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This research was conducted under the auspices of the Wageningen School of Social Sciences (WASS).

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Béla Teeken

PHD Thesis

submitted in fulfilment of the requirements for the degree of doctor at Wageningen University

by the authority of the Rector Magnificus

Prof. Dr A.P.J. Mol,

in the presence of the

Thesis Committee appointed by the Academic Board

to be defended in public

on Tuesday 1 September 2015

at 4 p.m. in the Aula.

Béla Teeken
African rice (*Oryza glaberrima*) cultivation in the Togo Hills:
ecological and socio-cultural cues in farmer seed selection and development
306 pages

PhD thesis, Wageningen University, Wageningen, NL (2015)
With references, with summaries in English and Dutch
ISBN: 978-94-6257-435-9

Abstract

Teeken B (2015). African rice (*Oryza glaberrima*) cultivation in the Togo Hills: ecological and socio-cultural cues in farmer seed selection and development. PhD thesis, Wageningen University, The Netherlands, 306 pp.

The low adoption rates of modern technologies in West Africa, such as improved rice varieties, suggest a gap between the motivations of farmers and development agencies. Many smallholder rice farmers in West Africa continue to rely on farmer varieties, farmer saved seeds and farmer seed system innovations. A better understanding of local farming practices and how they relate to farmer communities and their culture, as well as to the landscapes and climate within which the crop is grown might result in more successful initiatives to strengthen rice cultivation and improve food security and the livelihood of the many small scale rice growers in West Africa. As African rice has never been improved scientifically or commercially it is an important entry point to study farmers' variety selection and development. By studying farmer variety selection and development related to African rice within the Togo Hills in Ghana and Togo, a region that is ecologically as well as political-economically and culturally diverse, the research presented in this thesis tries to unravel the interactions between genetics, ecology and society (G × E × S).

Results show that in the Ghanaian Togo Hills cultural factors set additional and rice diversity enhancing criteria for selection, while in Togo selection criteria are mostly pragmatically agronomic and ecological factors dominate. This can be understood by the higher necessity in Ghana to construct identity and autonomy within the larger and more dynamic economic and political powers of competition and individualization. Here African rice has become a tool to shape such identity. Despite the ecological, cultural and political-economic differences within the Togo Hills, farmers in all the case studies selected a set of different varieties used for different purposes rather than a uniform type. This can be seen as a continuation of their earlier dynamic history in which the maintenance of diversity was part of a risk spreading strategy facilitating emergent innovations that suited such dynamics. Other examples from West Africa also show the different combinations of social and natural factors within the maintenance of rice diversity. Importantly farmers in West Africa have developed varieties that are robust and versatile: able to perform in very different ecologies and societal settings. African rice was found to be particularly robust.

This research therefore shows the importance of the "genealogies" between the genetic, the ecological and the social within variety development and food security issues. Therefore, it is the task of science to take an evolutionary perspective. These genealogies and their products should be made visible and need juxtaposition to formal scientific breeding strategies, strategies to tackle food security and agricultural and societal development issues in general. This indicates that there is a systemic alternative to a top-down Green Revolution in Africa. Trajectories of interaction between the social and the natural have produced a large variety of versatile resources and are crucial within tackling development issues in areas where such trajectories took place: there where farmer conditions are dynamic and suboptimal. Instead of anthropologically mapping local cultural preferences (these can change quickly over time and can vary over small distances) it is much more fruitful to emanate from and also disseminate the varieties farmers have already developed themselves.

Acknowledgements

This thesis is the result of a shared effort. A researcher not only looks for what he initially has planned to study but gradually explores what is relevant and feasible while going to the long trajectory of fieldwork and data gathering. He adjusts his questions to the reality that he encounters and builds on what he finds present. In the light of this thesis this implied an interdisciplinary research that asked for the cooperation of many people, from labourers, to farmers, to teachers, to scientists, drivers, car mechanics and many, many more. The least I can therefore do is to thank all the people that were involved in the research as I feel their voices and works all partly speak through me. The moment I heard that my thesis was approved for defence coincided with the arrival, after more than nine years travelling at around 50000 km/h, of the New Horizons probe at Pluto on its way to explore and discover new regions and knowledge of our solar system. I see this as a metaphor of the expansion of my view that this thesis has offered me. I hope it can also constitute a metaphor of many new innovative and interdisciplinary perspectives and research projects that are so much needed in this era.

Firstly I would like to thank my (co-)promotors Paul Struik, Paul Richards, Harro Maat and Edwin Nuijten for their confidence in me while writing the research proposal that let to this thesis. Throughout the trajectory we always had very inspiring conversations that were invaluable in the whole PhD process. I remember the relaxed, critical and often humorous lunch and coffee breaks with Paul Richards that were always mind opening. I also admired his firm determination. I remember the clear guidance by Harro Maat, who always kept in view clear argumentation and focus, something that has been very important to me. Invaluable are the many lengthy conversations I had with Edwin Nuijten who always was open to discuss everything from a philosophical to a very detailed and precise technical perspective. I highly admire your precision and dedication and your willingness to discuss, at length, all aspects at all times, while at the same always giving very practical advice, many thanks. Not enough can be said in favour of Professor Paul Struik who with his optimistic humane view and hardworking attitude has always made the time to help out with almost anything. He has enormously helped me to focus and to keep on going, many, many thanks Paul.

I also want to express my sincere gratitude to the Netherlands Organisation for Scientific Research (NWO) which financed this research.

As members of the same project on African rice I especially thank my colleague Florent Okry and Alfred Mokuwa. Florent, in Wageningen as well as at AfricaRice and at your home in Benin, we spent lots of hours together working on and discussing our research but also many more things. I greatly admire your flexibility and dedication. Thanks so much for your work and also for the warm welcome you gave us when I and my wife arrived in Cotonou. Alfred I also thank you for your work, perseverance and precision and important remarks and comments during the process. I very much enjoyed our stay in Sierra Leone together with Edwin Nuijten. I greatly enjoyed your humour.

My special thanks also goes to Inge Ruisch who has always been able to create the necessary relativizing, home coming, breathing space when focus and work got so serious that it was not serious anymore. As for other PhD students this has been very important to me as well. Thanks also for your humane and always flexible attitude.

Special gratitude goes to Marina Temudo for her inspiring and energetic support, enthusiasm and great work; it was great to publish an important paper with you.

Special thanks also go to Rob van Treuren as he offered important tools and knowledge for the genetic analysis of the rice samples. I also want to thank Cesar Ospina and Muhammed Khan for the time they took to share their knowledge on important software.

At the University of Ghana, I sincerely acknowledge Professor Kwame Offei for his advice and for facilitating my research. I also want to greatly acknowledge the CGIAR institute AfricaRice where I was given an office for several months in the last phase of my fieldwork period in Ghana and Togo. The last I greatly owe to Paul van Mele who I also thank for his valuable advice, and for the great moments we spent together at my wedding and also while sharing a passion for live music together with Gopi Warrier, Ramon Raman and Savatri Mohapatra. At AfricaRice I further thank Paul Kiepe and Marco Wopereis for their interest and time. Also many thanks go to Dr. Kofi Dartey at the Crop Research Institute Ghana and Dr. John Manful at that time at the Food Research Ghana for providing me with important data. At Leiden University special gratitude goes to Felix Ameka who provided me with valuable information on the Togo Hills and who introduced me to Mercy Bobuafor who took the time to teach me the elementary principles of the Ewe language; this has helped me so much in building up trust and facilitating communication during my fieldwork. Mercy, thank you so much. Special thanks also goes to Lynne Brydon for introducing me to the research area.

I continue with acknowledging three very important people who are largely responsible for the success of this research. Firstly I thank the farmer Joshua Amankwah from Akpafu Odomi who dedicated many hours to this research and who has been a great local mentor for me and has managed a very important field trial with total dedication. I thank you so much for offering me a home and the many, many meals prepared by your wife Stella belong the best I ever ate and were very important to my functioning. Similarly I thank the farmer James Asare from Lolobi Kumasi, I will never forget your hard working and perfectionist attitude. The many hours we spent together collecting samples, interviewing and managing field trials are engraved in my memory. The third person is the late Mr. Bosso Kokou from ICAT Togo with whom I managed to monitor as many as five different farmer experimentation sites on the Danyi Plateau. Unfortunately we cannot see each other anymore, but your passion will continue to inspire me. You and your family also offered me a home when I was in Togo which facilitated so many important contacts and hours of discussion.

Importantly, I want to thank all the famers and other people that took the time to respond to interviews and to cooperate in this research; those efforts are invaluable. Many, many thanks go to the people at ICAT and ITRA in Togo for their exceptional cooperation.

In Ghana I am also indebted to the late Nana Bedu II Agbenyo and his family who also offered me an important home, valuable information and help during interviews. In Togo I am indebted to Yawo Nyaku who carried out many important interviews and field measurements on the Danyi Plateau, often together with Daniel and the late Akakpo who unfortunately died way too young.

I also owe important debts to Ted Ahloye who offered me a home when I was in Lomé. I thank you so much for the many lengthy discussions we had about subjects ranging from history, economics to politics, food and music. I remember with great joy how you encouraged me to perform my music at the Centre Culturel Français (CCF) in Lomé as well as the CCF in Cotonou. These moments are very precious to me. I am also very much indebted to Theo Semekono who did so much in helping with formal arrangements in Lomé and who was always ready to help out any moment, you have become a good friend, thank you.

At our chair group I would like to thank Antonio Castellanos, Huan Yang, Debashish Sen, Rica Flor, Catherine Kilelu, Doreen Mnyulwa, Douglas Barraza-Ruiz, Simeon Maravanyika Paola Chaves Perez, Mirjam Schoonhoven, Horacio Narvaez Mena, Jaye de la Cruz, Marie Garnier Ortiz, Jacintha Vigelandzoon, Philip Idinoba, Sabarmatee Tiki, Kees Jansen, Dominic Glover, Conny Almekinders, Paul Hebinck and Cees Leeuwis and all the others I have forgotten, for their presentations, discussions and the good working atmosphere.

Special thanks go to Wil van der Hucht who spent so many hours to teach my wife the Dutch language; she has been of such a great help thank you so much.

I will end these acknowledgements by mentioning those who are closest to me and have been so important in making this all happen. I greatly thank my wife Georgette for her patience, sacrifices and constant support and love. I also thank my daughter Océane, who was born during the long trajectory of this thesis, for providing me with so much wisdom, energy and joy. My heartfelt and very special gratitude goes to my parents Toon and Elsa for their unmatched continuous support and love in all ways, thank you so much. I also have to greatly thank my wife's parents Gerson and Valentine Essiomle as well as Georgettes brothers and niece: Gustave, Bernard, Sena, Yao, Benjamin and Akofa for their love and care and for providing me with the best second home in Togo that I could wish.

I am sure I have forgotten to mention names that deserved to be mentioned in this acknowledgment section. Sorry, but I thank you all as much as the ones I mentioned.

Béla Teeken,

Wageningen, July 2015

To my parents and to Georgette and Océane

Content

CHAPTER ONE

General Introduction

Béla Teeken

1. Introduction

Rice cultivation is an important activity in several parts of coastal West Africa, and many small holder farmers rely on it for self-sufficiency as well as to generate income, since extensive regional and even international markets exist for the crop.

The low adoption rates of modern technology, such as improved rice varieties, within this region requires a better understanding of local farming practices and how they relate to farmer communities and their culture, as well as to the landscapes and climate within which the crop is grown.

Many smallholder rice farmers in West Africa continue to rely on farmer varieties, farmer saved seeds and farmer seed system innovations, despite many previous attempts to promote modern varieties. This suggests a gap between the motivations of farmers and development agencies.

To bridge this gap a better understanding of farmers' ecological - as well as social contexts and how variations in these contexts result into local practices of variety selection and development, is needed.

A better understanding of the ways in which farming is embedded in the local social as well as ecological matrix might result in more successful initiatives to strengthen rice cultivation and improve food security and the livelihood of the many small scale rice farmers in West Africa.

It is in keeping with such an agenda of concern that the present thesis seeks to shine a light on the varieties that farmers themselves have selected. At times it is not always clear which varieties have been selected and maintained by farmers, and which are long-forgotten introductions. Thus it is helpful to have a focus (though not an exclusive focus) on African rice (*Oryza glaberrima*), since this is a crop that has been neglected both by crop researchers and development agencies. It gives the closest approximation possible to a true picture of a crop subject only to local processes of selection and adoption.

African rice is an interesting crop not only because it is fully the product of farmers' selection - ruling out the possible and perhaps forgotten influence of the introduction of scientifically improved varieties - but it has also recently lost its former status as an "orphan"[1] crop. It has recently begun to attract more attention from formal plant breeding, especially as a source of genetic resources for the improvement of varieties of Asian rice.

African rice and two other West African "orphan" grain crops - fonio (*Digitaria exilis)* and a related species (*Digitaria iburua*) - have functioned, perhaps for several millennia, to ensure the food security of marginal montagnard peoples seeking to farm in suboptimal conditions while seeking refuge from slave raiders on the plains.

This association between food security and the physical security of marginal groups has provided African rice with an important sociocultural value (Brydon, 1981; Linares, 2002; Teeken *et al.*, 2012). African rice is known to produce well under sub-optimal conditions (Futakuchi *et al*., 2012) and because of the existence of varieties of very short duration it can function as an important hunger breaker, harvested before other crops ripen (Richards, 1986).

With regards to food security for marginal farmers today, the trajectories of selection and the related seed innovation related to African rice can be highly relevant because varieties of African rice might be well adapted to the highly dynamic circumstances that marginal farmers are once again facing in the region, not least as a result of climate change.

The cultivation of African rice is expected to be locally and culturally specific, and therefore the outcome of selection based on biological -as well as on socio-cultural criteria. Therefore this thesis combines perspectives from social sciences and plant sciences to study African rice within a case study area especially well-known for its cultivation and where cultural diversity of montagnard groups is also high, namely the Togo Hills. This area forms a significant portion of the border between the present states of Togo and Ghana.

African rice (*Oryza glaberrima*) has been viewed by science mainly as a source of useful genetic constructs for the improvement of Asian rice (Jones *et al*., 1997). Within West Africa African rice has largely been replaced by Asian rice but persists in pockets associated with marginal groups with a recent or longer-term history of refuge and/ or political oppression and armed conflicts (Richards, 2006; Brydon, 1981; Linares, 2002; Maroyi, 2012; van Andel 2010). The Togo hills is one such pocket.

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[1] The term orphan crops is used here for crops that have received little scientific and commercial attention and funding but often fulfill important roles in securing local and regional food security. They also often play a role in balancing otherwise unstable commercial production systems.

This area is home to several ethnic minorities speaking quite distinct languages but sharing a history of migration, refuge and creolisation. Situated in an area dominated by yam cultivation these ethnic minorities have traditionally subsisted on rice as their staple food (Brydon, 1981). Furthermore areas of the Togo Hills divided between the two countries have very distinct economic and political regimes.

All these differences within a relatively small geographical space and within relatively similar ecologies make the Togo Hills an ideal area to create a picture of distinct articulations of the interaction between genetic and environmental variation and social characteristics regarding farmer rice seed innovation. The study underlying this thesis therefore explored why farmers continue to value this under-studied crop and how they utilise and develop it, in two contrasted settings, across the Ghana-Togo border. These distinct articulations of African rice cultivation, this thesis argues, always balance cultural necessity (ritual practice) and pragmatic necessity (food security). Where at the Ghana side of the Togo Hills the balance moves clearly to the cultural side it is the reverse at the Togo side where mainly pragmatic agronomic factors are emphasised. The study uses an interdisciplinary, comparative approach combining plant genetic resources analysis with anthropological and farming systems analyses and crop physiological investigations to understand the role of socio-cultural factors within rice cultivation and variety development.

Although many researchers and breeders have become conscious that to improve smallholders agriculture attention to farmers' ecology is important (Ceccarelli & Grando, 2007), there is as yet less agreement on two further issues – namely, the extent to which farmers' technology is adapted to highly dynamic conditions, and the extent to which social rather than ecological factors alone influence farmers' innovations and preferences.

2. Culture and the organisation of society

2.1 Culture and technology: general theory

The ways people manage their human needs, cope with risks and insurance and thereby create culture, seem highly dependent on the strategising and defining of the self in relation to others. This notion can already be found in Durkheims' *Elementary forms of religious life*, in which it is explained that the totem is the moral countenance of the community and is always fed by contacts with others and therefore is based on difference (Durkheim, 1912). Marcel Mauss rightly argued nations are not the purified products of some essential or immemorial destiny; it is not tradition that makes the group but rather the group that makes tradition, an ‘invention’ spurred by contacts and admixtures (Mauss, 1953 as cited in Schlanger, 2006). Mauss thus extended Durkheim’s vision and stated that not only specific symbols but all practices and technologies within a community are religiously charged, and that therefore there is also a substantial connection and interaction between people’s notions of culture and the material landscape and technology that surrounds them. This focus on materiality within the social science that Mauss started to bring forward now resonates with approaches subsequently found in Science and Technology Studies (STS), e.g., Bijker & Law (1992), the hybridity of the social and natural within society (Callon & Law, 1995), and the compatibility of natural and social sciences within anthropology (Nettle, 2009) and archaeology (Fuller, 2013).

2.2 Minority groups and hill societies

The cultural diversity that characterises the Togo Hills seems typical for hill regions across the world. There is a range of literature that offers various explanations of how mountain ecologies have emerged as places where social interaction results in a particular cultural blend while at the same time showing a patchwork pattern of various seemingly distinct cultural, social and agricultural practices. Within West Africa, mountainous areas are often culturally highly diverse. The Jos Plateau in Nigeria, with its multiplicity of languages, is an obvious example. Often these areas have provided a home to marginal groups fleeing or resisting more dominant groups, forced religious conversion and slave raiding. Therefore, these groups often are mixtures of different streams of people converging on a single refuge point. The outspoken and firm cultural traditions of these groups including specific and uniform tropes of origin are often the products of intensive ritual activity intended to shape a single local identity to overlay highly heterogeneous origins. Specific customs, in their relentless reiteration, result from the necessity to generate cooperation and a sense of community identity among people originating in various places and sharing little common background.

An example of a well-known ethnic group of this sort is the Dogon people of Mali, now generally believed to be an amalgam of different peoples (van Beek, 2001) settling in a defensive position along the Bandiagara escarpment and united by their resistance to Islam. This common purpose created a firm integral system of Dogon rituals and beliefs.

Richard Fardon (1988) in his study of the mountainous area bordering Nigeria and Cameroon similarly shows the heterogeneous origins of the local people, who call themselves Chamba, apparent in that different branches of the Chamba speak entirely different languages. He shows that the origins of the Chamba are very diverse and most have a refugee history. The notable density of ritual activity among these groups is an expression of the need to make society anew.

The Kofyar people on the Jos plateau in Nigeria are another example of marginal farmers resisting incorporation into larger political units. The Kofyar intensified their production through terracing in the mountains (Netting, 1968). They basically comprise three tribes, seemingly again pointing to plural origins. Here, instead of having strong communal rituals, the intensification of agriculture through terracing itself seemed to have provided enough identity and cooperative linkage, and the Kofyar managed to anticipate and to connect well to the market economy introduced in colonial times. Importantly Glenn Stone (1996) shows that the settlement patterns ever since they started moving down into the Namu Plains in the 1950s cannot be understood only by looking at optimising access to natural resources or economic opportunities.

He exemplifies this by comparing the frontiers of the Kofyar and the Tiv, who also moved into the Namu Plains and shared similar resources and crops: the Tiv followed a strategy led by a culture of extensive agriculture: constantly looking for new ground on sandy savanna soils while the Kofyar only abandoned lands that could not be intensified but rarely abandoned savannas in the sandy zone as they responded well to intensification. So not only was the strategy of the Tiv and Kofyar linked to their pragmatic execution of agriculture but most importantly to the socio-cultural organisation that evolved during earlier adaptation to socio-ecological circumstances resulting in intensification for the Kofyar and extensification for the Tiv. In effect, the two groups had different models of agricultural expansion, and each group stuck to the model with which it was familiar, resulting in diversified agriculture, even while converging geographically in the same environment.

Plateaus and hill areas, however, are not always the residence of people who resist or flee from the dominance by larger ‘state’ societies. The Futa Jalon highland region in Guinea is known for the dominant Fula group who spearheaded the expansion of Islam as from around 1725 in Guinea and ruled over a great diversity of people. In this particular case the Fula conquered and displaced earlier groups such as the Jalonka and Susu, and perhaps even the Temne, who moved from the mountains into the coastal plain.

There are also regions where the model of cultural diversity and refuge from larger political powers does not apply. Lieberman (2010; cited in Brookfield, 2011) has criticised James Scott’s (2009) generalisation about hill refugia in mainland Sout East Asia by showing that in Borneo and New Guinea, just like in “Zomia” (Scott's term for the montagnard refugia of South East Asia), similar cultural diversification, and purely local levels of socio-political organisation, combined with shifting cultivation and isolated wet rice cultivation, as well as intensive dry farming systems, also existed, but with no evidence of larger organised states impinging upon these regions (as Scott's model requires) before the 20th century.

The frontier thesis

Taking notice of the above it seems that the identity and community of hill people has often been constructed on the basis of the resistance that they encountered. This brings to mind the reformulation of the famous frontier thesis of Fredrick Jackson Turner (1921) by Igor Kopytoff, in an influential book on the African frontier (Kopytoff, 1987). Kopytoff posits that the frontier is a process of constructing a new society by a subgroup of people separating themselves from a larger political entity. Separation or “ejection” is triggered by something beyond their control such as famine, exclusion or war. Instead of forgetting their origins a sense of origin is amplified and reinvented, taking on mythical forms articulated by rituals and practices. Instead of a geographical frontier Kopytoff’s frontier is therefore much more a social space constructed by frontiersmen to distinguish themselves and construct and define a community within the web of economic and socio-political as well as ecological forces. Inventions of traditions are very important in shaping new identities within dynamically changing circumstances and also within the formation of the modern nation state (Hobsbawm, 1983).

Because of the shelter mountainous regions offer, they have over time been populated by many different people who often are, in Kopytoff’s terms, ‘ejected’ from ‘metropoles’, and who then find that the hills offer the opportunity to stay out of reach and remain as independent as possible. Paul Nugent (1997) has argued that this applies in the Togo Hills, where local minorities have absorbed so many immigrants. In the Togo Hills a variant of the Kopytoff (1987) model applies, whereby: “a community made up of many parts would commonly be structured according to ideological notions of precedence, with rulers claiming superior right by virtue of being the first comers, or finding reason for subverting the principle. Subordinate lineages, however, might often harbour their own underground traditions” (Nugent, 1997, p. 5).

