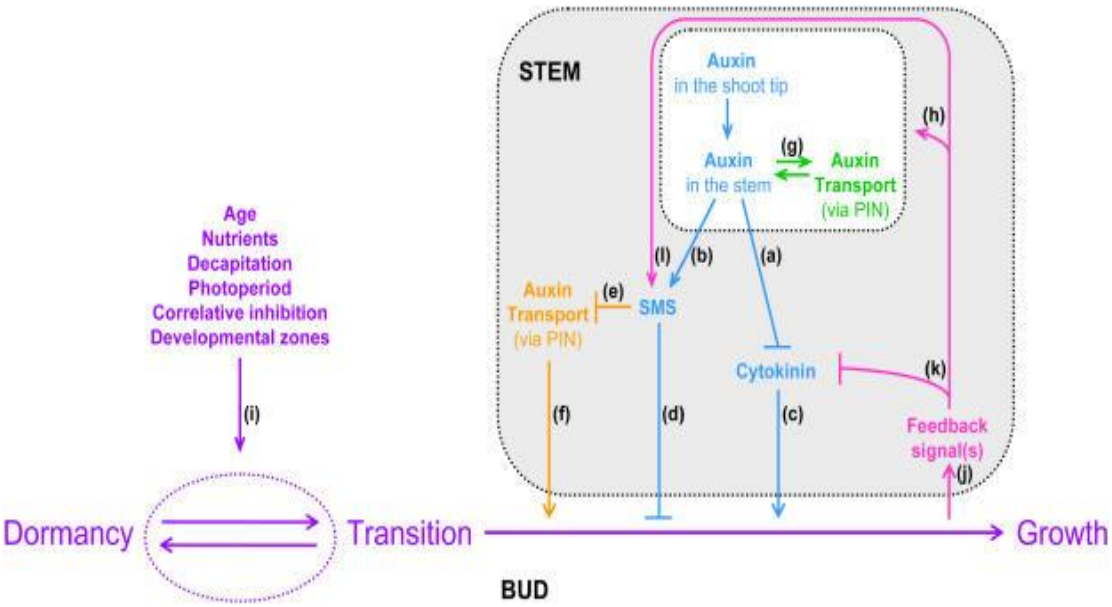


Fig. 5: Model for regulation of stages of bud outgrowth. The classical hypothesis is illustrated in blue (a, b, c, and d); the auxin transport hypothesis (Bennett *et al*., 2006) is illustrated in orange (e and f); an alternative interpretation of the auxin transport hypothesis is illustrated in green (g); hypothesized feedback interactions are illustrated in pink (h, j, k, and l); and the bud transition hypothesis is illustrated in purple, pink, blue, and green (a, b, c, d, g, h, i, j, k, and l). Arrowhead lines indicate promotion and flat-ended lines indicate inhibition (Adapted from Dun *et al*., 2006).

Apical auxin travels downwards and cannot move upwards into buds. Thus, two other hormone classes, strigolactanes and cytokinins, seem to act as long-distance second messengers to auxin for bud arrest, but display an antagonistic relationship with each other (Brewer *et al*., 2009; Dun *et al*., 2012). Strigolactanes inhibit bud growth (Gomez-Roldan *et al*., 2008; Umehara *et al*., 2008) and cytokinins promote bud growth (Wicson and Thimann, 1958) and both are regulated conversely by auxin (Chao *et al*., 2007; Dun *et al*., 2009) (see Fig. 6). Auxins levels decrease with distance from growing apex; this decrease eventually switches lateral buds to the active state, producing and acropetal activation sequence. After decapitation of growing plant, the lateral apex closest to the decapitation site is activated and becomes dominant (Shimisu-Sato *et al*., 2009). Meanwhile, several buds close to the decapitation site are activated in the case of overcompensation (Mazid *et al*., 2011).

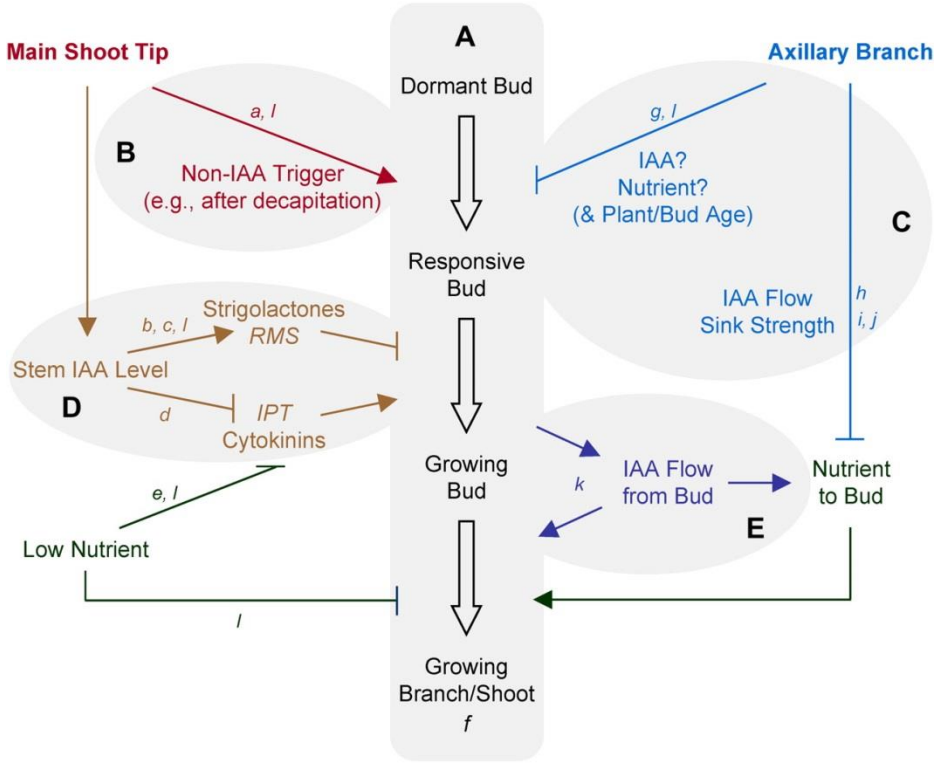


Fig. 6: Model of the developmental stages of bud outgrowth illustrating the regulatory roles of IAA, CK, strigolactone, and nutrients. A, Dormant buds must be triggered to a responsive state where they are receptive to outgrowth signals. B, Loss of the shoot tip (apical dominance) leads to a rapid trigger that is not IAA mediated. C, Growing axillary buds/branches (correlative inhibition) affect whether buds respond to depleted strigolactone and also reduce nutrient availability for bud growth and elongation. D, Strigolactone inhibits bud outgrowth, whereas CK promotes it. In intact plants, IAA negatively regulates bud outgrowth by maintaining high strigolactone and low CK contents. E, The IAA content of responsive buds increases and is exported into the stem, allowing the bud to develop a more effective and substantive vascular system and attract nutrients for growth. The extent of subsequent bud/branch growth is then strongly dependent on nutrient availability. This model illustrates the developmental stages of a growing bud/branch. The arrows shown between stages

represent the progression toward outgrowth but do not preclude the fact that bidirectional development can occur, where inhibition can cause buds to revert to a previous stage. References are indicated as follows: a, Morris et al. (2005); b, Beveridge (2000); c, Foo *et al*. (2005); d, Tanaka *et al*. (2006); e, Miyawaki *et al*. (2004); Takei *et al*. (2004); f, Stafstrom (1995); g, Napoli *et al*. (1999); h, Bangerth (1989); i, Davies and Wareing (1965); j, Phillips (1968); k, Ongaro and Leyser (2008); l, Ferguson and Beveridge study (Adapted from Ferguson and Beveridge, 2009).

Most of the time, funds have been provided to improve major cereals (rice, maize and sorghum) and pulses like groundnut, cowpea, wheat and faba bean (Onwubiko *et al.,* 2011; Yahuza, 2012). More attention to improve and diversify crop production can help to reach food self-sufficiency and its use can allow overcoming protein malnutrition. One of the urgent actions to address this problem is the adoption of agroforestry practices (Tchoundjeu *et al.,* 2006) which lead to the integration in farmers systems of native species with high nutritional and commercial values across the exotic fruit trees grown extensively (Leipzig, 1996).

In the fulfilment of cultivars development for priority tree species, studies on shoot branching which plays a pivotal role in the development of the aboveground plant structure is to be prioritized for future crop diversification programs (Siddique *et al.,* 1984; Dun *et al*., 2012). Nevertheless, success in breeding for yield superiority of indigenous fruit trees is still constrained by the lack of availability of improved germplasm (Akinnifesi *et al.,* 2008). In fact, managing their populations and improving the quality and regularity of fruit production are perceived as priorities for the economic development of rural populations (Diallo *et al.,* 2008; Venter and Witkowski, 2011). Additionally, wider crosses within a genus often produce favorable proportions of vigorous offspring, which can portray higher germination, seedling growth, and survival performances (Dinh Kha *et al.,* 2011). In the same line, branching in trees is not well understood (Fig. 25). In fact, branch formation in trees is controlled by two processes: (i) apical dominance (correlative inhibition), involving the regulation of axillary bud development by the terminal bud of a shoot, and (ii) apical control, the suppression of growth of existing branches imposed by younger more apical shoots (Leakey and Longman, 1986; Lapido *et al.,* 1992;). These mechanisms are under the control of hormones such as auxins, cytokinin and other growth substances (Brewer *et al*., 2009). In addition, branches can be classified as either proleptic, growing from buds previously inhibited by apical dominance, or sylleptic, uninhibited by apical dominance, growing immediately on appearance from the terminal bud (Leakey and Longman, 1986). Hence, in the tropical fruit tree *D. edulis*,

branching and crown development is basically conforms to Rauh's Model (Hallé *et al.,* 1978) and involves both proleptic and sylleptic branching.

In the other hand, larger size trees are not easily accessible to the grower and it is very risky when climbing to harvest fruits at an appropriate time whereas small-sized trees can be planted closer to each other, more trees per ha implies a further increase in the early harvest. Hence, dwarfed trees are much easier to manage (size, protection measures, harvesting), which significantly reduces production costs per kg of fruit and the risk of accidents during harvest (Tukey, 1964; Moot, 1993; Verheij, 2006). Growth habit is therefore very important in the cropping system of African plum and an influential character in its harvesting.

Among the selection criteria for the improvement of this species are the size and fruit flavour, colour and thickness of the pulp, pulp oil content, the fruiting season, disease resistance and pest, the frequency and regularity of fruiting performance (yield). Very little work has been done on the induction of early shoot branching to produce young seedlings with multiple twigs (spouted branches). This technique can help to reduce the size of the tree and thus facilitate the harvesting of fruits and silvicultural management (Kengue, 1990). The development of an early selection criterion for early shoot branching would be of particular value in this indigenous species where the techniques used for good quality fruit harvest appear to be strongly related to the plant architecture (Lauri, 2007; Vanderpuye, 2010). Consequently, this study part describes the first application of a decapitation test to this species.

Most previous investigations on timber tree species such as *Triplochiton scleroxylon, Cedrela odorata*, (Leakey and Longman, 1986; Tchoundjeu, and Lapido *et al.,* 1991), *Picea abies* (Tschaplinski and Blake, 1994) and even perennials such as *Petunia* (Snowden and Napoli, 2003) or procumbent herbs such as *Trifolium repens* (Thomas *et al*. 2003; Thomas and Hay, 2008; Dun *et al.,* 2006). The study was carried out under operational conditions in the nurseries, and it involved screening of large numbers of seedlings rather than clones. To our knowledge, no study has documented *D. edulis* seedlings' growth in response to decapitation. Such approach may help to characterize African plum control-pollinated seedlings with early multiple branches, in an attempt to select improved raw-material for the on-going breeding program.

2.9. Presentation of *Dacryodes edulis*

2.9.1. Systematic of *Dacryodes edulis*

D. edulis belongs to the Burseraceae family. The genus name is derived from the Greek word "Dakruon" (a tear) in reference to the resin droplets that appears on the bark surface of its species. The species-specific name "*edulis*" means edible. The genus *Dacryodes* comprises about 70 species, occurring in the American, Asian and African tropics. In Africa, the *Pachylobus* section counts about 20 species which have been described (Onana, 1998; 2008). The species has been described under different names, now considered synonyms. *Dacryodes edulis* responds to the following botanical classification (Table II):

Table II. Morphological and phylogenetical classification of *Dacryodes edulis*.

	Morphological	Phylogenetical
Kingdom:	*Plantae*	*Plantae*
Division: Sub-division:	*Phanerogams* *Angiosperms*	*Magnoliophyta*
Class:	*Dicotyledons*	*Magnoliopsida*
Subclass:	*Dialypetals*	*Rosidae*
Order:		*Sapindales*
Family:		*Burseraceae*
Genus:		*Dacryodes*
Species:		*Dacryodes edulis*

Dacryodes edulis (G. Don.) H. J. Lam (1932).
Pachylobus edulis G. Don. (1832),
Canarium edulis Hook. (1849),
Canarium saphu Engl. (1893),
Pachylobus saphu Engl. (1896),
Pachylobus edulis G. Don. var. *preussii* Engl. (1898),
Canarium mubafo (Ficalho) Engl. (1899),
Canarium manfeldianum Engl. (1910),
Pachylobus edulis G. Don.var. *glabra* A. Chev. (1916),
Pachylobus edulis G. Don.var. *sylvestris* A. Chev. (1916) and

Dacryodes edulis var *parvicarpa* (1983).

Dacryodes edulis is the typical species of the genus *Dacryodes*.

Common names are Safoutier, prunier du Gabon ou « atanga » in french. Butter fruit tree, bush butter tree, African pear tree, African plum tree, African palm tree in english. The name "bush butter" refers to its use as supplement for butter by some people. For local names, (see Table III).

Table III. *Dacryodes edulis* local names.

Country	Ethnical group	Nom local
Cameroon	Bamileke	Dschang: le-tsee; ekiep; tso Bangangte: tchou Bafang: che
	Bamoun et Banso	youom
	Bassa-Ewondo, Eton	assa; sa
	Bafia, Makenene	kiyom
	Douala	sao
	Bulu	assamingoum
	Bakoko	sas
	Banyangi	bekwa
	Bakweri	sibakwbri
	Fang	ollem
	Pygmee Bibaya	sene
Nigeria	Ibos	ube; abua; iben; oibo
	Afemai	oromi
	Edo Urhobo	orumu
	Efik	eben
	Boki	boshu
	Yorouba	elemie African
Democratic Republic of Congo	Kikongo, Lingala	nsafou, osaw
Congo	Kikongo, Lingala	nsafou
Gabon		atanga
Saô Tome and Principe		saô tome baum
Ivory Coast		abe vi; akye tsai; anyi karenda
Benin		orumu

Source: Okafor (1983); Kengue (1990); Silou *et al.*, (1994); Mpungi Buyungu (2000); Kengni (2004).

With regard to *D. edulis* yield per hectare, Hamid-Gony (2007) pointed out a performance within two years to about 1000 kg for seedlings, 1800 kg for cuttings and finally to 4000 kg for marcots. Likewise, studies on the morphology of the pollen grain of *D.edulis* by Kengue (1990) and Youmbi *et al.* (1998) gave values not very similar, respectively P= 28.2 µm for the polar axis and E =21.50 µm for the equatorial diameter against P= 41.0 µm and 30.9 µm. Based on these results, one might admit that Kengue (1990) took the sample of pollen from a pure male tree (a tree which never bears fruits, but regularly produces pollen for female trees), whereas the second authors have taken their sample on a male-hermaphrodite tree (a tree which can irregularly bear a few quantity of fruits).

2.9.2. Morphology and reproductive biology of *Dacryodes edulis*

2.9.2.1. Morphology

Dacryodes edulis is a small to medium-sized tree that grows up to 20-25 m tall with a bole up to 70-90 cm in diameter (Chevalier, 1916). It has a relatively short trunk and a deep, dense crown. The bark is pale grey and rough with droplets of resin. The leaves are compound with 5-8 pairs of leaflets (Onana, 2008). The upper surface of the leaves is glossy. Leaves are alternate and imparipinnate, whereas stipules are absent. The petiole is up to 7.5 cm long with 11-19 leaflets. Three types of flowers occur on two tree types. One tree type is the female tree, which bears which bears female flowers only. The second tree type is a male tree, which bears predominantly male flowers and sometimes, hermaphrodite flowers at varying proportions (Onana, 1998) (Fig. 7).

Dacryodes edulis has nutritive (Kinkela *et al.,* 2006; Ajayi and Adesanwo, 2009), and ethnobotanical value (Omonhinmin, 2012); pharmaceutical (Koudou *et al.,* 2008; Obame *et al.*, 2008; Ajibesin, 2011; Duru *et al.*, 2012), cosmetic (Dawodu, 2009; Ajibesin, 2011), melliferous (Messi *et al.*, 1994; Tchuenguem *et al.,* 2001; Azo'o Ela *et al.,* 2010) and ecological importance (Aiyelaagbe *et al.,* 1998; Okunomo *et al.,* 2007) are also recorded.

The fruit also called "safu" or "safou" in French, "African plum" or "bush butter" in the English-speaking parts of Cameroon and in Nigeria, is a monospermous drupe characterized by an extreme diversity in form, dimensions, color and taste. Major fruit forms are oblong, ellipsoidal, sub-globular, oval or conical. Diameter generally varies from 3-18 cm (Kengue, 2002; Kengue *et al*., 2011). Some fruits have longitudinal ridges on their surfaces.

Okafor (1983) described two varieties within Dacryodes species: *Dacryodes edulis* var *edulis* (the cultivated one) and *Dacryodes edulis* var *parvicarpa* (wild variety).

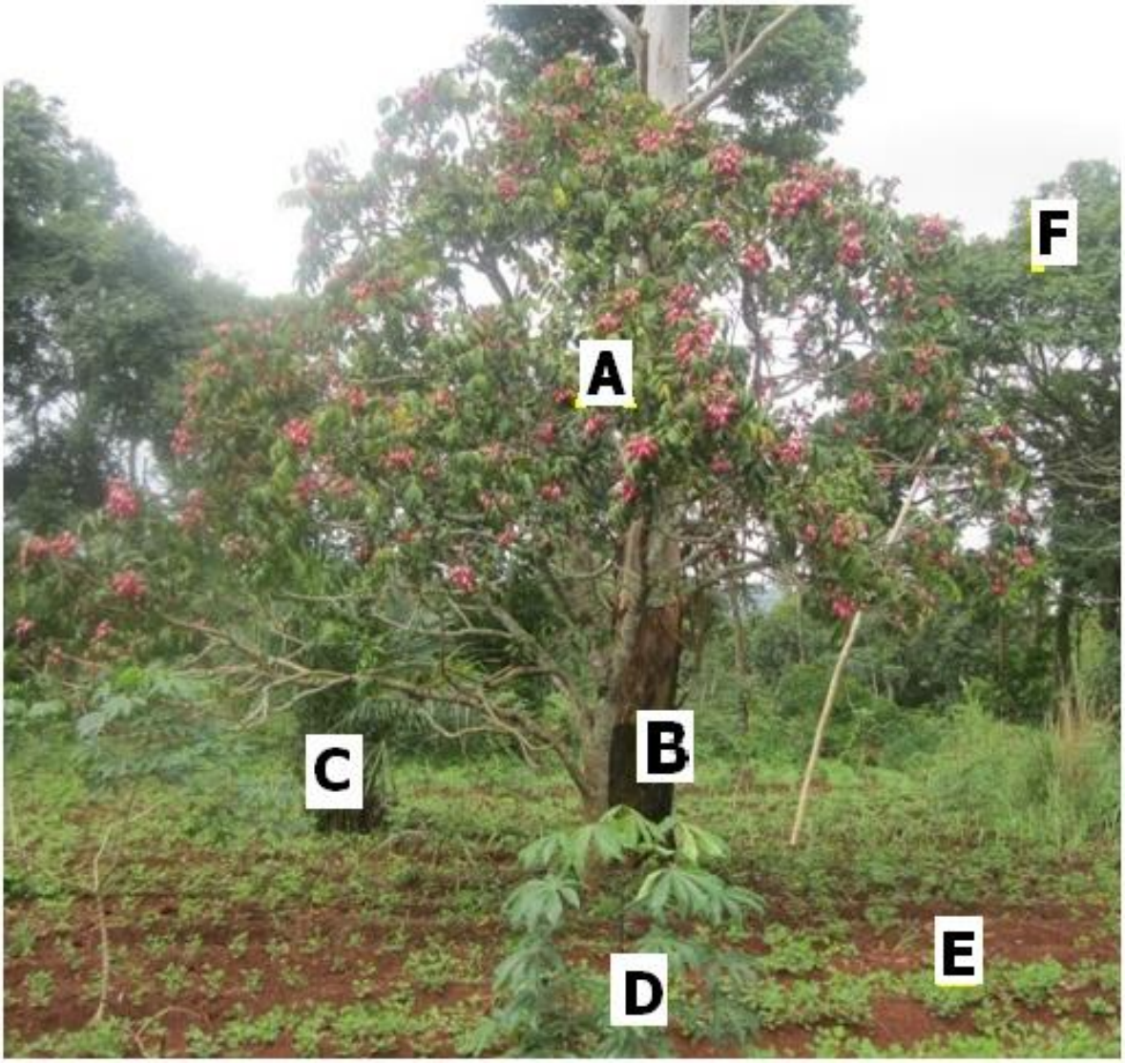


Fig. 7. Fruiting *Dacryodes edulis* tree in a cropping system

A: A fruiting African plum (*Dacryodes edulis*); B: Eucalyptus (*Eucalyptus grandis*); C: Palm tree (*Elaeis guinneensis*); D: Cassava (*Manihot esculenta*); E: Pea nut (*Arachis hypogea* and F: African canarium (*Canarium shweinfurthii*).

Epicarp color is pink in young fruits, and gradually turns to dark-blue, whitish green at maturity. The fruit has an oily, fleshy mesocarp, which also is the edible part. Mesocarp (pulp) color can be pink, whitish, greenish, yellowish or other similar colors. Within the fruit, one can generally find one or two seeds (kernels) enclosed in a smooth membranous tegument, but sometimes, seedless fruits can be found within fruits of particular tree provenances (pers. obs.). A smooth, thin and membranous tegument surrounds the kernel. Each cotyledon has an average of about five fleshy segments.

Kengue (2002) defined the breeding system of this species as allogamous. Cross-pollination is effectuated by insects notably honey bees of the species *Meliponula erythra* with possibilities of self-pollination in hermaphrodite flower, but an earlier controlled crossing study suggests that out-crossing is a frequent mode of reproduction (Kengue, 1990). The fact that African plum flowers are very small (3-8 mm long; 3-4 mm diameter) and are grouped into inflorescences, presents problems in the investigation of its reproductive biology (Fig. 8 and 9).

The inflorescence is axial and made up of a panicle with a biparous cyme on leafy branches. The male and/or hermaphrodite (up to 40 cm long) inflorescences have a pyramidal shape (Fig. 10) with a bright yellow color bearing about 300-500 flowers among which only 75-120 will rich anthesis. The female inflorescence (Fig. 11) is shorter (5-30 cm long) and bears only about 90 flowers due to its small size. Flowers with 3-8 mm long and 3-4 mm diameter in size are reddish-brown and open sequentially from basal to distal positions (acropetal blooming). Morphologically, the hermaphrodite flowers outwardly resemble the males, but bear potent female reproductive organs. The lifetime of a flower is three to four days. Both flower sexes produce copious amounts of sugar-rich nectar (melliferous tree) and have 3-5 free sepals and 2-4 petals. The androecium has 6 stamens that are about 3 mm long and the peri-ovarien disk has 6 lobes. The ovary is divided into two loges by a median placenta that is limited by a one-layered membrane. For both sexes, the blooming period is about 40 days.

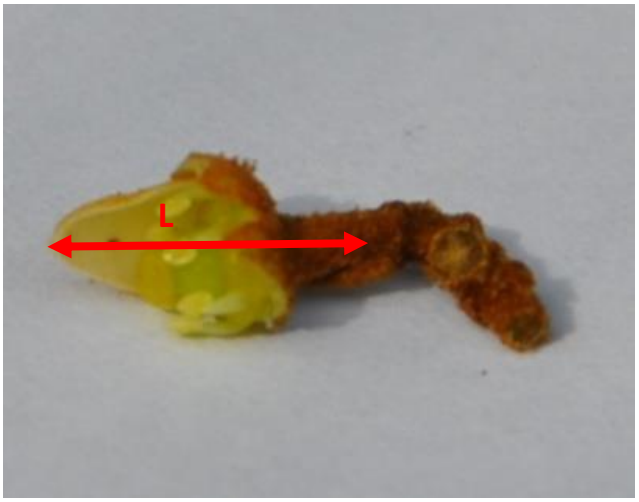


Fig. 8. *Dacryodes edulis* male or hermaphrodite flower

Legend**:** L = *D. edulis* flower length;

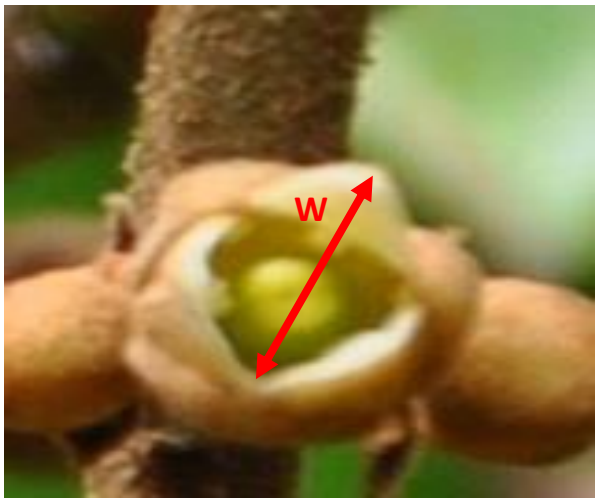


Fig. 9. *Dacryodes edulis* female flower

W = *D. edulis* flower width

Fig. 10. *Dacryodes edulis* male infloresecnce

Fig. 11. *Dacryodes edulis* female inflorescence

2.9.2.2. Reproductive biology of *Dacryodes edulis*

Flowering is generally stimulated by water stress, usually after two consecutive months of dryness. In Cameroon, this period falls at about late December in the climatic region of Littoral-Southwest (monomodal rainfall), late January in the Centre-South (bimodal rainfall) and the late February in the Western Highlands (monomodal rainfall) (Kengue, 2002). Some *D. edulis* trees flower earlier than expected, while others flower late and may

produce blossoms continuously for several months (ICRAF, 2007). This is the case with off-seasons trees. Flowers are pollinated by insects (entomophily) and wind (anemophily) and this may explain the large heterogeneity in organoleptical and pomological characters (Kengue, 1998).

Two types of fertilization take place on African plum trees. Autogamy or self-fertilization is the phenomenon where a pollen grain (male gamete) from a flower of a plant fertilizes its very ovule (female gamete) or the ovule of another flower on the same plant. Allogamy (syngamy) or cross-fertilization occurs when a pollen grain from a plant fertilizes the ovule of another plant. Fruits attain their maximum size after seven weeks but it takes about three months or more for physiological maturity to set in. Seed dispersion can either be zoochoric, hydrochloric or barochoric (Ayuk *et al.*, 1999a). Germination is epigeal (Kengue, 1990).

2.9.3. Habitat and geographical distribution of *Dacryodes edulis*

Dacryodes edulis is distrinuted in equatorial and humid tropical forest. It is originated from Central Africa and more precisely from the Gulf of Guinea (Cameroon and Nigeria) (Vivien et Faure, 1996). Older literature limited its geographical occurrence to the forest regions of Central Africa (Auberville, 1962). The current distribution as a result of human activities extends beyond its zone of origin to: Central African Republic (CAR), Gabon, Democratic Republic of Congo (DRC), Republic of Congo, and, then as far as Uganda in East Africa, Angola and northern Zimbabwe in the south of Africa (Bourdeault, 1971) (Fig. 12). Humans have extended its current distribution not only within Africa as Ivory Coast (Mpungi Buyungu, 2000), but also to tropical Asia (Aumeerudy et Pinglo, 1989). In Central Africa, it is a dominant fruit tree species in homegardens, cocoa and coffee agroforests, fallow land, and crop fields especially in Cameroon, Gabon, Congo, DRC, and southern Nigeria. The species is also sparsely distributed in secondary forests.

In the humid tropics of West and Central Africa, *D. edulis* manifests high climatic plasticity (Tchotsoua et Mapongmetsem, 1998). *D. edulis* can develop under light shade (hemi-sciaphile) but prefers open areas (heliophile) (Kengue, 2002). According to Tchotsoua *et al*. (1997) and Isseri (1998), temperature and rainfall are the two major climatic factors that influence growth and development of the tree. The tree develops well under an average

temperature range of 23-25°C, and with an annual rainfall range of 1400-4000 mm. Very high rainfall encourages vegetative development to the detriment of fruit production (Fig. 13). Average altitude for best performance is 1000 m. *D. edulis* grows on various soil types (Isseri, 1998). Nonetheless, it prefers slightly acidic, deep ferallitic and evolved volcanic soils with exploitable thick and humic horizons (Kengue, 2002). Where there is a well-marked dry season, it is found only in gallery forests and on wet soils.