This is in fact somewhat similar to James Scott's (2009) arguments concerning the mountainous regions in South-East Asia. Scott argues that the diversification as well as complex social organisation based on different lineages and myths of origin are mostly strategies to stay out of reach of the political influence of the rules and laws set by the ruling majorities on the plains. Ethnic minorities are vulnerable to much larger neighbouring societies organised on bureaucratic principles, and prove therefore to be extremely dynamic, falling apart into lineages at the moment circumstances so demand, in order to stay out of reach of policies, taxation and rules set by the dominating power on the plains. This provides mountain people with a specific dynamic and identity: flexible, segmentary, mobile and socially innovative.

Richard Fardon (1988) offers similar views when he analyses the cultural and ethnic mosaic around the upper Benue River around the international border between Cameroon and Nigeria, categorising the diverse ethnic groups as 'refugees' and the larger political powers on the plains as 'raiders'. In sum, high density of ceremonial activity is a characteristic of a certain kind of hill society, where social relations are regularly made and remade as political, and perhaps environmental, circumstances dictate. Togo Hills society has these characteristics, and this helps explain why rice has a ritual salience not found in other parts of the West African coastal rice belt.

2.3 Culture and food crops

We inherit from Durkheim the view that it are sacred symbols - the totems - that provide groups of people with identity and that these sacred symbols are recurrently revived and re-potentiated within repeated rituals. What was never made clear by Durkheim is how ritual density relates the world of technical practices. Work and technology were initially dealt with in a footnote in Durkheim's *Elementary forms of religious life*, (1912) but it was this footnote that Marcel Mauss turned into his principle object of study. Rather than only the sacred symbols, Mauss acknowledged the importance of the performance of daily work - technology, in a word - as equally value-creating, providing the task group with identity and value. Mary Douglas built on Mauss' perspectives when she preferred to relate religious belief to the experience of action within an institution rather than to sacred symbols or ideals alone. The body can be seen as the most fundamental and first technology, and is the basis of all action, and therefore plays an essential role in the articulation of the religious, or perhaps better, as the mechanism for creating shared values and affections:

> "Most symbolic behaviour must work through the human body.... The human body is common to us all. Only our social condition varies. The symbols based on the human body are based to express different social experiences." (Douglas, 1973, p. 110).

Eating is such a bodily and social experience and therefore food and the cultivation of food crops often constitute sites for ritual elaboration that provide identity and historical consciousness, especially there where shared sacred symbols are very much needed in the construction of a group identity such as in hill societies amalgamated from different people constantly having to stress and build up their togetherness. Cultivating a food crop is a mundane "technology" in Mauss' sense significantly influencing group identity because of the communal work tasks it entails. It might or might not also become a sacred symbol in the sense of Durkheim. It is also in this light that we have to approach the (African) rice cultivation in the Togo Hills. If we want to understand how rice operates we also need to study what makes rice suitable to fulfil such functions, i.e., what are the biological mechanisms that make the crop fit the community of its cultivators and importantly how do the communities get hold of such a suitable crop. This asks for a conceptual framework that not only integrates the interactions between genotypes and environment but also the interactions between genotypes and society as well as environment and society.

3. Conceptual framework: Genotype, Environment and Society and their interactions (G × E × S)

The present research emanates from the idea that not only Genotypes of varieties and Ecologies and their interactions are conducive within farmer innovations and selections (Ceccarelli *et al.*, 1994), but also that important interactions between Society and Genotype, and Society and Ecology, are involved, as well as the emergent outcomes that result from the interaction of all these three domains (Nuijten *et al*., 2013).

To unravel why farmers have appreciated African rice and to see in what way their other varieties of rice relate to African rice, genetic, physiological and agronomic data are required to be integrated with socio-cultural data. This will illustrate how Genetics, Environment and Society mutually shape each other (Figure 1).

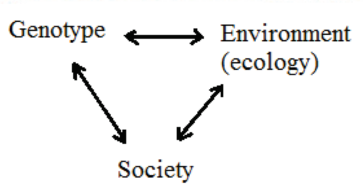

Figure 1*: The production of phenotypes of rice as occurring in farmers' fields*

Within the interactions between the three components the concept of what Richards calls 'performance' is important (Richards, 1993; Janssen & Vellema, 2011). This entails serendipitous discoveries and processes that are the outcome of practices – defined here as socially-situated action- with which people respond to unpredictable, contingent constellations of societal factors (including the contingencies of cultural, social and economic life) as well as ecological/climatic and genetic factors:

> "It seems more appropriate to conceptualise these practices as 'sequential adjustments' to unpredictable conditions rather than as a combinatorial logic. Rather than thinking about [e.g.] intercropping as a plan, Richards argues that it is better viewed as performance, thus inviting research that studies the performance skills and performance knowledge that underlie farmers' capacity to adjust to unpredictable and shifting conditions. Methods consequently emphasise observation and doing (participation) rather than relying on interviewing. It is the process of making and doing itself that is the starting point for research, rather than the intentions before the act or the rationalisations thereafter" (Janssen & Vellema, 2011, p. 171)

So rather than following a disciplinary perspective, the object of study, i.e. the cultivation of African rice, is here contextualised to do justice to the "performance" aspect. While contextualising rice as seed and food, social as well as natural science tools appeared to be relevant. Through such a contextualisation hitherto hidden but important, causalities and mechanisms become visible. The approach avoids treating social facts with natural science tools or natural facts with social science tools (reductionism). Richards calls this approach "technography", meaning by this neologism an ethnography that also operationalises and investigates the mutual interactions between human and material aspects of collective life. The first task of technography, he suggests is technographic "mapping", which attempts to establish the place of the item of study (here African rice) within the broader socio-technical framework. It does so by itemising and describing elements making up a domain (including labour, land, tools, crops, seed system processes, markets, politics, rituals, etc.). Technographic analysis then tries to uncover mechanisms through which activities, artefacts, and outputs are related.

Farmer practices can be various and attached to various entities and constellations of human and non-human entities, and this is a reason why the sequential adjustments and the concept of "performance" are so important, rather than simply taking a cultural materialist perspective (e.g., Harris, 1979). Therefore culture has to be understood by empirical investigation of the local practices and technologies, using tools of natural as well as social science. Practices that evoke effervescence and create value often make "poetic" connections between elements through which entities and contexts are formulated and charged with value and vitality.

4. The case study area: the Togo Hills

The Togo Hills are those parts of the mountain ranges that run from south eastern Ghana and south central Togo into northern Benin. In Ghana they are also known as the Togo Ranges that geographically can be seen as a continuation of the Akwapim ridge that starts north-east of Accra. In Benin the continuation of the range is known as the Atakora Mountains. In Ghana and Togo, the Togo Hills are home to several minority groups speaking languages characterised by the pioneer German linguist Westerman as "Togo Restsprachen" (Westerman, 1953). If they are thus a remainder then any notion of any inherent connections between them should perhaps be queried.

Although the groups and their languages and cultures might be traced back to migrating groups that finally settled in the area before the now dominant Ewe-speaking group arrived, it is much more probable that these groups have been largely the result of a process of creolisation (here defined as mixing of cultures) as the area has through time offered shelter to many different groups of "refugees" (Nugent 1997) and, therefore, these minorities are most probably an amalgam of several groups and genetic lineages of people coming to the area. The languages of the ethnic minority groups are now most often referred to, descriptively, as Ghana Togo Mountain (GTM) languages (Ring, 1995; cited in Ameka, 2007), a term that deliberately implies nothing about assumed processes of formation or inter-connection.

Many of these ethno-linguistic minorities state that African rice has been an important food crop within the context of displacement and insurgencies and the dependence on less fertile land and the numerous slopes and plateau areas in the area. Within the Togo Hills, two major adjacent plateaus exist: the Danyi and the Akposso Plateau. Both are situated on the Togo side of the international boundary. These plateaus are situated at a height of around 800 to 900 meters above sea-level, respectively. The Danyi Plateau is now peopled by Ewe people, who are more generally the main ethnic group in the areas around the Togo Hills, and the Akposso Plateau is populated mainly by Akposso people. Figure 2 shows a map of the Togo Hills and indicates the areas of the different minorities speaking the GTM languages as well as the location of the Danyi and Akposso Plateaus.

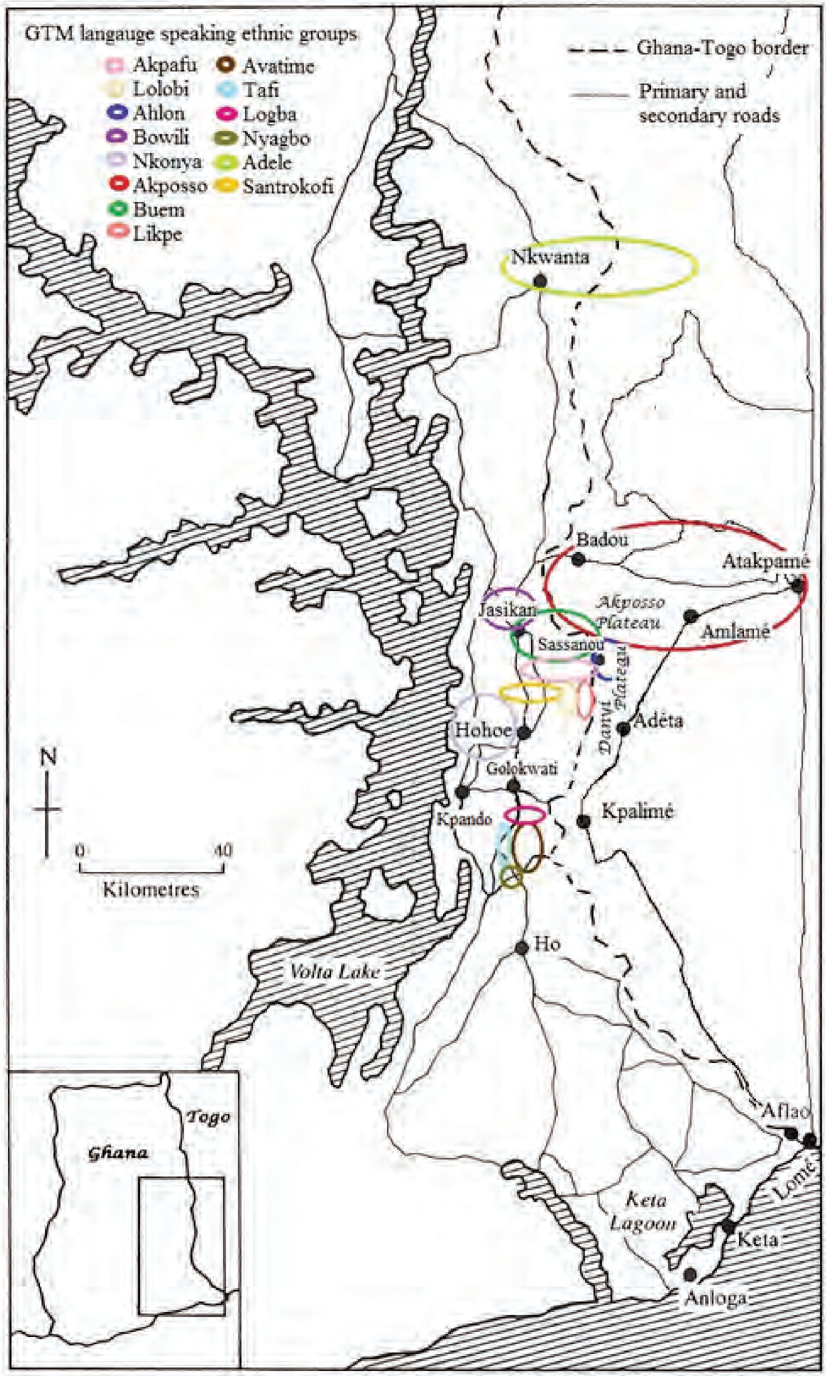

Figure 2 *:Map of the study area indicating the location of the Togo Mountain Languages speaking ethnic minority groups as well as the Danyi and Akposso plateaus.*

Importantly, the Akposso on the Akposso plateau traditionally cultivate fonio, and fonio is to them like African rice is to many of the other minority groups. Several interviews with the Ahlon minority group in Togo, now living halfway down the descent from the Danyi Plateau towards Ghana, indicate that they used to live on the Danyi plateau but were driven to the edges and down into the escarpments towards today's Ghana by the Ewe. The Ahlon stated that the Ewe even used their local African rice that they had been cultivating as bullets in the war against them.

The Ewe now living on the Danyi Plateau can also be considered a group with a refuge history. They state that they came to the area in the 15th century fleeing the cruel reign of the Dahomey king Agorkoli, who had constructed a large walled enclosure to imprison many people (Cornevin, 1969). The remnants of that wall can still be found around Notse in Togo (Quarcoopome, 1993) and the story of the cruel reign of Agorkoli is taught in all Togo's schools today as a myth of national origin. As the Togo Hills area constituted a natural as well as a political barrier between two traditional empires, the Asante and the Dahomey empire, the region traditionally might have been an area where refugees from oppressed groups found shelter and an opportunity to live their lives independently. When the Europeans started to trade along the West African coast it might then have become a region to seek shelter from slave raiding from the Dahomey side as well as the Asante side. Therefore the identity of the minority groups in this region can be seen as a constant manoeuvring and weighing of dangers and opportunities and connections to several interregional networks that have been linked up to the Trans-Sahara trade as well as to the Transatlantic trade (Brydon, 2008).

The continuing existence of the many minority groups, who even today predominantly use their own languages, can be seen as a frontier in the making, with each group carving, in relation to one another in a Kopytoffian way, their niche in a complex regional web of powers and influences and economic relations such as trade networks. Plehn (1889) predicted that GTM languages would soon die out because of the dominance of the surrounding Ewe and Twi languages. Thus it is significant that over a hundred years later the GTM languages are still actively spoken. Also the old idea, reflected in the name "Togo Restsprachen", that these languages in some way remnants of older languages, is no longer supported linguistically, hence the name change to GTM languages. In effect, the process of language fragmentation speaks to a still current process of group autonomy-making, for clear regional, political reasons (and active desire not to be subsumed by larger identities). This is well reflected in the debate among linguists about how best to classify the GTM languages. Because of the diversity among them it is hard to group them together in any satisfactory taxonomic tree, as well as hard to relate them to other wider language groups, and therefore a new bottom up approach of classification has been proposed (Blench, 2006 and Roger Blench, 2013 personal communication; Esther Kropp-Dakubu, 2013, personal communication; Bernd Heine, 2013 personal communication; Felix Ameka, 2013, personal communication). It seems that the active construction of highly localised political identities might also be applicable to the construction of these languages, which should be seen as emergent rather than the “relics” of long term isolation and preservation.

From the 19th century on, the mountainous region came to constitute another kind of barrier: that between the English colonial power and the German (and later French) colonial powers. According to Nugent (2002), this gave another impulse to create and reinforce the identity of minorities in the region and, instead of only a rupture and disturbance, the installation of the border between British and German Togoland - that later turned into the international border between Ghana and Togo - was something that people used to construct identities and formulate groups - a border that creates opportunities and reinforces identities, group formation and thus units of cooperation. Paul Nugent (1997) therefore hypothesises that the ethnic minorities, and their languages, are to a large extent a result of these dynamic processes, including border imposition, and thus it seems more appropriate to think in terms of the creolisation of different groups and lineages searching for shelter and refuge in the mountainous area at different moments in time. Brydon also stresses that the origin of one of these groups, the Avatime people, is plural: “Both oral histories and genealogies indicate that the present Avatime population comprises the descendants not only of the ‘proto-Avatime’ group and the Baya, but also of other individuals and groups who arrived in the area and were incorporated into Avatime well before the middle of the 19th century” (Brydon, 2008, p. 26). This is further clear evidence of the dynamics of group formation and ethnicity in the region. Kropp-Dakubu (2006) likewise stresses the plural origins of the GTM speaking communities. It is as if each mixed local group decides to invent its own new local tongue, to keep its secrets intact, and differentiate itself from neighbouring mixed but rival groups.

In his paper on iron melting in the Togo Hills among the Akpafu and Lolobi and Santrokofi ethnic groups Pole (2010) has shown that, given the vast investment and activity levels that can be deduced from archaeological findings in the area, it is most probable that iron smelting was going on for many generations, when the Europeans arrived and displaced the products of this proto-industrial region with cheaper iron and tools from Birmingham and the Ruhr. This, however, does not correspond with the migration history preceding the settlement of groups within the Togo Hills claiming traditionally to be blacksmiths – namely, the Akpafu/Lolobi and the Santrokofi. But each of these groups might have joined blacksmiths already settled in the Togo Hills. It might also point to an 'invented' tradition flowing from the political and economic manoeuvring just mentioned.

During interviews about the origin of the Akpafu, Lolobi, Likpe and Buem in Ghana and the Ahlon and Akposso in Togo, farmers stated mythic origins in ancient Nubia, via today's eastern Ghana, or Nigeria, and that they followed various routes to their current location (see also Ogbete, 1998). Simultaneously, farmers also indicated that their history is complex. In all likelihood the Nubia story is an invented tradition connected to a general and more recent trend in many West African communities to connect themselves to the lost tribes of Israel, perhaps reflecting missionary influence. That there were ancient connections between West Africa and Nubia, and even India and the Arabian peninsula, seems to be attested by the spread of western African crops such as sorghum and cowpea to eastern Africa and south Asia at an early date, but beyond this indication hard archaeological evidence for the nature of these contacts has yet to be uncovered.

This situation resembles what Richard Fardon found among the Chamba. The different histories of clans that are sketched are mythical and avoid any specific history. Also Matriclans might be divided or unified according to the situation: "Despite their avowals that matriclans have "one mother", in other contexts and in confidence, Chamba will say that in fact the different sections have "different mothers" (Fardon, 1988, p. 174). In all these situations no dogma exists, and categories such as corporate groups and witches (i.e. anti-social persons) are made in relation to arising issues.

5. Research methodology

5.1 Broader context of the research

This research is part of a larger project on the biology and anthropology of African rice (*Oryza glaberrrima*) in West Africa. One of its main objectives is to understand how and why the cultivation of African rice survives within West Africa in certain regions and to investigate how this influences variety development. The focus on interactions between genetic variation, environmental and social characteristics (G × E × S in short) is central in all the projects (Nuijten *et al*., 2013). In the study on seed flow in Guinée, the interaction expresses a parallel development of informal seed networks and formal seed dissemination by NARS and NGOs (Okry, 2011). A study on the influence of the recent war on the portfolios of varieties of farmers in Sierra Leone shows how, despite the material devastation and social disruption of war, seed portfolios of rice farmers remained relatively stable (Mokuwa, 2015).

5.2 Choice of research sites

Research was carried out mainly among the following GTM speaking minorities: the Akpafu and Lolobi in Ghana and the Ahlon in Togo. Furthermore research was carried out among the Ewe on the Danyi Plateau. Case studies were chosen because of the prominent role of rice cultivation in these areas together with the cultivation of African rice in particular. In Ghana, the Lolobi are known and mentioned by other ethnic groups for their prominent role in developing and innovating rice cultivation and most often varieties developed or selected by them diffuse to other GTM speaking minorities such as the adjacent Akpafu with whom the Lolobi share a common language. The Danyi plateau situated at about 800 m above sea level was particularly included in the research because almost all the rice cultivated on this plateau is African rice. The Ahlon were included because the prominent place rice has within their culture and history and because they are situated at around 400 m altitude in between the plateau ecology of the Danyi Plateau and the lower Togo mountain escarpments of the Ghanaian Togo Hills that are situated at an average height of about 250 m above sea level, therefore representing a transition between two major ecologies: the Ghanaian Togo Hills and the Danyi Plateau.

6. Research questions, objectives, hypotheses and chapter overview

Main research question:

> Why do farmers in the Togo Hills continue to grow African rice and what is its role within the dynamics and innovation of the farming system and to what extent do socio-cultural together with genetic and ecological factors determine this role?

Subquestions:

1. Do African rice and other farmer varieties of rice in West Africa possess specific agronomic and/or physiological mechanisms that facilitate cultivation under dynamic

suboptimal conditions and if so are these mechanisms partly the outcome of farmer selection steered by social factors?

2. Does genetic analysis of farmer varieties in West Africa reveal patterns of selections according to morphology or molecular similarity in relation to specific ecological and or social factors in the Togo Hills?
3. Does the cultural diversity in the Togo Hills result into rice variety preferences that are also different from region to region?

Research objectives:

- To study the crop physiology of African rice in relation to other farmer varieties of Asian rice.
- To genetically analyse West African farmer varieties to know how varieties from different regions relate to the different ecologies as well as farming societies living in these regions as well as to how botanical groups of rice relate to ecologies and farming societies.
- To evaluate the process of farmer selection of farmer varieties within the different regions in the Togo Hills.
- To compare the role African rice has within the Togo Moutain areas to the role in other pockets in West Africa where African rice is still cultivated.

Hypotheses:

- African rice possesses specific physiological mechanisms that explain why African rice performs well under various suboptimal farmer conditions.
- Genetically farmer varieties differ from region to region and can show specific adaptation to local communities as well as local ecology.
- Cultural factors determine variety choice and variety selection processes and therefore variety innovation and adoption as well as the genetic makeup of varieties.
- Local adaptation is not necessarily adaptation to a specific fixed local culture or ecology but can also entail adaptation to a local dynamic that is turbulent and changing in nature.

Chapter overview

Chapter 2 provides the reader with the agronomic as well as historical and socio-cultural context of rice cultivation for the different case study areas within the Togo Hills and shows its social as well as ecological diversity. It deals with the present cropping systems and rice variety portfolios. Importantly it shows that farmers mainly use farmer varieties and it illustrates the different entanglements of African rice with socio-cultural and ecological factors and puts them in a historical perspective.

Chapter 3 continues with an evaluation with farmers of a set of 14 different farmer varieties from 7 West African countries. The role of socio-cultural factors within the organisation of rice cultivation, farmer selection and variety development of the Togo Hills is studied. The same set of varieties was evaluated within all the three case study areas. Reflecting the different political economic regimes of the two countries, Ghanaian farmers set up individual trials while in Togo farmers formed groups. Despite this differences the social effects should not be considered necessarily different. The chapter shows that farmers select a set of different varieties rather than one or two ideotypes. Rather than limiting and narrowing rice diversity, cultural factors seem to contribute to the diversity as they determine variety development pathways. Apart from these pathways farmers are pragmatic and also select varieties that might open up other pathways and opportunities. Importantly, the different political, economic backgrounds of the Ghanaian and Togolese Togo Hills result in the different articulation of the cultivation of African rice. In the Ghanaian Togo Hills, African rice has become explicitly part of a cult that provides identity and union and determines development pathways within the cultivation of Asian rice. In the Togolese Togo Hills, rice cultivation is maintained as a communal tradition just like the cultivation of other crops.

Chapter 4 presents the genetic diversity, using molecular AFLP markers, among the collected farmer varieties in seven countries of West Africa. An important finding of this chapter is that farmers appear to have developed a new rice type that also shows high diversity: a group of varieties that are the result of interspecific hybridisation between Asian and African rice. This chapter partly answers the question what West African farmers have genetically achieved after long trajectories of variety selection and innovation.

Chapter 5 compares robustness, a physiological term to indicate a plant’s capacity to deal with stress factors, of farmer varieties of African rice and Asian rice from five countries in West Africa. It shows that a large group of the collected farmer varieties are robust: they are able to perform well within different ecologies, contrary to the received wisdom that farmer varieties are only adapted to a specific locality. Varieties of African rice and several other farmer varieties appear to be robust: they are able to perform well within different ecological and climatic regions under low input conditions - and this robustness is the result of adaptation to dynamic conditions and farmer selection. This chapter provides important insight in the biological reasons why certain groups of farmers continue to grow African rice and farmer varieties related to African rice, and studies if African rice and farmer varieties in general possess specific physiological mechanisms that favour cultivation under dynamic and suboptimal conditions.

Chapter 6 present results from a combined morphological and molecular analysis, showing the large genetic diversity of *O. glaberrima*, *O. sativa* (*japonica* as well as *indica*) and a group of natural farmer hybrids that farmers maintain. The chapter gives further insight in what farmers have genetically achieved looking at genetic characteristics visible to farmers: the plant morphology. It studies whether morphological and molecular analysis reveal patterns of selection according to morphological similarity in relation to ecology and/or socio-cultural factors and shows that farmers in each area maintain a wide variety of varieties and do not spot a uniform ideal type or validate a certain morphological trait. It also shows that recent human selection pressures limit the diversity within African rice while this is not the case for the other rice species. African rice however is still important in determining diversity enhancing development pathways within the other rice species.

Chapter 7 shows how in different regions in West Africa, the interplay between ecological, economic and socio-cultural factors determine the continuation or abandonment of African rice and illustrates that in each region these type of factors are all determinative in different proportions. Together with ecological factors socio-cultural and economic factors set selection criteria within the adoption abandonment and development of rice varieties and farmer agency has a prominent role herein.

Chapter 8 gives a discussion of results and draws the overall conclusions of this thesis. The different chapters provide insight in how social factors and natural factors articulate the cultivation of African rice and shows important emergent innovations that result from such articulation. In the Ghanaian Togo Hills cultural factors set extra criteria for selection while in Togo these are mostly pragmatically agronomic. This can be understood by the higher necessity in Ghana to construct identity and autonomy within the larger and more dynamic economic and political powers of competition and individualisation. African rice has become a tool to shape such identity. Other examples from West Africa show again different combinations of social and natural factors.

This thesis therefore asks for full attention for the “genealogies” between the biological, the ecological and the social within variety development and food security issues. Therefore, it is the task of science to take an evolutionary perspective. These genealogies and their products should be made visible and need juxtaposition to formal scientific breeding strategies and strategies to tackle food security, and agricultural and societal development issues in general. Trajectories of interaction between the social and the natural have produced a large variety of resources and are crucial within tackling development issues in such areas where such trajectories took place: there where farmer conditions are dynamic and suboptimal.

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CHAPTER TWO

Rice cultivation in the Togo Hills; diverse and dynamic pathways of adaptation to ecological and societal factors.

Béla Teeken

Abstract

Based on several case studies this chapter provides a characterisation of the present rice cultivation within the cropping systems in the Togo Hills and describes its historical and socio-cultural context. Results show that farmers mainly use farmer varieties and illustrate the different entanglements of African rice to socio-cultural and ecological factors and puts the them in a historical perspective. The different ethnic groups in the Togo Hills all seem to have had a certain earlier history of migration, refugees and conflict or war in their strategy to retain autonomy in relation to larger political powers such as the Ashanti - and Dahomey Empire and later on the various colonial powers: first the Germans, then the British and the French, and then the more liberal state model of Ghana and the more state-led model in Togo. This dynamic history seems important in understanding the cultural diversity in the area and in understanding the trajectories of farmer variety selection and development.

Introduction

Western African farming communities have adapted their agricultural practices and socio-cultural organisation to the ecological diversity of the region over many centuries. Rice is a major food crop in this region and farmers have continuously tried out different rice varieties. Local preferences for certain varieties and methods of seed selection are shaped by the ecology available to farming communities as well as their socio-economic and political situation (Richards, 1986). Some major factors are an overall scarcity of labour force due to historical low population densities and absence of a animal traction (due to disease constraints) and an associated plow-based cultivation system, creating a situation in which rice has to endure in uneven fields and requires to be resistant to a number of stress factors associated, in particular, with high weed competition (Goody, 1976). The Togo Hills constitute a mountainous ecology that has historically served as a refuge for groups escaping from ethnic rivalry and slave raiding (Brydon 2008; Nugent, 1997 and 2002). African rice (*Oryza glaberrima*) has played an important role in serving specific agro-ecological and cultural demands in this region. To get a better understanding of how farmers cultivate rice, and how they perceive what counts as quality in rice, both as a crop to cultivate and as a food item, two areas in the Ghanaian Togo Hills and two areas on the Togolese side of the Togo Hills are chosen as case studies. This chapter presents a detailed account of these areas, describing cultivation practices, documenting the different rice varieties farmers grow in their fields and recording how people express their preferences for rice varieties. This chapter thus provides a basis for the more specific analyses presented in following chapters about how and why farmers continue to rely on locally selected rice varieties, rather than adopting modern, i.e. scientifically improved, varieties offered by national and international rice improvement programmes.

Methodology

To study rice variety development pathways, rice cultivation technical choices, and their place within local cropping systems, four case studies within the Togo Hills are analysed. Specific attention is given to the role African rice plays within these farming systems and communities, because African rice is solely the product of farmer agency, as it has never been scientifically improved. The Togo hill area was chosen because African rice is still actively cultivated there, and because the area is ecologically as well as culturally highly diverse.

The Togo Hills run more or less north-south along the southern sector of the international border between Ghana and Togo. This area is home to several ethnic minority groups. The division imposed by the international border also coincides with an ecological division. A large part of the Togolese Togo Hills is constituted by the Danyi plateau and Akposso Plateau, situated 800-900 meters above sea level. The Ghanaian Togo Hills comprise mountain escarpments around 200 to 300 meters above sea level. The soils on the Danyi plateau are strongly weathered and are less fertile than those on the Ghanaian Togo Hills.

Research was carried out in 2007 and 2008 using a mix of methods, including structured and semi-structured interviews, participant observation, and discussion with key informants. The work was done in four case study areas, two on the Ghana side and two on the Togo side of the international border. Many fields of farmers were visited to cross check the answers on the varieties farmers said they cultivated. The researcher also participated in several ceremonies, and meetings were held to discuss the societal role of African rice and its related practices.

The villages of Akpafu Odomi and Lolobi Kumasi, 10 and 8 km north of Hohoe in the Volta Region in Ghana, were selected as case study villages. Both villages are very active in rice cultivation. In Akpafu and Lolobi, 150 and 103 persons were interviewed using questionnaires. Other research methods were mainly implemented in the villages Akpafu Odomi and Lolobi Kumasi. A few households from the neighboring villages of Lolobi Ashambi and Akpafu Mempeasem were also included. Conversion to world religions is an imporant part of the story to be unfolded. Thus it is important to note that the Lolobi group are mainly Catholics, but their beliefs are syncretic, and integrated with traditional religion. The Akpafu are mainly converts to protestant Christianity.

In Accra (the Ghanaian capital) nine sellers of red-brown rice (the means through which consumers identify red rice) were interviewed. The group comprised two street sellers in Dzorwulu and Shiashie, two sellers in the marketplace Salaga and Madina market, and five shops (Health and Wealth Consult, Ghana Rice Company Limited, Rhema Limited, Thrive Enterprise La Paz and Asepa Vegetarian Restaurant). Also customers who regularly bought rice were interviewed: four at Thrive Enterprise La Paz and two buying from the street seller at Shiashie. In Lomé Togo similarly sellers of brown rice were sought but not found.

On the Togo side of the international border data were collected in five Ewe villages on the Danyi plateau (Elevagno, Xexatro, Meampaseam, Dafor and Sassanou). Further data were collected in three Ahlon villages (Sassanou, Bogo and Tinipé) situated near the international border between Ghana and Togo, on the descent of the Danyi plateau towards the Ghanaian Togo Hills (Figure 1). In total 148 households were interviewed on the Danyi plateau including the Ahlon area, using questionnaires. An additional 18 farmers on the Danyi Plateau were interviewed in depth on rice cultivation practices, and all their fields were visited. The Danyi plateau in Togo, situated about 40 km east of the Lolobi case study villages (as the bird flies) at an average altitude of 800 metres, is home to the 'Danyiwo' (Ewe speakers). Most are Catholic converts, although traditional so-called "animist" practices are still common.

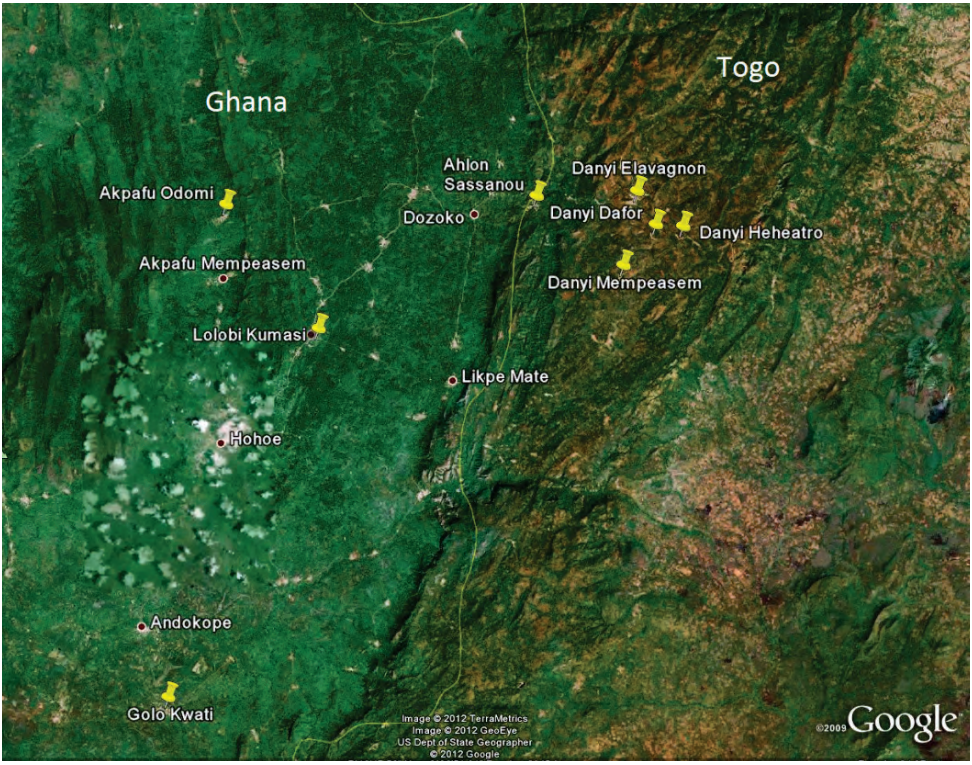

***Figure 1**: Map of the research area. Main case study villages are indicated by pushpins*

Farming the Togo Hills – between two major ecological zones and two countries.

The Togo Hills are home to several ethnic minority groups, as well as to a group of Ewe-speaking people inhabiting the Danyi Plateau in Togo. The Togo Hills are part of a larger mountain formation that runs as a more or less continuous ridge from southern Ghana to northern Nigeria. In southern Ghana and Togo this ridge partly coincides with and constitutes the international border between Ghana and Togo. The region has a long history in which different ethnic groups dynamically strategised to carve a “niche” to combine opportunities, create freedom and protect themselves against threats and make a living within a field dominated by larger political and economic powers (Brydon, 2008; Nugent, 1997 and 2002). It is in this light that we have to see the ethnic and thus cultural diversity in the area.

Former German Togoland (today Togo and Ghana’s Volta region that includes all of the Togo Hills) experienced early incorporation into market structures as the result of colonial tropical produce exports. Around 1912, under German rule, it was estimated that around 86% of the native farmers' cultivation, in today’s Togo, around Misahoe within the Togo Hills, was devoted to cacao (Darkoh, 1967). The farmers on the Danyi plateau have been producing coffee since the German colonial era 1887-1912, as the plateau ecology favoured coffee more than cacao.

Later this coffee production was intensified under French rule and largely influenced the social structure as the perennial nature of the coffee crop largely facilitated the appearance of individual property and the emergence of smaller household units, as the land now became individual property instead of being disposable for use for the whole community (Quesnel and Vimard, 1988).

During recent decades coffee production has waned especially since the international coffee prices started dropping dramatically from 1998 to 2002 (Hallam, 2003). During this most recent period the Togolese Togo Hills, and especially the Danyi Plateau, became a backward area that hardly received any government attention. This can also be attributed to the relatively poor soils on the Danyi Plateau and the limited economic opportunities in the country caused by a dictatorial of President Étienne Eyadéma Gnassingbé.

After a major drop of the coffee price in 2004, from 1000 cfa to 400 cfa per kg many farmers on the Danyi Plateau stopped coffee production altogether, which resulted in a significant increase in rice and maize production (Table 1). Rice and maize are good alternatives as both can be consumed as well as stored for longer periods of time without much processing, contrary to the dominant yam and cassava, providing food security as well as facilitating small sale in very small local markets. Only a small part of the major food crops output is sold in the market, and the only crops specifically produced for the market are vegetable crops like cabbage. This vegetable production is mainly done by a few wealthier farmers who came to specialise. The usually hire labor to maintain their farm. Although the soils are somewhat more fertile in the Ahlon area, situated on the international border between Togo and Ghana halfway down the descent from the Danyi Plateau into Ghana, these areas are limited and difficult to access. As we shall see, the Ahlon farming system is similar to that of the Ewe on the Danyi Plateau, because they are historically connected to this plateau and farmers say that the Danyi cropping system provides them with the certainty of good yields. This Ahlon area is also more humid, as rainfall is locally higher because of location on the lower slopes.

Table 1*: Rice production on the Danyi plateau 4 years before and 4 years after(in bold) the drop of the coffee price from 1000 to 400 fcfa per kilogram in 2004. (Source : Direction des Statistiques Agricoles de l'Informatique et de la Documentation (DSID)Togo)*

	Area(ha)	*Production(t)*
2002-2003	183	154
2003-2004	475	629
2004-2005	564	610
2005-2006	**770**	**1922**
2006-2007	**694**	**1388**
2007-2008	**322**	**690**
2008-2009	**487**	**1055**
Average 2002-2003	407	464
Average 2005-2009	**568**	**1264**

By contrast to the Danyi plateau, the ecology in the escarpments of the Togo hill ranges in Ghana is more favourable to cacao production. The cacao market is structured through the governmental “cacao board” that buys from farmers and regulates cacao production. Many farmers maintain a cocoa farm.

The more liberal and democratic political climate in Ghana has resulted in more economic opportunities than in Togo. This incorporation into liberal market structures has facilitated income streams from various domains. Out of the 148 people interviewed on the Danyi Plateau in total only 22 income contributing members of the household who were outside the village were mentioned, of whom only five stayed in larger towns, while nine were staying in neighbouring villages on the Danyi Plateau, and eight were staying in small villages further north. In contrast, in Ghana out of the 150 interviewed households from Akpafu Odomi and Akpafu Meampeseam in the Ghanaian Togo Hills 50 contributing household members were mentioned as staying outside the village, of whom 37 were staying in the larger cities like

Accra and Cape Coast, while 10 stayed in neighboring villages and three in more far off villages.

This shows the very limited access to capital and opportunities for investment of farmers on the Danyi plateau. Therefore, for the people in the Togolese Togo Hills there is much more dependence on self-sufficiency, and on cooperation in their livelihood strategies, compared to the Togo Hills area in Ghana.

Because of the long dictatorial regime in Togo the individualistic tendencies that came with the colonial plantation economy, as mentioned by Quesnel and Vimard (1988) have not continued, as they have in Ghana. In Ghana commodification resulted in the decline of 'family farms', which caused farmers to become more dependent on hired labour, and share cropping has tended to replace land inheritance (Amanor, 2010 and 2001). As chapter 3 of this thesis will show, this also holds partly for the ethnic minorities in the Ghanaian Togo Hills.

Rice cultivation in the Togo Hills.

African Rice has traditionally been the staple food that the minorities, as well as the Ewe on the Danyi plateau, grew in this mountainous region. The crop thrives on mountain slopes and in forests, where the minority groups carved their niche in the web of political economic powers, and where, otherwise, mainly yam cultivation on the plains was dominant. Rice cultivation and farmer selection, and the cultural importance of (African) rice, have also to be understood within this diverse frontier area of contestation and "niche carving". Farmers seek optimal combinations of profit from opportunities and alliances, while maintaining a large degree of independence as group.

Whether the African rice was brought to the Togo Hills from elsewhere is unclear, but the interviews with the minority groups as well as the Ewe on the Danyi plateau, indicate that African rice has been a major source of survival in dynamic circumstances of migration, insurgencies and war. Often mentioned are the conflicts with the Ashanti ethnic group. The Lolobi mentioned that one of their villages is even named after the Ashanti town Kumasi. The Ashanti had been impressed by the resistance of the Lolobi, and therefore nicknamed the Lolobi town Kumasi. The Asante war of 1868-1869 was one that reached as far east as the Togo Mountain area and disrupted the lives of many people (Johnson, 1965; Brydon, 2008). The minorities, as well as the Ewe on the plateau, state that the traditional rice perfectly suited their somewhat nomad life, as it is very versatile and allows cultivation in secure but infertile plateaus, and slopes, while its cycle is relatively short and its grain very nutritious. They also stated that the rice can even be consumed uncooked by grinding and mixing it with cold water. This offered an advantage in times of war. You survive without making a fire, so an enemy could not easily locate you by signs of smoke.

Currently rice cultivation within the Togo Hills consists of lowland and upland cultivation in the Ghanaian Togo Hills and almost only upland cultivation in the Togolese Togo Hills. This is mainly a result of the ecology of the region. The Lolobi, Santrokofi, Akpafu and Likpe minorities in the Ghanaian Togo Hills have, since the 1960's started to make use of the natural wetlands within the escarpments around their villages and even around more remote villages on the plains. These wetlands are mainly used for cultivating Asian rice varieties although a significantly smaller part remains planted to African rice. This has become their major activity and rice is used for selling as well as for own consumption. The variety they cultivate is actually a mixture of about 7 varieties of African rice, which they consider to be elements of a single land race.

We shall subsequently see that new Asian rice varieties selected or developed by farmers are often inspired by the qualities of traditional African rice, and therefore African rice remains an important reference. On the Danyi plateau in Togo rice cultivation is not a major activity, and comprises only upland African rice for home consumption (with the exception of some marshy areas). People do not have access to lowlands, and cannot afford to rent such land, as occurs east of Adeta, around the 600 m lower in altitude. On the Danyi plateau the seven different African rice varieties are cultivated separately, to make effective use of differences in duration (see below).

A characterisation is now attempted of the cropping systems within four case study areas within the Togo Hills based on field data collected in 2007 and 2008. Connections with sociocultural data are also explored. The Akpafu and Lolobi cases are located on the Ghanaian side of the Togo Hills. The Danyi plateau and the Ahlon cases are located on the Togo side. Figure 1 shows the main case study villages. It also shows the border between Ghana and Togo, following the western edges of the Danyi plateau. The village of Ahlon Sassonou is situated on this border (also shown in Figure 1)

The Ghanaian Togo Hills

The Lolobi and Akpafu cases

In the Lolobi and Akpafu areas rice is the most important food crop followed by cassava and maize (Tables 2 and 3). Most Lolobi and Akpafu farmers keep a cacao farm but as the Lolobi are more specialised in commercial production of rice they are less involved in cacao production and other activities outside rice cultivation than the Akpafu. Although in former times several Lolobi individuals are known to have become rich through the cultivation of cacao its role has now strongly diminished and rice has become their major business. Therefore the role of rice in these two areas in the Ghanaian Togo Hills is different.

Both villages also get income from other domains than agriculture and through jobs in Hohoe, Jasikan and other larger towns in Ghana. Although in both these areas upland African rice was once the main rice crop, similar to the Danyi plateau area, lowland cultivation was added to the cropping system around 1960. Before that, the lowlands were natural swamps unused because the people were not familiar with lowland cultivation. The Akpafu nowadays do their lowland cultivation close to their villages within the seasonally-flooded intra-mountain basins. The Lolobi villages are situated somewhat further into the mountains and naturally have fewer accessible marshy lowlands. Lolobi farmers do their lowland cultivation in the area around Golo Kwati and also around Gbi-Wgebe, two Ewe villages south of Hohoe, respectively about 23 km and 9 km south of Lolobi Kumasi. Just like the seasonally flooded intramontane basins adjacent to the Akpafu villages, these areas are naturally fertile and clayey, since they are situated in outwash areas at the foot of the mountains, absorbing nutrient-rich run off water from higher areas. Accordingly, farmers do not use fertilisers.