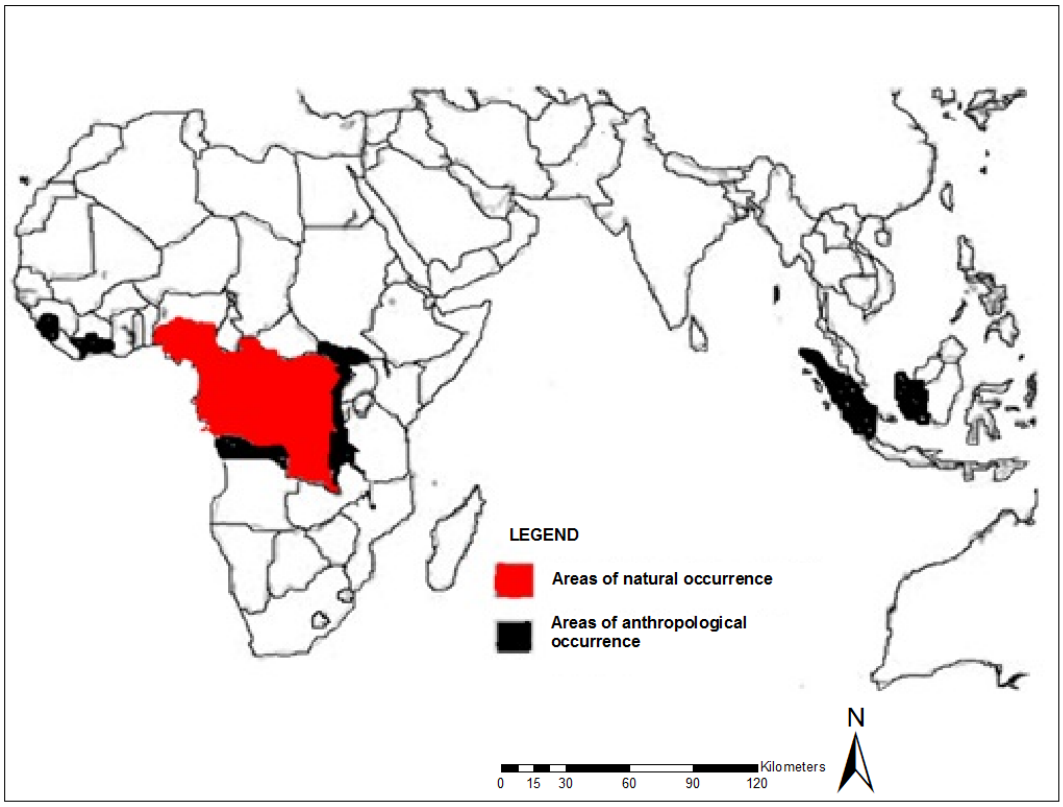


Fig. 12. *Dacryodes edulis* natural and cultivated areas (Adapted from Kengue, 2002).

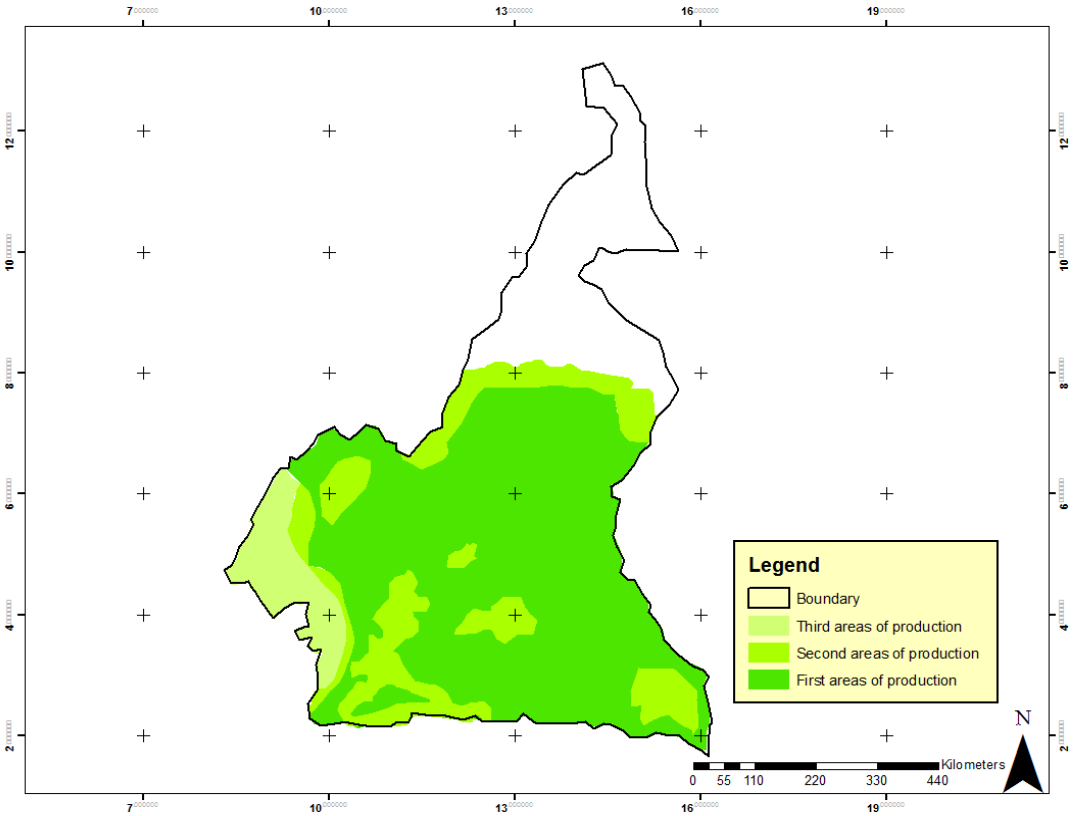


Fig. 13. Production zones of *Dacryodes edulis* in Cameroun (Adapted from Isseri, 1998).

2.9.4. Socio-economical importance of *Dacryodes edulis*

2.9.4.1. Economical importance of *Dacryodes edulis*

The fruit of *Dacryodes edulis* is the economic part that gives its true economic value to the species and explains why the tree is cultivated and/or under domestication (Leakey and Lapido, 1996; Kengue, 2002; Waruhiru *et al.*, 2004; Anegbeh *et al.*, 2005; Schreckenberg *et al.*, 2006). It is a staple food in some regions of Cameroon and Nigeria during fruit production season (June-September; Ndoye and Ruiz-Perez, 1999). The fruit is rich in lipids, proteins, minerals and vitamins making it an excellent snack to consumers. The economic importance of *D. edulis* fruits is quite pronounced in Central Africa in general, and Cameroon, in particular that *D. edulis* is the most-collected agroforestry tree product (AFTP) (quantity-wise) and the most commercialized AFTP in southern Cameroon (Ndoye *et al.*, 1998; Tabuna, 1999). In 1999, 2,324 t of bush butter were sold for a total amount of about US$ 1.5 million in nine big markets in Cameroon (Awono *et al.*, 2002). This quantity represented only about 14-23 % of total production in the national territory as Isseri and Temple (2000) estimated the

national production at 10,000 to 16,000 t. In Nigeria, 70% of fruits are home consumed whereas the average market price per ton of fruits ranges from US$ 300-700 (Ajibesin, 2011).

Awono *et al.,* (2002) stated that, between 1995 and 1996, among eight AFTPs widely commercialized in Humid Tropics of Central Africa, *D. edulis* fruits occurred at the first rank (Table IV). This resource is mostly exported by Cameroon (200 t), RDC (120 t) and Nigeria (6 t). These sales respectively generated 1.861.735 US$, 1.117.041 US$ and 71.987 US$ to these economies. In 1999, Cameroon exported 89 t to Gabon and Congo. *D. edulis* fruits have entered the international market. Of the 105 t of *D. edulis* exported to Europe (France and Belgium) in 1998, 100 t came from Cameroon, 3 t from DRC and 2 t from the Republic of Congo (Tabuna, 1999). Cameroon therefore occupies and undisputable position in sub-regional and international transactions in the production and the sales of the African plum. More in general, the principal importing countries of *D. edulis* are Belgium, France and United Kingdom from countries such as Cameroon, Nigeria, Republic of Cameroon, Democratic Republic of Congo, and Central Africa Republic. The estimated potential market in these importing countries was about 120,000 people (Awono *et al.*, 2002). *D. edulis* fruits therefore constitute an important source of food, income and employment, and enhance livelihood to farmers, transporters and traders (Schreckenberg *et al.,* 2006). According to Ingram and Shure (2010ab), *D. edulis* market value was estimated at 989.504 US$.

Table III. Value of AFTPs commercialized in the Humid Tropic zone of Cameroon between 1995 and 1996.

AFTP	Sales value of AFTPs in 1995 (millions FCA)	Sales value of AFTPs in 1996 (millions FCA)
***Dacryodes edulis* (fruit)**	**301.549**	**467.119**
Garcinia kola (fruit)	921	14.990
Garcinia kola (bark)	3.971	2.109
Garcinia lucida (bark)	10. 360	9.867
Gnetum spp (leave)	3.508	35.822
Irvingia spp (fruit and nut)	124.627	147.769
Cola acuminata (nut)	217.564	94.655
Elaeis guinensis (fruit)	14.896	4.722
Ricinodendron heudelotii (nut)	194.170	211.503

Source: Awono *et al.,* (2002); In 1995-1996, exchange rate was US$=685FCFA.

2.9.4.2. Nutritional importance of *Dacryodes edulis*

The contribution of fruits to a healthy and nutritious diet, the world over is a well-established fact that *Dacryodes edulis* is a tree cultivated widely for its edible and nutritious fruits. Generally, the fruit may be cooked in hot water, or roasted/baked in an oven at about 50º C. The cooked fruit can be eaten with maize, plantain, cocoyam (*Xanthosoma sagittifolium*), bread, etc. Unlike other oily fruits, both *D.edulis* fruit pulp and seed oil contain the same fatty acids and physicochemical properties (Table V) (Kalenda *et al*., 2002; Koudou *et al.,* 2008; Ajayi and Adesanwo, 2009) with the seeds containing as much as 18-70 % oil made of polyunsaturated fatty acid (Gunstone and Norris, 1982).

The fruit pulp of *Dacryodes edulis* is rich in lipids, with oil content determined on dry basis reported to range from 30-60 % (Silou and Kama Niamayoua, 1999). Kapseu and Tchiégang (1996) cited by Kengni (2002), stated that the fat content in terms of dry mater (g/100 g) of *D. edulis* pulp is 63.4 % which is not far from that of palm nut: *Elaeis guineensis* (69 %), closer to that of avocado: *Persea Americana* (65 %) and shea nut: *Vittelara paradoxa* (50 %), and higher than that of pea nut: *Arachis hypogea* (45 %), coconut: *Coccus nucefera* (38 %), and soybean (18 %). Furthermore, Kinkela *et al.*, (2006), maintains that oil content in *D. edulis* pulp could be as high as 70 %.

Furthermore, Ikhuoria and Maliki (2007) and Nwosuagwu *et al.,* (2009) reported lower oil content from *D.edulis* fruit pulp in Nigeria with values as low as 23.2 %. According to Omogbai and Ojeaburu (2010), *D. eduis* pulp oil content is considerably higher when compared to other fruits such as apple with 0.4 %, guava 0.4 %, banana 0.39 %, and pawpaw with traces of oil. The lipids yields numerous fatty acids such as palmitic acid (30-62 %), oleic acid (18-60 %), linoleic acid (15-24 %) and stearic acid (1.3-5.5 %) (Omoti and Okiy, 1987; Obasi and Okoli, 1993; Silou and Kama Niamayoua, 1999; Mbofung *et al.,* 2002; Kinkela *et al.,* 2006; Ikhuoria and Maliki, 2007). Arachidonic acid was recently identified in *D. edulis* fruit pulp and seed and reported as an important fatty acid (Ajayi and Adesanwo, 2009) (Table VI).

Table V. Physicochemical properties of *D. edulis* (approximate composition). Energy is expressed in kcal / 100 g; acid and saponification values are expressed in mg KOH / g of fat while iodine value is expressed in g iodine / 100 g fat. ND: not determined.

Constituents	Pulp	Seed	Research site
Moisture (%)	58.9-70.3	7.9-58.5	Cameroun Nigeria, RDC, Côte d'Ivoire Gabon
Ash (%)	3.4-4.7	6.8-12.6	
Fatty acids (%)	36.6-71.3	12.0-47.5	
Total Carbohydrates (%)	9.8-16.3	7.6-20	
Total energy (%)	444.7	273.6	
Protein (%)	6.6-27.1	13.8-33.8	
Fibre (%)	17.9-27.1	17.3-25.0	
Polyphenols (%)	1.2	ND	
Vitamin C (mg/100 g)	24.5-209.0	ND	
Vitamin A (mg/100 g)	0.65-67	ND	

Authors: Kapseu and Tchiégang (1996), Tchiendji *et al.*, (1981), Youmbi *et al.*, (1989), Ali *et al.*, (1998), Fonteh (1998), Koumpo (1998) et Kengni (2002) for Cameroon; Omoti and Okyi (1987) ; Obasi and okolie (1993), Achinewhu (1993) and Okafor *et al.*, 1996) for Nigeria ; Kikouama et Silou (1999), Silou (1991) for the la Republic of Congo and Laroussile (1964) for Ivory Coast.

Mbofung *et al.*, (2002) reported a 49-58 % variation in the fatty acid content of *D. edulis* fruits from Cameroon, Republic of Congo, Democratic Republic of Congo, and Gabon with some consistency observed in samples from Equatorial Guinea. The latter fatty acid values reported for countries within the Congo basin forest in Central Africa are higher than those reported for Nigeria (30.35-35.60 %) in West Africa (Omogbai and Ojeaburu, 2010). *D. edulis* fruit pulp and seed oil contain important polyunsaturated fatty acid such as linoleic acid, which are relevant to human food in the prevention of cardiovascular disorders.

The rich content of oleic acid in the oil gives it oxidative stability which is important for its use as frying oil (Ikhuoria and Maliki, 2007). Thus oil from *D. edulis* fruit pulp and seed can be exploited commercially as vegetable oil for home use as well as other industrial applications.

Table VI. Fatty acid profile of *Dacryodes edulis* pulp and seed.

Fatty acid	Fatty acid name	Mean	
		Pulp	Seed
C16:0	Palmitic acid	17,18	43,16
C18:0	Stearic acid	14,84	4,59
C18:1	Oleic acid	40,45	21,97
C18:2	Linoleic acid	23,17	12,63
C20:0	Arachidic acid	2,1	11,56
C20:1	Gadoleic acid	0,91	0,21
C20:2	Eicosadienoic acid	0,84	3,21
C20:3	Eicosatrienoic acid	0,51	1,72
C22:0	Behenic acid		0,32
C22:1	Erucic acid		0,27
C22:2	Brassic acid		0,12
C24:0	Lignoceric acid		0,06
C26:0	Cerotic acid		0,18
Saturated		34,12	59,87
Unsaturated		65,88	40,13

Source: Ajayi and Oderinde (2002).

Regarding analogy to common oils, a study on chemical and nutritional composition of safou in Republic of Congo (Table VII) stated that olive oil (*Olea europea*) had only 0.5 % of acylglycerols with two unsaturations, which is largely below safou oil (Dzondo-Gadet *et al.*, 2005). From this study, authors pointed out that the low saturated fatty acid contents of olive and soybean oils contribute to their low melting points and make them easy to use for dressings. Nevertheless, these oils are very unstable at high temperature. Safou pulp oil, with its composition as 50 % of saturated, 25 % of mono unsaturated and 25 % of polyunsaturated, appears as equilibrated oil.

From older studies, Kengni (2002) pointed out that the protein content of *D. edulis* defatted pulp is 25-27 % (Omoti and Okiy, 1987; Ali *et al.*, 1998), which is comparable to that of defatted kernel of *I. gabonensis* (Table VIII). The amino acid composition shows the concentrations (in terms of g per 100 g of protein) of lysine (6.27 %), leucine (9.57 %) and threonine (4.39 %) to be similar to those found in the proteins of hen's eggs (Lys 7 %; Leu 4.2 % and Thr 5.1 %) for Lys and Thr and higher for Leu. These concentrations are also comparable to those of cow's milk and beef muscle, but higher than in wheat, barley (*Hordeum vulgare*), rice, maize, sorghum and melon seed (*Cucurbita pepo*).

Table VI. Composition by percentage (%) of saturated and unsaturated fatty acid in major usual oils.

Seed or pulp	Carbon number							
	C14	C16:0	C16:1	C18:0	C18:1	C18:2	C18:3	C20
Peanut (USA)	0.04	10.6	0.13	2.41	47.05	30.77	0.14	1.31
Colza-Canola		5.56	0.12	1.38	58.25	22.17	8.9	0.22
Sunflower		6.27		4.86	19.69	67.44	0.03	0.31
Olive		14.31	1.65	2.48	66.68	13.91	0.5	
Soybean		11.03		3.91	23.04	56.84	7.9	
Maize		10.69	0.12	2	25.46	59.35	0.92	0.37
Palm	0.89	43.14	0.18	5.41	38.72	10.59	0.27	0.39
Safou		42.4 ± 0.4	0.2 ± 0.1	2.5 ± 0.1	27.8 ± 0.45	25.2 ± 0.1	1.2 ± 0.5	

Source : Dzondo-Gadet *et al.,* (2005).

Furthermore, the amino acid content of *Dacryodes edulis* fruit pulp has been reported to vary between 2.89-4.16 % (Omogbai and Ojeaburu, 2010). Though this figure is generally low, the latter pulp could still make significant contribution in starchy diet thereby ameliorating protein malnutrition. For example Mbofung *et al.,* (2002), reported a 39 % increase in protein contents of biscuits when ordinary margarine in the biscuit recipe was substituted by *D. edulis* pulp oil. The fruit pulp of *D. edulis*, following a chemical analysis of 100 g samples from five states in Nigeria, is a rich source of mineral elements such as sodium, potassium, calcium, phosphorus, magnesium, iron, copper, and zinc (Table IX) (Kengni, 2002). Thus, *D. edulis* pulp is highly nutritive if consumed. For instance, elements in the pulp like sodium are required for the regulation of acid-base equilibrium, maintenance of osmotic balance, whereas it protects against dehydration in the body (Kengni, 2002; Duru *et al.,* 2012).

Potassium is the chief cation of the intracellular fluid and is also involved in protein synthesis. Other elements like iron and calcium present in *D. edulis* fruits are vital for blood formation as well as providing hardness and/or strength to bones and teeth (Omogbai and Ojeaburu, 2010).

Table VIII. Amino acid profile of *Dacryodes edulis* pulp and seed. a = Methionin alone.

	Country			
Constituents	Congo		Nigeria	Ivory Coast
	Seed	Pulp	Seed	Seed
Essential amino acids (%)				
Lysine	3.45	6.27	8.41	2.13
Histidine	1.45	2.41		1.42
Phenylalanine	2.91	2.97	4.97	3.06
Leucine	5.41	9.57	18.56	5.70
Isoleucine	4.50	3.87	7.50	4.49
Threonine	3.54	4.39		5.58
Methionine & Cystine	2.50a	1.02	0.94a	3.56a
Valine	4.27	3.73	3.45	4.27
Arginine	3.75	3.34	2.90	2.85
Non-essential amino acids (%)				
Aspartic	11.47	15.04	13.08	11.04
Serine	4.30	4.86	4.49	4.63
Glutamic	9.37	17.04	12.02	9.26
Proline	4.37	6.59	5.72	4.63
Glycine	3.95	2.64	2.29	4.27
Alanine	4.79	7.71	7.12	4.98
Tyrosine	3.87	4.97	4.52	3.77

Source: Kengni (2002).

2.9.4.3. Medicinal and ethno-medicinal values of *Dacryodes edulis*

The entire plant of *Dacryodes edulis* has pharmaceutical and cosmetic properties that are variously exploited by many African communities (Dibong *et al.*, 2011; Omonhinmin, 2012). This is guaranteed by a quantity (1-2 %) and quality (sterols, triterpene alcohol and traces of tocopherols) of the unsaponifiable fraction of the oil in the fruits (Ajibesin, 2011). Prichard (1991) cited by Dawodu (2009), stated that the African plum seed oil content can be used in cosmetic industries. *D. edulis* oil can also be used in food industries (Mbofung *et al.*, 2002; Ajayi and Adesanwo, 2009). Moreover, a cut on a bark releases an exudate used in some societies as incense, which is used to cure skin diseases (Kengue, 2002; Verheij, 2002). No part of *D. edulis* is known to be toxic (Obasi and okolie, 1993; Ajibesin *et al.*, 2002). However, the findings of Hanson (2009) opposed this report when he found the seed to

contain antinutrient factors such as oxalate, tannins, and phytate and trypsin inhibitory activity, thorough processing of the seed before use was therefore suggested. Sometimes, the fruit sold in the market may be contaminated with metal pollutant (Akinola and Adenuga, 2008).

Table IX. Mineral composition of *Dacryodes edulis* pulp and seed.

	Mean (%)	
Constituents	Pulp	Seed
Na (mg/100 g)	0.19-89.00	30.00-80.00
K (mg/100 g)	0.86-230.00	2030.00-2680.00
Ca (mg/100 g)	0.53-690.0	340-730
Mg (mg/100 g)	0.73-450.00	241-3280
Fe (mg/100 g)	0.10	5112-6100
Zn (mg/100 g)	0.03	36-3747
Cu (mg/100 g)	0.01	5-3700
P (mg/100 g)	220.00	218-460
Water (%) for 100 g Dry Matter	50	

Source: Kengni (2002).

In Cameroon, people from Western Highland crushed the bark and used in concoctions against dysenteries while in central Cameroon the bark is used to treat toothache (Mapongmetsem, 1998). Species for the Burseraceae family generally contain a well-known oleoresin which chemical formula is $C_{30}H_{500}$ and whose melting point is between170° and 175°C, thus can be used to cure injuries and skin diseases (Onana, 1998; Kengne, 2002; Makueti, 2007). Nguefack (2009) reported the significant antioxidant and free radical scavenging activities in the aqueous and ethanol extracts of *D. edulis*. Similarly, Ogunmoyole *et al*. (2012) stated that *in vitro* boiling of *D. edulis* seeds highly potentiated on its phytochemical constituents and antioxidant properties. The leaves made into a plaster have been recently reported to treat snake bites in South West Cameroon (Jiofack *et al.*, 2010).

Leaves of African pear can also be used as forage (Duguma and Tonye, 1994). The seeds (3.2 % protein/unit dry matter) and pulp can be used to formulate livestock feed (Mbofung *et al.*, 2002). The wood is used for making tool handles, and occasionally for mortars, is suitable for wood working and is used as firewood. *D.edulis* is a melliferous tree (Kengue, 1990; Messi *et al.*, 1994; Tchuenguem *et al.*, 2001; Azo'o Ela *et al.*, 2010), the nectar produced appreciated honey.

In Gabon, the bark of the plant has long been reported to treat wounds (Raponda-Walker and Sillans, 1961). The essential oils of the plant resin were investigated for antimicrobial and antioxidant activities. The essential oil showed that more potent antibacterial effect against bacteria such as *Staphylococcus aureus*, *Bacillus cereus*, *Escherichia coli*, *Salmonella enteric* and *Proteus mirabilis* than fungal effect against *Candida albicans* and this effect was found to be due to the presence and high content of terpinen-4-ol (19,8 %) and alpha-pinene (17,4 %) (Obame *et al.*, 2008). In another study, the antibacterial effect of the essential oil of the plant resin was confirmed to be due to the presence and high content of the same foregoing terpenes (Table X), but antifungal effect of the oil was reported to be lacking (Koudou *et al.*, 2008). This essential oil of *D. edulis* resin also demonstrated an antioxidant activity (Ella Missang *et al.*, 2001; 2003; Obame *et al.*, 2008). Furthermore, this antioxidant capacity was ascribed to the mono and sesqui terpenes present in the plant essential oil. Employing similar antioxidant assay methods, Koudou *et al.*, (2008) reported significant antioxidant effect of the resin oil on the scavenging activities and inhibition of lipid peroxidation and suggesting that *D. edulis* may help to prevent oxidative damage in the human body such as lipid peroxidation associated with cancer, premature aging, atherosclerosis and diabetes.

In Nigeria, the leaves are crushed and the resultant juice used to treat skin diseases such as scabies, ring worm, rashes, while twigs from branches are sometimes used as chewing sticks (Igoli *et al.*, 2005; Ajibesin *et al.*, 2008; Okwu and Nnamdi, 2008). Its bark has long been used to cicatrize wound (Okunomo and Egho, 2010). The resin from the bark has long been reported to treat parasitic skin diseases and jiggers (Hutchinson, 1963) whereas when applied in lotions and body creams it smoothens the skin (Ekpa, 1993). The resin is also used in some communities as incense and is believed to send off evil spirits in Nigeria (Sofowora, 2008). Overall, the presence of bioactive compounds such as saponins, tannins, alkaloids and flavonoids identified in *D. edulis* has been suggested to be responsible for the various uses of the plant in traditional medicine (Ariza and Aworth, 2008; Okwu and Nnamdi, 2008).

Table X. Characteristics of the oil of the resin from the bark *of Dacryodes edulis.* RI= Retention Indices; tr = Trace percentage < 0.1%.

Level	RI	Constituents	%
1	927	*α-Thujne*	1.55
2	935	*α-Pinene*	17.47
3	951	*Camphene*	0.24
4	975	*Sabinene*	21.76
5	979	*β-Pinene*	4.27
6	1001	*Menth-3-ene*	0.37
7	1007	*&-phellandrene*	0.22
8	1009	*δ-3-carene*	0.23
9	1018	*α-terpinene*	1.22
10	1026	*p-cymene*	11.29
11	1031	*Limonene*	5.72
12	1032	*β-phellandrene*	0.99
13	1034	*1,8-cineole*	0.68
14	1060	*γ-terpinene*	5.84
15	1072	*Cis sabinene hydrat*	1.08
16	1086	*Terpinolene*	1.08
17	1091	*p-cymenene*	Tr
18	1102	*Trans sabinene hydrat*	0.39
19	1119	*β-thujene*	Tr
20	1127	*Cis p-menth-2-en-1-ol*	0.40
21	1138	*Terpinen-1-ol*	Tr
22	1142	*Trans sabinol*	Tr
23	1145	*Trans p-menth-2-en-1-ol*	0.37
24	1148	*Camphre*	Tr
25	1184	*Terpinen-4-ol*	19.79
26	1189	*p-cymene-8-ol*	0.13
27	1197	*α-terpineol*	3.01
28	1211	*Trans piperitol*	0.20
29	1257	*Piperitone*	0.22

Source: Koudou *et al.*, (2008).

In addition, the potential health-related functions of dietary plants were found to include antibiosis, immunostimulation, nervous system action, detoxification, anti-inflammatory, antigout, antioxidant, glycemic and hypolipidemic properties (Johns, 2001; Onocha *et al.,* 2011; Compaoré *et al.,* 2011).

In the Republic of Congo, Burkill (1985) reported that the decoction of the bark of *D. edulis*is rich in aromatics thus could heal diarrhea, dysentery, anemia, menstrual disorder, lung infections and mouth gargles. The bark of the root cures leprosy. The leaves are boiled in combination with *Lantana camara, Cymbopogon citratus* and *Persea americana* yielding a steam bath taken to treat fever/headaches (Bouet, 1980) and malaria (Diafouka, 1997). A study was carry out by Dzondo-Gadet *et al.,* (2005) on the characterization and nutritional interest of safou pulp oil and their results were in line with those reported by other authors from different countries in the sub-region.

In the Democratic Republic of Congo, a concoction of the bark is taken as oral treatment against leprosy and it is also gargled as mouth-wash for the treatment of tonsillitis (Bouquet, 1969).

2.9.5. Sylvicultural value of *Dacryodes edulis*

The settlement and the intensification of cultivation of African plum like the most AFTPs would meet the increasing famers' income, reducing slash and burn agriculture and the pressure of population on forest through the unsustainability management of these products. The rusticity of the plant and its possibilities to be use in the fight against erosion on marginal soils, are some positive aspects to environmental problems (Okorie, 1998). *D. edulis* adapts easily and is found in evergreen rainforest, gallery forest and marshes. It can still be found in the homegardens, cocoa and coffee plantations, fallow fields and crops.

In cropping systems, in addition to shading, *D. edulis* brings to perennial or annual mainly coffee (*Coffea* spp), cocoa (*Theobroma cacao*), cocoyam (*Colocasia* spp, *Xanthosoma* spp), cassava and yam (*Dioscorea* spp); it provides a large amount of litter, which helps to maintain soil fertility by improving its organic status (Mapongmetsem 1994; Okorie, 1998; Sonwa *et al.,* 2001). Leaves and fallen fruit produce a significant amount of biomass that improves soil fertility (Aiyelaagbe *et al.,* 1998; Okunomo *et al.,* 2000; Mpungi Buyungu, 2001; Okunomo and Orji, 2004; Okonomo *et al.,* 2007; Omokhua & Koyejo, 2009). According to Burkill (1985), *D. edulis* is a tree used as an agri-horticulture indicator (weather,

season, time) and as a shade tree. The *D. edulis* wood by its soft consistency and color yellowish pink is a soft wood easily scrollable and comparable to that of mahogany, *Khaya* spp (Norman, 1948; Raponda-Walker and Sillans, 1961).

2.9.6. Constraints to *Dacryodes edulis* fruit production

Production for fruits is limited by the gynodioecious nature of the species. This phenemenon has been outlined earlier by Renner and Ricklefs (1995). Trees with male-hermaphrodite flowers are generally characterized by low production. With the high inter-tree variability in the species, most farmers use vegetative propagation in an attempt to reproduce desired traits. Unfortunately, this method does not always produce awaited results. Fruit abortion is high in *D. edulis* and this leads to heavy pre-harvest loss in fruits. Cultivation techniques remain traditional and post-harvest losses are high due. This can be explained by the fact that the African plum is a very perishable fruit, thus, the problem of conservation is very acute. In the tropics, conservation of fruits under ambient conditions is hardly possible after 5 days (Nya Ngatchou, 1998). In Cameroon, post-harvest losses stand at 30 % (Isseri, 1998). Silou (1994) demonstrated that 50 % of the post-harvest losses result from early softening of the fruit pulp.

Regarding phyto-sanitary aspects of African plum, anthracnosis (irregular dead areas on leave margins and veins) and scab (swollen plant parts) are the two main diseases, which impact on its production. They are caused by the fungi: *Gloeosporium fructigenum* and *Colletotichum gloeosporioîdes*, respectively. These diseases can cause the loss of almost all the fruits on a tree. Some insects such as caterpillars, grasshoppers and beetles do attack and destroy plant parts such as the leaves, fruits, flowers, stems and roots (Kengue, 2002). *Botryodiplodia theobromae* and *Rhizopus stolonifer* have also been reported as being responsible for a post-harvest rot disease (Black and Janssens, 1996). The damage caused to the plant by these diseases and pests is usually high and heavily reduces the market value of the fruits (Mouaragadja and M'Batchi, 1994). This is explained by the fact that the period of pullulation of these pests generally coincides with that of active plant growth; period during which trees prepare to flower and fruit (Kengue, 2002). Avifauna visit and eat up fruit parts, thereby adding to the toll of fruit drop, which is naturally alarming (pers. obs.).

Partial conclusion

As important components of sustainable integrated agriculture, tree crops are attracting increasing attention for researchers and politics. Species like *D. edulis* under domestication, and in response to purposeful man-led selection, now have reduced juvenile phase to first fruit production, larger fruit size, extended fruiting season, and less competitive rooting system for belowground resources if intercropped in an agroforestry context with companion crops, all brought about by vegetative propagation methods. Hence, best candidates to be used for the establishment of long-lived perennials like *D. edulis* of vegetative origin must be produced through hand controlled pollination, a technique which may help to combine a number of desired fruit characters in one tree and increase the inter-tree variability between selected superior genotypes. The integration of the improved planting materials in different land use systems will provide food, and generate income through sales of fruits and could enhance the provision of ecological services (erosion control, habitat for flora and fauna, nutrient recycling, carbon sequestration and help to counter climate change).

Furthermore, filling the niches under the trees through intercropping with useful and marketable annuals herbs, cereals and grain legumes would be important for the further improvement and diversification of the livelihoods options of rural populations, and overall profitability and value of the system. This could lead to higher yields, increase rural incomes, resulting in greater food security and avoided emissions through the integration and retention of useful trees supplying diverse products in agricultural landscapes in the humid tropics of Africa where the species grow naturally. Similarly, farmers are encouraged to incorporate *D. edulis* trees into their farming systems and plant new *D. edulis* trees in areas where land has been cleared or abandoned. This form of smallholder agroforestry production contributes to better landscape connectivity and can help enhance the integrity of forest landscapes.

2.10. Research needs

From the findings of the preliminary studies on *D. edulis*, the main research needs are focused on the following axes:

- ❖ understanding the breeding system of the studied species in order to develop (through controlled hand cross-fertilization) and characterize improved planting materials which will serve as raw material for clonal test and vegetative propagation in the fulfilment of cultivars development;

- establishment of seed and/or clonal orchards for further clonal trials;
- development of improved dwarfed trees through a decapitation test for yield improvement by assessing relationship between branching habit, harvest index and yield improvement;
- creation of a pollen gene bank for further controlled crosses and reproductive biology purposes.

CHAPTER II. MATERIAL AND METHODS

II.1. Study sites

The present study was carried out during three flowering seasons (repetition), from January 2010 to September 2012 at two experimental field trials established by ICRAF (Fig. 14). The selected locations are known to be among the best in terms of *D. edulis* production, consumption and commercialization. The first living gene bank is situated at Minkoa-Meyos near Yaoundé, Cameroon (3°51'N Lat., 11°25'E Long.), which lies at an altitude of 813 m.a.s.l., with a mean annual rainfall of approx.1400 mm with bimodal distribution and a mean annual temperature of 25°C. The soils are moderately acid i.e pH 1:1 soil:water 5 to 6 and Al saturation 20. Nursery activities were taken at the ICRAF's central nursery situated at Nkolbison (3°51'N Lat., 11°27'E Long.) which lies at an altitude of 760 m.a.s.l. with a mean annual rainfall of approx.1300 mm.

Fig. 14. Localization of the studied sites.

Source: National Institute of Cartography 2006 (Redrawn by Priscilla Ngaukam).

The second living gene bank is situated at 65 Km from Yaoundé in the Mbalmayo division (3°10'N Lat., 11°00'E Long.), which lies at an altitude of 650 m a.s.l., with a mean annual rainfall of approx.1802 mm and a mean annual temperature of 24°C. The soils are deep ferralitic (Ambassa-Kiki, 2000).

II.1.2. Minkoa-Meyos

The mean annual rainfall stands at 1295 mm. Rainfall pattern is bimodal with a long rainy season from March to June and a short rainy season from September to November. December, January and February make up the long dry season (Fig. 15) (Ambassa-Kiki, 2002).

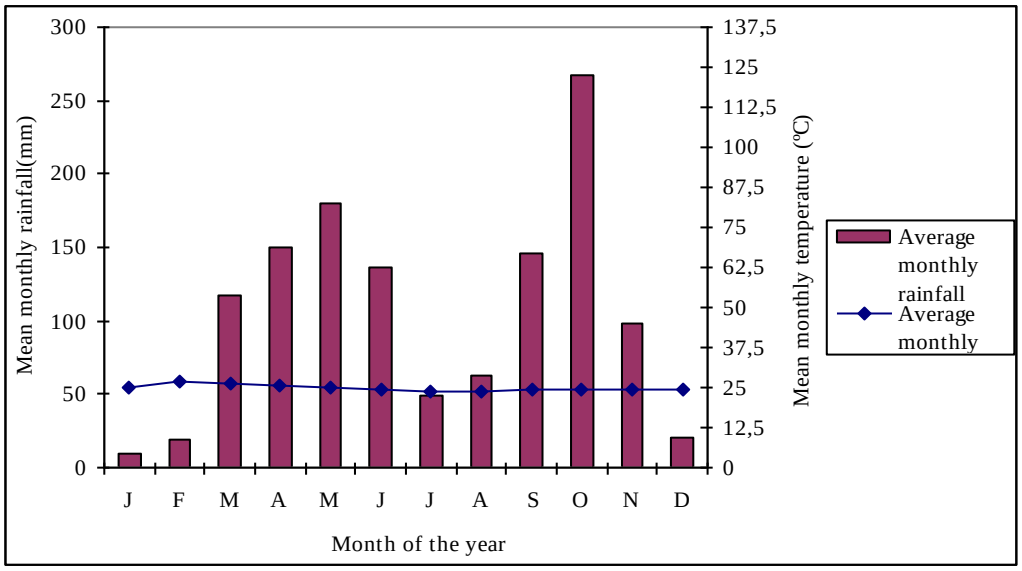


Fig. 15: Average monthly rainfall and average temperature for Minkoa-Meyos from 1999 to 2005 (Source: Provincial Service of Meteorology, Centre Province)

FAO classification classifies the soils of Minkoa-Meyos into the group ferric arisol. The vegetation is a degraded tropical forest dominated by species such as *Entandrophragma utile, Entandrophragma candollei, Triplochiton scleroxylon, Terminalia superba and Mansonia altissima.* Patches of secondary forest dominated by *Elaeis guineensis, Musa paradisiaca, Albizia zygia* and *Ceiba pentandra* occupy the rest of the site. In under growth, *Aframomum* spp, *Costus affer, Megaphrynium macrostachryum and Haumania*

danckelmaniana are abondant. There also exist *Chromolaena odorata* based fallows (Ambassa-Kiki, 2002).

II.2.2. Mbalmayo

The ICRAF experimental field trial of Mbalmayo is located in the equatorial humid forest zone of Cameroon (Ambassa-Kiki, 2002) between longitude 11° 00' and 11° 50' East and latitude 3° 10' and 3° 40' North. The altitude ranges between 600-700 m above sea level with undulating hills and broad valleys. It has Guinean type of climate, an average temperature of 24 °C with an average annual rainfall of 1802 mm from 1999 to 2005.

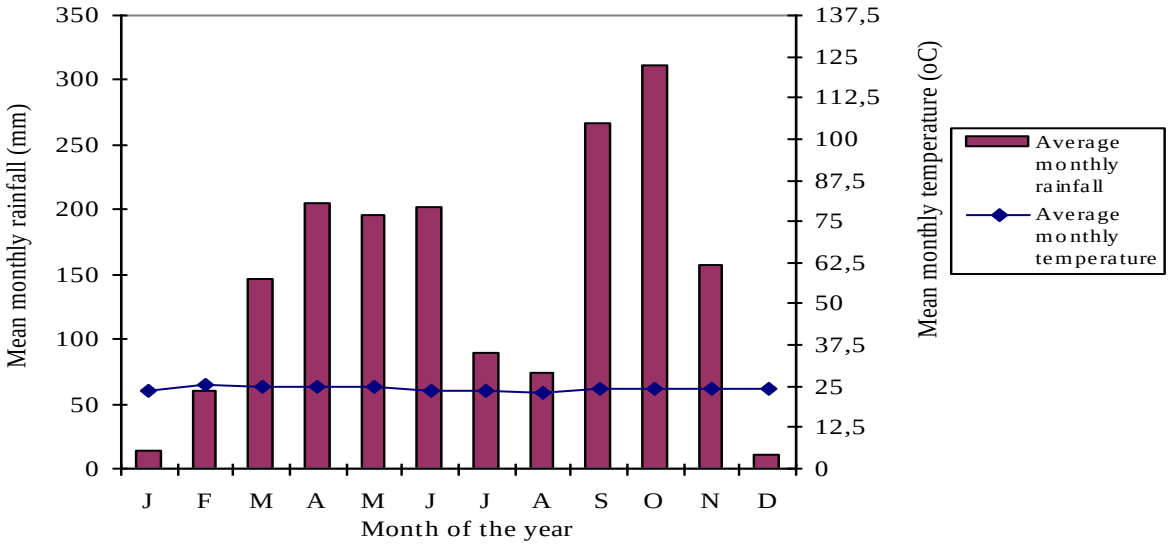


Fig. 16: Average monthly rainfall and average temperature for Mbalmayo from 1999 to 2005 (Source: Provincial Service of Meteorology, Centre Province)

Rainfall pattern is bimodal (Ambassa-Kiki, 2002) with a long rainy season from March to June and a short rainy season from September to November (Fig. 16).Total sunshine is estimated at 1500 per annum. FAO classification places the soil in the Ferrasol major soil group with soil unit Xanthic Ferrasol. The vegetation is composed of semi-deciduous and evergreen dense forest dominated by Sterculiaceae and Ulmaceae and a secondary forest with fallow areas colonized by *Chromolaena odorata* (Ambassa-Kiki, 2002).

II.2. Methodology

II.2.1. Plant material established by ICRAF and agro-morphological traits

The seedling gene banks in which the field experiments were carried out were established with the participation of farmers in 2001, and the first flowering took place in 2007 (Tchoundjeu *et al.*, 2002). The living gene banks are comprised of five provenances from which four were chosen for the implementation of this study, namely Boumnyebel (Littoral Region), Makenene (Central Region) and Kekem (West Region). Limbe (South-West Region) is the fourth and the 5th one named Ongot (Central Region) was victim of bush fires. These provenances represent the major agro-ecological zones where *D. edulis* grow naturally in Cameroon. Each provenance consists of two trees (accessions or "plus trees") (Table XI) on line each of five sub-populations, thirty progenies per sub-population arranged in randomized blocks of 150 trees per block, with a maximum distance between the blocks approximately 100 m. Each randomized block consisting of accessions of the same provenance, includes 15 repetitions. Distance between sub-populations was 200 km and between "plus trees" was 100 m apart (see Appendice 1).

The collected germplasm was accessions of well-known and appropriate origin from home gardens, crop fields, forest fallow, cocoa and coffee farms. The trees were also located using a Global Positioning System for further sites mapping (summary given in Table XII). Fifty seeds were collected from each tree, seeded and grown in polyethylene bags in the ICRAF's central nursery, Yaoundé, Cameroon. After six months of growth in the nursery, planting were transplanted as provenance test (field trials). These seedlings were planted in 40x40x60 cm hole sand filled at 30 cm depth with fertile soil at 5x5 m spacing. Provenance-plots were surrounded by buffer rows of unimproved and unknown *D. edulis* provenances. Trials were hand-weeded twice per year for at least the first seven years.

Characteristics selected for accessions include size and fruit flavor, color and thickness of the pulp, pulp oil content, the fruiting season, disease resistance and pest, the frequency and regularity of fruiting efficiency (yield).

The experimental plant material (Fig. 17) comprised of 25 (17 females and 8 male-hermaphrodites) selected superior genotypes accessions of African plum (9 years old) submitted to controlled hand cross-pollination using a full nested mating design (Zobel and Talbert, 1984).

Table XI. *Dacryodes edulis's* provenance and "plus tree" parents used for the crossbreeding test.

Provenance	Plus trees or accessions		
	Male tree	Hermaphrodite tree	Female tree
Boumnyebel (BUM29)	BUM/DE/29 Seedling 070	BUM/DE/29 Seedling 050	BUM/DE/26 Seedling 015 BUM/DE/25 Seedling 026 BUM/DE/37 Seedling 111 BUM/DE/25 Seedling 114 BUM/DE/26 Seedling 122
	BUM/DE/09/98 Seedling 12B1	BUM/DE/14/99 Seedling 16B4	
Makenene (MAK33)	MAK/DE/33 Seedling 106	MAK/DE/33 Seedling 126	MAK/DE/04 Seedling 078 MAK/DE/28 Seedling 104 MAK/DE/01 Seedling 116 MAK/DE/04 Seedling 144
Kekem (KEK02)	KEK/DE/02 Seedling 088	KEK/DE/02 Seedling 102	KEK/DE/18 Seedling 050 KEK/DE/18 Seedling 070 KEK/DE/07 Seedling 074 KEK/DE/13 Seedling 079 KEK/DE/07 Seedling 142

II.2.2. Selection of accessions for the crossbreeding test

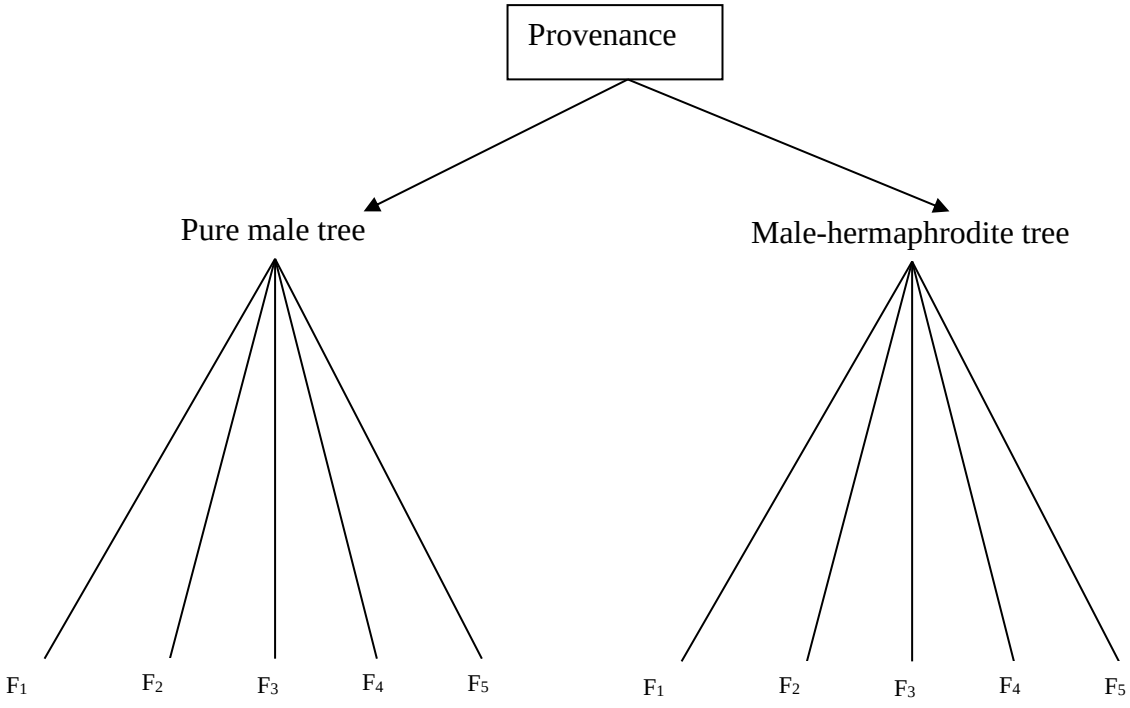
The choice of accessions used for controlled hand-pollination was based on Biakaiy's outcome (2008), which was focused on the biometric characterization of *D.edulis* fruits from the "plus trees" in plots referred above. Based on this work, within the major classes determined from the fruit characteristics used (size, shape, flavor, color of the epicarp and mesocarp of the fruit; seasonality and earliness of production, the resistance to diseases and pests, the regular production and yield), healthy accessions among the most powerful parents (plus trees) were selected according to the methodology chosen, that is 7 trees minimum per provenance, with either a pure male, a male-hermaphrodite and 5 females.

Following this methodology, in Makenene provenance, there were only 4 female trees in flowering instead of 5. In fact, in *D.edulis* as in the most fruit trees, years of mass production are usually followed either by low production or by simply a production defect (Herrera *et al.* 1998). This alternation and irregularity of production, very marked in the

African plum, is also well known in other fruit tree species (Gauthier, 1971) such as olive (Poli, 1979), mango (De la Rousilhe, 1980) and avocado (Gaillard, 1987).

II.2.3. Pollination experiments

The breeding test was conducted following a full nested mating design adapted from Zobel and Talbert (1984) and Nanson (2004). Three factors were studied: (i) the provenance of the male parent: Boumnyebel (BUM29), Makenene (MAK33) and Kekem (KEK02); (ii) the type of flower (male or hermaphrodite) which produced pollen used for hand fertilization and (iii) the female parent status.



F_n : Number of female trees

Fig.17. Nested mating design diagram (Zobel and Talbert, 1984; Nanson, 2004). In the diagram, the chosen male is crossed with five different female plants belonging to the same provenance, knowing that we used four provenances.

The experimental design included provenance as a fixed factor, treatment as within-subject (i.e. repeated measures) fixed factor and plant individual as a random factor (subject) (Fig. 17).

The pollination experiments were performed during three flowering seasons (repetition) between January 20 and March 3, 2010; 2011 and 2012 at the Minkoa-Meyos locality, whereas at Mbalmayo site they were carried out between March 17 and April 13, 2010; 2011 and 2012, using a full nested mating design. In each provenance we marked, labeled and bagged ten healthy and vigorous panicles on five female individuals and two male-hermaphrodites, one week prior to anthesis. Depending of the sex of the accession pre-determined by the morphology of the inflorescence, that is 8 to 40 cm in length for male and hermaphrodite panicles, and 5 to 20 cm for female accessions, selected panicles were bagged on both sexes with fine mesh cloth bags (1 mm^2) in size of 30 cm x 15 cm that allowed the passage of light and air, but not insects. In this way, we prevented flower deformation, unwanted insect visits and possible pollen removal (Fig. 18).

Pure male parents are those male trees that, since the first flowering of the accession, had never bore fruits and their essential role is the production of pollen for the fertilization of female trees. Contrary, male-hermaphrodite trees are those trees, which occasionally bore fruits compare to female trees, which bear fruits during each flowering season.

The bags were removed from anthesis when the first open flowers were in the female stage. In established provenances, fresh pollen harvested from 2 male trees were used to fertilize ovules on 5 female trees. The average number of 18 flowers was used and any unopened buds were removed. Pollen was collected with a pair of pliers and a fine paint brush with black hairs against which the pollen could be seen, and kept in a Petri dish (Fig. 19 and 20). Since there was a gradient of open flowers at both flowering branch and entire panicle, it was not possible to pollinate the flowers the same day. On each selected female tree, bags were removed every day at 9 a.m., recently opened flowers were pollinated once by fresh pollen previously harvested on two male-hermaphrodite between 6 and 8 a.m., located at least 10 m away from the targeted female. The petri dish and brush were carefully cleaned with alcohol between flowers and trees to prevent contamination.

Fig. 18. *Dacryodes edulis* floral panicle isolated with fine mesh bag and labeled

Fig. 19. *Dacryodes edulis* male flowers in a Petri dish

The panicles were then rebagged immediately after hand-pollination. Flowers were monitored every three to four days recording the number of fruit set per panicle and per female tree and bags were removed after eight days, Makueti *et al.*, (2012a). In total, 06 distinct male parents including 03 pure male and 03 male-hermaphrodites were used for the crossbreeding of 14 selected vigorous and healthy female trees, making 20 trees for the crossbreeding test.

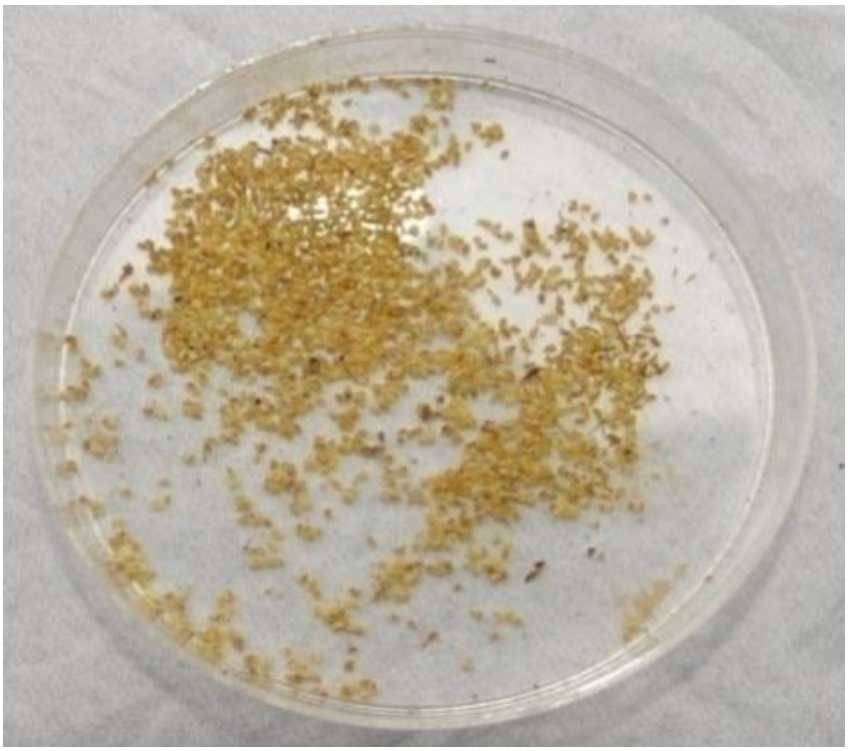


Fig. 20. *Dacryodes edulis* fresh pollen in a Petri dish

For the list of the 25 African plum accessions used for the study, see Table XI.

Table XII. List of the 25 studied *Dacryodes edulis* accessions collected from the agro-ecological zones in favour with growth and development in Cameroon. ACC= Accession.

Acc. no.	Code in gene bank	Collection sites	Accession sex	Latitude	Longitude	Altitude (m)
ACC-01	BUM/DE/26 Seedling 015	Boumnyebel	Female	$3^0$52'58.34"N	$10^0$50'57.62"E	358
ACC-02	BUM/DE/25 Seedling 026	Boumnyebel	Female	$3^0$52'58.34"N	$10^0$50'57.62"E	358
ACC-03	BUM/DE/37 Seedling 111	Boumnyebel	Female	$3^0$52'58.34"N	$10^0$50'57.62"E	358
ACC-04	BUM/DE/25 Seedling 114	Boumnyebel	Female	$3^0$52'58.34"N	$10^0$50'57.62"E	358
ACC-05	BUM/DE/26 Seedling 122	Boumnyebel	Female	$3^0$52'58.34"N	$10^0$50'57.62"E	358
ACC-06	MAK/DE/04 Seedling 078	Makenene	Female	$4^0$53'03.84"N	$10^0$47'41.44"E	696
ACC-07	MAK/DE/28 Seedling 104	Makenene	Female	$4^0$53'03.84"N	$10^0$47'41.44"E	696
ACC-08	MAK/DE/01 Seedling 116	Makenene	Female	$4^0$53'03.84"N	$10^0$47'41.44"E	696
ACC-09	MAK/DE/04 Seedling 144	Makenene	Female	$4^0$53'03.84"N	$10^0$47'41.44"E	696
ACC-10	KEK/DE/18 Seedling 050	Kekem	Female	$5^0$09'05.91"N	$10^0$01'16.07"E	715
ACC-11	KEK/DE/18 Seedling 070	Kekem	Female	$5^0$09'05.91"N	$10^0$01'16.07"E	715
ACC-12	KEK/DE/07 Seedling 074	Kekem	Female	$5^0$09'05.91"N	$10^0$01'16.07"E	715
ACC-13	KEK/DE/13 Seedling 079	Kekem	Female	$5^0$09'05.91"N	$10^0$01'16.07"E	715
ACC-14	KEK/DE/07 Seedling 142	Kekem	Female	$5^0$09'05.91"N	$10^0$01'16.07"E	715
ACC-15	MAK/DE/35 Seedling1B1	Makenene	Female	$4^0$53'03.84"N	$10^0$47'41.44"E	696
ACC-16	BUM/DE/14/99 Seedling5B3	Boumnyebel	Female	$3^0$52'58.34"N	$10^0$50'57.62"E	358
ACC-17	MAK/DE/94 Seedling13B3	Makenene	Female	$4^0$53'03.84"N	$10^0$47'41.44"E	696
ACC-18	BUM/DE/29 Seedling 070	Boumnyebel	Pure male	$3^0$52'58.34"N	$10^0$50'57.62"E	358
ACC-19	BUM/DE/29 Seedling 050	Boumnyebel	Male-hermaphrodite	$3^0$52'58.34"N	$10^0$50'57.62"E	358
ACC-20	MAK/DE/33 Seedling 106	Makenene	Pure male	$4^0$53'03.84"N	$10^0$47'41.44"E	696
ACC-21	MAK/DE/33 Seedling 126	Makenene	Male-hermaphrodite	$4^0$53'03.84"N	$10^0$47'41.44"E	696
ACC-22	KEK/DE/02 Seedling 088	Kekem	Pure male	$5^0$09'05.91"N	$10^0$01'16.07"E	715
ACC-23	KEK/DE/02 Seedling 102	Kekem	Male-hermaphrodite	$5^0$09'05.91"N	$10^0$01'16.07"E	715
ACC-24	BUM/DE/09/98 Seedling 12B1	Boumnyebel	Pure male	$3^0$52'58.34"N	$10^0$50'57.62"E	358
ACC-25	BUM/DE/14/99 Seedling 16B4	Boumnyebel	Male-hermaphrodite	$3^0$52'58.34"N	$10^0$50'57.62"E	358

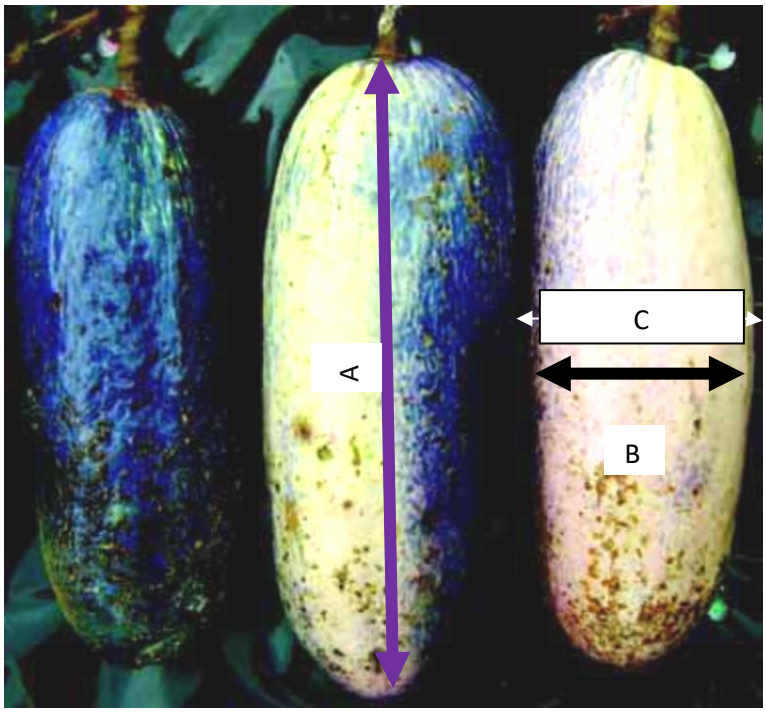
II.2.4. Experimental details

Upon physiological maturity stage (17-21 weeks after hand cross-pollination), control-pollinated fruits were collected in open-weave collection bags (Fig.21), labeled and transported to ICRAF's laboratory at Nkolbison for characterization as soon as possible (within 2-3 days). Fruit length, fruit width and pulp thickness were measured using 0.1 mm digital calipers, while fruit weight and kernel weight were determined using a 0.1 g electronic balance (Ohaus HP-320), based on the methods of Leakey *et al.*, (2002a) and Waruhiu *et al.*, (2004) for the same species. Pulp weight (fruit-kernel weight) was derived by difference. Fruit

length:width ratio, fruit:kernel weight ratio, fruit:pulp weight ratio were assessed and the number of kernel per fruit recorded.