***Table 2**: Estimation of the share of rice in relation to other carbohydrate crops in Lolobi area Ghana, average of the years 2007 and 2008 N=103 (survey 2008) Villages: Lolobi Kumasi and partly Ashambi Population: 3208 and 1626 inhabitants respectively- source Ghana statistical service, 2000 Population and housing Census.*

Crop	% production	% of total area cultivated with carbohydrate crops	Average field size (ha)	Dry yield (kg/ha)	% of farmers cultivating the crop
rice	35.0	37.4	0.24	3621	100.0
maize	13.4	21.5	0.23	2439	59.2
cassava	27.2	16.6	0.45	6400	23.3
yam	4.8	4.4	0.47	4320	5.8
plantain	19.5	20.2	0.54	3750	23.8

***Table 3**: Estimation of the share of rice in relation to other carbohydrate crops in Akpafu area Ghana in 2007, N=109 (survey 2008) village and population: Akpafu Odomi 2231 (source Ghana statistical service, 2000 Population and housing Census, unpublished)*

Crop	% production	% of the total area cultivated with carbohydrate crops	Average field size	Dry yield (kg/ha)	% of farmers cultivating the crop
rice	45.4	52.9	0.40	1984	97.2
maize	9.0	24.6	0.22	844	83.5
cassava	41.2	19.9	0.29	4800	49.5
yam	1.6	0.8	0.22	4320	2.8
plantain	2.9	1.8	0.24	3750	5.5

During the growing season people from Lolobi Kumasi take turns and stay in basic temporary sheds next to their fields. Lolobi Kumasi is known in the region to be the most active and innovative centre for rice cultivation. Many new varieties are first discovered and tried out by

Lolobi farmers and often disseminate among the other minorities, and among Ewe farmers in the region. An example is the highly popular variety *Viono*, discovered around 1992 in the Santrokofi area and taken up rapidly by the Lolobi. In Lolobi a farmer then discovered a shorter type among the *Viono* that yielded even more. This '*Viono short*' is now the most widely cultivated rice variety among the minority groups speaking Ghana Togo Mountain (GTM) languages, as well as among the Ewe from Golo Kwati to Hohoe, Jasikan and Kadjebi. Tables 4 and 5 show the rice varieties and their proportions as cultivated in the Lolobi and Akpafu areas. As can be seen, the share of *Viono* (upland + lowland) ranges from 30- 35% in Lolobi to 70 -76% in Akpafu.

A more recent example is *Aworema*, discovered within *Viono short*. Although very similar to the variety *Viono*, *Aworema* has a panicle flag leaf that stands straight up which makes it more uncomfortable for birds to eat the seeds. *Aworema* means "hide from the enemy" in Siwu language, the language of the Lolobi and Akpafu. As can be read from Table 4 *Aworema* is highly popular in Lolobi but in Akpafu they have just started to cultivate it (Table 5). Although the Akpafu still continue with *Viono*, the Lolobi people are already cultivating a large quantity of the new variety *Aworema*: The combined percentage of *Viono* and *Aworema* is 48 and 53 percent, in 2007 and 2008 respectively. Farmers in Lolobi as well as Akpafu clearly state that the criteria set to select *Viono* or any other variety for consumption are determined by the characteristics of their traditional African rice.

Farmers in Akpafu and Lolobi both state that red rice types, and especially African rice, are more nutritious and stay in the stomach for longer, and therefore facilitate more hours of work before becoming hungry again. That red rices are more nutritious is attributed to the red pericarp that farmers often do not (especially when the rice is used to make porridge or rice fufu) fully remove. Full removal is possible by milling the rice more than once. This is nowadays done in milling machines.

A nutritional analysis was made by the CSIR Food Research Institute in Accra Ghana which in fact showed that single milled *Viono* contained significantly more nutrients than double milled *Viono*, the double milling resulting in almost entirely removing the pericarp (see annex 1). Dr. John Tewiah Manful (Augustus 2007, personal communication) from the same institute also declared that for African rice it is almost impossible to remove the pericarp entirely and almost always a part remains on the endosperm, but this is not the case with white rice, where the pericarp comes off easily. Therefore maintaining a tradition in which the pericarp is only partly removed results in consuming rice that contains more nutrients.

Although Asian rice, *Viono* and *Aworema* are both red (having a red pericarp just like African rice) and farmers state that these varieties swell and fill the stomach when cooked. Both Akpafu and Lolobi prefer red rice types where the pericarp is not (fully) removed for consumption, which explains the dominant share of red rice varieties in these places.

The exploration and development of new local Asian varieties can therefore be considered as an extrapolation of the cultivation of African rice. All new Asian red rice varieties can be readily identified as farmer varieties, since the Ghanaian extension services and agricultural research stations have always promoted only white pericarp rice varieties. Interestingly the variety Nerica 1, highly promoted in the area by the Ministry of Food and Agriculture (MOFA) is only cultivated in places where it was not intended – namely, in the lowland where it is cultivated in small quantities for experimentation. The Akpafu did not cultivate it at all. There were however two Akpafu farmers, encountered after the survey was done, who had cultivated Nerica 1 as an experiment in a corner of their field, stating that many farmers in Akpafu had tried it out without much success, not because they did not like the grain or the plant morphology, but because other local varieties largely outperformed it. For one of these informants Nerica 1 had become her principal variety, because she had been cooperating with the University of Reading (UK) (see Dorward, 2007) and afterwards became a seed provider for the MOFA in Hohoe. It is clear from these data that farmers deploy mainly the varieties that they have developed or selected for themselves.

***Table 4**: Varieties and important characteristics and an estimate of their proportion within the total rice production within the Lolobi area: botanical group, pericarp colour, percentage of farmers cultivating the variety, percentage of the total rice production, percentage of the total area under rice cultivation ,average field size and average yield per hectare. Bold numbers indicate the data for African rice and the major Asian varieties as well as the dominant pericarp color of the cultivated varieties. (Survey, 2008 among 135 farmers in the Lolobi villages: Kumasi and Ashambi for the year 2007, N=70 and for the year 2008, N=90)*

Variety	**botanical group**	**pericarp colour**	**% of upland or lowland farmers cultivating**		**% of total farmers cultivating**		**yield % upland or lowland**		**total yield% (upland + lowland)**		**area % upland or lowland**		**total area % (upland + lowland)**		**average fieldsize (ha)**		**average yield (kg/ha)**	
Year			2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008
Upland ecology																		
Boadekamo	African	red/brown	**80.00**	**94.29**	**22.86**	**36.67**	**39.3**	**76.3**	**3.9**	**7.3**	**45.7**	**83.7**	**7.5**	**13.6**	**0.10**	**0.13**	**1783**	**1940**
Viono	Asian (ind.)	red/brown	**10.00**	**5.71**	**2.86**	**2.22**	**30.0**	**9.5**	**3.0**	**0.9**	**28.3**	**7.4**	**4.6**	**1.2**	**0.48**	**0.18**	**2200**	**2723**
Aworema	Asian (ind.)	red/brown	5.00	2.86	1.43	1.11	22.9	14.2	2.3	1.4	19.6	8.9	3.2	1.4	0.66	0.44	2421	3404
Adeisi	Asian (ind.)	white	5.00		1.43		7.9		0.8		6.5		1.1		0.22		2496	
Total white rice			**5.00**		**1.43**		**7.9**		**0.8**		**6.5**		**1.1**		**0.22**		**2496**	
Total red rice			**95.00**	**100.00**	**27.14**	**38.89**	**92.1**	**100.0**	**9.1**	**9.6**	**93.5**	**100.0**	**15.3**	**16.3**	**0.17**	**0.14**	**2043**	**2128**
Total upland			100.00	100.00	28.57	38.89	100.0	100.0	9.9	9.6	100.0	100.0	16.3	16.3	0.17	0.14	2072	2128
Lowland ecology																		
Boadekamo	African	red/brown	**29.63**	**13.51**	**22.86**	**11.11**	**9.1**	**3.6**	**8.2**	**3.2**	**14.6**	**4.8**	**12.3**	**4.0**	**0.16**	**0.12**	**2289**	**2930**
Viono	Asian (ind.)	red/brown	**40.74**	**40.54**	**31.43**	**33.33**	**35.2**	**32.2**	**31.8**	**29.1**	**32.1**	**29.1**	**26.8**	**24.4**	**0.25**	**0.25**	**4067**	**4308**
Aworema	Asian (ind.)	red/brown	**18.52**	**40.54**	**14.29**	**33.33**	**12.5**	**24.8**	**11.3**	**22.4**	**10.4**	**25.7**	**8.7**	**21.5**	**0.18**	**0.22**	**4446**	**3764**
Addeisi	Asian (ind.)	white	**35.19**	**18.92**	**27.14**	**15.56**	**21.1**	**12.1**	**19.0**	**10.9**	**20.8**	**12.1**	**17.4**	**10.1**	**0.19**	**0.22**	**3752**	**3891**
Akpesse	Asian (ind.)	white	12.96	14.86	10.00	12.22	10.0	9.7	9.0	8.8	9.8	9.8	8.2	8.2	0.24	0.23	3789	3845
Damansah	Asian (ind.)	red/brown	5.56	6.76	4.29	5.56	4.2	4.1	3.8	3.7	2.8	3.5	2.3	2.9	0.16	0.18	5656	4596
Longgrain	Asian (ind.)	white		6.76		5.56		3.4	0.0	3.1		4.6		3.9		0.24		2894
Nerica	Hybrid	white	7.41	6.76	5.71	5.56	2.1	3.5	1.9	3.2	3.8	3.9	3.2	3.3	0.17	0.20	2043	3530
Perfume	Asian (ind.)	white	9.26	10.81	7.14	8.89	5.8	6.5	5.2	5.9	5.7	6.5	4.8	5.4	0.20	0.21	3732	3904
Total white rice			**55.56**	45.95	42.86	37.78	39.0	35.3	35.1	31.9	40.1	36.9	33.6	30.9	0.20	0.22	3595	3718
Total red rice			**72.22**	83.78	55.71	68.89	61.0	64.7	55.0	58.5	59.9	63.1	50.1	52.8	0.20	0.21	3771	3998
Total lowland			100.00	100.00	77.14	82.22	100.0	100.0	90.1	90.4	100.0	100.0	83.7	83.7	0.20	0.22	3701	3894

Table 5*: Varieties and important characteristics and an estimate of their proportion within the total rice production within the Akpafu area: botanical group, pericarp colour, percentage of farmers cultivating the variety, percentage of the total rice production, percentage of the total area under rice cultivation, average field size and average yield per hectare. Bold numbers indicate the data for African rice and the major Asian variety cultivated as well as the dominant pericarp color of the cultivated varieties. (Survey, 2008 among 135 farmers in the Akpafu villages: Odomi and Mempaseam. For the year 2007, N=68 and for the year 2008, N=100).*

Variety	**botanical group**	**pericarp colour**	**% of upland or lowland farmers cultivating**		**% of total farmers cultivating**		**yield % upland or lowland**		**total yield% (upland + lowland)**		**area % upland or lowland**		**total area % (upland + lowland)**		**average fieldsize (ha)**		**average yield (kg/ha)**	
Year			2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008
upland ecology																		
Boadekamo	African	red/brown	**27.3**	**20.0**	**4.4**	**4.0**	**24.2**	**13.5**	**2.3**	**1.3**	**24.7**	**12.2**	**3.4**	**1.7**	**0.35**	**0.22**	**916**	**1101**
Viono	Asian (ind.)	red/brown	**63.6**	**35.0**	**10.3**	**7.0**	**68.3**	**28.5**	**6.4**	**2.8**	**68.5**	**41.5**	**9.4**	**5.8**	**0.42**	**0.43**	**932**	**685**
Aworema	Asian (ind.)	red/brown		5.0		1.0		4.2		0.4		8.1		1.1		0.59		511
perfume	Asian (ind.)	white		5.0		1.0		5.6		0.5		1.5		0.2		0.11		3631
kabila	Asian (ind.)	white		15.0		3.0		18.0		1.8		8.1		1.1		0.20		2213
Damansah	Asian (ind.)	red/brown		5.0		1.0		16.7		1.6		20.4		2.9		1.47		817
Aqua Blue	Asian (jap.)	white		5.0		1.0		0.5		0.0		1.5		0.2		0.11		300
Adeisi	Asian (ind.)	white	9.1	5.0	1.5	1.0	7.5	6.2	0.7	0.6	6.8	4.1	0.9	0.6	0.29	0.29	1021	1532
Saka(rouge)	Asian (ind.)	red/brown		5.0		1.0		6.9		0.7		2.5		0.4		0.18		2723
Total white rice			9.1	30.0	1.5	6.0	7.5	30.3	0.7	3.0	6.8	15.3	0.9	2.1	0.29	0.18	1021	1982
Total red rice			**90.9**	**75.0**	**14.7**	**15.0**	**92.5**	**69.7**	**8.6**	**6.9**	**93.2**	**84.7**	**12.8**	**11.9**	**0.40**	**0.41**	**928**	**821**
Total upland			100.0	100.0	16.2	20.0	100.0	100.0	9.3	9.8	100.0	100.0	13.7	14.0	0.39	0.34	934	998
lowland ecology																		
Boadekamo	African	red/brown	**5.3**	**8.5**	**4.4**	**7.0**	**1.5**	**2.0**	**1.4**	**1.8**	**3.0**	**4.0**	**2.6**	**3.4**	**0.27**	**0.25**	**743**	**738**
Viono	Asian (ind.)	red/brown	**73.7**	**79.3**	**61.8**	**65.0**	**69.9**	**81.2**	**63.4**	**73.2**	**73.3**	**80.9**	**63.3**	**69.6**	**0.47**	**0.55**	**1378**	**1500**
aworema	Asian (ind.)	red/brown		1.2		1.0		1.1		1.0		0.6		0.5		0.24		2860
perfume	Asian (ind.)	white	7.0	12.2	5.9	10.0	12.3	12.3	11.1	11.1	8.1	10.3	7.0	8.8	0.55	0.45	2179	1795
kabila	Asian (ind.)	white	7.0	6.1	5.9	5.0	4.2	2.3	3.8	2.0	4.6	3.2	4.0	2.7	0.31	0.28	1322	1075
Damansah	Asian (ind.)	red/brown	1.8	1.2	1.5	1.0	3.7	0.7	3.4	0.6	2.2	0.4	1.9	0.4	0.59	0.18	2468	2451
Saka(rouge)	Asian (ind.)	red/brown	5.3	1.2	4.4	1.0	7.2	0.5	6.5	0.4	7.6	0.7	6.6	0.6	0.69	0.29	1354	1021
Mateggi	Asian (jap)	red/brown	1.8		1.5		1.2		1.0		1.1		0.9		0.29		1532	
Total white rice			**14.0**	**18.3**	**11.8**	**15.0**	**16.5**	**14.6**	**15.0**	**13.2**	**12.8**	**13.4**	**11.0**	**11.6**	**0.43**	**0.40**	**1869**	**1626**
Total red rice			**87.7**	**87.8**	**73.5**	**72.0**	**83.5**	**85.4**	**75.7**	**77.0**	**87.2**	**86.6**	**75.2**	**74.4**	**0.47**	**0.51**	**1383**	**1475**
Total lowland			100.0	100.0	83.8	82.0	100.0	100.0	90.7	90.2	100.0	100.0	86.3	86.0	0.47	0.49	1445	1495

Table 4 and 5 also clearly show that the Lolobi farmers have much higher average yields and production than the Akpafu. While the Akpafu 68 and 200 farmers produced 14141 kg and 20765 kg respectively (an average of 208kg and 103 kg per farmer), 60 and 90 Lolobi farmers produced 71000 and 109650 kg respectively (an average 1183kg and 1218kg per farmer). It is also remarkable that farmers in Lolobi combine more different varieties and therefore the average plot size per variety becomes much smaller while the number of fields is larger. As a consequence of the Lolobi being more involved in produce for the market they also produce a large quantity of white rice next to their highly preferred red rice; around one third of their total output is white rice. When Lolobi farmers consume some of their white rice it is most often mixed with red rice. The Akpafu produce less white rice; only 16-18% of total rice production is white. The Akpafu have more hydromorphic upland (rain fed) soils than those of the Lolobi; the upland fields of the Lolobi are all close to the village where there is hardly any hydromorphic area available. This explains why the Akpafu cultivate a larger number of the varieties cultivated in both lowland and upland. The Lolobi cultivate a larger percentage of African rice than the Akpafu (3.9% and 7.3% against 2.3% and 1.3% of total output). This can on the one hand be explained by the suitability of African rice in the upland conditions more commonly encountered in Lolobi but also by the strong attachment of African rice to important customary rites around Lolobi gods and ancestors – rites that cannot be performed with any other rice. In Lolobi the Catholic church accepted and was even inspired by traditional religion (beginning its mission around 1903) while the Presbyterian church of Bremen (beginning its mission in the early 19th cenutry) prohibited it among the Akpafu, a reason why customary rites have almost vanished among these Protestants. Lolobi farmers stated that the earlier intrusion of Bremen Presbyterian was rejected, while later the Catholic mission was accepted. An interview with Father Akpalu, and catechist Leo, at the Catholic church of Lolobi Kumasi confirmed this.

Here it is important to mention that during German colonisation many villages within the Togo Hills were divided between Catholics and Bremen Presbyterians largely influencing a differential reshaping of the local social and moral order: “After having in many cases disturbed the social order in villages new social divisions were created: most towns and villages were divided between Catholics and Bremen Presbyterians, leading to frequent discord between members of the churches. Intermarriage and other forms of interactions were often prohibited.” (Gavua, 2006, p. 142). The Lolobi also cultivate small quantities of African rice (*Boadekamo*) in parts of the lowlands, to have it always close by whenever they need it.

This also shows the salience of the cultural and religious reasons to cultivate African rice. The quantities are not that small; 4-10 percent of total lowland production is *Boadekamo.*

Cultural practices within the Akpafu region – there are no longer any customary religious rites - that require red skinned rice, such as local dishes consumed at special occasions, can equally well be prepared with red Asian rice such as *Viono.*

An indication of the greater Lolobi community integration around rice, is that they use much less paid labour within rice cultivation than the Akpafu (Table 6). The labour exchange principle is much stronger in Lolobi; a group of workers will work on one's farm today and will work on another one's farm another day until all the group members' fields are dealt with. In Akpafu this organisation is less common, and more farmers will prefer to ask several people to come to work on their farm and pay them in cash. This way, when the job is done there is no longer any obligation, which makes payment in cash more individualistic. It seems probable that the importance of *Boadekamo* rice in community ceremonies and the continued functioning of the labour group exchange system in Lolobi are correlated. In Akpafu the world of religion and community is no longer directly connected to the world of agriculture because religious practices that generate an essential communal spirit are no longer connected to the locality, due to the intervention of Protestantism.

But this is almost certainly not the full story. In group discussions with youths in Akpafu and Lolobi, and with youths living in the villages of the Danyi plateau the diminished cooperation among people was mentioned as the key major factor to diminishing returns in agriculture. But the decrease and abandonment of traditional religious practices directly connected to agriculture with the community were also mentioned. When further discussing this issue many youths commented that the community spirit achieved in the modern Christian church is often not used to stimulate working together in the field but on the contrary to distract from it. However, exceptions were the church choirs, of which several were also working together in the field. On the Danyi plateau football teams were mentioned in a similar vein; they also foster agricultural working groups and a spirit of shared effort. Farmers on the Danyi plateau visiting the Akpafu area also indicated that they experienced a more individualistic attitude and lack of mutual dedication to that the experienced among the Lolobi, who were according to the Danyi farmers much more communally oriented.

***Table 6**: Percentage of farmers using hired paid labour for different activities of rice cultivation (survey 2008)*

Activity on rice farm	2006 n=102 Lolobi	2006 n=114 Akpafu	2007 n=102 Lolobi	2007 n=114 Akpafu
Clearing	61	94	60	82
Ploughing/Hoeing	52	96	51	84
Sowing	23	76	23	67
Weeding	19	54	19	47
Bird scaring	18	9	18	8
Harvesting	51	88	50	77
Threshing	19	83	19	73

In Lolobi Kumasi *Boadekamo* (which literally means "the rice of our people") plays a very important role in offerings to ancestors and local gods. *Viono* cannot be used here. Also no other food crops are used for these ceremonies, as the ancient staple food is *Boadekamo.* At family level *Boadekamo* is used for offerings to the family stool and the family's shrine (an earth model with cowries). Both the stool and the shrine reside with an important family elder. This stool helps women and men to have children. Kamo Kra (rice stew) with palm nut soup is prepared. Since *Boadekamo Kraa* may not be enough to feed all the people also *Viono* and any other red variety is cooked to feed the people, but the *Boadekamo* is obligatory and central in the offering. Those who pledge, bring gin, palm wine and money. Each cowry represents the spirit of a celebrated forefather of the family. Each time an important celebrated member of the family dies a cowry is added to the earth model. Both the family stool and the shrinecan kill evil people. When the stool or shrine kills a person the family pays a ram, palmwine, *Boadekamo*, palmnuts for soup, gin and other drinks, as the custom demands. Failure to do this might cause someone to fall sick. This is a sign to show you that you have to perform the customary rites before you are saved.

At village level *Boadekamo* is also used as the only food to be offered to local gods (served by priests called *Mobia*). These gods are, through the priests, consulted to ask for prosperity and to solve problems. There are seven local gods in Lolobi Kumasi. Ceremonies of offering are frequently held (See box 1). Ceremonies of this sort can only be held on two particular days of the week, *Ikulu* and *Ipo.* These are also the days people are not supposed to go farming. The other days in the week are called first and second day after *Ikulu* and first and second day after *Ipo.* The Lolobi Calender has 6 days, just like the Akpafu Calender, except that in Akpafu this 6 day week is rarely referred to because of the dominance of the Protestant church.

So, at family as well as at village level, African rice is an important component attached to the moral and physical well-being. Also among the younger generation the *Mobia* and the traditional morals and rules (like the taboo days for farming: *Ikulu* and *Ipo*) which they safegaurd, are still important. Several meetings with youths showed that they feared not respecting taboo days might bring you bad luck. Several youth also remarked that a number of today's problems, like diminishing cooperation and yields, can be ascribed to not observing these days and the moral rules represented by the *Mobia* (Box 2). The absence of African rice in offerings to foreign gods also illustrates the interconnectedness of African rice and the local social and moral order.

***Box 1:** A description of an offering to the Lolobi village god, Sangrey, illustrates the role rice plays in the ceremony and how rice is also shared by the people who take part in the ceremony. Such offerings to gods do no longer exist in Akpafu Odomi.*

Around eight o'clock in the morning we leave together with the *Mobia* Mr. Martin A. and Ms. Abovi A. who are both dressed in white. We are five: three men and two women. One of them is the family member that is going to offer to Sangrey because the problem that he had one year ago, he didn't have a job, is now solved. A year ago he also came to Sangrey with the demand to do something about his problem. He has got what he wanted and he is now to thank the god.