To improve accuracy, fruit's width was measured at the first, the second and the third quarter of each fruit and the arithmetic means were considered as the fruit's width (Fig. 22). Pulp thickness was measured at four points on a longitudinal split half (Fig. 23). The mean value gave the pulp thickness. Epicarp and mesocarp colours were assessed using a Home base colour chart; values were recorded on characterization forms developed by ICRAF.

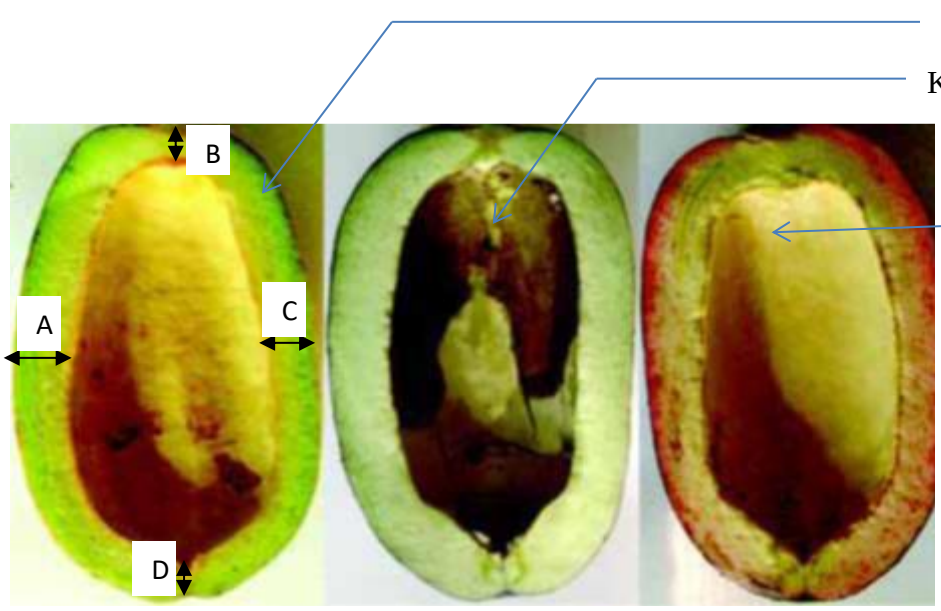
Fig. 21. *Dacryodes edulis* control-pollinated fruits harvested, labelled and gathered in wave bags for characterization in the laboratory: a, b and c are control-pollinated fruits from Makenene provenance while d and e are from Boumnyebel provenance; f represents fruits form Kekem provenance.



Fruit length = A

Fruit width = $\frac{B+C}{2}$

Fig. 22. Measurement of fruit length and fruit width



Pulp or flesh thickness=

$$\frac{A+B+C+D}{4}$$

Fig. 23. Measurement of pulp or flesh thickness

For seedlings nurseries activities, the experiment was carried out in the ICRAF's central nursery at Nkolbison (3°51'N Lat., 11°27'E Long.), Cameroon. This site lies at an altitude of 760 m.a.s.l., with a mean annual precipitation of approx.1400 mm and a mean annual temperature of 25, 1°C. From four provenances established in two experimental field trials as living gene banks, control-pollinated seeds were collected from twenty six selected and well-known accessions using a full nested mating design (Makueti *et al.*, 2012a), immediately characterized (Makueti *et al.*, 2012b), labelled and sown directly into black bags (4 l capacity) containing a 2:1 mixture of forest soil and sand. After 28 weeks, the plants were reported into larger buckets (15 l capacity) filled with the same potting mixture at the ICRAF's experimental net house at Mbalmayo (3°10'N Lat., 11°00'E Long.), for management and evaluation of shoot branching growth as determined by decapitation (Fig. 24). This site lies at an altitude of 650 m a.s.l. with a mean annual precipitation of approx. 1802 mm and a mean annual temperature of 24°C. The buckets were treated with fungicide (Ridomil Plus) and insecticide (Cyperdim 220 EC) three days prior to the beginning of the experiment and throughout the seedlings' growth in the net house.

Fig. 24. Assessment of control-pollinated *D. edulis* seedlings in the net house at Mbalmayo, Cameroon

The experiment included 13 progenies belonging to 4 provenances. In the net house, the plants (F_1 hybrids) were labelled and arranged at a constant spacing of 35 cm x 35 cm in randomized blocks, with 5 to 6 seedlings per provenance per block arranged in line, and 7 blocks in total, giving a mean total of 42 seedlings per provenance. The buckets were hand-weeded at regular intervals. Seedlings in the net house were grown under shade and watering daily. The sides of the net house were made of shade-cloth allowing 40 % ambient light transmission to reduce air temperatures in the net house. For dwarfism induction, the seedlings were decapitated on 28 April 2011, 39 weeks after sowing (WAS), by which time they were 46 cm to 70 cm tall (Fig. 25). All plants were cut to a constant height of 40 cm as recommended by Leaky and Lapido (1987), by removing the apex or the uppermost node. Cuttings were labelled and taken to the ICRAF's central nursery at Nkolbison for management and evaluation (Makueti *et al.,* 2013.).

Seedling assessment was carried out at weekly intervals beginning from the 24 day after sowing (DAS). Parameters assessed include: (i) seedling height and shoot length (using meter rule); (ii) collar diameter (using veneer caliper); (iii) numbers of leaves; (iv) numbers of twigs sprouted after decapitation; (v) and numbers of vigorous twigs. These numbers were counted manually. Lengths of lateral shoots (considered in this study as twigs) were measured at two-week intervals over a 6-8 week period. Shoots were considered to be actively growing if they grew by more than 2 mm $week^{-1}$. There was no lateral shoot present at the time of decapitation. After decapitation, a solid fertilizer namely 12 g urea (N:P:K; 20:10:10) was added in each bucket.

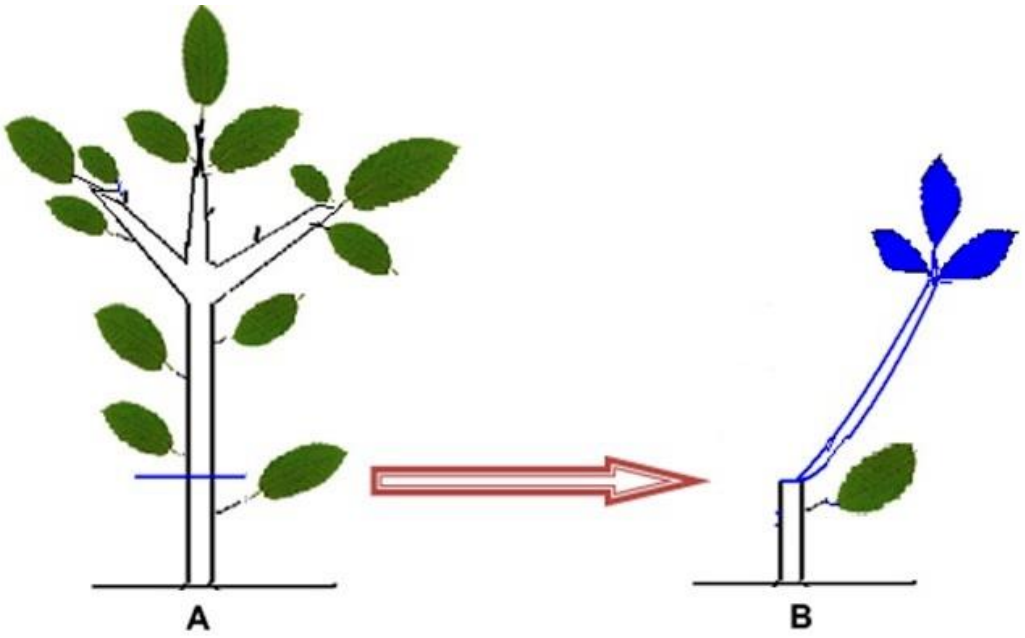


Fig. 25. Apical dominance's sketch following decapitation in a timber tree.

II.2.5. Data recording and analysis

To assess the fertilizing capacity and the fruiting efficiency of the tested plus-trees (Fig. 26), depending on the provenance of the male parent and the pollen type used for hand-pollination, four variables were observed during the study: (i) the number of flowers pollinated, (ii) the number of fruits set, (iii) the number of mature fruits and (iv) the number of fruits dropped. The fruit began to develop with enlargement of an ovary (Palanichamy *et al.*, 2011), turning from green to pink at physiological maturity stage (Fig. 27), then dark-blue, whitish green or purple at maturity (Fig. 28) within 3-5 months. After hand pollination, the number of flowers effectively pollinated per panicle and per female tree was counted immediately. Young fruits were counted three days after pollination and continued every 2 days for 8 days on each female tree. At the end of this observation period, all unopened flowers on the labelled panicles were removed. Upon physiological maturity stage (17-21 weeks after hand-cross-pollination), control-pollinated fruits were collected in open-weave collection bags, labelled and transported to ICRAF's laboratory at Nkolbison for characterization as soon as possible (within 2-3 days).

Fig. 26. Fruit set in *Dacryodes edulis* under controlled hand-pollination

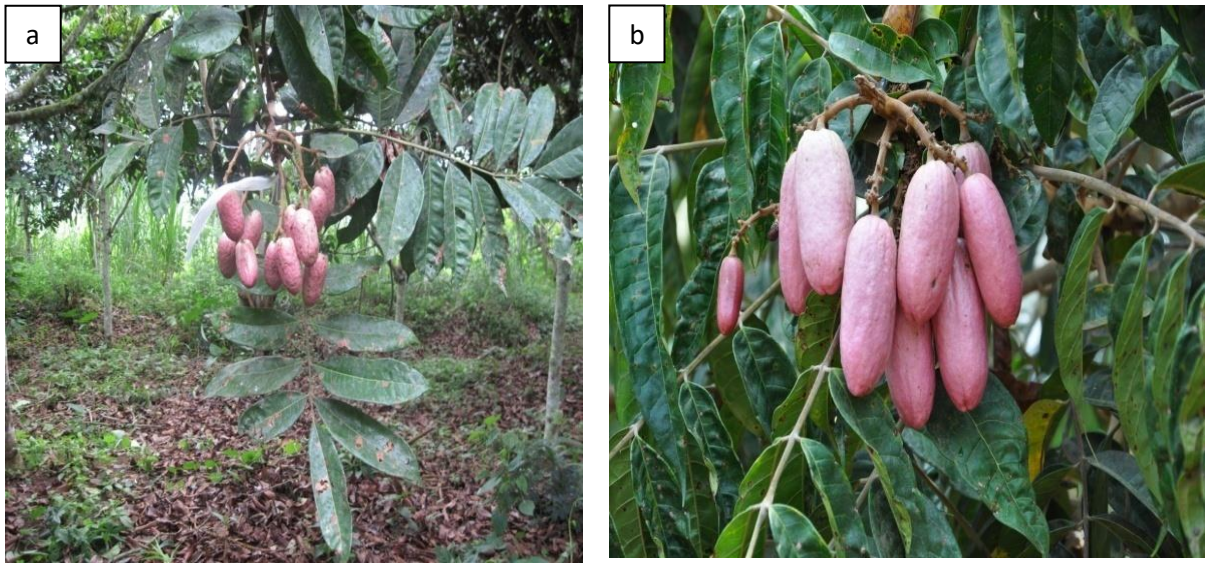


Fig. 27. *Dacryodes edulis* control-pollinated fruits at physiological maturity (pink colour): (a) Makenene gene bank; (b): Boumnyebel gene bank.

Depending on the number of flowers pollinated for each crossing, fruit-setting rate (FSR), fruiting index (FI) and fruit-dropping rate (FDR) were calculated using equations 1, 2 and 3 below.

- $$FSR(\%) = \frac{number\ of\ fruits\ effectively\ set}{number\ of\ flowers\ pollinated} \times 100 \ldots\ldots\ldots\ldots\ldots\ldots EQ_1$$
- $$FI = \frac{Number\ of\ mature\ fruits}{number\ of\ flowers\ pollinated} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots EQ_2$$
- $$FDR(\%) = \frac{number\ of\ mature\ fruits - number\ of\ fruits\ set}{number\ of\ flowers\ pollinated} \times 100 \ldots EQ_3$$

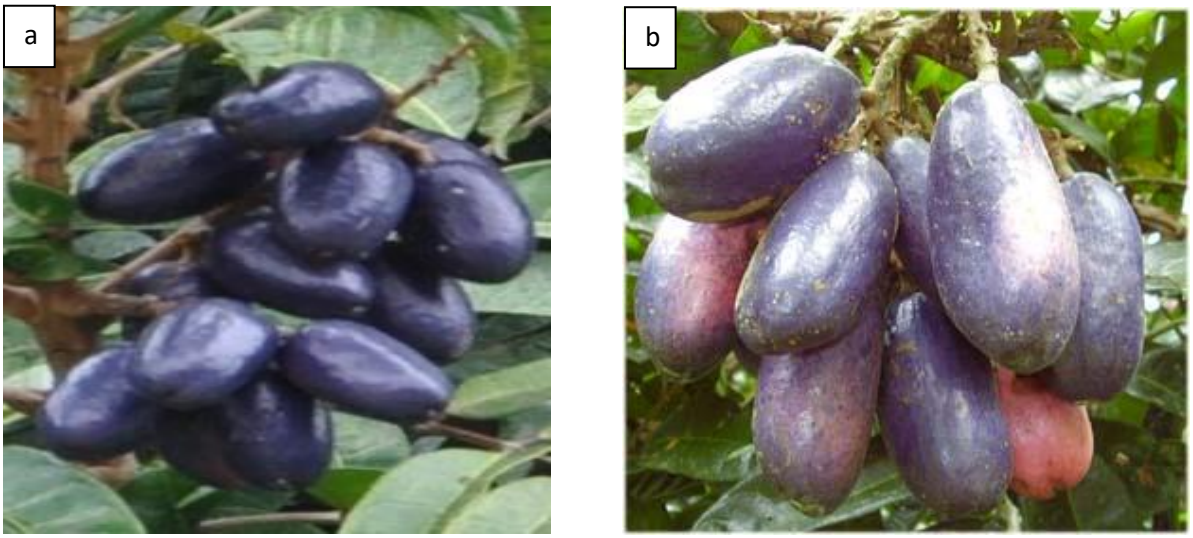


Fig. 28. *Dacryodes edulis* fruits at maturity stage: (a) dark-blue and (b) purple).

The degree of relationship between the fruit-setting rate, the fruit-dropping rate and the fruiting index was assessed using an analysis of correlation. Then, data were subjected to analysis of variance using procedure 'General Treatment Structure' Genstat v14 software. For factors showing a significant effect on the observed variables (fruit-setting rate, fruiting index and fruit-dropping rate), the means were calculated and separated using the more significant small difference (Atil and Unver, 2001; Allan *et al.,* 2006; Kizungu, 2011) with a threshold of 5 % probability. Finally, to determine the most efficient crosses on the basis of the three evaluated criteria used in this study (fruit-setting rate, fruit-dropping rate and fruiting index), means obtained were grouped into similar performance class using the ascending hierarchical classification (cluster analysis). Cluster analysis is the partitioning set of objects into groups so that objects within a group are similar and objects in different groups are dissimilar. It is efficient in grouping objects with similar characters (Hodgkin *et al.,* 1995). Average linkage cluster between provenances was analyzed. Clusters were defined based on their unique characters. Detailed results are presented in tabular or graphical in the next section.

To assess *Dacryodes edulis* fruit traits characterization, analysis of variance was performed to determine the descriptive statistics such as mean, standard error, standard deviation and variance for each one of nine quantitative traits over twelve studied traits. Pearson test was used to assess correlation among variables. Hierarchical clustering analysis (dendrogram) using Ward's hierarchical algorithm based on squared Euclidean distances was performed to study selected accessions with some promising crosses out of which those with high performing traits could be selected. Prior to squared Euclidean distance calculation, the data were standardized by variable to have a mean of zero and a variance of one. In addition, Principal Component Analysis (PCA) was carried out on the resultant matrix to summarize the major patterns of morphological variation. In fact, PCA is an unsupervised ordination technique that enables the low-dimensional representation of multivariate data, allowing the data to be explored visually in two dimensional correlations plotting of factors or biplots. Thereafter, those PCs with eigen values greater than one (> 1.0) and cumulative proportion explained were selected, as proposed by Jeffers (1967) and Thattil and Samita (2007), to identify number of principal components. Multivariate ANOVA Tests were used to confirm the accuracy of grouping that produced by cluster analysis. Significant differences at $P < 0.05$ were further tested using Student-Newman-Keuls multiple comparison test to identify the discriminative traits within and between clusters.

As the pulp is the principal trait of commercial importance, we also carried out a linear regression to identify predictors of pulp yield per fruit and to test if predicting power of the explanatory variables differs between crosses. We built a linear regression for pulp weight per fruit, with four independent variables measured on fruits (length, width, thickness and weight). Pearson's correlation was performed between the independent variables to test multicollinearity. Since there were significant strong correlations between pairs of variables ($r > 0.60$, $P < 0.001$) only one independent variable, (fruit weight) was finally used in the regression model. We insert crosses classified in 3 clusters in the model as dummy variable (Kutner *et al.*, 2005). Three models shown in the equations below were tested:

- $Pulp\ weight = \beta_0 + \beta_1(fruit\ weight) + \varepsilon \ldots\ldots EQ_4$
- $Pulp\ weight = \beta_0 + \beta_1(fruit\ weight) + \beta_2(cluster) + \varepsilon \ldots\ldots EQ_5$
- $Pulp\ weight = \beta_0 + \beta 1(fruit\ weight) + \beta_2(cluster) + \beta_3(fruit\ weight \times cluster) + \varepsilon \ldots\ldots EQ_6$

β_0 indicates the intercept, β_1, β_2 and β_3 the partial regression slopes and ε the unexplained error associated to the model. The residuals normality plot, the residual vs. fitted plot and the residuals vs. advantage plots with Cook distance were used to diagnose the regressions models (Quinn and Keough, 2005).

For the seedlings' dwarfism induction, clustering of accessions into similarity groups was performed using Ward's hierarchical algorithm based on squared Euclidean distances. Prior to squared Euclidean distance calculation, the data were standardized by variable to have a mean of zero and a variance of one. Analysis of variance was performed to determine the descriptive statistics such as mean, standard error, standard deviation and variance for each studied trait. Pearson test was used to assess correlation among variables. A One Way ANOVA test was performed to confirm the accuracy of grouping that produced by cluster analysis. Student-Newman-Keuls Test was used to identify the discriminative traits within and between clusters. We also carried out a linear regression to identify predictors of shoot length's growth. Data were processed under SPSS version 17.0.0 (Aug 23, 2008).

CHAPTER III.

RESULTS AND DISCUSSION

Part I: Parents and pollen type effects on the fruiting efficiency of *Dacryodes edulis* (G. Don) H. J. Lam. under controlled pollination conditions.

The present study aims at improving the availability of quality germplasm in *D. edulis* through hand pollination crossbreeding tests. More specifically, the study aims at evaluating the provenance of the male parent and the pollen type effects on (i) the fruit-setting rate, (ii) the fruiting index, (iii) the fruit-dropping rate in *D.edulis* females' accessions under cross hand-controlled pollination and (iv) determining the most efficient crosses to be chosen for the on-going breeding program. The obtained F_1 hybrids will serve as improved raw material for further new cultivars development. Onto these cultivars, vegetative propagation could be undertaken for the enrichment of African plum plantations with good quality planting material.

III.1.1. Results

III.1.1.1.Fruit-setting rate and fruiting index of African plum female accessions

- ***Fruit-setting rate (FSR)***

The analysis of data obtained from this study revealed a main highly significant effect ($p = 0.044$) of parents provenance and a significant interaction ($p = 0.005$) of the type of flower which produced pollen used and female parent on the fruit-setting rate of *D. edulis* flowers pollinated manually. The type of flower which produced pollen used for the crossbreeding test has no significant effect ($p = 0.15$) on the percentage of fruit set (Table XIII). Table XIV presents the average fruit set obtained according to the provenance of male parents, the type of flower which produced pollen used for fertilization and the female parent crossed. It appears that in the Makenene provenance (MAK33), the fruit-setting rate is significantly high (76.65 %) than in the Boumnyebel (BUM29) (70.18 %) and Kekem (KEK02) (69.90 %) provenances respectively.

Table XIII. ANOVA of fruit-setting rate, fruit-dropping rate and fruiting index of *Dacryodes edulis* based on the male parent provenance, the type of flower which produced pollen used for fertilization and the female parent status in each provenance.

		Fruit-setting rate		Fruiting index		Fruit-dropping rate	
Source of variation	D.F.	SCE	F pr.	SCE.	F pr.	SCE	F pr.
Parent provenance	2	125,7	**0,044**	**0,042**	0,369	282,6	0,479
Provenance. Type of flower which produced pollen used	3	1050,4	0,151	0,095	0,214	485,6	0,470
Provenance. Type of flower which produced pollen used. Female parent	22	9265,9	**0,005**	0,909	**0,010**	8254,5	**0,012**
Residue	112	21752,1		2,323		21371,5	
Total	139	33319		3,368		30394,2	

In the Boumnyebel provenance, fertilization with pollen from hermaphrodite flowers indicated that the BUM/DE/25 Seedling026 accession showed a lower statistically fruit-setting rate (50.94 %) whereas this rate exceeded 75 % for the other four accessions of this provenance. These are: BUM/DE/37 Seedling111 (79.23 %), BUM/DE/25 Seedling114 (78.44 %), BUM/DE/26 Seedling122 (76.06 %) and BUM/DE/26 Seedling015 (75.38 %).

Moreover, fertilization with pollen from male flowers indicated the same trend, except that three groups can be distinguished: (i) BUM/DE/25 Seedling114 has the highest fruit-setting rate (76.14 %); (ii) BUM/DE/25 Seedling026 showed the lowest rate (55.93 %) while BUM/DE/37 Seedling111, BUM/DE/26 Seedling122 and BUM/DE/26 Seedling015 occupy intermediate positions with respectively 72.45 %, 68.56 % and 68.69 % of fruit-setting rate.

For crosses with pollen from hermaphrodite flowers in the Kekem provenance, the KEK/DE/07 Seedling074 accession showed a lower and significant fruit-setting rate (51.35 %), while KEK/DE/13 Seedling079 and KEK/DE/18 Seedling070 accessions showed the highest fruit-setting rate (74.89 and 72.22 %) respectively.

Meanwhile, KEK/DE/18 Seedling050 and KEK/DE/07 Seedling142 accessions occupy an intermediate position with a fruit-setting rate of 67.15 % and 63.33 % respectively. According for accessions crossed with pollen from male flowers, the percentage of fruit set

per female accession after hand-pollination vary from 65 to 80 %, but the differences observed are not significant at 5 %.

In the Makenene provenance, fertilization with pollen from hermaphrodite flowers induced the highest fruit-setting rate on the MAK/DE/04 accession and the lowest fruit-setting rate was observed on MAK/DE/04 Seedling 116 (64.40 %). Meanwhile, these accessions indicated the highest fruit-setting rate (80 %) when fertilized with pollen from male flowers. MAK/DE/04 Seedling078 with only 49 % of fruit-setting rate is least efficient female accession. With a fruit-setting rate of 78 %, MAK/DE/28 Seedling104 occupies an intermediate position whatever the type of pollen used for its fertilization.

- ***Fruiting index (FI)***

The average of the fruiting index of 14 female accessions tested through controlled hand-pollination in this study (Table XV) varies depending on the provenance of the male parent, the type of flower which produced pollen used and the status of the female parent subjected to the crossbreeding test. Analysis of variance (Table XIII) shown that the variation of the fruiting index was highly related to the combined action of the three factors studied: the provenance of the male parent, the female parent in the provenance and the type of flower which produced pollen used for the crossbreeding test ($p = 0.01$). None of these three studied factors taken individually showed a significant effect on the number of mature fruits ($p = 0.21$ and 0.37 respectively), neither for the flower which produced pollen used nor for the provenance of the male parent.

Thus, in the MAK33 provenance, MAK/DE/04 Seedling144 and MAK/DE/28 Seedling 104 showed a statistically identical fruiting index (0.68) when fertilized by pollen from hermaphrodite flowers. This value is higher than those obtained from MAK/DE/04 Seedling078 (0.41) and MAK/DE/04 Seedling116 (0.37) accessions. Meanwhile, when fertilized with pollen from male flowers, three of the four studied females had a similar fruiting index (0.54) and significantly higher than that obtained from MAK/DE/04 Seedling116 (0.37). Those three females are MAK/DE/04 Seedling144, MAK/DE/28 Seedling104 and MAK/DE/04 Seedling 078.

Table XIV. Fruit-setting rate of *Dacryodes edulis* under controlled hand-pollination conditions.

Provenance	Female parent	Type of flower which produced pollen used		
		Hermaphrodite	Male	Rate
BUM29	BUM/DE/25 Seedling114	78,44 a	**76,14 a**	70,18 b
	BUM/DE/37 Seedling111	79,23 a	72,45 ab	
	BUM/DE/26 Seedling122	76,06 a	68,56 ab	
	BUM/DE/26 Seedling015	75,38 a	68,69 ab	
	BUM/DE/25 Seedling026	50,94 b	55,93 b	
	Mean	**72,01**	**68,35**	
KEK02	KEK/DE/13 Seedling079	**74,89 a**	74,10 a	69,90 b
	KEK/DE/18 Seedling070	**72,22 a**	75,13 a	
	KEK/DE/18 Seedling050	67,15 ab	77,05 a	
	KEK/DE/07 Seedling142	63,33 ab	78,50 a	
	KEK/DE/07 Seedling074	51,35 b	65,26 a	
	Mean	**65,79**	**74,01**	
MAK33	MAK/DE/04 Seedling144	**88,20 a**	**86,51 a**	**76.65 a**
	MAK/DE/28 Seedling104	78,03 ab	77,77 ab	
	MAK/DE/04 Seedling116	64,40 b	82,80 a	
	MAK/DE/04 Seedling078	72,01 ab	63,49 b	
	Mean	**75,66**	**77,64**	

Means followed by a common letter within a column are not significantly different at *P< 0.05* (Student-Newman-Keuls test).

Table XV. Fruiting index of *Dacryodes edulis* under controlled hand-pollination condition.

Provenance	Female parent	Type of flower which produced pollen used		
		Hermaphrodite	Male	Rate
BUM29	BUM/DE/25 Seedling114	0,50 a	0,53 a	0,47a
	BUM/DE/37 Seedling111	0,53 a	0,51 a	
	BUM/DE/26 Seedling122	0,42 a	0,38 a	
	BUM/DE/26 Seedling015	0,53 a	0,46 a	
	BUM/DE/25 Seedling026	0,38 a	0,48 a	
	Mean	**0,47**	**0,47**	
KEK02	KEK/DE/13 Seedling079	0,42 a	0,59 ab	0,48a
	KEK/DE/18 Seedling070	0,54 a	0,48 ab	
	KEK/DE/18 Seedling050	0,38 a	0,62 a	
	KEK/DE/07 Seedling142	0,40 a	0,42 b	
	KEK/DE/07 Seedling074	0,46 a	0,51 ab	
	Mean	**0,44**	**0,52**	
MAK33	MAK/DE/04 Seedling144	0,68 a	0,54 a	0,51a
	MAK/DE/28 Seedling104	0,68 a	0,54 a	
	MAK/DE/04 Seedling116	0,37 b	0,54 a	
	MAK/DE/04 Seedling078	0,41 b	0,37 b	
	Mean	**0,53**	**0,50**	

Means followed by a common letter within a column are not significantly different at *P< 0.05* (Student-Newman-Keuls test).

Regarding the BUM29 provenance, all the 5 accessions tested (BUM/DE/25 Seedling114, BUM/DE/37 Seedling111, BUM/DE/26 Seedling122, BUM/DE/26 Seedling015 and BUM/DE/25 Seedling026) have showed a fruiting index ranging from 0.38 to 0.53. The differences observed between the averages were not significant at 5 %, whatever females were crossed with pollen from a hermaphrodite or a male flower.

In the KEK02 provenance, the same trend was observed but only in crosses with pollen from the hermaphrodite flower. It has been observed that in this provenance, all the female accessions had a statistically similar fruiting index (0.38-0.54). Meanwhile, when crossed with pollen from a male flower, three groups were identified: (i) the best accession KEK/DE/18 Seedling050 with a fruiting index of 0.62; (ii) the least efficient one KEK/DE/07 Seedling142 (0.42) and intermediate accessions KEK/DE/13 Seedling079, and KEK/DE/07 Seedling074, KEK/DE/18 Seedling070 with indices between 0.45 and 0.60.

III.1.1.2. Fruit-dropping rate of African plum female accessions (FDR)

Table XVI shows the average fruit-dropping rate after fruit set at the end of a hand-pollination test in *Dacryodes edulis* depending on the provenance of the male parents, the type of flower, which produced pollen used and the female parent. It appears that the fruit-dropping rate varies in each provenance, from a female accession to another, depending on the type of flower which produced pollen used for the crossbreeding test. Analysis of variance (Table XIII) showed that apart from the combined action of flower type used and plant mother ($p = 0.012$) in a given provenance, none of the three studied factors taken individually did not significantly affected ($p \geq 0.470$) the fruit-dropping rate after fruit set in *D. edulis.*

Thus, in the BUM29 provenance, when female accessions are crossed with pollen from hermaphrodite flower in the same provenance, the BUM/DE/25 Seedling026 accession showed the lowest dropping rate that is only 13.17 %, against 34.29 % for the BUM/DE/26 Seedling122 accession. The fruit-dropping rate is average and statistically similar in BUM/DE/26 Seedling015 individuals (22.71 %), BUM/DE/37 Seedling111 (26.12 %) and BUM/DE/25 Seedling114 (28.44 %). With pollen from a male flower, the same trend is observed between five female accessions and values are apparently lower than in crosses involving hermaphrodite as well as male flowers; min 7.9 % and max 30.73 % for BUM/DE/25 Seedling026 and BUM/DE/26 Seedling122 respectively.

Regarding the KEK33 provenance, the KEK/DE/07 Seedling074 accession crossed with pollen from hermaphrodite flower of the same origin had the best fruit-dropping rate 5.15 % against 32.53 % and 29.07 % for KEK/DE/13 Seedling079 and KEK/DE/18 Seedling050. When crossed with pollen from male flower, KEK/DE/07 Seedling074 accession maintained the lowest dropping rate (14.49 %) but this time with KEK/DE/13 Seedling079 (14.94 %) and KEK/DE/18 Seedling050 (15.33 %) accessions. The highest fruit-dropping rate was recorded on KEK/DE/07 Seedling142 (36.29 %).

In MAK33 provenance, the lowest fruit-dropping rate after fruit set was recorded on MAK/DE/28 Seedling104 (10.47 %) crossed with pollen from hermaphrodite flower. For the other three accessions, the rates were higher than 20 %: MAK/DE/04 Seedling144 (20.73 %), MAK/DE/04 Seedling116 (27.67 %) and MAK/DE/04 Seedling078 (31.28 %). It has been noticed that, in this provenance, when crossed with pollen from male flower, all the six female accessions recorded a fruit dropping rate above 20 % and statistically equivalent.

Table XVI. Fruit-dropping rate in *Dacryodes edulis* under controlled pollination.

Provenance	Female parent	Type of flower which produced pollen used		
		Hermaphrodite	Male	Rate
BUM29	BUM/DE/25 Seedling114	28,44 ab	22,93 ab	22,97 a
	BUM/DE/37 Seedling111	26,12 ab	21,04 ab	
	BUM/DE/26 Seedling122	34,29 a	30,73 a	
	BUM/DE/26 Seedling015	22,71 ab	22,71 ab	
	BUM/DE/25 Seedling026	**13,17 b**	**07,90 b**	
	Mean	24,95	20,99	
KEK02	KEK/DE/07 Seedling142	23,22 ab	36,29 a	21,68 a
	KEK/DE/13 Seedling079	32,53 a	**14,94 b**	
	KEK/DE/18 Seedling070	18,22 ab	27,54 ab	
	KEK/DE/18 Seedling050	29,07 a	**15,33 b**	
	KEK/DE/07 Seedling074	**05,15 b**	**14,49 b**	
	Mean	21,64	21,72	
MAK33	MAK/DE/04 Seedling144	20,73 ab	32,10 a	25,23 a
	MAK/DE/28 Seedling104	**10,47 b**	23,70 a	
	MAK/DE/04 Seedling116	27,67 a	29,06 a	
	MAK/DE/04 Seedling078	31,28 a	26,80 a	
	Mean	22,54	27,92	

Means followed by a common letter within a column are not significantly different at $P < 0.05$ (Student-Newman-Keuls test

III.1.1.3. Hierarchical classification dendrogram of the studied accessions

Figure 29 shows the dendrogram grouping the 28 genetic crossbreeding tests conducted during this study depending on the similarity of the performance based on the evaluated criteria (the fruit-setting rate, the fruit-dropping rate and the fruiting index). It shows that crosses can be classified into five distinct groups:

- Group I consists of four crosses from exclusively Kekem provenance. It is characterized by a greater fruit-setting rate (> 70 %) and fruiting index (> 50 %), but a fruit-dropping rate that exceeds 25 % of the flowers pollinated.
- Group II includes six crosses mainly characterized by high fruit-setting rate (> 70 %) and high fruiting index (> 50 %), followed by low fruit-dropping rate (< 25 %) respectively after fruit set. Those best accessions are from Boumnyebel and Makenene provenances as follow:
    - BUM_050*015;
    - BUM_070*111;
    - BUM_070*114;
    - MAK_106*104;
    - MAK_126*104 and
    - MAK_126 *144.
- Group III consisting of crosses with low levels of fruit-setting rate (< 70 %), fruiting index (< 50 %) and fruit-dropping rate (< 25 %) respectively.
- With regard to group IV crosses, the fruit-setting rate (>70 %) and the fruiting index (> 50 %) are higher, but contrary to the results described above in group II, dropping is abundant (> 25 %).
- The group V then has the same trend as the group III unlike the fact that the fruit-dropping rate is high (> 25 %). It includes four crosses, 2 with pollen from the Makenene male parent (MAK_106*078 and MAK_126*116), and one with pollen from Boumnyebel (BUM_070*122) and Kekem (KEK_088*142) male parent.

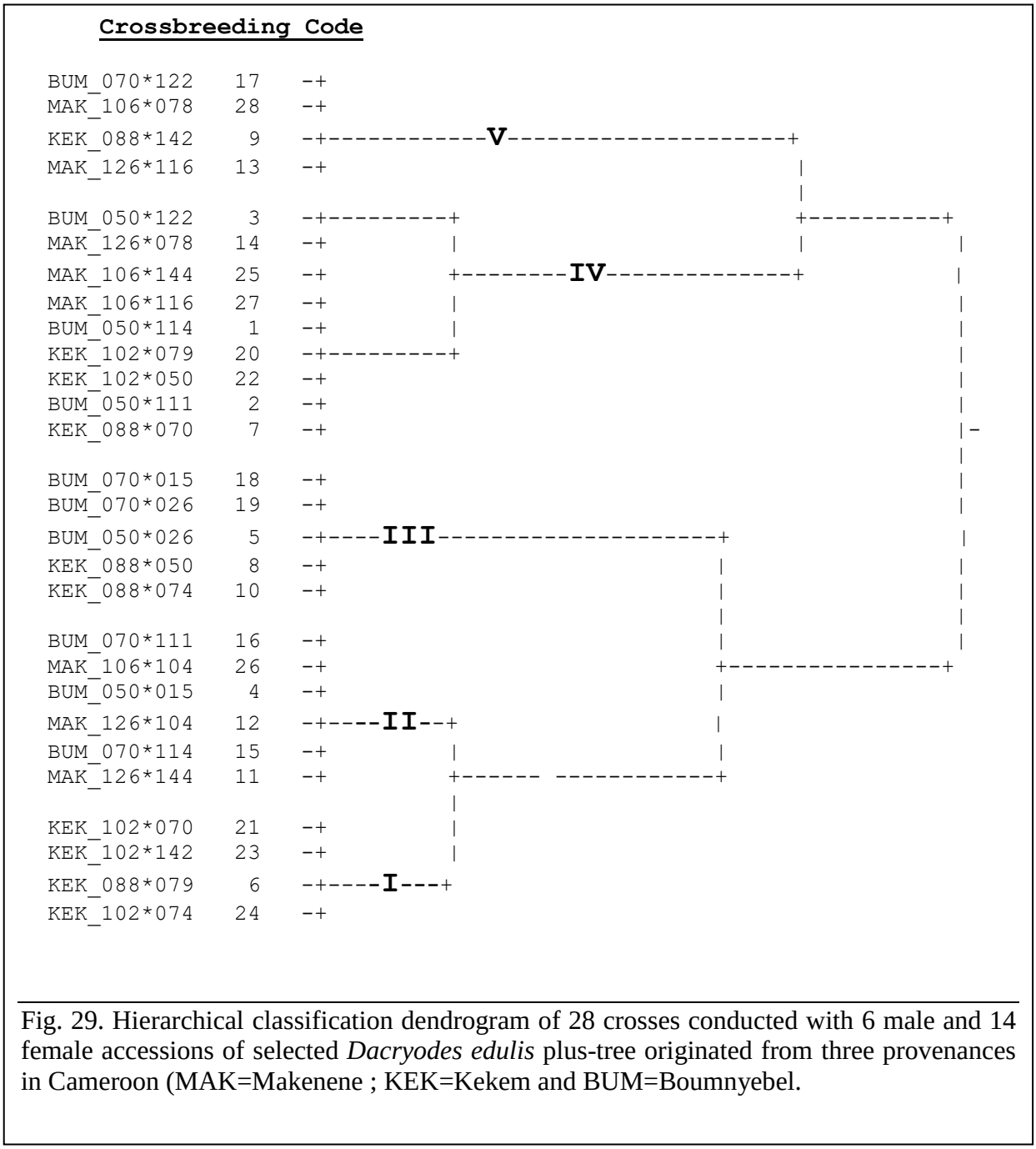


Fig. 29. Hierarchical classification dendrogram of 28 crosses conducted with 6 male and 14 female accessions of selected *Dacryodes edulis* plus-tree originated from three provenances in Cameroon (MAK=Makenene ; KEK=Kekem and BUM=Boumnyebel.

III.1.2.Discussion

During the crossbreeding experiments, manual pollination has seemed to be very difficult for pollen from pure male trees because of their agglutinated nature and very small size, therefore difficult to collect. This type of pollen withered rapidly in the contact with ambient air or when kept in the Petri dish (pers. obs.). Contrary to this observation, given the significant size of pollen from hermaphrodite flowers, it was easy to harvest and more accurately deposed on the stigma of the flower. Given these observations, one could expect that hand pollination performed with pollen from hermaphrodite flowers may lead to best results (high fruit set and fruiting index and low fruit drop). This hypothesis was confirmed for Boumnyebel and Makenene provenances, Kekem provenance having presented a reverse trend. From this study, one might think that pollen from male flower, taking into account its small size, is more able to adhere to the micropyle of the ovule, thus reducing handling errors. This ability explains the phenomenon, which happens in natural conditions when the honeybee, main pollinator of the species, disperses pollen.

Fruit development is an exquisitely plant specific process under the control of a complex interplay of endogenous and environmental factors. Likewise, the process of fruit set is defined as the commitment of the ovary tissues to undergo transformation into a fruit (Gillaspy et al., 1993). This process is gaining increasing interest also for its potential exploitation to control parthenocarpic fruit development, in the absence of pollination/fertilization.

Regarding the estimation of the fruit-setting rate, the results of this study are almost in line with those reported by Kengue (1990) on *D. edulis*. In fact, this author obtained an average fruit-setting rate of 93.62 % in the first hand-pollination test on a sample of three trees in the studied species. The difference observed between these two results can be attributed to: (i) the size of the sample; (ii) the genetic disposition of the sample coupled to environmental conditions wherein it is located and/or (ii) the applied methodology (studied factors).

Results from this study on *D. edulis* hand-pollination, compared to studies performed on the open-pollination of some fruit species under the natural conditions, would let one admit that hand-pollination process improves fruit set. These results are fairly in line with those

reported by Johannsmeier and Morudu (1999) and Omokhua and Koyejo (2009) on avocado (*Persea americana*), Kalinganire *et al.,* (2001) on silky oak (*Grevillea robusta),* Omokhua and Ukoimah (2008) on *Teprapleura tetraptera*, Omokhua and Koyejo (2009) on *D. edulis* and Iqbal *et al*., (2010) on palm date (*Phoenix dactylifera*). This improvement can be attributed to the precision with which the pollen is applied on the stigma of the flower.

Increasing outcross pollen from one to four did not alter fruit set, nor did increasing the quantity of eggs per flower. These results are in line with those reported by Lovatt (1999), Niesenbaum (1999), Young *et al.,* (1982), Margriet *et al.*, (2000), Bots and Mariani (2005), and De la Bandera and Trasevet (2006). These results mean that all flowers had an equal chance of fruit set regardless of pollen quantity, pollen type or egg number. Vander Kloet (1983) pointed out similar results from a study on the relationship between seed number and pollen viability of *Vaccinium corymbosum* and Allison (1990) on a study related to the reproductive biology of *Taxus canadensis*. Similarly, these results are also consistent with those reported by Winsor *et al.* (1987) on *Cucurbita pepo*, Holland *et al.,* (2004) on senita cacti (*Lophocereus schottii*) and Jorge *et al.* (2005) on *Bauhinia ungulata*. Generally, the effective pollination period is determined by length of stigma receptivity, pollen tube growth rate, and ovule longevity.

Naturally, in the plant kingdom, the fruiting index is heavily correlated with the flowering index (Stephenson, 1981; Bawa and Webb, 1984; Murawski and Hamnick, 1991; Sedgley *et al.,* 1992; Niang, 2002; Gassana-Dia *et al.,* 2003). Many proximate (ecological) and ultimate (evolutionary) hypotheses have been proposed to explain excess flower production and low fruit-to-flower ratios (Stephenson, 1971; Sutherland and Delph, 1984; Are and Whelan, 1989; De la Bandera and Traveset, 2006).

Among the array of reproductive parameters in tropical forest species, fruiting efficiency is the most remarkable (important) to the commercial farmer, because it determines the overall yield of his crops per hectare. Moreover, low fruiting efficiency implies low harvest yield and vice versa (Delph, 1986; DiFazio *et al.,* 1998; Koenig and Knops, 2000; Sakai, 2001, 2002; Koenig *et al.,* 2003; Wright *et al.*, 2005). The mean fruiting efficiency of 48 % recorded for *D. edulis* in this study is higher than the 1.31 and 1.36 % obtained by

Omokhua and Koyejo (2009) respectively on *D. edulis* var. *edulis* and var. *parvicarpa* in Nigeria in natural conditions. On the same line, this result is also higher than those obtained by Oni (1990) working on *Terminalia ivorensis* as well as Oni and Adedire (1987) working on *T. catappa*. These authors reported 21 % and 26 % fruiting efficiency respectively for these species. This result could mean that hand pollination increases fruit set and fruiting index.

Additionally, many fruit species bear an abundance of flowers, which produce a surplus of fruits that the tree is unable to support. In *D. edulis*, a pure male or male-hermaphrodite inflorescence can carry between 300 to 500 flowers with 75-120 only, given their positions, rich at anthesis (Kengue, 1990). In this species, in female trees, flowering shoots are 5-10 inflorescences each consisting of 90 flowers. According to this physiology, it is obvious that a large number of flowers formed would not develop into fruits. This situation tends to deplete resources of the tree. Thus, for pollination experiment, whatever in natural or controlled (manual) conditions, it would be wise to check the phenomenon of fruit set (fraction of flowers beginning fruit development) because in *D. edulis*, panicles having a certain high fruit-setting rate particularly loose prematurely much fruits. This result is in line with those reported by many other authors whose studies were carried out on fruit trees (Anila and Radha, 2003; Basharat *et al.*, 2008; Al-Naggar *et al.*, 2009). To solve this problem, one method would be the spray of a growth inhibitor as ethephon or 2-chloroethyl phosphoric acid, gibberellic acid (AG3) and the perlagonic acid or endothall during flowering to reduce the fruit-setting rate. This technique may help reducing fruit load and improve tree fruiting efficiency as earlier pointed out by Liao *et al.* (2006), Chamet and Delaunay (2007), Férré *et al.* (2008) and Modise *et al.* (2009).

Likewise, fruit trees have evolved a system to control fruit load in relation to their nutritional status, thus allowing the plant to make efficient use of resources. This is naturally achieved by a process called physiological drop, involving the abscission of young developing fruits mainly due to a correlative dominance effect of adjacent fruit and/or nearby shoots (Bangerth, 2000). In order to control fruit load, the major fruit species developed an immature fruit (fruitlet) physiological drop as a self-regulatory mechanism. This process is at least in part a consequence of the competition among fruits and between fruits and shoots for carbon assimilates. The phenomenon of fruit drop is very pronounced in most of fruit trees as pointed out by Lebon *et al.* (2004) and Iqbal and Karacali (2004). It can be a physiological fruit drop (fruit abortion) or the abscission of ripe fruit (fruit abscission), all related to factors that could

be explored in further work for the present studied species. To avoid these effects, farmers could perform blossom or fruitlet thinning to adjust crop load and ensure a satisfactory fruit quality at harvest for commercial purposes.

Moreover, it is known that from the fruit set to maturity and repining, fruit may drop at different stages as it was demonstrated in other nuclei fruit trees (Lebon *et al.,* 2005; Alcaraz and Hormaza, 2009; Muhammad *et al.,* 2011). The physiological drop may depend on the success of the fertilization, which is essential to the maintaining of the fruit on the tree, or on climatic conditions such as the adverse effects of drought, winds and heavy rains (Udovic and Aker, 1981; Sutherland, 1984; Moncur *et al.,* 1991; Tybirk, 1993; Levri, 1998; Holland and DeAngelis, 2002).

Similarly, abscission is a natural self-regulatory mechanism whereby fruit trees shed part of the fruitlets, and is an important agricultural event from the farmer's point of view because it directly affects the final size and quality of the commodity. In spite of this self-regulatory mechanism, fruit trees set too many fruitlets negatively affecting not only the final quality, but also the returning bloom (Eccher *et al*., 2013). With regard to fruit abscission (Eccher *et al*., 2013), some factors can reduce the accuracy of the estimation of the pollination activity as early pointed out by Allison (1990); Bots and Mariani (2005) and Madyen *et al*. (2011). These factors can be:

(i) competition both between young fruit and the growth of vegetative organs, and secondly between the fruits themselves for minerals, growth hormones and especially for carbohydrates. Studies related to this competition have been carried out by many authors such as Pas Suarez (1984); Lebon (2005); Brevis (2005; Sheard, 2008 or Omokhua and Chima (2009);

(ii) risk of fruits predation and diseases (Bos *et al.,* 2007);

(iii) the environmental conditions.

The interaction of these physiological and environmental factors could explain the selection that operates on the level of the tree between the fruit drop and those who remain on the tree as early pointed out by Vaugton and Carthew (1993); Guitan (1994); Susko and Lovett-Doust (1998); Shiell *et al.* (2001); Mehdi *et al.* (2007) and De Smedt *et al*. (2012). The mean fruit-dropping rate of 24.89 % recorded for *D. edulis* in this study is lower than the 98.79 and 98.64 % obtained by Omokhua and Koyejo (2009) respectively for *D. edulis* var. *edulis* and var. *parvicarpa* in open-pollination. The difference observed can be explained as

result of mass selection did by farmers during many years and the fact that our study was carried out on controlled conditions. In fact, mass selection may have contributed to the selection of superior genotypes with low fruit drop and controlled pollination may help increase fruit set and by so doing, reduce fruit drop. This result is also lower than that reported by Omukhua and Chima (2009) working on avocado. These authors reported 99.21 % fruit-dropping rate (open-pollination condition).

Furthermore, the phenomenon of fruit drop is also probably under the control of growth hormones such as ethylene (Hilt and Bessis, 2003), cytokinins (Ollat *et al.*, 2002), gibberellins and auxins (Roberts *et al.,* 2002) and finally the polyamines (Malik and Singh, 2003). In fact, auxins and gibberellins play a pivotal role in the inductive phase of fruit set and parthenocarpic development of fruits. Like many other tropical forest fruit trees, the reasons for low average yields of *D. edulis* are complex and need further research. In fact, evolutionary history, stage of domestication and vegetative-reproduction competition for photosynthate at critical stages is speculated as contributory factors to the low yields of the studied species. McFadyen *et al*. (2011) have obtained similar results on a study related to shoot growth post-pruning of macadamia in Australia. In addition, Blumenfeld *et al.*, (1983) reported that vegetative-reproductive growth competition involving the partitioning of photosynthate is a major limitation to some cultivated fruit trees yield potential such as avocado. Similarly, Bawa and Webb (1984) as well as Allison (1990) stated that pollination limitations and fertilization failures are contributory factors to low fruiting efficiency in tropical plants. As our study was focused on controlled hand-pollination, pollen limitations could not be a limiting factor for low fruiting efficiency.

From the present study, we can deduce that during the pollination process, several factors can influence the fruiting efficiency of a tree in a given species. It can include:

(i) the success of pollination guaranteed by the methodology used. In fact, during this process, pollen viability (Firmage and Dafni, 2001; Bots and Mariani, 2005; Ferreira *et al.*, 2007) and the stigma receptivity may be questioned, the micropyle of the ovule may be damaged when applying the pollen;

(ii) the amount of resources available during flowering. In fact, during flowering, competition for water and nutrients between the various parts of the plant, including floral panicles initiation and the growth of vegetative organs may be a limiting factor of the fruit set;

(iii) the genetic status of the sample;

(iv) the environmental factors may also influence the process.

Additionally, Lahav and Gazit (1994), Lahav and Lavi (2002) as well as Klein *et al.*, (2003) believe that with the process of controlled pollination (manual or hand pollination), there is substantial evidence that cross-pollinated fruits have a better chance of maturing. In fact, it is well know that fruits initiated from early flowers have a lower probability of aborting than the fruits initiating late. This hypothesis is fairly in line with the results of the present study.

Partial conclusion

The present study highlighted that Boumnyebel and Makenene provenances have the best combinations, characterized by high fruit-setting rate and fruiting index (> 70 % and > 50 % respectively), followed by low fruit-dropping rate (< 25 %). These crosses are potential best candidates onto which mass multiplication though vegetative propagation techniques could be undertaken for cultivar development. For Boumnyebel provenance, these accessions are BUM/DE/37 Seedling111 and BUM/DE/25 Seedling 114 crossed with pollen from male flower, then BUM/DE/26 Seedling015 crossed with pollen from hermaphrodite flower. With regard to Makenene accessions, they are MAK/DE/28 Seedling104 crossed with pollen from male flower, then MAK/DE/28 Seedling104 and MAK/DE/04 Seedling144 crossed with pollen from hermaphrodite flower.

Results from this study showed that variation in fruiting index that determines the species' yield is highly in strong relationship with the combination of the three factors studied (male parent provenance, the pollen type used for the crossbreeding test and the status of the female parent). None of the three individual factors has had a significant effect on the number of mature fruits at the end of the crossbreeding test. Therefore, under hand pollination, the assessment of *D. edulis* fruiting efficiency depends not only on the male parent provenance and the type of flower which produced pollen used for fertilization, but also on the specifically genetic disposition of each female parent (potential). Moreover, during flowering, several factors that may affect the species' yield need to be explored in future works, namely: (i) the position of the flower on the female panicle (ii) the pollen viability, (iii) the genetic status of the embryo and (iv) competition for water and nutrients.

In addition, excessively heavy flowering can be seen to be wasteful of scarce resources at a critical time. Therefore, it is necessary to explore ways of reducing fruit set in order to reduce the fruit load by using an inhibitor of growth during flowering that would improve yield. Furthermore, farmers could perform blossom or fruitlet thinning to adjust fruit load and ensure a satisfactory fruit quality at harvest for commercial purposes. Although we did not observe increasing in fruit size as compare to breeding in *Citrus* spp, the process of controlled cross-pollination investigate in this study significantly increase the fruit set. This can help controlling the early fruit drop that negatively affects the species' yield. The spatio-temporal regulation of the molecular factors involved in early steps of fruit set and development should be investigated. This information may help to understand how a plant response to endogenous/environmental perturbations. Seeds from the resultant fruits (F_1 hybrids) were harvested from each crossed female tree, then characterized and pot-grown in polyethylene bags at the ICRAF's nursery for further improvement work.

Part II: Morphological fruits characterization of control-pollinated F_1 hybrids of *Dacryodes edulis*

To our knowledge, no study has documented morphological and genetic characterization of African plum fruits obtained through controlled-cross-pollination. The approach may help to develop and characterize progenies, improve raw material for breeding and clonal development while allowing the species to better express its potential (i.e. fruit size and yield, pulp productivity, pulp taste, pulp oil content, etc.) and identify links between traits. The current study aims at (i) assessing control-pollinated African plum morphological fruit traits (ii) analyzing its relationship with intra-provenances performance and, (iii) analyzing the implications to further breeding improvement leading to the expression of the genetic gain in F_2 and F_3 generations. Thus, the following questions were addressed:

(i) Does controlled pollination increase the quality of the quantitative fruit traits of well-known African plum accessions?

(ii) Which African plum's ecological provenances possess best fruits traits for selection through controlled pollination? Information presented herein, will help breeders to develop high yielding and good quality African plum hybrids for further breeding, clonal selection and cultivar development.

III.2.1. Results

III.2.1.1. Description of fruit traits from control-pollinated accessions of African plum

Epicarp and mesocarp colors of studied fruits varied from one tree to another. Five different epicarp colors and seven different mesocarp colors were registered (Table XVII and XVIII). The most common epicarp color was Hereford heather found in 72.6 % of the fruits. Green pastures and Eucalyptus were the most common mesocarp colors (34.9 % and 33.0 % respectively).

Table XVII. Frequency of epicrap fruit color appearance in 18 African plum accessions (n = 1261).

Code	Qualitative descriptor	Frequency	Percent (%)
EC01	Hereford heather	916	72.6
EC02	Malvern blue	56	4.4
EC03	Mulberry	61	4.8
EC04	Royal blue	81	6.4
EC05	Viola	147	11.6
Total		1261	100

Table XVIII. Frequency of mesocrap fruit color appearance in 18 African plum accessions (n = 1261).

Code	Qualitative descriptor	Frequency	Percent (%)
MC01	Eucalyptus	440	34.9
MC02	Green pastures	416	33.0
MC03	Lime	81	6.4
MC04	Misty green	82	6.5
MC05	Spring green	125	9.9
MC06	Summer rose	56	4.4
MC07	White wine	61	4.8
Total		1261	100

Fruit, pulp and kernel weight displayed continuous and highly significant ($P < 0.05$) tree-to tree variation in all crosses combined (Table XIX and Fig. 30). Mean fruit weight was 68.49 g. The heaviest fruits were registered from crosses from Boumnyebel, Makenene and Kekem accessions respectively. Mean pulp weight was 56.92 g. The heaviest pulp was also recorded in Boumnyebel, Makenene and Kekem accessions respectively. Mean kernel weight was 11.57 g. Mean kernel weight differ significantly ($P < 0.05$) between crosses. Variation was between fruits within each crossing and between tree provenances. Fruit:kernel weight ratio range from 1.67 to 14.80 with a mean of 5.93 ± 0.05 g whereas fruit:pulp weight ratio range from 1.00 to 2.50 with a mean of 1.25 ± 0.00 g.

Mean fruit length and width differed significantly ($P < 0.05$) between crosses with continuous tree-to-tree variation (Table XIX; Fig. 30). Mean fruit length was 78.83 mm and the longest fruits were registered from Boumnyebel (88.15 mm) and Makenene (76.54 mm) crosses. Mean fruit width was 40.15 mm and the largest fruits were recorded from Boumnyebel (42.51 mm) crosses. Mean fruit width differed significantly ($P < 0.05$) between crosses. Fruit length:width ratio range from 0.83 to 4.02 with a mean of 1.97 ± 0.00 mm.

Table XIX. Quantitative agro-morphologic traits in 18 African plum accessions (n = 1261).

Code	Descriptors	Minimum	Maximum	Mean	SE	SD	Variance
T01	Fruit length (mm)	33.90	112.00	78.33	0.38	13.83	191.27
T02	Fruit width (mm)	18.35	57.75	40.15	0.17	6.17	38.11
T03	Pulp thickness (mm)	4.08	9.38	6.80	**0.02**	0.81	0.66
T04	Fruit weight (g)	10.00	118.00	68.49	0.66	23.66	559.84
T05	Pulp weight (g)	6.60	99.00	56.92	0.63	22.70	515.63
T06	Kernel weight (g)	0.00	25.00	11.57	0.10	3.66	13.40
T07	Fruit length:width ratio (fruit form)	0.83	4.02	1.97	**0.00**	0.26	**0.06**
T08	Fruit:pulp weight ratio	1.00	2.50	1.25	**0.00**	0.17	**0.03**
T09	Fruit:kernel weight ratio	1.67	14.80	5.93	**0.05**	2.05	4.24

SE: Standard Error; SD: Standard Deviation

As compare to the results from opened pollination by Okafor (1983), Table XX shows that results from controlled pollination have highest fruit trait mensurations.

Table XX. Comparison between opened and control-pollinated *D. edulis* fruit traits according to varieties.

Trait	Opened pollination Okafor (1983)		Controlled pollination
	D. edulis var *parvicarpa*	*D. edulis* var *edulis*	*D. edulis* var *edulis*
Fruit length (mm)	< 50	> 50	33.9 – 112
Fruit width (mm)	< 20.5	>20.5	18.35 – 57.75
Pulp thickness (mm)	2.5 – 3.5	3.5 – 9	4.08 – 9.38

Fig. 30.Variation in fruit width (a) and fruit length (b) of the African plum

Mean pulp thickness differed significantly ($P < 0.05$) between trees with continuous tree-to-tree variation (Table XIX). Mean pulp thickness was 6.80 mm. The pulp thickness differ significantly ($P < 0.05$) between crosses and the highest pulp thickness was registered from Makenene (7.01 mm) crosses.