We walk into the forest for about 40 minutes before we get to a very narrow and small clearing. On the sides simple benches in the form of tree trunks are arranged. Around a small tree in one corner several knifes are stung into the ground. Each knife represents somebody who died and was guilty. Empty bottles of gin are piled up behind the tree. Mr. Agblor Martin starts to ask permission to the god to accept the man's offer: palm wine, several bottles of gin and a he-goat. Somewhat later more people arrive until we are about 30 and a big calabash of palm wine is brought to the front. The calabash is covered with a "crown" made from palm leaves. Before the palm wine will be served to the tree with the knifes, a prayer is said to sanctify the wine. Several people tell me that the fetish priest Mr. Martin A. and Ms Abovi A. resemble a referent father and sister: "there is not much difference the rituals are very similar ….you see how he and his female colleague are dressed up and how the wine is transformed?"

After that milled and totally peeled *Boadekamo* powder is put around the tree in 5 little heaps. The red husk is totally removed from the rice as the powder is very white. Each heap represents a gift to a different entity: 1. to the land; 2. to the ancestors; 3. to the spirits of the village Lolobi; 4. to the messenger of the shrine; and 5. to those who died and where guilty (the evil spirits). This last heap is formed with the left hand and is placed somewhat away from the other heaps; the contrast of the white powder on the ground is fluorescent. While doing this the priest calls upon the ancestors who were there before to do similar offerings and asks the different entities to accept the offer to the god Sangrey. As I was told to do, I contribute two bottles of gin and three Ghana Cedis. The priest then informs everybody (including the different entities) of my presence and states that I am studying all the aspects of their rice for the good of all of us. At the same time a group of women have arrived and have started to prepare *Boudekamo Kra*: red rice flour cooked and for this occasion made into balls. This time the husk of the rice is not peeled of, which makes the rice flower turn red. Meanwhile men have slaughtered the goat and the blood is being used to cook palm nut soup. Palm nut soup with goat blood is called *Igpupou*, and is prepared only on ritual occasions. Palm wine is now given to all the participants to drink. The rain starts to fall and many people look for banana leaves to cover themselves. We almost get soaked by the rain but everybody stays and the rain doesn't prevent people from chattering in a very cozy and empathic way. The rice balls and the palm nut soup together with pieces of goat meat are handed round. Everybody eats with visible enjoyment. I shortly talk to the women who prepared the rice balls and ask them if they are prepared with the red *Viono* rice just to verify one more time if the rice that the people eat is also *Boadekamo*. "No" the women utter," it is the traditional rice of Lolobi: *Boadekamo*, it is only this rice that the god accepts".

Box 2: *On 5 May 2009 a meeting with youth from Lolobi was organised to talk about the importance of the Mobia, the importance of their advice and the practices that they maintain.*

The meeting starts with a discussion on how the youth organise their work in the field.

A young farmer of about 27 starts:

"Before we did communal labour but nowadays we notice that this communal spirit is getting weaker. When we go to a communal field there are always a significant number of persons who are lazy and it are these people that demotivate, discourage the work spirit. But it is not only that, it is also related to our way of farming that has changed. We use a lot of chemicals like herbicides that make it less necessary to weed. Herbicides and fertiliser hamper collective work. Because of this we are only thriving on the fruits of our parents as we no longer want to go to farm like them"

Then a boy of about 19 years old joins the meeting:

"I have just arrived but what I know is that the local gods represented by the Mobia transfer a lot of messages to us concerning our food security and the Mobia have the power to pray and to do sacrifices at the moment of sowing of rice or other crops. I am a specialist in rice cultivation and I always bring a small quantity of *Viono* and our local *Boadekamo* rice (because I cultivate two varieties) to the Mobia to ask permission of the gods for cultivating my rice".

Another youngster of about 25 adds to this:

"Yes according to me the days of Taboo *Ikulu* and *Ipo* have to be respected especially by us the youth who are the future of agriculture, and I am not only talking about rice and cacao because a lot of people think that the gods only come to the rice and cacao farms."

Then another young man continues:

The days of Taboo and the offerings by the *Mobia* are very important to everybody who lives in this region of Lolobi. We have to respect these days to stay in the same spirit as our gods who have been there since the days of our forefathers".

Then we ask a group of girls that are in the church choir:

"You girls who are related to the modern church, how do you respect the days of Taboo?

"We think it is self-evident to respect the days of Taboo even if you are a Christian."

We then pose the following question:

"What has changed concerning the connection between religion and agriculture?

A young active farmer of about 30 responds:

"According to me the connection between religion and agriculture is diminishing. Nowadays we see everything separated: the rice cultivation, the modern religion and the traditional religion. This situation always results into a low yield because there are no longer any obligations for farmers towards the gods"

Among the Akpafu, who speak the same language and have the same origin as the Lolobi, the family rituals and the local gods have more or less become extinct. A strong ‘anti-traditional religion’ attitude is present, one that is totally absent in Lolobi. People who still perform rituals related to these gods are therefore openly called ‘pagans’. However, African rice is still cultivated (although in relatively smaller quantities than in Lolobi - see Table 4 and 5) for cultural reasons: it remains part of funeral and marriage ceremonies and is an important ingredient for dishes eaten at all special occasions. During marriages, funerals and other gatherings the following is often stated: “If you eat the local *fufu* made with rice flour you will learn to speak our local language (Siwu) very fast”. The statement was attested by Mark Dingemanse, a linguist working on the Sewu language (2007, personal communication). However the local dish called *Kamokra* that goes along with bean stew can often also be made with the Asian rice variety *Viono* and served on ordinary occasions.

A discussion with a farmer on the religious role that African rice used to play ran as follows:

We talk to Akua Bedu aged 74, ‘pagan’ and farmer at Akpafu Odomi. He says he has always been dedicated to the traditional religion. However, nowadays he starts to doubt the traditional religion especially now he gets closer to his death. He thinks of converting to Christianity. He remembers that in 1953 the elders of Akpafu Todzi, Odomi and Meampaseam organised an ‘excursion’ to visit the former settlement of the Akpafu, the settlement where their forefathers had stayed. This excursion was open to everybody who was interested. Although Christian religion prohibited the traditional religion it was decided that some customary rites, of which African rice was part, would be performed during the excursion as an illustration and respect to the culture of their forefathers.

This was later confirmed by the paramount chief of Akpafu. He also talked about an excursion, not a ceremony or pilgrimage. In this way, he stated, practicing libations and offerings to the ancestors and ancient gods were legitimised as it was done in the name of respect to their local culture and tradition, not in the name of the religion, as that would be considered a sin. In some sense one could state that these practices have therefore become at least partly ‘museumized’ (Vishvanathan, 2007). Instead of ‘religion’, the rites and ceremonies that include African rice or *Viono* flour are explicitly considered as ‘culture’ and ‘tradition’ and are therefore no longer connected to the transcendental, and perhaps for that reason (as Durkheim once suggested about ceremonial experienced as entertainment) have become less important in constituting the social norms and structure.

In effect, African rice has become a cultural identity marker, as can be seen from the proportion of rice of this type that the Akpafu still cultivate. It is in this manner that African rice continues to set criteria for rice cultivation, selection and variety adoption. During interviews farmers several times stated that one of the reasons (apart from the good taste and nutritious value) why the original *Boadekamo* had not vanished was because older farmers were familiar with cultivating it, and because outsiders told them that it was a very good rice. In a blind tasting test between *Viono* and *Boadekamo* involving 20 Akpafu people all farmers, without exception, easily distinguished the *Boadekamo* from the *Viono.*

During the annual rice festival (celebrated around Easter), traditional dishes made with *Boadekamo*, *Viono* or any other rice that resembles *Boadekamo* are presented. This rice festival is tribute to the old tradition of offerings to the mountain Molito that provided the Akpafu with rice when stocks were lost, as well as to Tokpaiko, the god that protects the rice in the fields, as well as the god protecting people in time of war. Most importantly it is a way to invite officials, and attract investors, buyers and rice dealers, and to showcase specific local products, such as Red rice. A specific rice festival is also celebrated in Lolobi and similarly is a way to attract buyers and invite officials and government members and farmers, and to expose the different varieties cultivated during a special farmers' market.

In Accra there is a growing demand by the wealthier classes for red rice, and at several places red rice from the Volta region can be bought where it is promoted as nutritious local rice that is directly bought from farmers. Nine interviews with shop owners as well as street sellers offering brown rice from the Volta Region revealed that it is mostly the rich health-conscious consumers who come to buy this rice. Doctors' advice in case of diabetes also makes people to come to buy local brown rice. The rice is also known to be beneficial for pregnant women who also come to buy. In-depth interviews with six buyers of brown rice from the Volta region at a local food store specialised in brown rice confirmed this. The health conscious rich think the local rice is more healthy. All six buyers owned a car. Also one customer who runs a successful food place in the La Paz area in Accra buys local rice to prepare all his dishes, such as the popular *Watché,* as well as fried rice. He says he only needs a little of this rice to get a good quantity of cooked rice. Customers highly appreciate the rice as they say it is full of taste and fills the stomach for a longer time. He said a large part of the reason his fast food restaurant is so successful is because of the brown rice he uses.

When talking to several farmers in Akpafu Odomi they state that African rice has played a central role within their history and also plays a central role in their myth of origin, which states that ancestors moved out of Nubia, and after wandering far and encountering many conflicts settled where they are today (Box 3). These mythic histories usefuly show that African rice, and rice in general, occupies a central place within the local culture. They also illustrate the relation between the Akpafu and the Lolobi people and illustrate the central place that the African rice has occupied in the lives of the Lolobi as well.

Interestingly the initial division between the Akpafu and the Lolobi is also ascribed to an issue around rice cultivation:

The Akpafu and the Lolobi share the same language and originate from the same Kawu people. During a severe drought the whole of the rice harvest was destroyed and only one clan, the Magadagbe, was able to produce some rice and therefore was the only provider of seed. The Magadagbe sold the rice to the Omamain clan, but before selling they roasted the grains so that they would not germinate. The head clan of the Kawu people was Omamain and when they found out about the roasting the younger chiefs refused to punish the Magadagbe and so settle the case. The head chief felt demoted and decided to leave and settled eastwards of the river Daye, today's Lolobi area.

This shows again that although these stories are myths, rice appears as a crucial element. The Akpafu and Lolobi (as well as the Santrokofi) smelted iron to produce tools and weapons, and were the enemies of the Ashanti and the Ewe, but also provided these same people with tools and weapons. The Kawu people somehow divided up into two different groups and in difficult times cooperation was enforced by reviving a mythic past and stressing the origins of a common interest in rice cultivation. These oral materials also speak to ecological factors such as the presence of iron, the relief of the area in which the rice was cultivated, and various political, social and religious factors associated with survival, such as group formation based on a shared cult. In short, the mix between crop type, food security, culture and identity is historically salient.

Box 3: *The history of the origin of the Akpafu told by an Akpafu teacher as he heard it when he was around 10 years old when his father sent him to Efia Katani Srodja who was the oldest 'Mancrado' or founder of the oldest Apafu village: Akpafu Todji situated on a mountain top**:***

The Akpafu people originate from Nubie in north Africa that was situated between Soudan and Egypt. They were blacksmiths and made hoes and other farming utensils. This resulted in an exchange of farming utensils for rice with the people around them. Then there was a great faminine in Egypt and the Akpafu could no longer find buyers. From that time they started to use their own utensils to cultivate rice themselves, with large success. When they could not find sufficient iron anymore and had limited access to land they started migrating to the Gold Coast and settled in what is now the Ashanti region and continued to cultivate their rice for their food security. Around 1750 they left there and came to Tsito (Peki) in Ghana. The Akpafu continued to cultivate rice and sometimes they were not able to harvest it because of the many conflicts with other ethnic groups. When the raiding for slaves started the Akpafu crossed the river Volta and settled at Akomufie where you can still find traces of melted iron. Then there was another war between the Ewe and the Akpafu and the Akpafu finally fled to the Todji Mountain and created Akpafu Todji that is still one of their villages today. After that a group of Akpafu continued to a mountian '*Tsokpé*' north of Todji to look for more iron. During that time their iron melting and the making of farming utensils as well as arms flourished and the Ewe as well as the Ashanti bought from them. The Akpafu that stayed at Todji focused more on rice cultivation on the hills. After that the Akpafu that went to Tsokpé returned and the Akpafu split up. Part of them went to the Danyi plateau in Togo where they met other ethnic groups such as the Akposso, before coming back to the Todji area because of the Ashanti war. During the year 1890 there was no rain and Efia Katani, a fetisch priest widely known in the area stated that the rain had not come because of the disturbance and influence of the Ashanti. During that drought all the stocks of rice were consumed and only a very small quantity of rice was left and people started to die of hunger. This is also the moment that people started to decent to the plains and rely on other crops such as yam. During a meeting the elder Togbui Efiakatani and the other elders decided that it was necessary to return to the adoration of the ancient gods of Egypt, Soudan and the big loop of the Nile River. These gods were abandoned during the many slave raidings that disturbed the Akpafu people. It was also decided that a large sacrifice of rice should be given to Amou Ra to which they used to give sacrifices on a mountain in Egypt. So they sacrificed their last rice to the local mountain *Limoikabemi* and two weeks later a large rain fell on the mountain and soon rice started to germinate on a large area on the mountain. This area had never been cultivated before. At harvest they sacrificed a large quantity of rice to the mountain of *Limoikabemi* that also became known as *Molito* [Siwu for Rice Mountain] and since then it is this mountain god that has to eat first before the people can eat. Nowadays these practices have almost vanished because of the Christian religion.

Summarising the two Ghanaian cases

Data from the Lolobi and Akpfu case studies show that the particular role rice cultivation occupies within their cropping system and community influences variety preferences and the trajectories of variety development.

Among the Lolobi, involved most in commercial rice production, a very different set of varieties is cultivated, and although preferences are still strongly influenced by the characteristics of their traditional African rice, the Lolobi people add any white variety that can bring them profit, even when it strongly deviates from their preferred red African rice. Asian white varieties such as Perfume, Adeisi and Kabila are popular and mainly serve a market demand. The very strong cultural significance of African rice seems to be part of a cultural stratum that creates local identity, cooperation and unity, but does not at all hamper innovation or the acceptance of other (Asian) varieties, but seems rather to stimulate it by creating focus and dedication. This focus and dedication is necessary within a liberal market economy where income from other domains and from cities, attracts youth and are a potential danger to the functioning of the Lolobi rice production economy. Young people are no longer dedicated to agricultural group work. It seems that for the Lolobi youth rice cultivation is now a rather unattractive business, even if it enables the strong cultural identity the older generation continues to value.

Among the Akpafu yet another pattern is observed. Although rice cultivation is a major occupation for the Akpafu, income from cacao, and as importantly, from other domains than agriculture, like income from city jobs, seem to make them leave the development of varieties to other groups more dedicated to its demands (such as the Lolobi). Therefore they easily adopt new varieties that have proven their potential elsewhere (like *Aworema*). The significantly lower rice yields in Akpafu, compared to Lolobi lowland output, also indicates that rice cultivation among the Akpafu is less important than a comprehensive strategy based on multiple income streams. Although the Akpafu largely cultivate red rice varieties, some white varieties are also cultivated alongside, representing about 14 % of their total rice production. The cultural significance of African rice, although less than in Lolobi, is still of some significance, and influences the adoption of new varieties, while constituting an important part of Akpafu identity.

In both Akpafu and Lolobi varieties promoted by the extension service are mostly neglected by farmers, because farmers are usually more knowledgeable about what suits them best and because the varieties provided are outperformed by farmer material.

The particular culture of red rice cultivation in the Ghanaian Togo Hills seems also to result in a connection of their production to an emergent demand for red rice in cities by an increasingly affluent middle class convinced of its nutritional benefits.

The Togolese Togo Hills

The case of the Ewe and the Ahlon

On the Danyi plateau cassava is the most important food crop (Table 7). Although rice only constitutes about 9% of the total food crop yield on the Danyi plateau, farmers confirm that rice is an important variation to their diet and about 75% of the farmers cultivate rice. Another very important reason to cultivate rice is that rice can relatively easily be stored and conserved for times when food is scarce, contrary to cassava and yam, which both need processing to flour for longer term storage. Rice used to be their principle food at the time insecurity drove them on to the plateau. The cruel rule of the King Agorkoli at the end of the 15th century (Cornevin, 1969; Quarcoopome, 1993) is often mentioned here by farmers. The data from the Sassanou village in the Ahlon area were taken together with those of the Danyi Plateau as no difference in farming system could be observed and the Ahlon villages belong to the Danyi prefecture. The Ahlon village Tinipé is even situated on the Danyi Plateau. The other four Ahlon villages Bogo, Denou, Ounadjassi and Sassanou are situated on the descent towards Ghana.

Remarkable are the very low yields for rice and maize for the Danyi Plateau area, which can be ascribed to the lower fertility of the soils but also to the more marginal role rice and maize play within the cropping systems, with priority to cassava and yam. Also important to note is that while only nine percent of the total production of carbohydrate crops is rice, three-quarters of the population cultivates the crop. That the area cultivated with rice is greater than that cultivated with cassava can be explained by intercropping; rice is most often intercropped with cassava and yam. This intercropping pattern is also practiced in the upland rice areas in the Lolobi and Akpafu areas.

***Table 7**: Estimation of the share of rice in relation to other carbohydrate crops on the Danyi Plateau Togo and the Ahlon village of Sassanou, average of the years 2006 and 2007, N=150 (survey 2008). Villages and population: Elevagno 2715, Dafor 493, Meampasem 839, Heheatro 412, Sassanou 790 (source: Population census Direction des Statistiques Agricoles, de l'Informatique et de la Documentation (DSID) Togo 1997)*

Crop	% production	% of the total area cultivated with carbohydrate crops	average field size (ha)	Dry yield (kg/ha)	% of farmers cultivating the crop
rice	8.7	33	0.32	494	75.5
maize	9.5	34	0.29	520	84.9
cassava	62.3	24	0.23	4800	77.9
yam	19.4	8	0.41	4320	14.9

On the Danyi plateau rice is a crop purely used for subsistence. African rice seems to be the only rice that thrives when no fertiliser is used, and farmers do not have means to acquire fertilisers. The about seven African rice varieties that make up the traditional *Boadekamo* in Akpafu and Lolobi are cultivated separately here, as respecting the differences in cycle length results into advantages in yield. This advantage is no longer valued by the Lolobi and Akpafu. Although all the varieties ripen at more or less the same time (November-December) because of photoperiod sensitivity, the optimal cycle length can be utilised by planting the varieties at different times; from the end of July to the end of September (the cycles vary from 2 to 4 months). For instance, the variety *Xleti Eve* (“two months” [Ewe language]) will ripen over four months if planted early (at the end of July), but this results in very large plants with few panicles.

During ceremonies and rituals for ancestors African rice is not used exclusively. Other crops such as maize, cassava and yam figure as well. The ‘symbol’ of the people of Danyi includes all the crops they cultivate and not the shape and form of a specific crop. Almost all farmers (146 out of 148) stated that it does not matter what kind of rice variety is used in ceremonies as long as it has been cultivated on their land. During in-depth interviews with a fetish priest and five other people familiar with performing funeral and marriage rites all informants stated at the outset that African rice is necessary. However afterwards they all state that the morphology of the plant is not important, it is only important that the rice is red and cultivated on their own land.

In a detailed semi structured questionnaire administered among 18 farmers all stated they would readily leave the traditional *glaberrima* variety if they could find a variety that yielded more. Without any problem this rice could then also be used within ceremonies. African rice, with its specific plant and seed characteristics, has not become a religious symbol, unlike among the Lolobi. Instead of a religious or cultural symbol the cultivation of African rice on the Danyi plateau has to be seen differently, as a longterm tradition within an agriculture dominated by cassava and yam. Instead of providing totemic identity in the Durkheimian sense, the cultivation of African rice should be seen as a communal practice that confers identity through the shared practice of its cultivation and therefore could be said to have cultural value in Mauss' sense of the term.

In short, the cultivation of rice is something that is part and parcel of the Danyi community but it has not taken on explicit cultural or religious significance. As we shall see in chapter 6, where a farmer experiment carried out in all the case study areas is described, the main criterion for rice selection by farmers on the Danyi plateau is ecological; it should be able to perform well in their ecology.

Although farmers already stated that they hardly sold their local rice there also appeared not to be a demand for it in the capital of Lomé .Within the markets in Lomé we could not find any people selling African rice from the Danyi plateau. Asking around at several markets and rice shops did not yield any result either. A demand for red rice, or healthy local rice, was not apparent, unlike the situation in Accra, where an open, liberal economy appears to have stimulated consumer interests in red rice as a health and gourmet product.

According to the farmers, as well as the government extension officers, the people on the Danyi plateau have never cultivated Asian rice. They say they have been growing *O. glaberrima* ever since they arrived on the Danyi Plateau. It is true that the region has been neglected by government programmes, and to this day no electricity is available, contrary to the Ghanaian villages in the Togo Hills. In colonial times agricultural officers seem not to promote or advise on rice cultivation, as they were mainly focused on the then major cash crops, coffee and cacao (TNAL 8APA/155). Around 2007 researchers from AfricaRice in Cotonou started field trials in farmer fields but to date none of this material has disseminated significantly among local farmers. This implies that there is more to it than just a lack of government extension work or a conservative and passive attitude among farmers when it comes to the variety portfolio. When talking to farmers they simply state that other varieties then the *O. glaberrima* do not grow well. During several group meetings in the different villages on the Danyi plateau farmers confirmed that they knew about other varieties and that they have occasionally been buying lowland rice, from for example Adeta, to eat but only very rarely do they try to sow these varieties since they are sure they would not do well on the Danyi plateau. *O. sativa* varieties are only cultivated very occasionally in the backlands. Table 8 shows to what extent each variety is cultivated. It can be seen that 90 to 95 percent of the rice cultivated is *O. glaberrima*. All the non-African rice varieties in table 8 are cultivated in the marshy backlands. This information is important not for the area sown, but for the evidence it provides that farmers have access to other varieties than *glaberrima*.

These Asian varieties are not only provided by the Togolese gouvernment extension service (Institut de Conseil et d'Appui Technique - ICAT-) but also by farmers themselves. Varieties provided by ICAT were named ICAT as many farmers did not know the variety name. Although ICAT has been providing lowland varieties to be cultivated in backland marshes, they only very recently became involved in the promotion of alternative upland material, mainly through research carried out by AfricaRice.