The number of kernel per fruit varied from zero (00) to one (01). Occasionally, crossing from the four provenances had fruits with no kernels and sometimes many fruits of a particular crossing had no kernels (C_106*104 and C_106*116 within Makenene provenance). Among the 1604 fruits obtained after controlled pollination, 42 appear with no kernel making a frequency of 3.3 % (Fig. 31). This seedlessness phenomenon needs to be investigated.

Fig. 31. Seedless African plum.

Nonetheless, it is worth nothing sometimes, some fruits may contain two seeds, but this phenomenon is very rare (Fig. 32).

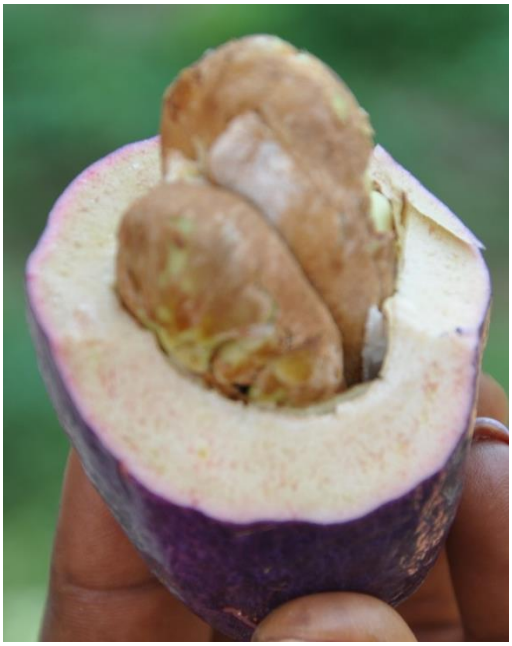


Fig. 32: An atypical African plum with two seeds or kernels

III.2.1.2. Principal Component Analysis

The principal component analysis (PCA) performed on nine agro-morphological fruit traits of 18 African plum accessions showed that the first two principal components (fruit:kernel weight ratio and fruit width) had eigen values greater than one and accounted for 87.01 % of the total variation. Table XXI presents the correlation between the axes and quantitative traits.

The first component (PC1), which explained 68.6 % of the total variation showed a strong and positive link with and between fruit length, fruit width, fruit and pulp weight, pulp thickness, fruit:kernel weight ratio, whereas it was negatively correlated with fruit:pulp weight ratio. This result mean that fruits from crosses with high PC1 values have greater fruit length, fruit width, fruit and pulp weight and fruit:kernel weight ratio whereas they have lower kernel weight and fruit length:width ratio.

Figure 33 shows the projection of the individuals from the four crossed provenances onto axes 1 and 2 and the crosses' position on the scatter plot. PC2 explained 21.41 % of the total variation and was positively influenced by kernel weight and fruit length:width ratio. This means that crossing with high PC2 values have high kernel weight and fruit length:width ratio. Nevertheless, this second component was negatively correlated with fruit:kernel weight ratio.

From this plot (Fig. 33) and Table XXI, it can be deduced that all crosses located in the upper positive part of the axis 1 outclassed the others for most of the quantitative traits, but showed low values for the fruit:kernel weight ratio. In contrast, the other crosses had high values for the ratio fruit weight/kernel weight.

Table XXI. Correlation between quantitative morphological traits of control-pollinated African plum fruits and Rotated Component Matrix.

Code	Quantitative descriptors	PC1	PC2
T01	Fruit:kernel weight ratio	**0.973**	-0.071
T02	Fruit width	**0.971**	0.167
T03	Fruit:pulp weight ratio	-0.968	0.182
T04	Pulp weight	0.964	0.173
T05	Fruit weight	0.949	0.234
T06	Fruit length	0.838	0.499
T07	Pulp thickness	0.731	0.311
T08	Kernel weight	0.081	**0.876**
T09	Fruit length:width ratio	0.076	**0.815**
Eigen value		6.181	1.651
Proportion		68.677	18.339
Cumulative		68.677	**87.016**

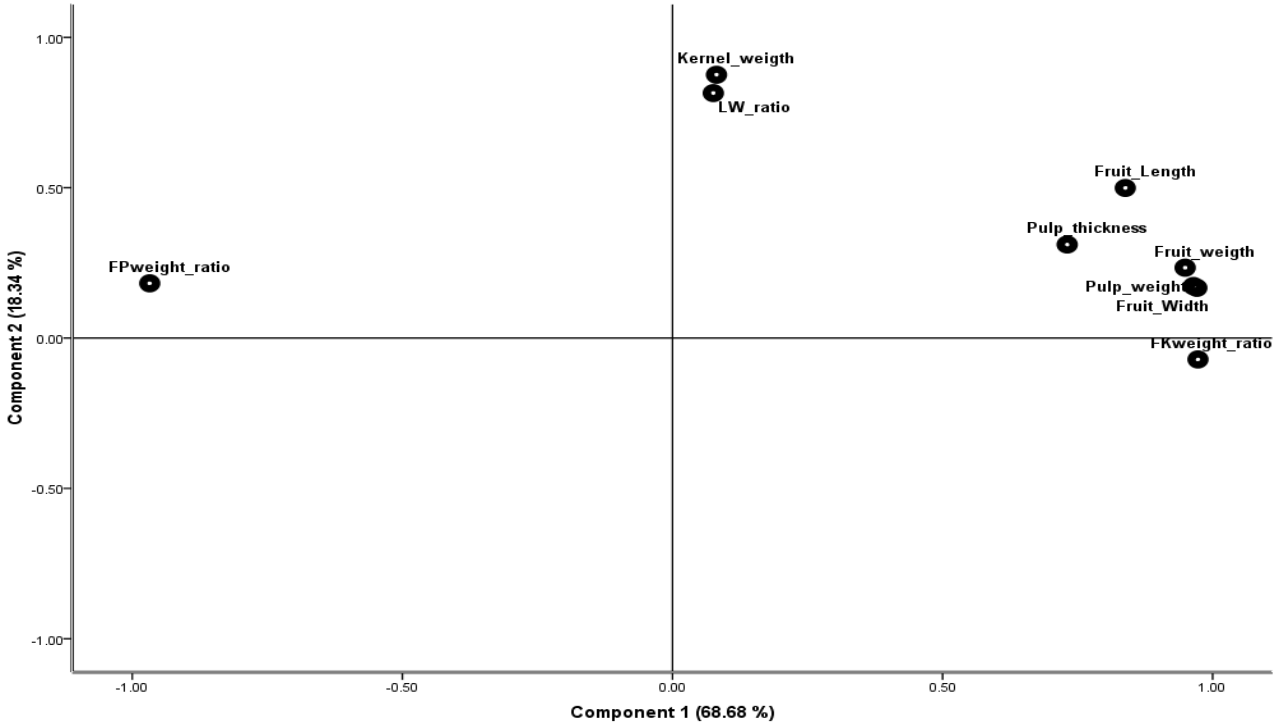


Fig. 33.Scatter plot of the PCA analysis showing links between African plum control-pollinated fruit traits.

III.2.3.3. Cluster analysis

The 25 African plum accessions grouped in 36 crosses based on nine over twelve morphological traits were classified in three groups using Ward's hierarchical algorithm as shown in Figure 34.

Cluster 1 contained sixteen accessions from Boumnyebel (10) and Makenene (6). Crosses from these provenances are characterized by greater values of eight over nine quantitative fruit traits studied, except fruit:pulp weight ratio.

Cluster 2 comprises nine accessions from Boumnyebel (2), Kekem (2), Makenene (3) and Limbe (2). In this cluster, except in fruit:pulp weight ratio, crosses are characterized by lower values in all studied traits.

The third cluster included eleven accessions from Kekem (8) and Makenene (3) and is intermediate between clusters 1 and 2.

Accuracy of produced groups by cluster analysis was done using multivariate ANOVA (Table XVIII).

III.2.1.4. Modelling *Dacryodes edulis* pulp yield per fruit

Regression equations were used to build predictive models for pulp yield (the principal trait for commercial importance) based on fruit weight (Table XXII). There were highly significant and strong relationships (Table XXIII) between fruit weight and pulp weight (R^2 = 0.988). However, fruit weight was a strong predictor of pulp weight (Fig. 35). Results showed that only the first model tested was significant, thus the standard linear regression for African plum pulp yield per fruit was:

- *Pulp weight = -8.040 (0.004) + 0.948 (0.299) x fruit weight……EQ7*

Table XXII. Means and standard errors of quantitative morphological traits of control-pollinated African plum fruits.

Code	Quantitative descriptors	Cluster1	Cluster2	Cluster3	*P*
T01	Fruit length (mm)	90.339 ± 1.098^{a*}	63.423 ± 1.644^{b}	72.213 ± 1.324^{c}	**0.000**
T02	Fruit width (mm)	43.838 ± 0.412^{a}	32.351 ± 0.550^{b}	39.985 ± 0.497^{c}	**0.000**
T03	Pulp thickness (mm)	7.239 ± 0.068^{a}	6.083 ± 0.09^{b}	6.178 ± 0.082^{c}	**0.000**
T04	Fruit weight (g)	83.688 ± 2.76^{a}	38.249 ± 3.691^{b}	67.291 ± 3.33^{c}	**0.000**
T05	Pulp weight (g)	71.264 ± 2.642^{a}	26.573 ± 3.523^{b}	57.215 ± 3.187^{c}	**0.000**
T06	Kernel weight (g)	12.424 ± 0.310^{a}	11.706 ± 0.414^{a}	10.076 ± 0.374^{b}	**0.000**
T07	Fruit length:width ratio (fruit form)	2.071 ± 0.022^{a}	1.999 ± 0.029^{a}	1.818 ± 0.026^{b}	**0.000**
T08	Fruit:pulp weight ratio	1.177 ± 0.011^{a}	1.443 ± 0.015^{b}	1.186 ± 0.014^{a}	**0.000**
T09	Fruit:kernel weight ratio	6.0874 ± 0.210^{a}	3.374 ± 0.280^{b}	6.393 ± 0.253^{a}	**0.000**

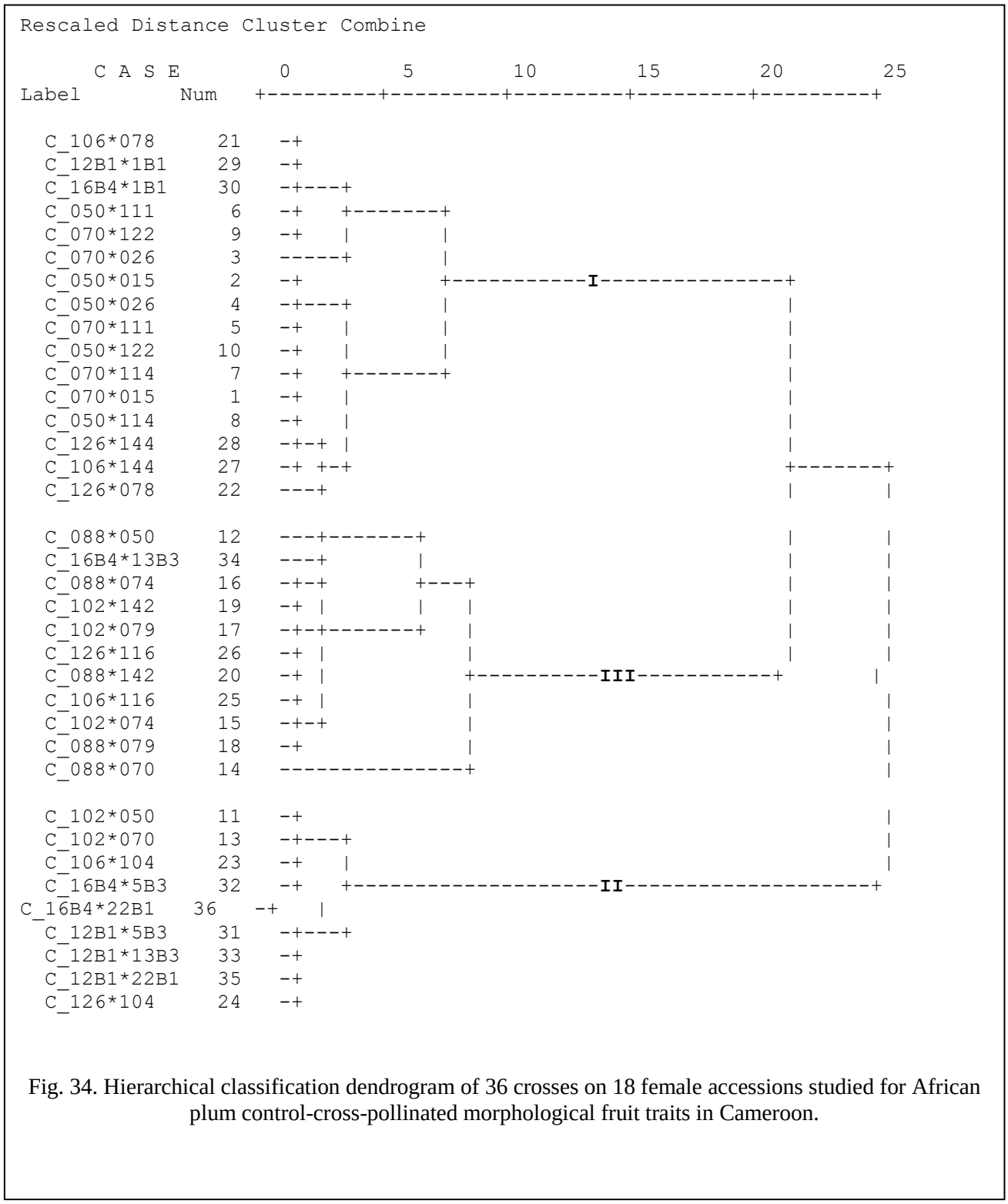


Fig. 34. Hierarchical classification dendrogram of 36 crosses on 18 female accessions studied for African plum control-cross-pollinated morphological fruit traits in Cameroon.

Table XXIII. Calculated correlations coefficients

	Fruit length	Fruit width	Fruit lenght:width ratio	Pulp Thickness	Fruit weight	Kernel weight	Fruit :kernel weight ratio	Pulp weight
Fruit length	1							
Fruit width	0.760**	1						
Fruit lenght:width ratio	0.396	-0.267	1					
Pulp Thickness	0.590**	0.646**	-0.025	1				
Fruit weight	0.800**	0.797**	-0.090	0.544**	1			
Kernel weight	0.316	0.248	0.120	0.321	0.333	1		
Fruit:kernel weight ratio	0.558**	0.623**	-0.018	0.324	0.716**	-0.353	1	
Pulp weight	0.782**	0.791**	0.074	0.515**	0.988**	0.185	0.791**	1

**: Very significant at 5%.

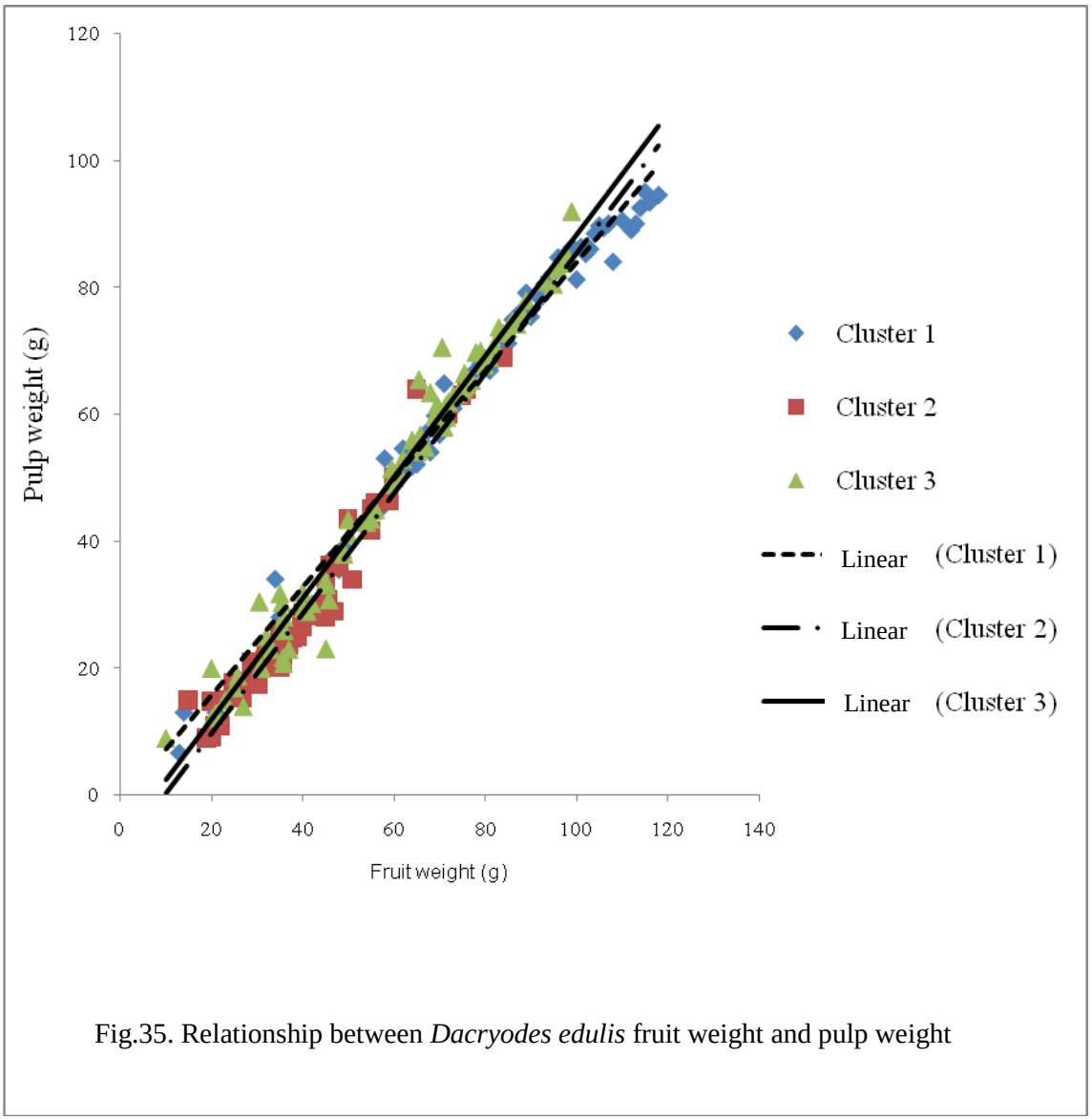


Fig.35. Relationship between *Dacryodes edulis* fruit weight and pulp weight

III.2.2. Discussion

This pioneer study quantifies variation in fruit traits from control-hand-cross-pollinated accessions of African plum and provides basic knowledge on the range of variation of several morphological fruit traits within and between well-known provenance accessions. The studied accessions displayed considerable variation in fruit and pulp weight traits as well as moderate variation for fruit length, fruit width, kernel weight and fruit:kernel weight ratio whereas they showed lower variation in pulp thickness, fruit length:width ratio and fruit:pulp weight ratio. These results suggest that fruits smaller in size and lower in weight have lower fruit:pulp weight ratio. This may imply that in superior trees, increase in pulp weight is greater than that of the kernel weight.

Respectively in Cameroon and Nigeria, the very extensive variation found irrespective of the studied traits is consistent with previous studies on the same species in wild and planted village populations (Akamba, 2000; Leakey *et al.*, 2002a). In fact, phenotypic characterization studies on *D. edulis* fruit traits (fruit length, width and pulp thickness) observed a frequent occurrence (about 80%) of intraspecific variation in the above-measured fruit traits. The observed tree-to-tree variation in fruit size was 3-to-10-fold (Waruhui *et al*., 2004; Anegbeh *et al*., 2005). The same trend was pointed out for many other indigenous fruit trees such as: *Irvingia gabonenis* (Atangana *et al.,* 2001, 2002); *Sclerocarya birrea* subsp. *caffra* (Leakey *et al.,* 2002b); *Balanites aegyptiaca* (Elfeel and Warrag, 2006); *Detarium microcarpum* (Kouyaté *et al.,* 2009); *Ziziphus mauritiana* (Koné *et al.,* 2009); *Allanblackia floribunda* (Atangana, 2010); *Adansonia digitata* (Kouyaté *et al.,* 2011; De Smedt *et al.,* 2011b; Parkouda *et al*., 2012) and *Vitellaria paradoxa* (Maranz and Wiesman, 2003; Ugese *et al*., 2010).

The relatively strong relationships between fruit weight and pulp weight suggested by the predictive models indicate that selection for pulp can be based on fruit weight. The variability of the relation between fruit weight and pulp weight confirms the moderate differences between clusters and may have been driven by both ecological and genetic variation. This result is fully in line with those reported early on others indigenous fruit trees by Kouyaté (2005) on *D. microcarpum*; Sanou *et al.,* (2006) and Ugese *et al*. (2010) on *V. paradoxa*; Diallo *et al.,* (2008) and Fandohan *et al.,* (2011a) on *Tamarindus indica* and Assogbadjo *et al.,* (2011) on *A. digitata*. Thus, further use of the obtained models should be made with respect to the provenances or progenies (Achigan *et al.,* 2006). This study indicates that based on the quantitative traits, most of the observed variation is held within provenances. Nevertheless, the between provenances variation was found to be relatively high, particularly for fruit length, fruit width, fruit weight, pulp weight and pulp thickness. These results are in line with the results outlined by Leakey *et al.,* (2002a); Waruhiu *et al.,* (2004) and Anegbeh *et al.,* (2005) in the same species respectively in West and Central Africa. Similar results was pointed out by Thiong'o *et al.,* (2002); Kadzere *et al.,* (2006); Yakushiji *et al.,* (2006); Assogbadjo *et al.,* (2011) and Simbo *et al.,* (2012), respectively on *Sclerocarya birrea*, *Uapaca kirkiana* in South Africa and *A. digitata* in West Africa.

The evidence of continuous intraspecific variation found in the open-pollinated fruit and nut traits of *D. edulis* and other indigenous fruit trees such as *I. gabonensis*, *V. paradoxa*, *A. digitata*, *D. microcarpum* represents the normal variability arising from out-breeding. The reported results are in line with results of the present study, which was focused on controlled pollination of well-known accessions. Nevertheless, this occurrence of continuous variation also questions the validity of Okafor (1983; 1990) who postulated the existence of two varieties with different sizes and Youmbi *et al.*, (1989); Ndoye *et al.*, (1997), Onuegbu (2004) and Silou *et al.*, (2000). These authors' categorized *D. edulis* fruits into size classes for market studies. In addition, the results of the present study suggest that fruit size is not necessarily related to other fruit traits and they are in fairly agreement with those reported by Akamba (2000), Leakey *et al.*, (2002) and Waruhiu *et al.*, (2004) in the same species.

The variation in fruit:kernel weight ratio reported here supports earlier evidence from Akamba (2000) and Kengue (2002) that a few trees from a specific provenance produce kernel-less fruits, especially those trees that produce late in the season, so called "off-season" trees (Kengue, 1990). In fact, it was observed in this study that, all crosses occasionally had fruits with no kernels and sometimes many fruits of a particular crossing had no kernels. In general, kernel number per fruit is one in this species, thus the variation within individual tree fruit samples from 0 to 1 kernel per fruit may suggest that this trait is affected by some environmental factors in addition to genetics. It is also known that seedless fruits can develop in one of two ways: (i) either the fruit develops without any fertilisation (parthenocarpy) or (ii) pollination triggers fruit development but the ovules or embryos abort without producing mature seeds (stenospermocarpy) (Vander Kloet, 1983).

In fruits obtained through opened-cross-pollination, a possible explanation for this variability in kernel number per fruit could be that, not all ovules were successfully pollinated, perhaps as a result of lack of pollinators, adverse hormonal levels or competition for carbohydrate and/or nutrients, excessive distances between trees, or inappropriate weather for pollination activity and even predation on developing seeds (Diallo *et al.,* 2008). One of the urgent actions to address this problem is the setting of beehives in a male tree for dioecious species such as marula (*S. birrea*), *A. floribunda*, African canarium (*Canarium schweinfurthii*) and masuku (*U. kirkiana*), or in a hermaphrodite tree for monoieciuos species such as baobab (*A. digitata*), ber (*Z. mauritiana*), tamarind (*T. indica*), *D. microcarpum*, she butter tree (*V. paradoxa*) and African locust bean (*Parkia biglobosa*).

Our study was focused on well-known accessions submitted to controlled-cross-pollination, a process that permits the breeder to deposit pollen exactly onto the stigma of an open flower. Thus, the existence of fruit with no kernel in this present work can only be explained by parthenocarpy, a phenomenon that is the natural or artificially induced production of fruit without fertilization of ovules, the fruit is therefore seedless (Zeven *et al.*, 1982; Parent, 1990). Fruits with a high proportion of zero kernels were among those with highest pulp weight and lowest mean kernel weight, while those with 1 kernel were among those with highest mean kernel weight and lowest pulp weight. This result is fairly in line with that reported by Akamba (2000) on the same species. Kengue (1998), Akamba (2000) and Kengni (2002) outlined that parthenopcarpic fruits are generally the heaviest (due to the highest pulp weight) and are also known as fruits with best organoleptic qualities. Therefore, African plum tree samples that produce such fruits are eligible for cultivars development.

Furthermore, studies on avocado (Alcaraz *et al.*, 2009), mango (Anila and Rhada, 2003), *Ziziphus* (Koné *et al*., 2009) and *Citrus* species (Muhammad *et al.*, 2011; Ladaniya and Mahalle, 2011) confirmed this hypothesis. Vander Kloet (1983) stated that in dioecious species, parthenocarpy increases fruit production because staminate trees do not need to be planted to provide pollen. Moreover, some "plus trees" from Makenene provenance reputed as off-season tree have many fruits with no kernel (pers. obs.). As the kernel is of obvious importance for sexual regeneration, it would be of little importance in vegetatively regenerated cultivars and consequently seedless cultivars could be a desirable market trait. In fact, in seedless fruits, the fruit weight corresponds to the weight of the edible part, thus, they will be suitable for any improvement program geared towards human consumption.

Additionally, results from the present study showed that crosses, which lead to high PC1 values, have better fruits traits and can be selected for breeding and cultivar development. Otherwise, crosses with high PC2 values have high kernel weight thus low pulp weight and high fruit length:with ratio. Kernel weight and fruit length:width ratio traits did not have significant importance as selected traits. According to breeding goal, African plum breeders could select accessions by considering appropriate PCs values. In fact, any studies aimed at determining the physiological traits and their genetic parameters (genetic variation, heritability, genetic correlations, repeatability), must utilize genotypes representative of breeder's populations (Zhou, 2005).

Principal component analysis has been widely used in studying agro-morphological fruit characterization in germplasm collections of many exotic crops such as sorghum (Mujaju *et al.,* 2008), *Cucumis melo* (Lotti *et al.,* 2008), *Helianthus annuus* (Nooryazdan *et al.,* 2010); groundnut (*Vigna subterranea*) (Onwubiko *et al.,* 2011; Cobbinah *et al.,* 2011), castor bean (*Ricinus communis*) (Goodarzi *et al.,* 2012) and Soursop (*Annona muricata*) (Padmini *et al.,* 2013). This methodology has been also used for morphological fruit traits characterization of some native indigenous fruit trees such as *Uapaca kirkiana* (Mwase *et al.,* 2006), *Canarium indicum* (Leakey *et al.,* 2008), tamarind (Fandohan *et al*., 2011a), baobab (Assogbadjo *et al.,* 2011) and yellow passion fruit (Castro *et al*., 2012). The high variability indicates great potential for further improvement through the development of cultivars from elite trees using horticultural techniques. Speedy benefits may be obtained by selecting superior hybrids from control-cross-pollination, establishing them as seed orchards and propagating such stocks as clones. Since crosses belonging to clusters 1 and 3 from Boumnyebel, Makenene and Kekem provenances portrayed the highest values for most of the investigated traits, especially pulp weight per fruit, they may be of particular interest for breeding with the purpose of improving pulp yield per fruit. Such candidate trees could later in seed orchard be cloned via air-layering and/or leafy stem-cutting (Mialoundama *et al.,* 2002). Crosses from Limbe provenance belong to cluster 2 and showed intermediate or low fruits size, low fruit and pulp weight but high fruit:kernel weight ratio.

Additionally, the perceived qualitative variation (pulp oil content, pulp taste, epicarp and mesocarp colors) may be genetically determined and should not be neglected. Our studied showed that the most common epicarp color was Hereford heather whereas the most common mesocarp colors were “Green pastures” and “Eucalyptus”. These results are in line with the results reported by Leakey *et al.,* (2002a), and Waruhiu *et al.,* (2004), on the same species. The higher the amount of variation presents for a character in the breeding materials, the greater the scope for its improvement through selection (De Smedt *et al.,* 2011a; Simbo *et al*., 2012). From these results, it is clear that although controlled cross-pollination better increase fruit set, it did not increase African plum fruit size as observed in *Citrus* species (Iqbal and Karacali, 2004; Basharat *et al.,* 2008; Al-Naggar *et al.,* 2009) as well as in *Z. mauritiana* (Koné *et al.,* 2009). Nevertheless, the qualitative genetic gain (pulp taste, pulp oil content) will be tested from the obtained F_1 hybrids (already set on a field trial as orchard) during the first production. As cultivars are developed for their morphological attributes (Waruhiu *et al.,*2004), it is clear from this study and previous that detailed study of tree-to-tree variation in

taste, nutritional qualities and oil content in African plum control-pollinated fruits is required to meet the food and industrial markets, respectively.

Morphological characters have traditionally been used to obtain information on variation within plant species. These characters are usually controlled by many loci and may be affected by environment, which can complicate the evaluation of genetic diversity (Jermyn and Slinkard, 1977). By contrast, molecular markers are not generally influenced by environment; they are often but not always selectively neutral and, if chosen carefully throughout the genome, supposedly unbiased (Wani *et al*., 2010; Coster *et al*., 2012). Random Amplified Polymorphic DNA (RAPD) is one of these methods, which do not require previous knowledge of DNA sequences is easy to perform, and is one of the most cost-effective methods for obtaining polymorphic markers in many plant genera (Ngo-Mpeck, 2004; Muchugi-Mwangi *et al*., 2008). For the on-going African plum scaled-up breeding program, we suggested that studies on molecular markers should be investigated for further genetic diversity for fruit traits improvement as early outlined by Todou *et al*., (2013).

Partial conclusion

This study has highlighted required information for African plum improvement breeding program based on crosses of well-known accessions. The studied accessions showed high variability in fruit and pulp weight traits as well as moderate variation for fruit length, fruit width, kernel weight and fruit:kernel weight ratio whereas they showed low variability in pulp thickness, fruit length:width ratio and fruit:pulp weight ratio. The 18 females accessions based on studied traits were classified in three groups. Results showed that the most studied accessions have been clustered together in groups 1 and 3 indicating high genetic variability in African plum germplasm. Principal component analysis (PCA) revealed that the first two principal components accounted for 87.01% of the total variation. Among the studied traits, fruit length, fruit width, fruit and pulp weight, pulp thickness and fruit:kernel weight ratio showed strong and high positive link with the first component (PC1) whereas kernel weight and fruit length:width ratio showed positive link with the second component (PC2). According to breeding goal, breeders can chose accessions by considering appropriate PCs values.

Likewise, the developed predictive models could allow researchers and policy makers in partnership with local people to make more quantitative assessment of the pulp potential of African plum trees established in traditional agroforestry systems. In fact, phenotypically superior candidate African plum individuals will be coppiced, brought into clonal propagation via air-layering or stem-cuttings, followed by clonal testing of those clones that are easy to propagate. From this study, it is clear that controlled cross-pollination did not increase African plum fruit size, but the fruit set was better increase; otherwise, the perceived qualitative variation (in pulp oil content, pulp taste, epicarp and mesocarp colours) should not be neglected and would be tested in the F_2 and F_3 generations (genetic gain evaluation) in further investigations. In addition, as the tree-to-tree variation is higher within provenances, this result suggests that the improvement of indigenous fruit trees germplasm through vegetative propagation does not narrow the genetic diversity in the studied species. For the on-going scaled-up African plum breeding program, we suggested that tree-to-tree variation in taste, nutritional qualities and oil content in African plum control-pollinated fruits must be taken into account to meet the food and industrial markets. Studies on molecular markers should be investigated for further genetic diversity for fruit traits improvement.

Part III. Decapitation test on African plum control-pollinated seedlings and consequences on subsequent growth

The main objectives were three fold: (i) characterizing the branching habit of control-pollinated African plum seedlings submitted to an early decapitation test; (ii) analyzing its relationship with intra-progeny performance and (iii) analyzing the implications for further breeding improvement leading to branching habit, harvest index and yield improvement. Thus, the main question addressed was: Do control-pollinated African plum seedlings' behavior in the nursery depend on the progeny and the crossing to which they belong?

III.3.1. Results

III.3.1.1. Description of African plum control-pollinated seedlings in the nursery

Seedling height (SH) did not showed tree-to-tree variation ($P > 0.05$) in all crosses combined (Table XXIV), 39 weeks after seeds sowing (WAS). Seedling height mean was 54.66 cm. The highest seedling height was registered from crosses belonging to clusters 1 and 2 respectively.

Seedling collar diameter (SCD) differed significantly ($p < 0.05$) in all crosses combined between crosses with continuous tree-to-tree variation (Table XXIV), 39 WAS. Mean seedling collar diameter was 3.48 cm and the biggest collar diameters were registered from crosses belonging to clusters 1 and 2 respectively.

The numbers of leaves per seedling (NLs) differed significantly ($p < 0.05$) between crosses with continuous tree-to-tree variation (Table XXIV), 39 WAS. Mean number of leaves per seedling was 5.06 and the maximum number of leaves per seedling was registered from crosses belonging to clusters 1 and 2 respectively.

The number of twigs sprouted after decapitation (NTAD) did not showed tree-to-tree variation ($P > 0.05$) in all crosses combined (Table XXIV), 8 weeks after decapitation (WAD). Mean number of twigs was 4.58 and the maximum number of twigs sprouted after decapitation was registered from crosses belonging to clusters 1 and 2 respectively.

The numbers of vigorous twigs (NVT) recorded also followed the same trend as obtained for seedling collar diameter and the numbers of leaves ($P < 0.05$) between crosses, 8 weeks after decapitation (WAD). Mean number of vigorous twigs was 3.44. As others studied

traits, the maximum number of vigorous twigs was registered from crosses belonging to clusters 1 and 2 respectively. Table XXV shows variation in shoot elongation according to clusters and crosses belonging to cluster 1 show best physiological growth.

Moreover, the decapitation test in *D. edulis* showed synchronous growing in buds released within each cluster (Fig. 36).

III.3.1.2 Modelling *Dacryodes edulis* shoot elongation

Regression equations were used to build predictive models for shoot elongation. There were highly significant and strong relationships between seedling height and seedling collar diameter (R^2 = 0.909) and between the numbers of twigs and the numbers of vigorous twigs (R^2 = 0.899). However, the numbers of weeks after decapitation (WAD) was a strong predictor of shoot elongation (Fig. 37). The standard linear regression for African plum decapitated seedling was:

- *Shoot length (cm) = -8.808 (0.328) + 0.909 (-2,46) x WAD……..EQ₈*

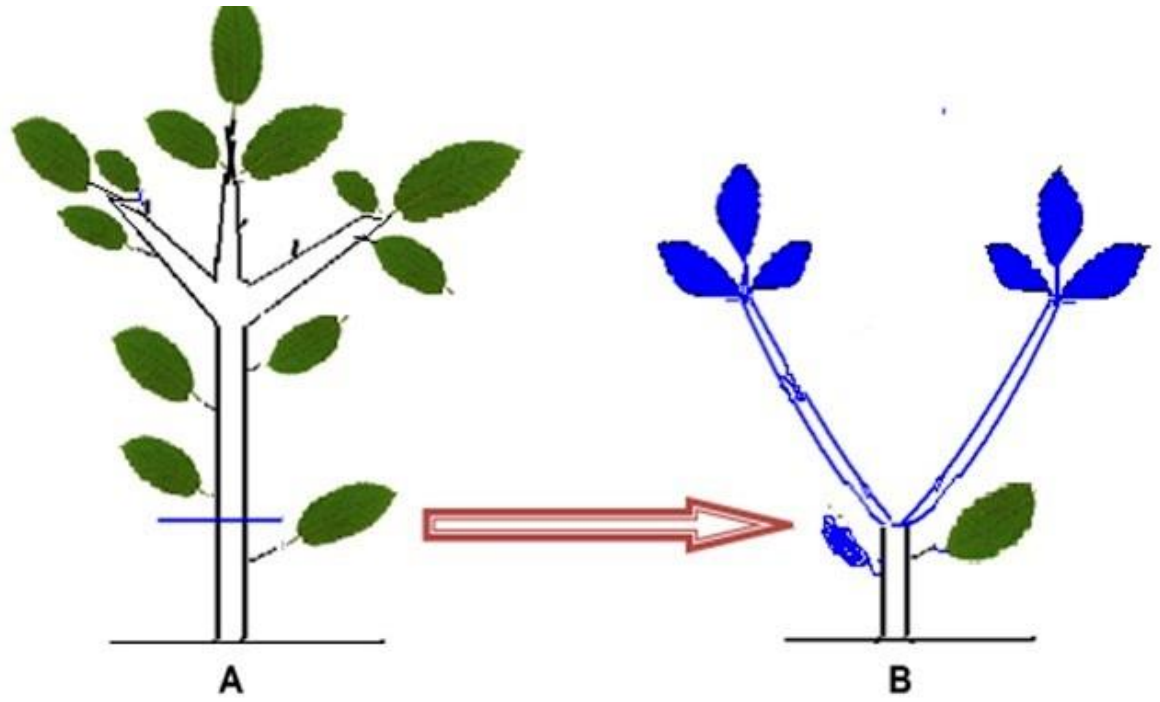


Fig. 36. *Dacryodes edulis* synchronous lateral buds releasing following decapitation

Table XXIV. Basic statistics for control-pollinated seedlings physiological traits within 39 WAS and 8 WAD (n=108). SH: seedling height; SCD: seedling collar diameter; NLs: number of leaves per seedling; NTAD: number of twigs sprouted after decapitation; NVT: number of vigorous twigs.

Traits	Cluster	N	Minimum	Maximum	Mean	SE	SD	95% Confidence Interval	
								Lower bound	Upper bound
SH (cm)	1	16	47.00	66.33	56.95	1.73	6.92	53.26	60.64
	2	9	45.33	66.33	54.59	2.56	7.68	48.68	60.50
	3	11	42.67	67.00	51.39	2.82	9.37	45.09	57.69
SCD (cm)	1	16	3.03	4.27	3.68	0.08	0.35	3.49	3.86
	2	9	2.90	4.20	3.51	0.14	0.42	3.18	3.83
	3	11	2.50	4.03	3.18	0.16	0.55	2.80	3.55
NLs	1	16	4	7	5.35	0.18	0.73	4.96	5.75
	2	9	4	6	5.15	0.17	0.53	4.74	5.56
	3	11	4	5	4.54	0.15	0.50	4.21	4.88
NTAD	1	16	3	7	4.96	0.21	0.85	4.50	5.41
	2	9	3	6	4.52	0.34	0.12	3.73	5.31
	3	11	3	6	4.09	0.28	0.94	3.46	4.72
NVT	1	16	3	5	3.73	0.11	0.44	3.49	3.97
	2	9	3	4	3.41	0.19	.057	2.97	3.85
	3	11	2	4	3.03	0.21	.070	2.56	3.50

Table XXV. Means values for control-pollinated seedling characteristics within 39 WAS and 8 WAD (n=108).

Code	Traits	Cluster1	Cluster2	Cluster3	*P*
T01	Seedling height (cm)	56.95±1.73^{a}	54.59±2.56^{a}	51.39±2.82^{a}	0.216
T02	Seedling collar diameter (cm)	3.68±0.08^{a}	3.51±0.14^{ab}	3.18±0.55^{b}	**0.023**
T03	Number of leave per seedling	5.35±0.18^{a}	5.15±0.53^{a}	4.54±0.50^{b}	**0.008**
T04	Number of twigs sprouted after decapitation	4.96±0.21^{a}	4.52±0.34^{a}	4.09±0.28^{a}	0.069
T05	Number of vigorous twigs	3.73±0.11^{a}	3.41±0.19^{ab}	3.03±0.21^{b}	**0.013**

Means followed by the same letter within a column are not significantly different at P< 0.01 (Student-Newman-Keuls test).

Table XXVI. Basic statistics for shoot elongation 8 WAD (n=108).

Cluster	Minimum	Maximum	Mean	SE	SD	Variance	N
Cluster 1	10.68	21.87	14.02	0.32	2.22	4.96	48
Cluster 2	8.37	25.80	14.37	0.73	3.81	14.51	27
Cluster 3	9.02	21.25	13.43	0.52	3.01	9.11	33

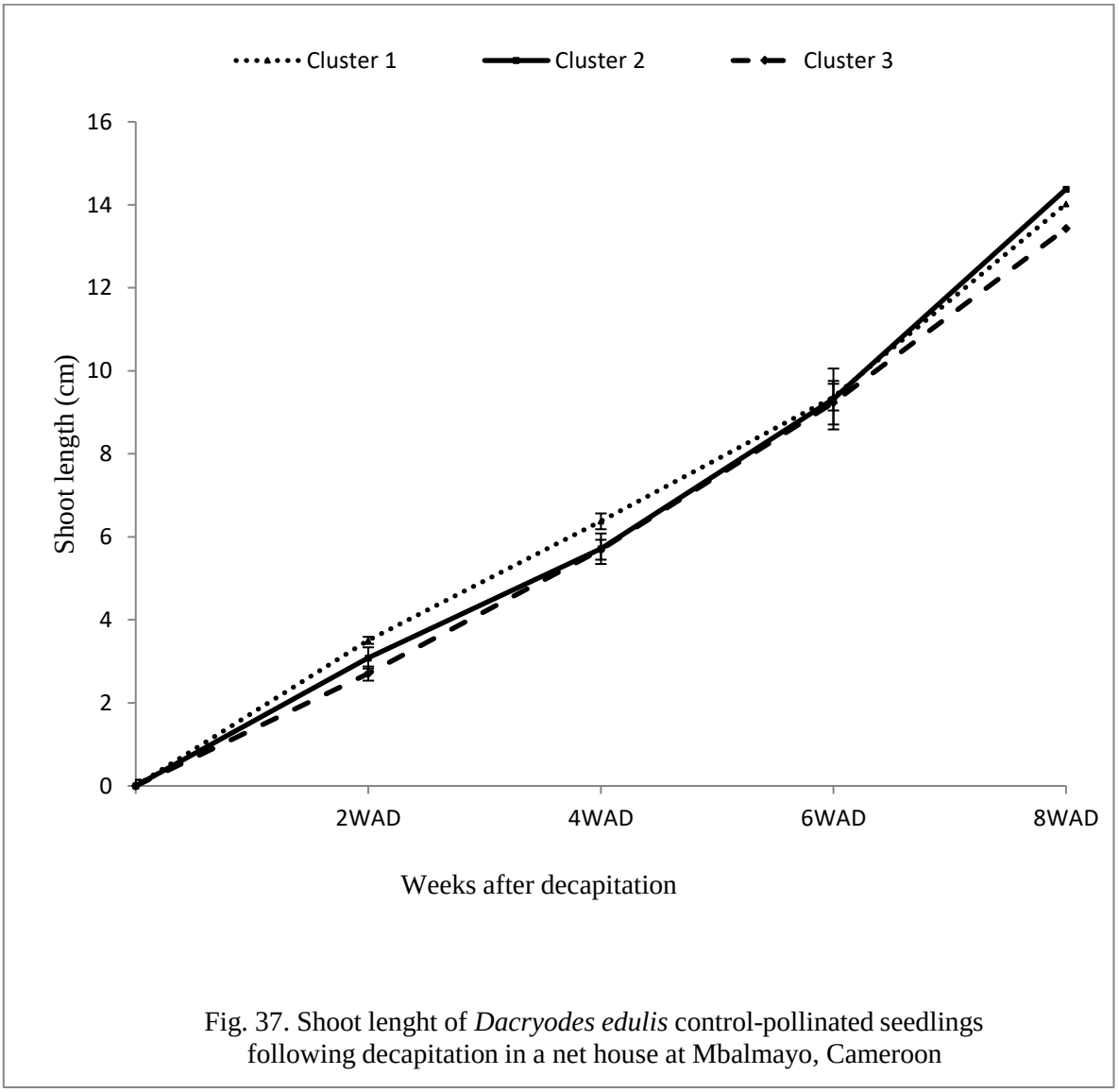


Fig. 37. Shoot lenght of *Dacryodes edulis* control-pollinated seedlings following decapitation in a net house at Mbalmayo, Cameroon

III.3.2. Discussion

The variations observed among the seedling growth characteristics such as collar diameter, shoot length, numbers of leaves, numbers of twigs sprouted after decapitation and numbers of vigorous twigs can be attributed to the progenies and the crosses to which they belong. This result is in fairly agreement with those reported by Akinnagbe and Oni (2007) and Okunlola *et al.*, (2011) respectively on *Prosopis africana*, and *Parkia biglobosa*. The results of the Analysis of variance (ANOVA) carried out to test the significance of variation at $P < 0.01$ among the progenies of different provenances using the growth variables revealed that significant variation existed in collar diameter, numbers of leaves and numbers of vigorous twigs. In general, increment in growth variables is an indication of growth, which is a common characteristic of biological organism base on the submission of Fogg (1970). This author asserted that the activities of the various meristematic cells are correlated; the correlation is such that as the shoot increases in length, it also increases in thickness and the root system extends proportionally.

In the present study, it was observed that there was no significant variation in the seedlings' height. This result is not in line with those reported by Mahoney and Fins (1995), Cochrane *et al.*, (2001); Etisso *et al.*, (2003); Karaguzel *et al.*, (2004), Upadhaya *et al.*, (2007), Janmohammadi *et al.*, (2008), Tian *et al.*, (2010), Batin (2011), Omokhua and Godwin-Egein (2011), and Soliman and Abbas (2013). These authors reported that significant variation existed only in seedlings' height among growth-studied variables. According for these authors, seedling height could serve as a trait for identifying genetically superior progenies. Furthermore, strong correlation that exist between height and other growth parameters support that height could serve as a trait for selecting superior progenies. In general, variation in the growth of seedlings may be due to a genetic factor of individual tree and less importantly to soil conditions, soil structures, weed competition and environmental factors (Fandohan *et al*., 2011b; De Smedt *et al*., 2012).

Previous investigations on some timber trees as *Triplochiton sceroxylon*, *Cedrela odorata* proposed that decapitation test was characterized by apical dominance in young plants which identified two phases of bud activity: the "Sprouting Phase", in which many buds are released from correlative inhibition, and the "Dominance Phase", during which (in

vertically oriented plants) the uppermost lateral shoots begin to assert dominance and suppress the growth of lower shoots (Phillips, 1969; Leakey and Longman, 1986; Lapido *et al.,* 1991; Newton *et al.,* 1995). Following this conceptual basis for interpretation, it is assumed that clones or seedlings with strong apical dominance release few lateral shoots after decapitation, while those with weak apical dominance sprout more freely. From these previous results, the first assumption indicated the behavior of timber trees' growth and the second was in line with results from the present study where no growth's phases were identified after decapitation. Surprisingly, the decapitation test in *D. edulis* did not showed an apical dominance effect. Results obtained showed synchronous growing in buds released within each cluster. From the relationship between branching habit and harvest index in the studied species, synchronous growing after decapitation may contribute to produce young seedlings with multiple twigs (sprouted branches). This architecture may contribute to yield improvement and facilitate handling experiments for the farmer (tree management). Additionally, this architecture can be compare to dwarfism, which has been documented in avocado (*Persea americana*), castor bean (*Ricinus communis*) and coconut (*Coccus nucifera*) (Miller and Gross, 2011).

Results for the present study showed that in all crosses combined, there was no significant variation in the numbers of twigs sprouted after decapitation and the number of weeks after decapitation was the only predictor variable for the shoot length among and within clusters. For branching frequency (Evers *et al.,* 2011), these results indicate that decapitation test could be used as an early predictive test on vigorous offspring which can portray higher germination, seedling growth and survival performances (Khan *et al*., 2002; Khan, 2004; Loha *et al*., 2006 and Diallo *et al*., 2010). These results are fairly in line with those outlined by Siddique *et al.,* (1984) and Pulkkinen and Pöykko (1990). This test could be used to screen a large number of seedlings, which could then be selected and vegetatively propagated for the establishment of seed orchards for further clonal tests. The advantage of screening seedlings in a progeny test design, as in the current investigation, is that genetic values may be estimated for the individual progenies, which may then form the basis of selection.

Hormonal response is a key adaptation that radically alters whole-plant architecture in order to optimize growth and development under diverse environmental conditions. Concerning this statement, further studies on the diverse role of hormone interactions, mainly auxin and cytokinin in the control of shoot branching must be taken into consideration to

improve the development of *D. edulis* plant material (seedlings, marcots or cuttings). Such studies have been undertaken for many crops like pea (*Pisum sativum*) and *Arabidopsis* (Li and Bangerth, 1999; Brewer *et al*., 2009) or sunflower (*Helianthus annuus*) (Nagarathma *et al*., 2010).

When considered as a result of a propagation technique, dwarfing offers an advantage in fruit tree management such as pruning, fruit thinning, spraying and fruit harvesting. These activities become easy and low-cost. Furthermore, fruit damage as the fruits drop down from dwarf trees is reduced. The use of dwarf trees could be important to households with small land holdings. Among many factors, slow growth of mature trees from which air layers and cuttings are collected could be a major factor contributing to dwarfing. However, there is a need for further investigation on dwarfing mechanism. Grafting and bark ringing have been used as dwarfing mechanisms in peach trees (Hossain *et al*., 2006), but the main cause of dwarfness has been speculated. This has been linked to low cytokinin production and possibly scion and rootstock union disturbing cytokinin translocation from the roots to the shoots (Mng'omba *et al*., 2008).

Partial conclusion

Early decapitation test can help breeders to produce young improved *D. edulis* trees with multiples branches in order to satisfy farmers' need for cultivar selection. This may help farmers to capitalize the relationship between branching habit, harvest index and yield improvement. Further studies on the diverse role of hormone interactions, mainly auxin and cytokinin in the control of shoot branching must be taken into consideration to improve the development of *D. edulis* planting material stock.

GENERAL DISCUSSION, CONCLUSION, RECOMMENDATIONS AND SUGGESTIONS FOR FURTHER RESEARCH

General discussions

The present work covers studies on *D. edulis* fruits (safou) and seedlings because of the important number of small scale farmers involved in its production and consumption, its naturally high degree of organoleptic characteristics and the associated consumers' attitudes and perceptions. This indigenous fruit tree is economically important and makes significant contributions to the daily nutritional requirements as well as income of the majority of rural populations in Cameroon. The study was therefore based on the assessment of the advantage of controlled pollination technique on the improvement of the overall production and food quality, and the evaluation of what it can offer to the scientific community involved in the rural development research.

However, domestication of indigenous fruit trees has received far less attention than that of annual crop plants (Leakey and van Damme, 2014). This process is a multidimensional process that involves identification, production, management and the adoption of the desired germplasm (Simons and Leakey, 2004; Degrande *et al.*, 2007). Overtime, this purposeful man-led selection has cause cultivated populations to diverge morphologically and genetically from their wild progenitors (Emshwiller, 2006). The domestication process therefore produces a continuum of plant populations that cannot survive without human intervention (Clement *et al*., 2010). As a result of these morphological and genetic dynamics, *D. edulis* has emerged within the domestication continuum in the humid tropics of Africa. This indigenous fruit tree could be considered to be at an intermediate phase in the domestication continuum (Asaah, 2012).

For the on-going breeding program initiated on *D. edulis* by the World Agroforestry Centre since 1998, despite the important results obtained through vegetative propagation methods well developed for the species, there was a need on enhanced production for the species. One option was to conduct controlled pollination on the studied species. This technique may help to develop new varieties or cultivars to satisfy the sub-regional and the international market needs. The options are either to rehabilitate old *D. edulis* trees to increase yields on farm or to replace the old trees with improved seedlings or high quality planting stock. As part of the participatory tree domestication process of high-value native species for the fight against poverty, environmental rehabilitation and biodiversity conservation, one fundamental objective of agricultural plant breeding is to increase crop yield (Islam *et al*., 2012). Among the array of reproductive parameters in tropical forest species, fruiting

efficiency is the most remarkable (important) to the commercial farmer, because it determines the overall yield of his crops per hectare. Specifically, early generation material is screened to improve disease resistance, and the second priority is selection for improved yield (Franzel *et al.*, 1996). Ultimately, the breeder aims to release a high yielding, stable cultivar with disease resistance and adaptability to many environments. Thus, yield components have often been used as selection criteria because they provide readily definable contrasts between genotypes that are presumed to be associated with yield differences. Therefore, breeders have aimed to produce higher yielding and good quality cultivars by exploiting variation in these components. Such studies have been carried out by Moot (1993); Ugese *et al*. (2010); Cuni Sanchez *et al*. (2011) and Parkouda *et al*., (2011). To exploit variations in these components for yield improvement, it is first necessary to apportion the variations to genetic and non-genetic factors (Jermyn and Slinkard, 1977). There is usually an interaction between the effects of these two groups (Poehlman and Borthakur, 1977) which means that the relative performance of genotypes may change in different environments (De Smedt *et al*., 2012).

Thus, as the main objective of this study was to develop and characterize improved planting material (best crosses) onto which vegetative propagation could be undertaken for cultivars development through hand cross-pollination in *D. edulis*, the crossbreeding test was carefully conducted. Concomitantly, we investigated (i) the fruiting efficiency of *D. edulis* well-known accessions also called superior genotypes or "plus tress"; (ii) the characterization of the control-pollinated fruits obtained and (iii) the assessment the decapitation test on the species in relation with branching habit, harvest index and yield improvement. Various experiments were designed and the results of these investigations are reported in chapters 2 and 3 of this thesis.

For the assessment of the fruiting efficiency of *D. edulis* selected plus trees, four main factors were to be considered:

- the parent (male and female "plus tree") provenance and family;
- the type of flower (male or hermaphrodite) which produced the pollen used for hand-fertilization as the species is andromonoic (two type of trees: one which bears only female flowers and the second type which bears male and hermaphrodite flowers in varying proportions);
- the genetic status of the female accession;
- the crossing to which each tested female accession belongs.

The species potential for successful breeding propagation through controlled hand cross-pollination suggested that breeding in *D. edulis* could be better managed. In fact, the fruiting efficiency of the studied species was under the control of many factors such as:

(i) the male parent family;
(ii) the type of flower (male or hermaphrodite) which produced pollen used for fertilization;
(iii) the genetic status of the female parent;
(iv) the resources limitations (water, soil nutrients);
(v) the experiment handling;
(vi) the overall environmental conditions.

For the present study, pollen limitation was not considered as a factor affecting the fruiting efficiency because the breeding test was undertaken in controlled conditions. Among the three provenances used for the crossbreeding test, two could be chosen for the on-going breeding program for progeny trials establishment and further clonal test. These are mainly accessions from Boumnyebel and Makekene crosses. In fact, clustering crosses into groups revealed that Group II combined the best potential candidates for further breeding. It included six crosses mainly characterized by a high fruit-setting rate (>70 %) and a high fruiting index (>50 %), then a low fruit-dropping rate (<20 %) respectively after fruit set. These comprised three crosses from Boumnyebel provenance (BUM_050*015; BUM_070*111; BUM_070*114) and three others from Makenene provenances (MAK_106*104; MAK_126*104 and MAK_126 *144).

Although we did not observe increasing in fruit size as compare to breeding in *Citrus* spp. as early outlined by Basharat *et al.* (2008); Al-Naggar *et al.,* (2009) as well as in *Ziziphus mauritiana* by Koné *et al.,* (2009), the process of controlled cross-pollination investigated in this study significantly increase the fruit set. This can help controlling the early fruit drop, which negatively impacts on the species' yield. Moreover, control-pollinated seedlings (F_1 hybrids) obtained with greater weight, and which portrayed higher germination, seedling growth and survival performances were established as progeny trial. These results are fairly in line with those reported by Cordazzo (2002) and Khan (2004). They will be monitored and managed until the first flowering and fructification, for genetic gain estimation (F_2). F_2

seedlings will be established within agro-ecological zones in the country, as clonal or progeny trials for cultivars development through vegetative propagation methods well-developed for the species. Nonetheless, the spatio-temporal regulation of the molecular factors involved in early steps of fruit set and development should be investigated.

In addition, from this study, we can deduce that during flowering, several factors that may affect the yield of the studied species must be explored during further works, namely:

(i) the position of the flower on the floral panicle (In fact, it is well know that fruits initiated from early flowers have a lower probability of aborting than the fruits initiating late);
(ii) the pollen viability;
(iii) the genetic status of the embryo;
(iv) the vegetative-reproductive growth competition and;
(v) the competition for water and nutrients. It is also necessary to explore the possibilities of reducing fruit-set that will help decreasing the fruit load by using a growth inhibitor during flowering which would improve yield (Liao *et al*., 2006; Modise *et al*., 2009).

With regard to control-pollinated fruits characterization, the studied accessions showed high variability in fruit and pulp weight traits as well as moderate variation for fruit length, fruit width, kernel weight and fruit:kernel weight ratio whereas they showed low variability in pulp thickness, fruit length:width ratio and fruit:pulp weight ratio. Results showed that the most studied accessions have been clustered together in groups 1 and 3 indicating high genetic variability in African plum germplasm. Principal component analysis (PCA) revealed that the first two principal components accounted for 87.01% of the total variation. Among the studied traits, fruit length, fruit width, fruit and pulp weight, pulp thickness and fruit:kernel weight ratio showed strong and high positive link with the first component (PC1) whereas kernel weight and fruit length:width ratio showed positive link with the second component (PC2). According to breeding goal, breeders can chose accessions by considering appropriate PCs values.

Likewise, the developed predictive models could allow researchers and policy makers in partnership with local people to make more quantitative assessment of the pulp potential of African plum trees established in traditional agroforestry systems. In fact, phenotypically

superior candidate of African plum individuals will be coppiced, brought into clonal propagation via air-layering or leafy stem-cuttings, followed by clonal testing of those clones that are easy to propagate. From this study, it is clear that controlled cross-pollination did not increase African plum fruit size, but the fruit set was better increase; otherwise, the perceived qualitative variation (in pulp oil content, pulp taste, epicarp and mesocarp colours) should not be neglected and would be tested in the F_2 and F_3 generations (genetic gain evaluation) in further investigations. In addition, as the tree-to-tree variation is higher within provenances, this result suggests that the improvement of indigenous fruit trees germplasm through vegetative propagation does not narrow the genetic diversity in the studied species.