The data coming from the Ahlon village of Sassanou are added to those of the Danyi plateau as no difference in variety portfolio could be observed, and Sassanou also belongs to the prefecture of Danyi. In total seven different varieties of African rice are cultivated.

***Table 8**: Varieties and important characteristics and an estimate of their proportion within the total rice production on the Danyi Plateau (including the Ahlon Area): botanical group, pericarp colour, percentage of farmers cultivating the variety, percentage of the total rice production, percentage of the total area under rice cultivation, average field size and average yield per hectare. Bold numbers indicate the major varieties cultivated (Survey, 2008 among 135 farmers in the Danyi villages: Elevagno, Heatro, Meampaseam, Dafor and the Ahlon village Sassanou. For the year 2006, N= 93 and for the year 2007, N=134).*

Variety	botanical group	pericarp colour	% of total farmers cultivating the variety		% of the total production		% of the total rice cultivated area		Average fieldsize (ha)		Average yield (kg/ha)	
Year			2006	2007	2006	2007	2006	2007	2006	2007	2006	2007
Awinto	African	red/brown	**36.6**	**23.9**	**32.6**	**21.9**	**36.1**	**23.4**	**0.32**	**0.31**	**421**	**453**
Danyi moli	African	red/brown	**34.4**	**37.3**	**31.6**	**38.6**	**33.4**	**38.4**	**0.32**	**0.33**	**441**	**484**
Xleti Eto	African	red/brown	**21.5**	**22.4**	**27.5**	**21.9**	**22.7**	**21.8**	**0.34**	**0.31**	**565**	**484**
Xleti Eve	African	red/brown	2.2	5.2	1.6	5.1	1.9	5.1	0.28	0.31	409	485
Kpakpalipke	African	red/brown	1.1	0.7	1.1	0.6	1.6	0.7	0.50	0.31	320	384
ICAT	Asian	white	2.2	3.0	2.5	2.9	0.8	2.5	0.13	0.27	1400	565
Wuwulili	Asian (ind)	white	1.1	4.5	1.0	5.2	0.6	3.9	0.19	0.28	747	640
awuie	Asian (ind)	white/red	1.1	0.7	1.4	0.8	1.6	0.7	0.50	0.31	400	512
moli yibo	African	red/brown	1.1	1.5	0.7	1.3	1.2	1.7	0.38	0.38	267	347
khaki moli	Asian (jap)	white		0.7		0.4		0.6		0.25		320
yovo moli	Asian (ind)	white		0.7		1.4		1.2		0.50		600

The case of the Ahlon

The variety portfolio of farmers in the Ahlon area does not differ from that in the Ewe villages on the Danyi Plateau. This might be due to the limited availability of farmland and the fact that two of the other Ahlon villages are geographically situated close to the Danyi plateau. Tinipe is on the Danyi plateau proper and Bogo on the descent between Sassanou and Tinipe. Farmers also state that for security reasons they rely on varieties that are also cultivated on the Danyi plateau, and this way they are sure their crop will not fail. Another factor might be the role the *Adjafanugbabe* clan in Sassanou traditionally serving the god *Adjafa*. *Adjafa* is a supreme deity said to have been there since their forefathers left Nubia or revealed himself when the Ahlon stayed in Ile-Ife, the spiritual home of the Yoruba-speaking peoples in Nigeria (Ewe is taxonomically somewhat close to the Yoruba language).

Adjafa was traditionally known to protect the rice stocks, and balls of red rice flour were centrally made and ritually invested to be given out to everyone in the village to place in their granaries before filling them in order to protect the granaries and to function as a graduator to control the speed with which the rice was consumed. Brydon (1981) reports a similar system for the Avatime, where rice and its rituals also involved everyone in the village and connected people to the gods. The *Adjafanugbabe* clan in Sassanou is the clan charged with the task of serving *Adjafa* on behalf all of the Ahlon villages. These clan members are traditionally not allowed to eat white rice, as *Adjafa* only consumes and supports traditional red rice. Even today when a new chief is installed in any of the Ahlon villages three clan members have to be present and red rice *fufu* is prepared and eaten with bush meat.

The Ahlon also stated that they fought the Ewe when the Ewe arrived on the Danyi Plateau and that the Ewe drove the Ahlon to the edges of the plateau and that the Ewe used rice as bullets. This is a reason given why people in Tinipe say that they do not cultivate rice anymore, a story reinforced by the recent case of a politician who started a rice project in Tinipe. As soon as people came to suspect this project was mainly to promote the ruling political party it was abandoned by all farmers in the project, who then became aversive to further rice cultivation. Tinipe also has a very limited amount of farmland suitable for rice cultivation, as the local farmland is mainly rocky.

So given the limited economic opportunities, the heterogeneous environment around Sassanou, the connection to the Danyi Plateau, the small quantity of backlands and other suitable farm land for rice together with a tradition of *glaberrima* cultivation might be thought to have had the effect that the only local choice was to stick to African rice, or to abandon rice altogether. Yet as we shall see, this is too extreme a conclusion, for in chapter 3 it will be shown that the introduction of Asian and African farmer rice varieties from other West African countries was well received in this area, and most varieties actually performed very well in this environment, and better perhaps than farmers had expected.

Summarising the Ewe and Ahlon cases

Among the Ewe local rice production of almost exclusively African is mainly used for subsistence and although part of their tradition rice has little or no significance within cultural or agricultural practices. The presence of red and white Asian varieties in occasional marshy places shows also that farmers are open to try varieties different from their African rice. Farmers say they are even prepared to abandon their African rice if they encounter any other variety that performs better. Although farmers state that they like rice with a red pericarp this is not mentioned as an important criterion within the selection and development of new rice varieties. The morphology of the plant or seed type, or the color of the seed of African rice, seems to have little influence on the selection and adoption of new varieties.

No indications for an existing national demand for red (African) rice could be distinguished. A demand by the middle and upper class for red "healthy" rice as found in Accra, but could not be found in Lomé. Because of the more limited level of economic development in Togo the middle and upper classes are small, and wealth-related health issues such as Type-2 diabetes or high blood pressure do not yet attract widespread comment or attention.

TheAhlon, like the Akpafu and Lolobi are an ethnic minority, and share a similar history with these two other groups. They traditionally also prefer red rice but this does not prevent them from also cultivating white varieties like '*Yovo moli*' and '*ICAT*' in the very few marshy places available to them. But the cultural importance of red rice might assure that some red rice varieties might remain as part of their future rice seed development and selection strategy.

Conclusion

This chapter has given an indication of different trajectories of rice variety development within the Togo Hills. Among the Lolobi the cultivation of African rice is a part of an important cultural stratum that confers identity on rice producers. Here the characteristics of the traditional African rice provide important criteria for selection, development and maintenance of other rice varieties. These criteria seem to contribute to the diversity of the rice portfolio, as well as to innovation and adoption of new varieties, rather than hampering innovation and change. In Akpufa, where rice cultivation is less intensive, less white rice is cultivated, as rice is here mainly used for subsistence, and farmers prefer to consume red rice. However farmers also cultivate some white rice and pick up innovations quickly when they have proven their capacity. So here also we can conclude that farmer practices embedded in their cultural or historical context are little constraint on variety development and adoption.

Within the Togolese Togo Hills cultural considerations attached to rice are found among the Ahlon, but again this only seems to add to the purely pragmatic selection criteria of robustness and yield, and thus increases diversity, because here also farmers seem to try out any variety that can do well in their environment and conditions. Although the ecology of the Ahlon resembles that of the Ghanaian Togo Hills economic constraints and limited amounts of farmland seem to make farmers stick with the assurance African rice provides them, and therefore no other (Asian) varieties are used in the upland. For them the cultivation of Asian varieties in a few marshy places seems more lucrative than trying to further improve their upland cultivation by exploring other varieties.

Among the Ewe on the Danyi plateau farmers maintain the maximum of African rice varieties to benefit from differences in cycle length. The same strategy is no longer practiced by case study groups in the Ghanaian Togo Hills, where all African rice varieties are now cultivated together as one traditional upland landrace, *Boadekamo* [the rice of our people] because focusing on lowland cultivation provides more benefits. However where possible farmers try out other varieties and use marshy places to cultivate non-African rice varieties. This is because outside the marshes African rice varieties are outperformed by the African ones. Also here cultural factors and the tradition of African rice cultivation seem in no way to hamper innovation or variety development. Here farmers even stated that they would abandon all their African rice varieties if other varieties would perform better.

Although all the case studies show different trajectories of rice seed development they all seem part of a proactive attitude to changing social as well as ecological factors. Cultural factors and traditions combine with ecological and economic factors to contribute to trajectories of innovation, and thus assure the maintenance of a diverse set of rice varieties from which future innovations might emerge.

So in the context of strategies of improving food security via rice production system development in West Africa it seems relevant to take notice of these “mixed” strategies as well as the varieties that have sprouted from them. So rather than regarding cultural and social factors as being conservative and barriers to change they should be understood as part of an open trajectory of technical and social elaboration.

A clear alternative to focusing on the introduction of Nerica within the Ghanaian Togo Hills region (the strategy to date) the Ghanaian extension services should more take notion of the popular varieties *Viono* and *Aworema* and define with farmers how the cultivation of these varieties can be improved. And rather than focusing on the introduction of Asian varieties or Nerica hybrids the Togolese extension service might find more progress by introducing other farmer varieties of African rice, or by improving African rice.

Importantly, it is in the case study where cultural factors seem to be most developed and important for the maintenance of rice diversity and within rice seed development that rice cultivation is also most strongly entrenched within the liberal market economy. This is the case of the Lolobi. For small scale farmers acquiring income mainly by producing rice means hard work under harsh circumstances. To keep such an activity going within a liberal market economy framework - that offers many other and more enticing ways to make a living - strong symbols that provide meaning to the activity of rice cultivation seem most necessary. This speaks against the widely assumed idea that cultures and traditions, as well as rice diversity connected to them, are most likely to disappear there where people enter a modern market economy.

In ironic contrast, it is in the case study where farmers were the least incorporated within commercial rice farming - on the Danyi plateau - that farmers said that they would most readily give up all their traditional varieties if something better was provided. This also provides us with an important insight into how to organise successful extension. Creating change and improvement demands a culture of attention in which objects are infused with value and meaning. Such a culture demands an open cooperation with farmers, rooted in a culture of fascination for farming, diversity and experimentation. It is not because cultural and varietal diversity is good in itself but because this diversity provides the conditions for innovation and local adaptation to emerge.

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TNAL 8APA/155 Rapport sur la tournée faite du 21 juillet au 1 Aout 1932 par M. Mancion Chef du secteur des cultures arbustives dans le cercle de Klouto. Fait 15 aout 1932. Territoire du Togo, Sous le Mandat de la France, Service de l'agriculture secteur des cultures arbustives, No. 15

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Annexes

Annex 1:*Nutritional value of Viono rice: a comparison between a single milled an double milled sample. Single milled leaves more of the red pericarp on the rice grain. Source: Laboratory report by the Food Research Institute ghana P. O. Box M20 Accra Ghana.*

FRI (Food Research Institute) laboratory reference nr:CID No.04/52 Lab nr 089-090/04				
Date of analyses 8-4-2004 supervised by William Amevor				
Parameter	***Method***	***Unit***	***Results***	
			Single milled	Double milled
Moisture	AOAC 925.09 (2000) 17th ed.	g/100g	10.9	11.6
Ash	AOAC 923.03 (2000) 17th ed	g/100g	1.4	0.9
Fat	AOAC 920.39 (2000) 17th ed	g/100g	2.2	1.7
Protein	AOAC 984.13 (2000) 17th ed	g/100g	7.3	6.8
Carbohydrate	By difference	g/100g	79.2	79
Energy	Atwater factor	Kcal/100g	361.8	358.8
Phosphorus	AOAC 948.09 (1990) 15th ed	mg/100g	81.5	61.6
Calcium	AOAC 941.41 (1990) 15th ed	mg/100g	35.9	19.7
Iron	AOAC 945.50 (1990) 15th ed	mg/100g	2.6	1.7
Fibre	AOAC 955.29 (1990) 15th ed	g/100g	0.29	0.25

CHAPTER THREE

What is the role of culture in farmer variety development and selection? A study in the West African Togo Hills

Béla Teeken

Abstract

This chapter presents results of a number of field trials with farmer varieties designed to reveal the selection methods of farmers cultivating varieties of African rice in three different cultural and ecological settings within the Togo Hills in Ghana and Togo, a borderland known for its cultural and ecological diversity and long term dynamic socio-political history. 15 farmer varieties from 6 West African countries were evaluated among different ethnic communities. Rather than a regular farmer managed trial it was an evaluation of how farmers would organise an experimental trial. Farmers in the less dynamic economy of Togo organised their trial communally and mainly ecological factors were important in setting criteria for their variety selection, while farmers in Ghana organised their trial individually and cultural and religious factors connected to African rice were also important in setting criteria for variety selection. In all the three areas not one specific variety or a number of varieties of matching properties was selected, but rather a set of very different varieties used for different purposes. We argue that a dynamic long-term history of strategising within a borderland between several political economic powers have resulted in ecological and cultural differences and in farmers being alive to the potential of farmer varieties with properties able to serve various market demands, ritual purposes and home consumption needs. Here cultural and social practices can directly connect well-being and cooperation to technologies such as seed as such practices provide additional selection criteria that enlarge varietal diversity and appear to secure varieties that are versatile and robust.

Keywords: Farmer varieties, Culture, *Oryza glaberrima*, *Oryza sativa*, Seed system

Introduction

The southern Ghana-Togo border is marked by the TogoHills. The study area, about 200 kilometers north from the coast, covers both the Ghana and Togo side of the Togo Hills. African rice (*Oryza glaberrima*) has a different position in the farming systems on each side of the border. On the Ghana side rice production is incorporated into a liberal market economy and rice is cultivated in both upland and lowland conditions. African rice has a minor but persistent place in this area and is grown mainly for cultural reasons. On the Danyi Plateau, on the Togo side of the border, African rice is the only rice cultivated and consumed locally, as marketing opportunities are few, relating to the more centrally planned and less dynamic economy in Togo. This chapter addresses the question how these distinct cultural conditions have an impact on farmers' preferences for different farmer varieties of African or varieties related to African rice. Results from the genetic and morphological analysis (Chapters 4 and 6, Nuijten *et al.* 2009 and Mokuwa *et al*. 2014) show that recent socio-cultural selection pressures within African rice restrict genetic diversity while this is not observed for Asian rice (*Oryza sativa*) and farmer hybrids. African rice as a full product of farmer agency, however, continues to set pathways and criteria for the development and selection of Asian rice varieties, and therefore nurtures the diversity within Asian rice varieties and has caused the appearance and further selection of natural hybrids between Asian and African rice. The findings from Chapter 5 (Mokuwa *et al*. 2013) show that African rice is robust, referring to a physiological capacity to adjust to different (often unfavourable) ecological conditions. Robustness is an important characteristic for rice varieties in areas where growth conditions are non-uniform and sub-optimal. Although ecological conditions and physiological characteristics are important, it is known that cultural preferences also play a role in variety selection. Experiences with participatory varietal selection show that cultural preferences, once identified, can be included in breeding programs (Almekinders *et al*., 2009; Bentley *et al*. 2010). However, cultures are not fixed entities and change due to community dynamics and external influences. Moreover, different communities with distinct cultural preferences may exist in the same geographical area. Hill regions typically show such cultural diversity (see Chapter 2). The occurrence of similar African rice varieties across the Togo Hills thus suggests a combination of physiological robustness and wide socio-cultural suitability.

This chapter presents results of a number of experiments designed to reveal the selection methods of farmers cultivating varieties of African rice in three different cultural and ecological settings within the Togo Hills. On the Ghana side this includes both lowland- and upland rice cultivation by the Akpafu ethnic group - a group for which customs and rituals related to rice and food are disconnected from religion due to the influence of the Bremen Presbyterian mission, a religious organisation that prohibited local religious practices - and the Lolobi ethnic group who maintained and developed specific rituals and customary rites tolerated by the Catholic mission in recent centuries. The third site is on the Danyi plateau in Togo, an area inhabited mainly by Ewe and a minority of Ahlon, who both grow rice varieties from the African rice species in upland conditions, and no Asian rice. Within the customs and rituals of the Ewe, rice does not have a special function, and is represented just like other food crops. Also here the Catholic mission tradition has tolerated local customs and beliefs, although for most local people the practices of the Catholic faith have become stronger than the religious observance of customary rites.

The Akpafu and the Lolobi cultivate mainly farmer varieties (and few modern variaties) within upland and lowland ecologies. Around 90 and 70 percent respectively of (Asian) rice grown by these two groups has a red pericarp, and in this respect resembles *O. glaberrima*. On the Danyi Plateau farmers cultivate African rice in upland ecologies, and all types have red pericarp. No lowland ecologies are available to them. Only very few *glaberrima* varieties exist with a white pericarp (see Gross *et al.* 2010), and so far is known none of these are found in this area. Akpafu farmers use the lowland (wetland) ecologies that are present around their villages for rice cultivation. Around the Lolobi villages lowland ecologies are rare and therefore they practice lowland cultivation about 30 km south of their villages, around the villages of W’egbé and Goli Kwati, where they rent land for this purpose. During the growing season the Lolobi migrants set up temporary shelters next to their rented wetlands.

Many West African farmer rice varieties, and especially African rice varieties, are the outcome of farming under dynamic social and economic conditions. The variety development in the Ghanaian Togo Hills can be seen as a continuation of the cultivation of African rice, since many Asian farmer varieties in that region resemble African rice in pericarp colour, as well as also having the desired characteristic associated with African rice of 'heaviness on the stomach' (they digest slowly), while the Ewe on the Danyi plateau still only cultivate African rice. Although differentiated culturally the distinct areas within the Togo hills share a history of dynamic social and economic conditions on the frontiers of pre-colonial African states such as Ashanti. It is therefore hypothesised that farmers will have a wide interest in other farmer varieties of African rice, or Asian varieties showing some resemblance to African rice, irrespective of the different cultural and ecological settings within the Togo Hills. In effect, therefore, the hypothesis presupposes that a shared history of cultural dynamics is more determinative within variety selection than the localised cultural practices that exist within the Togo Hills. This is due to a shared history of relocation in these frontier refuges. The farming systems of poor farmers in hazard-prone and politically insecure environments in West Africa are often “portable” (Richards, 1995). In this chapter, therefore, we argue that farming communities with a history of uncertainty might still set criteria for crop type selection in accordance with a need for portability and rapid relocation opportunities.

Materials and Methods

The ecology of the area

The Togolese Togo Hills

The soils on the Danyi Plateau in Togo are known to be poor and acidic, as they are strongly weathered. The government Institute Togolais de Recherche Agronomique (ITRA) classifies the soil on the Danyi Plateau as ‘ferrallic soils with concretions’ which are chemically poor and acidic (pH between 5.17 and 5.52) (see also Leveque, 1965) for the villages Dafo, Meampaseam and Hiheatro, and ‘young soils with little profile development (lithosols) and strongly to moderately colluvial, that are very poor in phosphate and moderately acidic, for the village of Elevagnon. The soil in Ahlon village of Sassanou, downhill towards Ghana, is classified as “unweathered mineral soil” with at the foot of the hills colluvial or lithic soils, with green vegetation even during the dry season offering small patches of fertile soil (ITRA, unpublished). Given that the soils on slopes are often poor farmers make use of these small patches of fertile soil where they can.

Rainfall in the Togolese Togo Hills on average measures about 1650mm per year, a little more than in the Ghanaian Togo hills, as the higher mountains induce rainfall. The Danyi Plateau is 700 to - 950 m above sea level. The Ahlon area is in terms of height situated between the lowland Lolobi-Akpafu area and the Danyi Plateau, at around about 400 m above sea level.

The Ghanaian Togo Hills

Ethnic minorities in Ghana like the Akpafu and the Lolobi also (in the days of insecurity) used to rely on mountainous soils on often steep slopes, and small plateau areas, but nowadays have transferred most of their rice cultivations to the intra mountain basins and plains where they cultivate rice on lowlands and on hydromorphic soils in areas that are more easily accessible. The soils of these intra-mountain basins are classed as dystric plinthosols.

Rainfall in the Ghanaian Togo hills on average measures about 1500 mm per year. The Lolobi and Akpafu areas are situated at about 220 - 240 m above sea level.

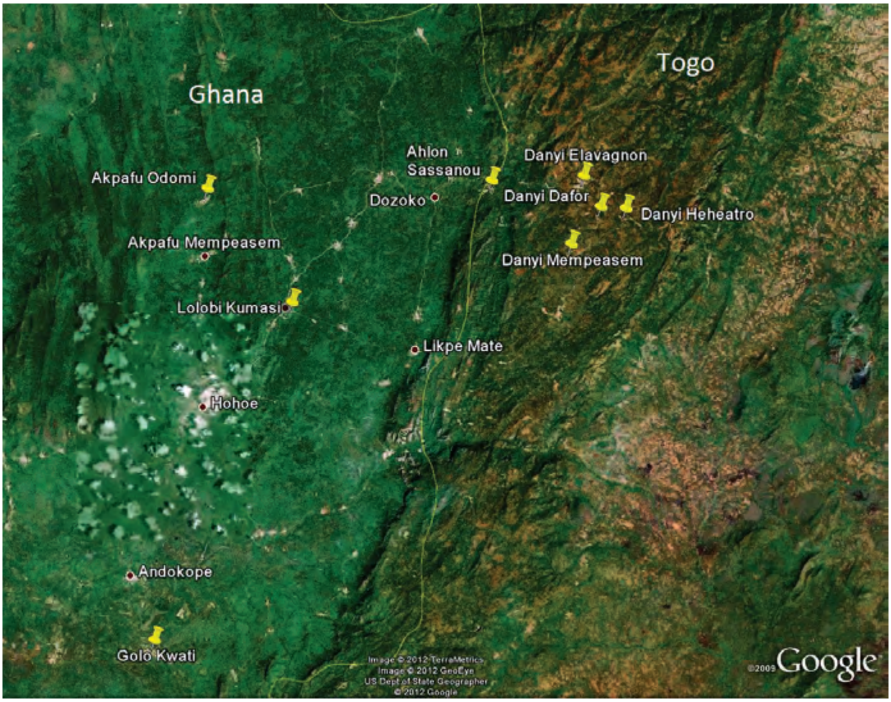

***Figure 1**: Map of the research area. Main case study villages are indicated by pushpins. The Danyi villages are situated on the Danyi Plateau, shown to be part of a mountain range that runs from southern Ghana to northern Nigeria. The major Western edge of this mountain range coincides with the border between the Ghanaian and Togolese Togo Hills.*

Farmer experimentation

The varieties for farmer experimentation were collected in farmers' fields in seven West African countries in 2007 and 2008: The Gambia, Ghana, Guinea, Guinea Bissau, Senegal, Sierra Leone and Togo. They were a selection from the set of farmer varieties listed in Nuijten *et al.* (2009). Selection criteria included that the varieties were popular among farmers and had characteristics in common with African rice, such as pericarp color or shared genetic background. Special attention was given to four farmer hybrids, now known to be crosses of *Oryza sativa* and *Oryza glaberrima*, and therefore presumably evolved in farmer fields and genetically constitute a distinct botanical group (Nuijten *et al*. 2009; Mokuwa 2014). As farmers in Togo were very curious about the varieties cultivated by their Ghanaian neighbours some extra Ghanaian varieties were included in the farmer experimentation trials as well. The experiment was not a 'farmer managed trial' as normally understood by plant breeders (where the experimental protocol has been set by researchers) but was an 'experiment on how farmers would do an experiment'. Thus, for example, observing the way farmers chose to organise the field trials was part of the set-up of the study. As a result the field trials were managed differently in each area. The results and discussion section evaluates these differences. The following section summarises the practical organisation in each of the areas.

It was proposed that each farmer would try out two or three varieties. In total, 13 to 14 farmer varieties were tested in each village (Table 1). *Nerica 1* was added as a reference variety because it had been promoted actively by the Ghanaian Ministry of Food and Agriculture, and more recently on the Danyi Plateau by the Africa Rice Center in cooperation with the Togolese Government extension service, Institut de Conseil et Appui Technique (ICAT). The idea was to give each variety to two farmers so that two replications per village would be obtained. Farmers were chosen from those explicitly showing interest in cooperating with the experiment. Traditionally both men and women work in rice; therefore men and women were included in each group. Table 1 shows the varieties planted in the trials and some of their characteristics. Pericarp colour is mentioned, as it was an important trait especially for the Akpafu and Lolobi farmers. The assigned variety numbers (Table 1, col. 1) correspond to the numbering of the varieties reported in Nuijten *et al*. (2009), this thesis, chapter 4, and Mokuwa *et al*. (2014), chapter 6.

***Table 1**: Varieties used in the farmer experimentation*

Nr.	Botanical group	Sub cluster botanical group	Variety name	Pericarp colour	Origin
125	*glaberrima*		*Danyi Molni*	red/brown	Togo
249	*glaberrima*		*Malaay*	red/brown	Sierra Leone
318	*glaberrima*		*Sali Fore*	red/brown	Guinea
402	*glaberrima*		*Wansarang*	red/brown	Guinea Bissau
164	hybrid	*Unclassified*	*Nerica 1*	white	Ghana
426	hybrid	*4-1erect*	*Untufa*	red	Guinea Bissau
450/30	hybrid	*4-2*	*Binta Sambou*	white	Gambia
460/462	hybrid	*4-2*	*Madina Wuleng*	red	Senegal
489/59	hybrid	*4-2*	*Barafita*	white	Gambia
102	*indica*		*Aworema*	red	Ghana
128	*indica*		*Viono tall*	red	Ghana
130	*indica*		*Zomojo*	white	Ghana
349	*indica*		*Saidou Gbeeli*	red	Guinea
141	*japonica*		*Aqua Blue*	white	Ghana
131	*japonica*		*Khaki*	red	Togo

Farmer experimentation in the Togolese villages on the Danyi Plateau and in one border village representing the Ghanaian Togo Mountain ecology, together with the one trial in Lolobi were more uniformly managed and this allowed for a statistical analysis of the measured parameters. Table 2 shows the measured parameters, the methodology of assessment and the trials in which they were measured. The damage by soil acidity was measured by the extent to which the plants suffered from brown spots. This plant disease is known to manifest itself when nutrient availability is hampered. An acid soil makes available less of the crucial nutrients Nitrogen, Phosphorus and Potassium. Farmers, as well as ICAT extension officers, stated that plants not resistant to the acid soil on the Danyi Plateau more readily suffered from brown spots, and that the brown spots disappeared when the acid soil was neutralised with lime.

To evaluate plant growth and development with farmers each plot was evaluated with all members of the group that managed the field trial. In Golo Kwati, six farmers who regularly visited the trial were asked to evaluate the varieties, as the trial was managed mainly by one farmer. Two weeks before panicle initiation, farmers judged the varieties on their plant growth and development, thus facilitating a judgement on growth and development without knowing the result of the reproductive stage and the harvest. In so doing the potentialities that farmers can read from the growth and development were included more accurately. Plant growth and development were evaluated on a scale from 1 to 10 for each plot by all members of the group, and in case of the Golo Kwati trial by the six farmers that most regularly visited the trial.

After harvest all members of the group were asked to name their favourite varieties and the reasons why.

In Sassanou the group members and some additional people who regularly visited the field and occasionally helped out decided to hold a meeting and together made a list of their favourite varieties.

In Golo Kwati the Lolobi farmer who managed the trial took many farmers to the trial. Later every variety was judged on the basis of the percentage of farmers liking that variety. A total of 29 farmers were asked to give their opinion. These were all farmers regularly visiting the field and included those that evaluated the field about 2 weeks before panicle initiation. During a meeting with these 29 farmers the varieties were evaluated and a list of characteristics for each variety was made together with the farmers that chose that variety. This list was an outcome of a discussion among these farmers. The discussion was led by the farmer who managed the trial.

As the ecological conditions in the four villages on the Danyi Plateau (Elevagnon, Meampeaseam, Heheatro, and Dafor) are similar the trials in these villages were considered as replications to allow for better statistical evaluation. The ecology in Sassanou, being halfway downhill from the Danyi Plateau, is different, as suitable soils are less abundant but more fertile. The ecology in Golo Kwati in Ghana is also different. That is why the trials in these last two villages were dealt with separately. Table 3 shows the characteristics of the trial sites.

***Table 2**: Measurements performed in the trials*

Parameters	**Indication on methods of measurement**	**Type of determination**	**Trials where parameters were measured**
Acidity damage/brown spots	Measured by estimating the percentage of the leaf area damaged (brown spots on the leaves) 1 = 1 to 10 3 = 11 to 30 5 = 31 to 50 7 = 51 to 75	Visual assessment of the whole plot	Dafor, Elevagnon, Heheatro, Meampeasem, Sassanou
Nitrogen status*	Estimated from -2 to +2 using a colour chart looking at the tip of the youngest fully expanded leaf. -2 = too light -1 = slightly light 0 = normal 1 = slightly dark 2 = dark	Visual assessment	Dafor, Elevagnon, Heheatro, Meampeasem, Golo Kwati (Lolobi)
Panicle exsertion*	Extent of coverage of panicle by flag leaf sheath (%) 1 = 0 3 = 1 to 10 5 = 11 to 25 7 = 26 to 40 9 = above 40	Measurement	Dafor, Elevagnon, Heheatro, Meampeasem, Sassanou, Golo Kwati (Lolobi)
Plant height (cm)*	Measured from the base of the plant to the tip of the panicle of the main tiller	Measurement	Dafor, Elevagnon, Heheatro, Meampeasem, Sassanou, Golo Kwati
Panicle length (cm)*	Measured from the base to the tip of the panicle of the main axis	Measurement	Elevagnon, Sassanou, Golo Kwati (Lolobi)
Number of tillers*	Total number of tillers per plant	Count	Dafor, Elevagnon, Heheatro, Mempeasem, Sassanou , Golo Kwati
Plot yield (kg ha^{-1})	Weight of the yield from the inner rows of the plot	Measurement	Dafor, Heheatro, Meampeasem, Golo Kwati (Lolobi)

*Measured on 10 plants randomly selected from the inner rows.

***Table 3**: Characteristics of the trial sites*

	Dafor (Ewe)	Elevagnon (Ewe)	Mempeasem (Ewe)	Heheatro (Ewe)	Sassanou (Ahlon)	Golo Kwati (Lolobi)
GPS coordinates	N 7.25668 W 0.72547 m asl 861	N 7.27919 W 0.70410 m asl 777	N 7.24129 W 0.70709 m asl 785	N 7.26384 W 0.73131 m asl 875	N 7.27679 W 0.65478 m asl 381	N 7.00589 W 0.45475 m asl 161
Ecology	Upland	Upland	Upland	Upland	Upland	Upland
Soil characteristics pH (water) OC% total N g kg^{-1} ppm Meh P sand% clay% silt% soil type	 5.3 3.8 0.48 50.2 77 12 7 Sandy loam	 4.8 5.5 0.8 7.0 64 18 10 Sandy (clay) loam	 4.8 1.3 0.7 5.6 75 16 6 Sandy loam	 4.9 3.3 0.42 6.7 69 16 8 Sandy loam	 5.6 5.1 1.08 5.3 61 12 23 Sandy loam	 6.1 3.3 0.86 97.5 52 10 32 Loam
Background of experiment sites	At least 5 years of fallow Previous crops (successively): rice, intercropped with cassava (*Manihot esculenta*)	At least 5 years of fallow Previous crop: maize (*Zea mays*)	At least 3 year fallow Previous crop: maize (*Zea mays*)	5 years fallow Previous crop: maize (*Zea mays*) intercropped with cassava (*Manihot esculenta*)	3 years fallow Previous crops: rice	5 years of follow Previous crops; legumes: tomato (*Solanum lycopersicum*), eggplant (*Solanum* spp.), pepper (*Capsicum* spp.)
Average annual rainfall (mm)	1700	1700	1700	1700	1700	1500
Duration rainfall (months)	6 to 7	6 to 7	6 to 7	6 to 7	6 to 7	6 to 7
General observation		Birds ate all harvest.	Some damage by rabbits within the first three weeks. Only leaves were damaged, no plants uprooted.		Very good growth. All plants bore panicles only birds ate all grains in one day, just before harvest.	Good growth and germination
Trial set-up dates Sowing	27 June 2008	24 June 2008	27 June 2008	28June 2008	30 June 2008	18 July 2008

Results

Management of farmer experimentation

Togo

The strategy followed during the farmer experiments in Togo was different from the one in Ghana. Farmers in Togo were very interested in varieties from Ghana, but apart from that they were also very open to the other varieties presented, and were highly motivated to try out all of them, even if they looked like one of the seven varieties of African rice that they already cultivated.

Farmers in all villages in Togo immediately decided to try out the varieties in a communal field in which they would work as a group.

In Togo a technician of the government extension service (Institut de Conseil et d' Appui Technique - ICAT-) who was also a native of the area became very interested in the idea of trying out the set of farmer varieties, and this resulted in official cooperation with his organisation: the director of ICAT was approached and asked for permission to carry out the experimentation and permission was granted. In contrast to the Ghana government extension service the Togolese extension service was very involved in what farmers were doing, especially because of the highly-motivated technician in charge. He often stated how important it was to do something concrete for the farmers in his area, and moreover something in line with what they were capable of doing, and willing to do. This resulted in a very smooth horizontal cooperation with extension staff and farmers. Rather than making money by jobs on the side - many ICAT employees often complained about unpaid salaries - the technician in charge saw the development of agriculture in his region as a mission and passion, and this attitude inspired and was shared by other ICAT workers he influenced. When he learned about my objective to try out farmer varieties from other West African countries he was very pleased and said that, that was exactly in line with what ICAT was doing. Also the general director of ICAT was very positive about the research proposal and supported the activities to be carried out on the Danyi Plateau. When farmers started out with the experiments no judgements on the seed, nor suggestions or remarks about the varieties to be incorporated were made.

Ghana

In Ghana the government extension service of the Ministry of Food and Agriculture (MOFA) was informed about the research. However it showed little interest, as staff was basically concerned with the promotion of Nerica rice, and this undermined interest in the local varieties. Although some technicians initially showed some interest it did not result in any cooperation with them. One technician who was promoting Nerica in Akpafu Odomi once invited the researcher to a meeting to talk about his and MOFA's activities, but when the researcher arrived at the meeting he was sent away with the announcement that the meeting was for staff only. While ICAT was no less hierarchical than MOFA in organisation, in practice MOFA seemed much more vertical and more detached from the farmers' culture and practices. Farmers in Ghana also stated that Nerica rice - and agricultural extension in general - had not benefitted them, as their own methods and varieties were superior to the ones that were being promoted. Also farmers often made ironic remarks about extension officers using their position for their own benefit, such as using government vehicles to collect firewood and other goods in villages. Farmers in Togo never made such remarks in the researcher's hearing.

In Akpafu and Lolobi in Ghana, farmers preferred to test 3 to 4 varieties individually, and farmers sometimes had to be convinced of the benefit they might get before they could commit to cooperate. In the Akpafu area farmers also had to be convinced that some of the *glaberrima* varieties from other countries would be different from the ones they already knew, even if they looked similar. For the Akpafu farmers the experimentation was seen as mere additional work and given little priority, reasons why trials were often neglected and sowing was very late: after all the other farm work had been done.

When comparing farmer experimentation in Akpafu and Lolobi it can be concluded that farmers in Lolobi were more motivated than those in Akpafu. All the trials carried out in Lolobi were dealt with seriously, and farmers remained motivated. Even when trials could not be maintained because of unforeseen circumstances, the results of what was left and the results of other farmers' experiments were evaluated with high interest. Importantly, one individual experimental field trial by a Lolobi farmer grew out to become a trial visited by many Lolobi farmers. In this last trial all 14 varieties were included, but the variety *Danyi Molni* was replaced by the *japonica* variety *Khaki*, found with only one farmer in Togo but of great interest to the Lolobi farmer organising the trial, because of its distinct khaki brown husk colour. Other farmers compared the remarkable husk colour of *Khaki* with the remarkable husk colours that are found in *Boadekamo*: from straw, to coffee, as well as black. *Boadekamo* is actually a mixture of six to seven varieties of African rice (Teeken *et al*. 2012). To Lolobi farmers the variety *Danyi Molni* from Togo was similar to the *Boadekamo* African rice, and therefore the farmer who organised the trial was more eager to incorporate *Khaki*.

Khaki actually seems to originate from Ghana, as the woman who was cultivating it on the Danyi Plateau said that she got it from Danyi people who installed themselves around N'kwanta Ghana mainly cultivating lowland rice. However the variety was looked for in that area but could not be found.

The Lolobi farmer initially doubled the trial as he also set up a separate trial in a lowland ecology in Golo Kwati. This trial was set up using a seed bed of which the seedlings were later transplanted to the trial. However, more than three quarters of the trial was destroyed by rodents (mice) one week after transplanting.

Teeken *et al*. (2012), chapter 7 (this thesis), and Chapter 2 (this thesis) show that the Lolobi are known in the region for their innovation in variety development and selection, and that rice occupies a special position even within ancestral and religious practices. They also have invested more to be able to continue their lowland cultivation, as they do not have lowlands close to their village but travel south to the Golo Kwati and Wgbe to undertake lowland cultivation. Therefore, there is a rich matrix of culture around rice innovation in Lolobi, helping to explain the interest in the experiment that emerged. Although this interest was initiated by one farmer it soon grew to be a hub that included more farmers.

These results show how the difference in not only ecology but also in socio economic and social context influenced the way rice cultivation was performed and variety selection took place. It is interesting that although rice on the Danyi Plateau only constitutes 9% of the total area of carbohydrate crops (Chapter 2) against 45% and 35% for the Akpafu and Lolobi, respectively, this was not a measure at all of local motivation and interest to cooperate with the experiment. More than food security other aspects of material self-interest might be at stake.

Farmer experimentation

Figure 2-7 show the agronomic and physiological variables measured during the farmer experimentation for the Danyi Plateau (Ewe), Sassanou (Ahlon) and Golo Kwati (Lolobi). The data for the Danyi Plateau are statistically strongest. On the Danyi Plateau the variety *Sali Fore* and the local variety *Danyi Molni* yielded highest and yielded significantly more than non-glaberrimas.

On the Danyi Plateau none of the indicas (*O. Sativa*) from Ghana (*Viono, Aworema* or *Zomojo*) yielded, and all farmers concluded that these varieties needed to be cultivated in more hydromorphic or lowland ecologies. Apparently even the upland ecology in Ghana

(Golo Kwati) was also not meeting these more humid requirements as these varieties did not yield there either. They did yield in Sassanou, although the harvest was eaten by birds just one day before harvest. The specific hill ecology halfway down the steep descent from the Dany Plateau offered enough humidity and nutrients to make all varieties yield. Although the yield could not be measured because of the bird damage, it can be said that if not for this factor the Sassanou experiments would almost certainly have shown the highest yields. The Pearson correlation between yield and plant height ($r= 0.547$; $P < 0.01$) and yield and panicle exsertion ($r= -0.239$; $P < 0.05$) are significant and the lowest values for panicle exsertion and the highest values for plant height can be found in Sassanou, suggesting that the ecology in Sassanou was the most favourable of the three locations. Also observations in the field support this, since all plants were very well developed and all bore panicles, even *Zomojo.* Annex 1-3 show the outcome of the statistical analysis. *Viono* cultivation within uplands was also noticed within similar upland conditions in Lolobi, Akpafu, Buem, Likpe and Avatime areas within the Togo Hills.

Sali Fore shows the best exsertion as it shows the lowest values, but statistically not different from those for *Danyi Molni and Saidou Gbeeli*. The next best panicle exsertion was observed for *Danyi Molni*, the remaining glaberrimas *Malaay* and *Wansarang* together with the hybrids *Untufa, Madina Wuleng* and *Nerica 1* as well as the *japonica Aqua Blue*. The indicas (that hardly produced any yield) showed the lowest values for panicle exsertion.

The resistance to acidity was the best for *Sali Fore* although the result is not statistically different from all the other varieties except for the *glaberrima Wansarang*, the hybrids *Untufa* and *Binta Sambou*, which showed a significantly stronger response to acidity.

Sali Fore showed the highest N status but this was not statistically significant when compared to the glaberrimas *Danyi Molni* and *Wansarang*, as well as the hybrids *Madina Wuleng Nerica 1* and the indicas *Saidou Gbeeli*, *Aworema* and *Zomojo.* Remarkable is the relatively good N status of some of the indicas, even though they did not yield at all.

On the Danyi Plateau the *indica* varieties showed the highest tillering, with no statistical difference from the two glaberrimas *Sali Fore* and *Danyi Molni* as well as the hybrid *Binta Sambou*, even though the indicas yielded almost nothing on the Danyi Plateau. This supports the finding in (Mokuwa *et al*. 2013) about the strategy followed by the indicas; the higher the stress conditions the stronger the tillering.

In general the glaberrimas, *Sali Fore*, *Danyi Molni* and *Malaay* performed best. Apparently not all glaberrimas do well, as *Wansarang* performed poorly. It is also worth noting that the farmer hybrids did not do less well than the *Nerica* in this experiment. The indicas *Aworema*, *Viono* and *Zomojo* are not suitable to be grown on the Danyi Plateau, but seem suitable to certain locations in the Ahlon area. This confirms the findings by Mokuwa *et al*. (2013) who stated that *Viono* and *Aworema* are to be grown in certain niches, specifically, the more hydromorphic part of the upland ecology.