As far as the decapitation test in control-pollinated *D. edulis* seedlings is concerned, results showed that in all crosses combined, there was no significant variation in the numbers of twigs sprouted after decapitation, and the number of weeks after decapitation was the only predictor variable for the shoot length among and within clusters. In fact, the apical dominance effect was not observed for *D. edulis*. Each decapitated seedling sprouted among two to four synchronous branches. For branching frequency (Evers *et al.*, 2011), these results indicate that decapitation test could be used as an early predictive test on vigorous offspring which can portray higher germination, seedling growth and survival performances (Khan *et al*., 2002; Khan, 2004; Loha *et al*., 2006 and Diallo *et al*., 2010). These results are fairly in line with those early outlined by Siddique *et al.*, (1984), Pulkkinen and Pöykko (1990). This test could be used to screen a large number of seedlings, which could then be selected and vegetatively propagated for the establishment of seed orchards for further clonal tests. The advantage of screening seedlings in a progeny test design, as in the current investigation, is that genetic values may be estimated for the individual progenies, which may then form the basis of selection.

Hormonal response that is a key adaptation that radically alters whole-plant architecture in order to optimize growth and development under diverse environmental conditions must be investigated. Concerning this statement, emphasis must be put on further studies on the diverse role of hormone interactions, mainly auxin and cytokinin in the control of shoot branching. This may help to produce improved *D. edulis* plant material (seedlings, marcots or cuttings). Such studies have been undertaken for many crops like pea and *Arabidopsis* (Li and Bangerth, 1999; Brewer *et al*., 2009) or sunflower (Nagarathma *et al*., 2010).

They are features that were assessed in the course of this work and that should be mentioned:

(i) the germination test of control-pollinated seeds and

(ii) the evaluation in a non-mist propagator of the control-pollinated cuttings obtained after seedling decapitation.

Raw data obtained from these experiments were in line with those reported in the species by Kengue (1990), Youmbi *et al.*, (1994b), and many others tropical fruits trees Cordazzo (2002), Khan *et al*., (2002); Khan (2004) and Diallo *et al*. (2010). These results will be published in a further scientific paper.

General conclusions

With a clearly understood breeding system and with standardized controlled pollinations techniques, *D. edulis* needs to be further exploited for its variations. Results from this study showed that variation in fruiting index that determines the species' yield is highly in strong relationship with the combination of the three factors studied (male parent provenance, the pollen type used for the crossbreeding test and the genetic status of the female parent). None of the three individual factors has had a significant effect on the number of mature fruits at the end of the crossbreeding test. Therefore, under hand pollination, the assessment of *D. edulis* fruiting efficiency depends not only on the male parent provenance and the pollen type used for fertilization, but also on the specifically genetic disposition of each female parent.

During blooming, several factors that need to be explored in future works may affect the species' yield, namely: (i) the position of the flower on the female panicle (ii) the pollen viability, (iii) the genetic status of the embryo and (iv) the competition for water and nutrients. Likewise, excessively heavy flowering can be seen to be wasteful of scarce resources at a critical time. Therefore, it is necessary to explore ways of reducing fruit set in order to reduce the fruit load by using an inhibitor of growth during flowering that would improve yield. Furthermore, farmers could perform blossom or fruitlet thinning to adjust fruit load and ensure a satisfactory fruit quality at harvest for commercial purposes. The present study also highlighted that Boumnyebel and Makenene provenances have the best combinations, characterized by high fruit-setting rate and fruiting index (>70% and >50% respectively),

followed by low fruit-dropping rate (<20%). These crosses are potential best candidates onto which mass multiplication though vegetative propagation techniques could be undertaken for cultivars development.

The relatively strong relationships between fruit and pulp weight suggested by the predictive models used in this study indicate that selection for pulp can be based on fruit weight. The variability of the relation between fruit weight and pulp weight confirms the moderate differences between clusters and may have been driven by both ecological and genetic variation. Thus, further use of the obtained models should be made with respect to the provenances or progenies. This study indicates that based on the quantitative traits, most of the observed variation is held within provenances. Nevertheless, the between provenances variation was found to relatively high, particularly for fruit length, fruit width, fruit weight, pulp weight and pulp thickness. In addition, as the tree-to-tree variation is higher within provenances, this result suggests that the improvement of indigenous fruit trees germplasm through vegetative propagation does not narrow the genetic diversity in the studied species. Overall, there exists a considerable genetic variation mostly between trees within provenances than between distinct provenances. Seeds from control-pollinated fruit (F_1 hybrids) obtained from this study were harvested, labeled, characterized and seedlings produced in the nurseries for further improvement.

Regarding the decapitation test and its consequences on the subsequent growth, the present study showed that plant height seems to be less important as morphological characteristic and the number of weeks after decapitation is the strong predictor for shoot elongation among and within clusters. The decapitation conceptual interpretation based on “sprouting phase” and “dominance phase” was not observed in the species, which contrary showed a synchronous shoots branching after decapitation. This architecture may contribute to the production of young trees with multiple branches, which can be compared to dwarfed trees. Synchronous branching may lead to yield improvement and easier tree management (handling experiments by farmers). This test could be used as a predictive test according to the relationship between branching habit, harvest index and yield improvement.

Likewise, *D. edulis* can suffer a certain degree of inbreeding depression that may negatively affect plant demography and thus pose a threat to the conservation of the species. Because the expression of inbreeding depression may vary across a plant's life cycle, more

research is needed to quantify the extent of inbreeding depression of *D. edulis* throughout its life cycle.

With regard to the genetic resources' conservation of this species, there is urgent need to implement conservation strategies in both genetically distinct units. *D. edulis* samples in or close to homesteads which were used for gene bank established for the present study showed slightly higher tree-to-tree variation in fruit characters within provenances compared to trees far from homesteads ("wild"). This observation may indicated that human-mediated seed admixture from various provenances (origins) have possibly enriched the genetic base in the homesteads stands. The development of provenance-specific and sustainable management strategies as part of *circa situm* conservation approaches will contribute to maintain the genetic resources of this important species in Cameroon. In addition, an approach of creating a pollen gene bank is underway. In fact, during pollination experiments, the best pollen was collected and conserved at different conditions at ICRAF's laboratory at Nkolbison, for further crosses and reproductive biology purposes.

Recommendations and suggestions for further research

Considering the fact that *D. edulis* seems capable of tackling problems of the poor, of the malnourished, and of the land, it can become a basis for rural development. Obviously, a productive, high-energy, high-protein food like this is worth developing. Now that better growing techniques are known, governments, individuals, and organizations throughout its range should get involved.

Steps to achieve better use of the species' potentials include the following:

- More germplasm collections (both wild and in cultivation) are needed to preserve the range of variation. Special attention should be paid to collecting germplasm in the species' in the West and Central African region for genetic diversity in other to avoid bottlenecks;

- Develop a marker-assisted selection protocol for *D. edulis* to facilitate development of distinct cultivars of desirable traits. For this purpose, deeper studies should be undertaken on the best provenance ideotypes and the wild to avoid bottlenecks;

- More research is needed to quantify the extent of inbreeding depression of *D. edulis* throughout its life cycle;

- Yield improvement: for this component, emphasis should be oriented on the possibilities of reducing fruit set that will help decreasing the fruit load by using a growth inhibitor during flowering. This will also lead to reducing premature fruit drop (abortion);

- More studies should be undertaken on the "off-season" ideotypes mainly from the Makenene provenance; In fact, fruits with a high proportion of zero kernels were among those with highest pulp thickness and lowest mean kernel weight, while those with 1 kernel were among those with highest mean kernel weight and lowest pulp thickness. So, further and deeper studies should be undertaken especially on the Makenene accessions which regularly showed many seedless fruits;

- Replacing old trees with high-quality trees; for this purpose, F_1 hybrids obtained from this study have been already settled on a field trial with the assistance of the ICRAF's technicians and will be monitored until the first flowering and fruit production (genetic gain expectation). Then F_2 hybrids obtained will be established in all agro-ecological zones in the country (multi-sites establishment) for further clonal trials and cultivars development; In other words, quantifying genetic gain that could be derived from multiplying *D. edulis* both sexually and vegetatively; Hence, F_2 hybrids will be evaluated and compared to the F_1 hybrids and to the mother trees (plus-trees) used for the crossing test in this study;

- Encourage the production of early seedlings with multiple branches (dwarfism). As with avocados, apples, castor and even coconut, creating smaller plants with multiple branches will make the African plum more productive and manageable;

- Urgent need to implement further studies on the diverse role of hormones, mainly auxin and cytokinin, on the control of shoot branching in the development of *D. edulis* improved planting materials;

- Increased planting with improved planting materials: *Dacryodes edulis* is a promising candidate for organized production on an organized scale. Programs to mass-produce selected plants and distribute the improved planting materials to farmers could be especially helpful. In this way, the health and welfare of the people especially children, the elderly, and the poor will be improved. Vegetative propagation from the established seed orchards (results from the present study) will lead to plantations of highly productive clones, which would transform this crop almost overnight. In fact, phenotypically superior candidate of African plum individuals will be coppiced, brought into clonal propagation via air-layering or stem-cuttings, followed by clonal testing of those clones that are easy to propagate;

- Increase market-chains in order to regenerate more revenues to farmers. Any increase in "demand pull" will see farmers and traders leaping in to produce and sell more safou;

- The ploidy of the cultivated populations is not well known. Further works should be initiated on this biological parameter.

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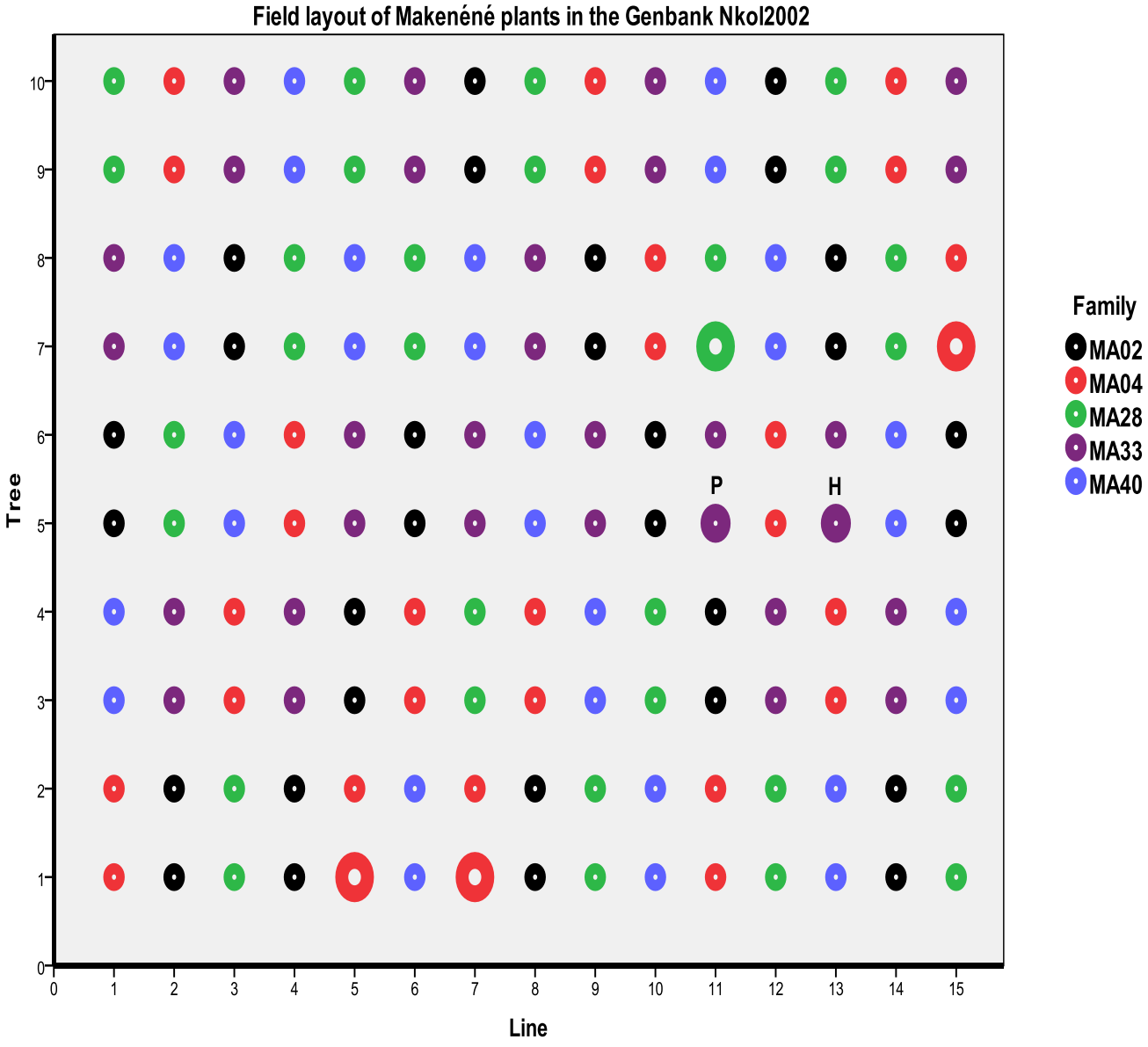
APPENDICES

Appendice 1: *Dacryodes edulis* mother trees or "plus-trees" positions' in the field layouts.

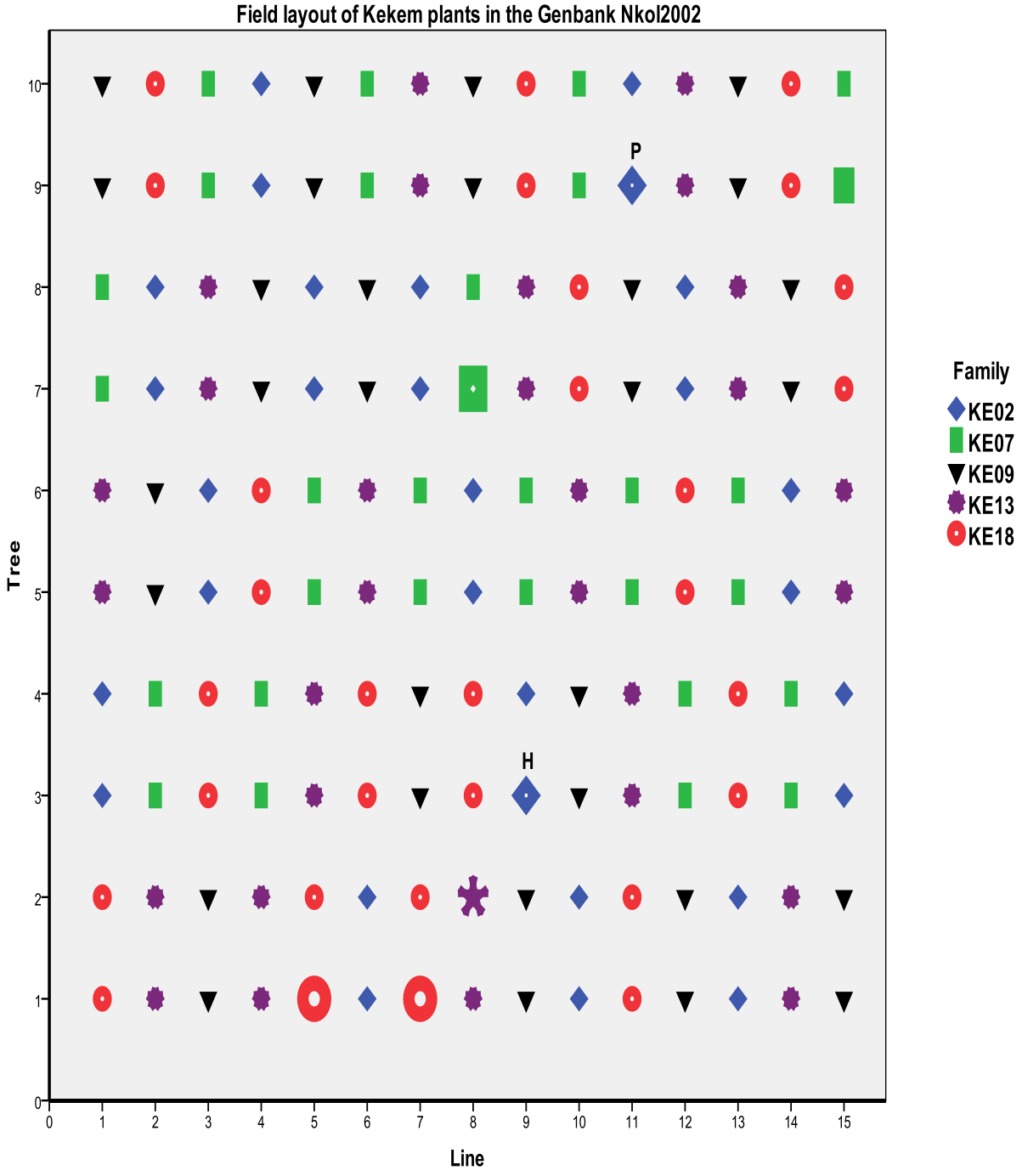
Makenene provenance



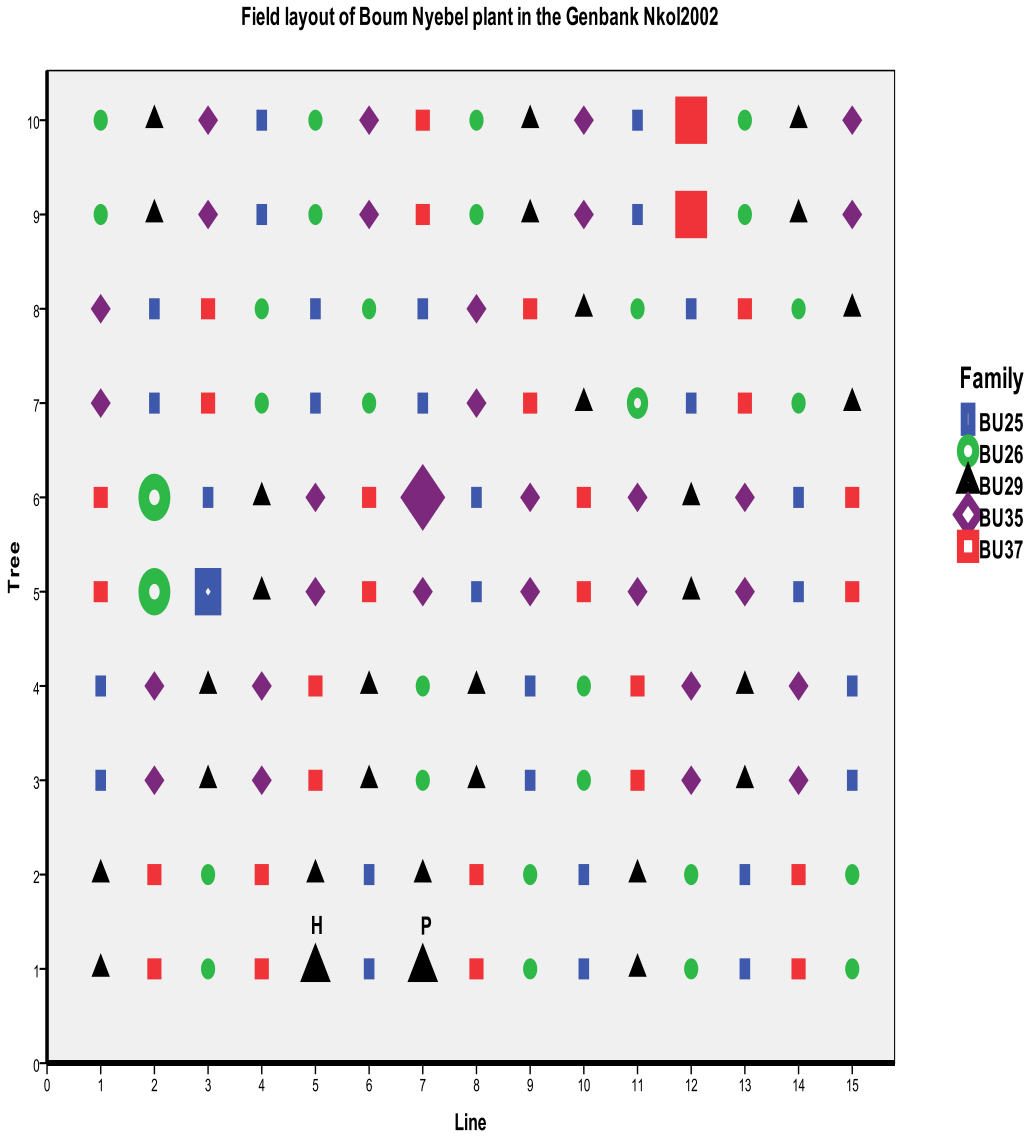
H: Male tree producing a great number of hermaphrodite flower (H)

P: Male tree producing a great number of male flower (P)

Kekem provenance



Boumnyebel provenance



Appendice 2: Pollination experiments

(i) *Dacryodes edulis* isolated floral panicles in a field trial at Minkoa-Meyos

(ii) *Dacryodes edulis* female flower real size (really small for hand pollination)

(iii) *Dacryodes edulis* male flower showing six etamins

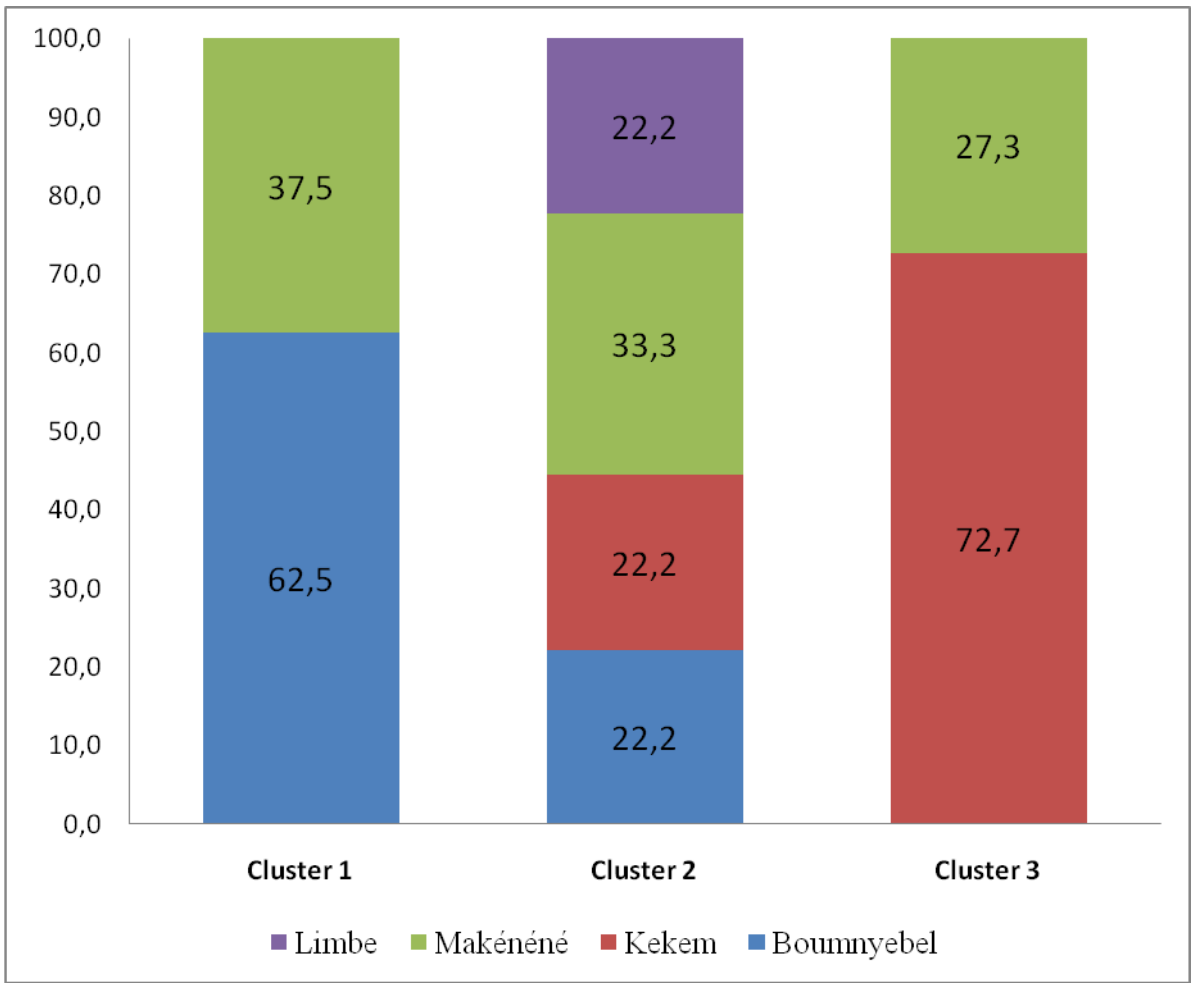
(iv) Field assistant ICRAF's technician staff carrying the ladder from on tree to another

Control-pollinated experiment 1: removing fine mesh bag for pollination

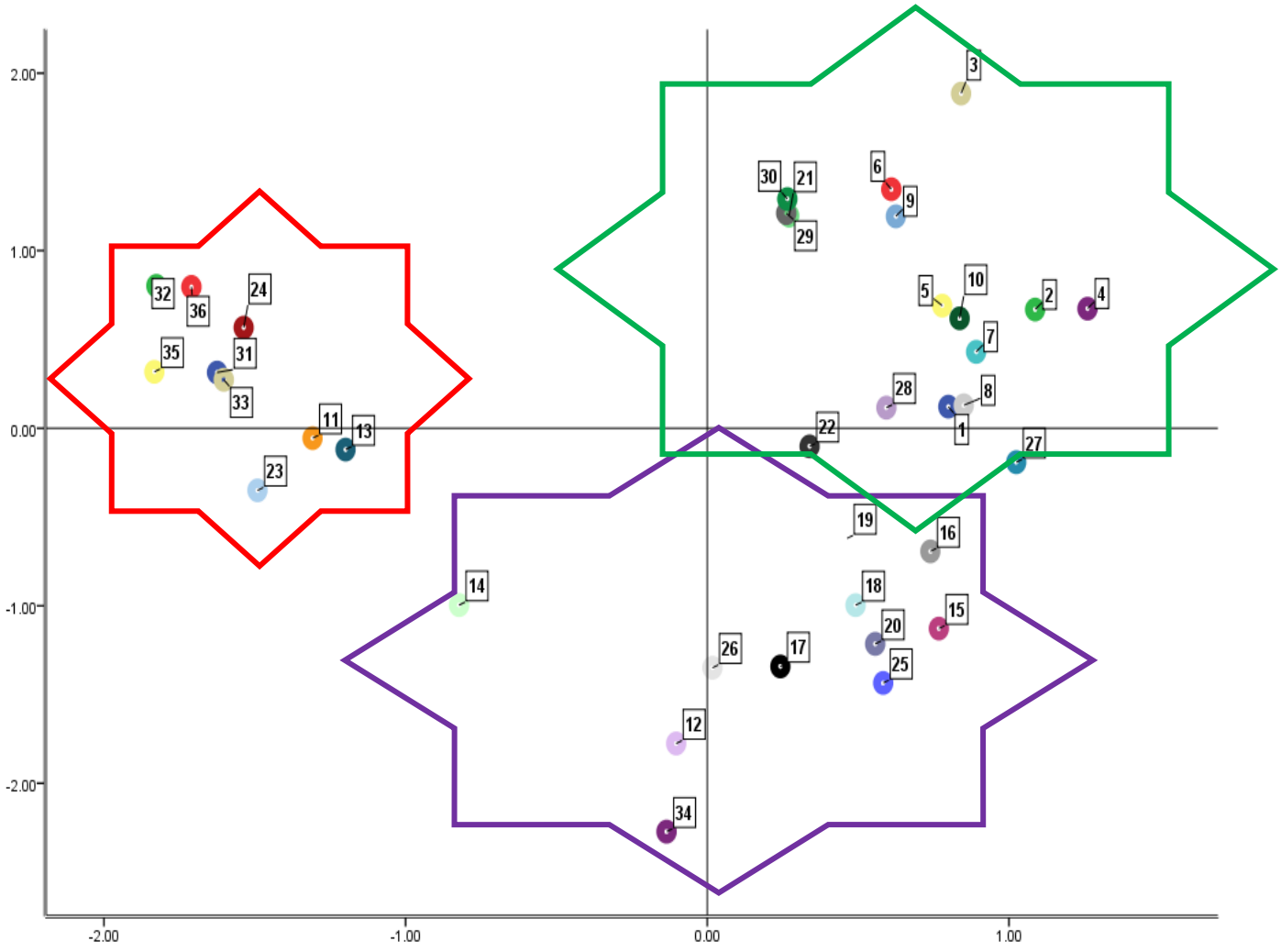
Control-pollinated experiment 2: controlled pollination properly

Control-pollinated experiment 3: rebagging of the female panicle after pollination

Appendice 3: Others usefull data from *Dacryodes edulis* controlled pollination



a. *Dacryodes edulis* provenances' distribution depending on clusters



b. Clusters discriminating *Dacryodes edulis* quantitative agro-morphological traits following controlled pollination

Appendice 4: Index of scientific names