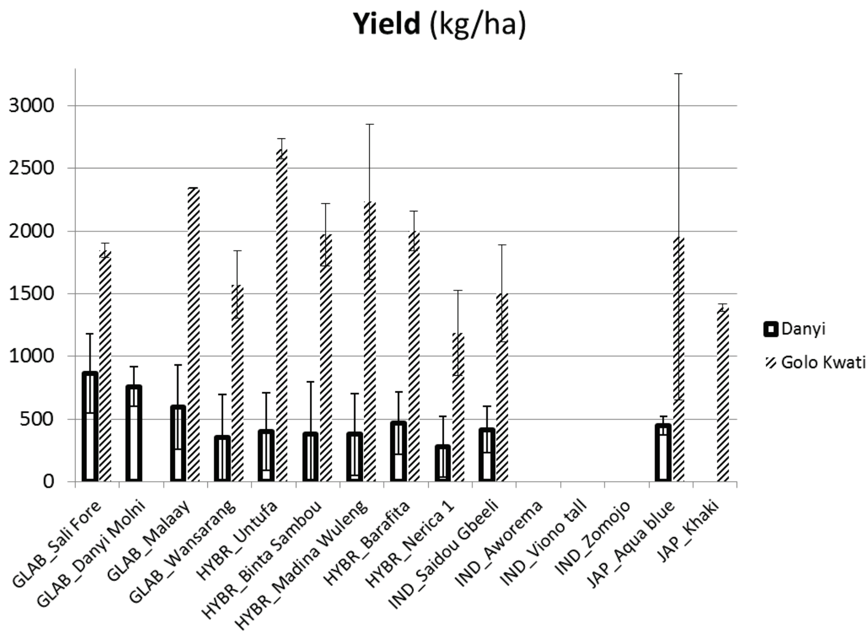

Figure 2*: Average performance of the 15 varieties used in the farmer experimentation for yield, in four Togolese villages on the Danyi Plateau: Danyi Elevagno, Xexatro, Dafor, Meampaseam and one village in Ghana: Golo Kwati (Lolobi). GLAB: glaberrima; HYBR: interspecific hybrid; IND: indica; JAP: japonica*

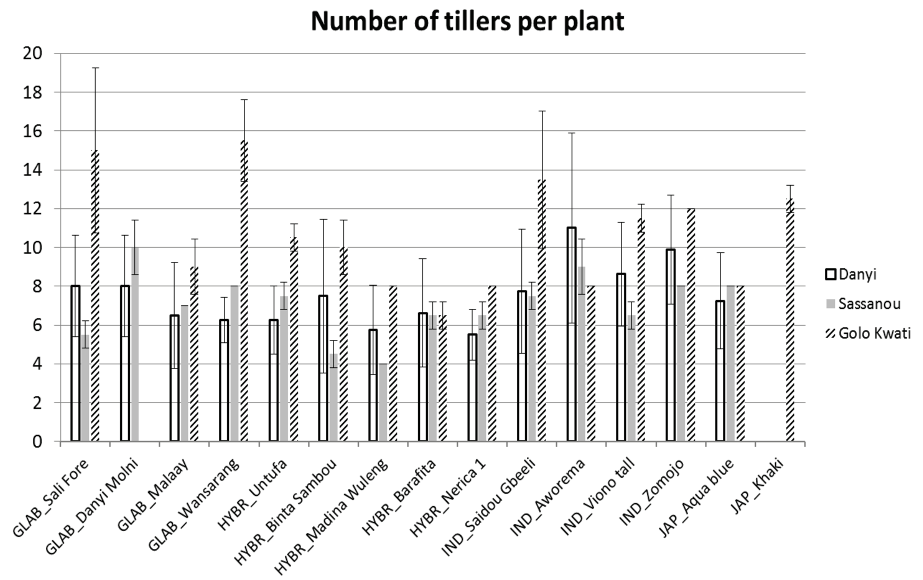

Figure 3*: Average performance of the 15 varieties used in the farmer experimentation for number of tillers in four Togolese villages on the Danyi Plateau: Danyi Elevagno, Xexatro, Dafor, Meampaseam, one village in the Ahlon Area: Sassanou and one village in Ghana: Golo Kwati (Lolobi). GLAB: glaberrima; HYBR: interspecific hybrid; IND: indica; JAP: japonica*

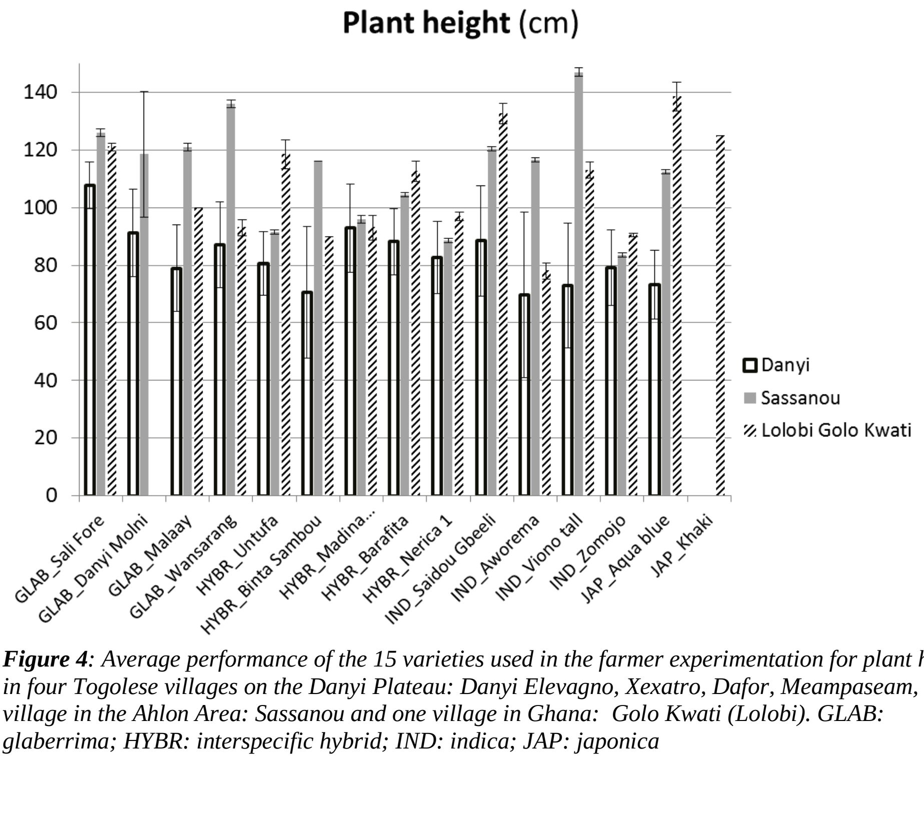

Figure 4*: Average performance of the 15 varieties used in the farmer experimentation for plant height in four Togolese villages on the Danyi Plateau: Danyi Elevagno, Xexatro, Dafor, Meampaseam, one village in the Ahlon Area: Sassanou and one village in Ghana: Golo Kwati (Lolobi). GLAB: glaberrima; HYBR: interspecific hybrid; IND: indica; JAP: japonica*

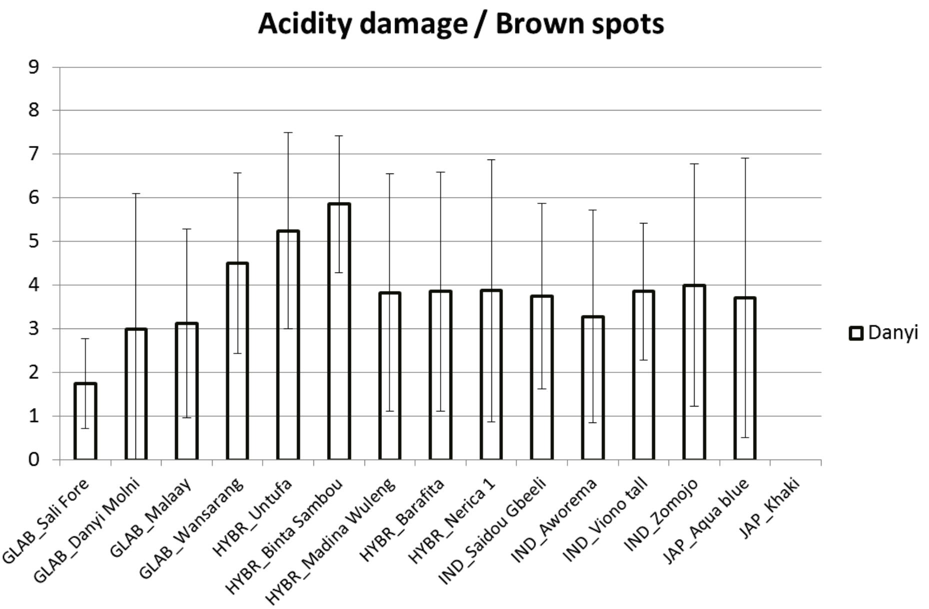

Figure 5*: Average performance of the 14 varieties used in the farmer experimentation for acidity damage/brown spots in four Togolese villages on the Danyi Plateau: Danyi Elevagno, Xexatro, Dafor, and Meampaseam. GLAB: glaberrima; HYBR: interspecific hybrid; IND: indica; JAP: japonica*

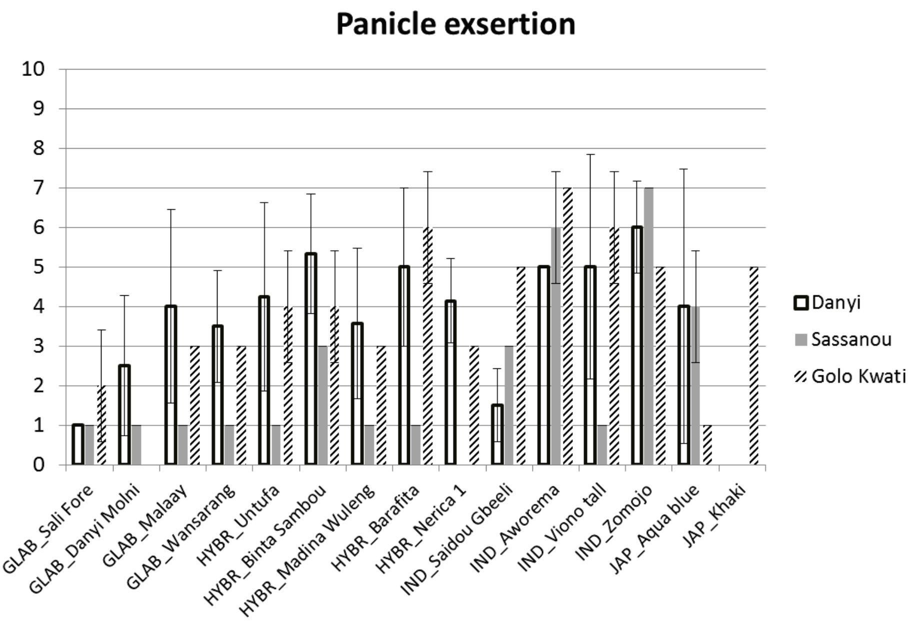

Figure 6*: Average performance of the 15 varieties used in the farmer experimentation for panicle exertion in four Togolese villages on the Danyi Plateau: Danyi Elevagno, Xexatro, Dafor, Meampaseam, one village in the Ahlon Area: Sassanou and one village in Ghana: Golo Kwati (Lolobi). GLAB: glaberrima; HYBR: interspecific hybrid; IND: indica; JAP: japonica*

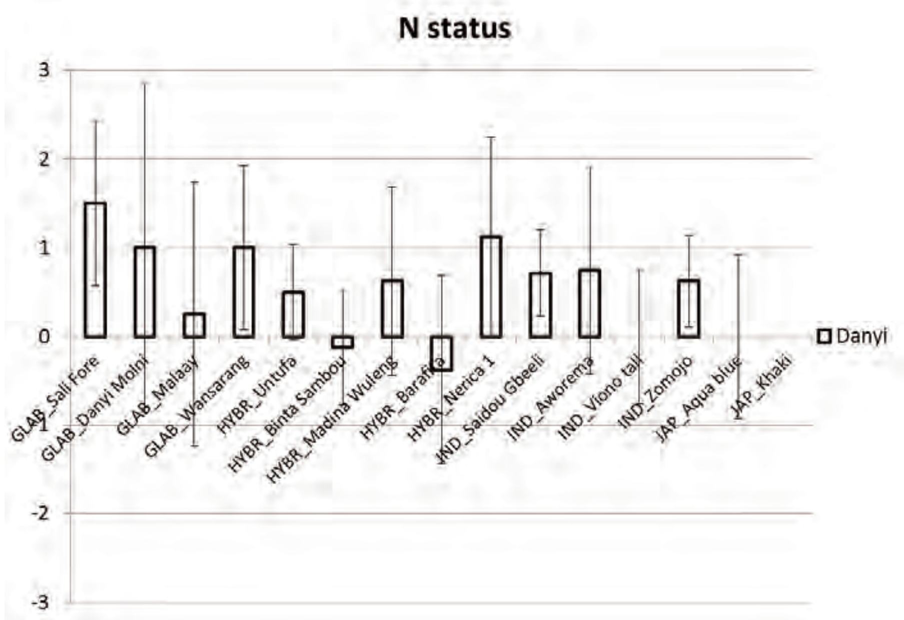

Figure 7: *Average performance of the 14 varieties used in the farmer experimentation for nitrogen status in four Togolese villages on the Danyi Plateau: Danyi Elevagno, Xexatro, Dafor and Meampaseam. GLAB: glaberrima; HYBR: interspecific hybrid; IND: indica; JAP: japonica*

Farmers' evaluation of growth and development

Figure 8 shows the evaluation by farmers of the growth and development of all varieties just before panicle initiation on a scale of 1 to 10. Annex 1 shows the outcome of the statistical analysis in the sixth column named “farmers’ evaluation”.

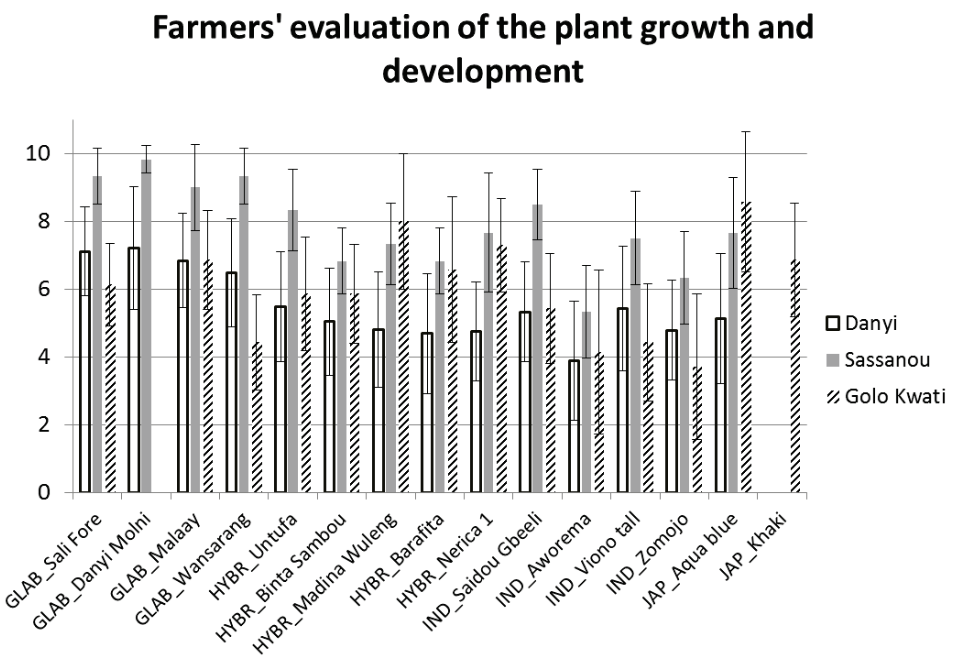

Figure 8*: Evaluation of the 15 varieties by the farmers in four Togolese villages on the Danyi Plateau: Danyi Elevagno, Xexatro, Dafor, Meampaseam, one village in the Ahlon Area: Sassanou and one village in Ghana: Golo Kwati (Lolobi). Evaluation was done just before panicle initiation. GLAB: glaberrima; HYBR: interspecific hybrid; IND: indica; JAP: japonica*

On the Danyi Plateau the growth and development of the *glaberrima* varieties was valued significantly better than those of the other varieties. There was no significant difference between the *glaberrima* varieties. Second best evaluated were the hybrid varieties and the indicas *Saidou Gbeeli, Viono tall, Zomojo,* as well as the *japonica Aqua Blue*. The variety valued least was *Aworema,* although it was not valued significantly differently from the hybrids *Madina Wuleng, Barafita, Nerica* and the *indica Zomojo.*

In Sassanou in the Ahlon area the varieties *Sali Fore* and *Danyi Molni* were evaluated best but were statistically not different from the other glaberrimas and the hybrids *Untufa* and *Nerica 1* or the indicas *Saidou Gbeeli* and *Viono tall* and the *japonica Aqua Blue*. The only varieties that were valued as 'poor' were *Aworema* and *Zomojo,* although they were not statistically significantly lower valued than the hybrids *Binta sambou, Madina Wuleng, Barafita, Nerica 1* and the *indica Viono tall* and the *japonica Aqua blue*. This confirms the overall good growth of all varieties in Sassanou.

In *Golo Kwati* the hybrid *Madina Wuleng* and the *japonica Aqua Blue* were valued highest but not significantly differently from the glaberrimas *Sali Fore* and *Malaay*, the hybrids *Untufa, Binta Sambou, Barafita, Nerica 1*, the *indica Saidou Gbeeli*, and the *japonica Khaki*. The indicas *Aworema, Viono tall* and *Zomojo* as well as the *glaberrima* variety Wansarang were equally poorly rated.

Farmers' choice of varieties after experience of the entire growth cycle

Table 4 indicates the varieties chosen by the farmers on the Danyi Plateau and in Sassanou. The reason why each of these varietis was ranked as a favourite is also shown, as well as the frequency with which these reasons were given by farmers. Eighty-four percent of Danyi farmers chose *Danyi Molni* (their local rice). The figure was 100% for *Nerica 1* and 79% for *Sali Fore*. Remarkable is the popularity of *Nerica 1,* which did not yield well at all, did not do very well on the other agronomic parameters and also did not score high on the farmers' evaluation of growth and development. However the large grains and the aesthetics of the grain - having a yellow-straw husk colour with clear black ends -took the interest of the farmers. As can be seen from Table 4 the reason "nice to look at" was mentioned by 17 out of the 19 farmers, and was not mentioned for any other variety. When a group of farmers was later interviewed and asked to explain why they liked the *Nerica 1* so much they stated that the grains looked nice, were easy to identify, were big and sturdy and were well developed. Another reason given was that in relation to the vegetative parts of the plant *Nerica 1* was said to have a higher harvest index than the other varieties. Apart from these three varieties it is only the *indica Saidou Gbeeli*, the hybrid *Madina Wuleng* and the *japonica Aqua blue* that were nominated as favourites, although in very small numbers. This suggests that the farmer variety *Danyi Molni* and the *glaberrima Sali Fore* (a variety from Guinea) are most advantageous for farmers as both did very well according to the measured agronomic and physiological parameters, as well as according to farmers experience and preferences.

***Table 4**: Varieties chosen by Ewe farmers on the Danyi Plateau and Ahlon farmers in Sassanou, after their experience with the farmer experimentation*

Location	Variety and botanical group	Appreciation (%)	Number of farmers (N=19)	Reasons given why the variety is chosen
Danyi Plateau	Sali Fore (*glaberrima*)	79	15	Easy to harvest 13/15, Good yield 12/15, Big grains 8/15 , Long panicle 6/15, Good height 6/15, Leaves stay green until harvest 3/15, Well adapted to the environment 2/15, Long grain 1/15, Difficult for birds to attack 1/15
	Danyi Molni (*glaberrima*)	84	16	Easy to harvest 15/16, Good yield 14/16 Big grains 11/16, Good height 6/16, Well adapted to the environment 6/16, Does not lodge 4/16, Leaves stay green until harvest 3/16, Long grain 2/16, Long panicle 2/16, Not many white empty panicles (worms) 1/16
	Nerica 1 (hybrid)	100	19	Good yield 18/19, Easy to harvest 18/19, Nice to look at 17/19, Large grains 15/19, Well adapted to the environment 7/19, Average height 5/19, Leaves stay green until harvest 4/19, Does not lodge 3/19, Droopy panicle good against birds 2/19, No empty panicles 1/19
	Madina Wuleng (hybrid)	5	1	Well adapted to the environment but has to be cultivated earlier (in June) 1/1.
	Saidou Gbeeli (*indica*)	21	4	Good yield 4/4, Easy to harvest 4/4, Good tillering 3/4, Big grains 2/4, Not many empty (worm attack) panicles 1/4
	Aqua Blue (*japonica*)	11	2	Difficult for birds to attack 1/1, Good yield 1/1, Big grains 1/1
Sassanou	Binta sambou (hybrid)	*	8	High yield, small grains but very good for home consumption
	Aqua Blue (*japonica*)	*	8	High yield, big grains
	Viono tall (*indica*)	*	8	Short variety but with high yield potential
	Nerica 1 (hybrid)	*	8	Nice to look at, good yield, because of morphology of plant it protects well against birds.

*A choice of varieties “to be kept” was made on basis of common agreement within the group

In Ahlon Sassanou farmers made different choices. Remarkable is the choice of *Viono tall* that did very well in the Sassanou experimental field. A disadvantage mentioned was that it was short (and therefore more difficult to harvest) but the high yield largely compensated for that. Also remarkable is the choice of *Binta Sambou*, a variety with very small, short grains. Interestingly the farmers stated that it was perfect for home consumption, but not to sell out.

***Table 5**: Appreciation of the varieties in the farmer experimentation trial at Golo Kwati by Lolobi farmers after their experience with the trial.*

Variety and botanical group	Appreciation (%)	Number of farmers (N=29)	Farmers evaluation after discussion with the group that chose the variety
Malaay (*glaberrima*)	79	23	Very easy to thresh, though pecked by birds, high yielding, does not lodge, early maturing
Sali Fore (*glaberrima*)	83	24	Very easy to thresh, no difference with Boadekamo only higher yield potential, can be used for customary rites
Wansarang (*glaberrima*)	28	8	Easy to thresh, birds peck it, high yielding, lodges because of long panicles, grains are too short
Nerica 1 (hybrid)	48	14	Early maturing, can be cultivated late, yield is not bad but there are better alternatives, familiar with this variety through MOFA.
Untufa (hybrid)	93	27	High yielding, does not lodge, not liked by birds, resembles Boadekamo so can be used for rituals, very good!
Binta Sambou (hybrid)	41	12	High yielding, of all the varieties it is most liked by birds because of the shiny character of its grains, it does not lodge
Madina Wuleng (hybrid)	62	18	Good yield, does not lodge, early maturing liked as new variety especially by women who do upland cultivation in Lolobi
Barafita (hybrid)	62	18	Very easy to thresh, early maturing, good panicles, liked because of its colour (paddy), birds do not peck it.
Aworema (*indica*)	0	0	Highest number of tillers, long cycle, lack of water, perfect in lowland
Viono tall (*indica*)	7	2	Good tillers, but lack of water, only does well in upland if there is a lot of rain, perfect in lowland
Zomojo (*indica*)	0	0	Few tillers, long cycle, lodges.
Saidou Gbeeli (*indica*)	10	3	Long cycle, not drought resistant
Aqua Blue (*indica*)	83	24	Very good, high yielding, birds do not peck it because of blue colour, does not lodge, already familiar with this variety.
Khaki (*japonica*)	21	6	Very hard to thresh, poor germination, good high yielding

In Golo Kwati 90% of the Lolobi farmers preferred *Untufa*. Next to the agronomic advantages (high yield, not liked by birds and not lodging) an important issue was its resemblance to

Boadekamo the local *glaberrima* rice. Farmers stated that it yielded better than *Boadekamo* and then again that it resembled it perfectly. It could therefore be recognised by their forefathers. That it originated from Guinea Bissau was not an issue at all. The fact that its panicles were also standing straight up just like the local *Boadekamo* and that the grains also resembled *Boadekamo* was what mattered (see also Teeken *et al*. 2012). These kinds of cultural considerations were not mentioned by people on the Danyi Plateau. *Untufa* is an example of a hybrid that morphologically resembles its *glaberrima* parent rather than its *sativa* parent (see Nuijten *et al*. 2009). Equally liked was *Sali Fore,* only that farmers saw more yield potential in Untufa. This is also reflected in the field trial - although the result is not statistically valid (Annex 1). In Golo Kwati the *glaberrima Wansarang* was not liked, not because it was not high yielding but because the grains were found to be too short and so there was no advantage over *Boadekamo.* Also the farmer hybrids *Madina Wuleng* and *Binta Sambou* that more resembled their *sativa* parents in panicle attitude and seed shape (droopy panicles and long grains) were liked by more than half of the farmers. Interesting is that *Barafita* is a white variety but equally well liked. Although red rice is normally preferred this is apparently not a reason not to choose a white variety. “We will make sure we have a lot of red rice but we will cultivate any good white variety in addition” was a statement that was made several times in discussions with farmers as well as during the meeting of the final evaluation. Although *Viono* and *Aworema* were not evaluated very positively in this experiment all farmers knew these varieties as ones that do very well in the lowlands and hydromorphic areas. Another white variety that was liked by at least 50% of the farmers was *Aqua Blue* (80%), a variety with which they were already familiar. Interesting also is that farmers not only chose the varieties they liked but chose to evaluate all the varieties.

Individual trials

At Lolobi Kumasi out of the six people each given four varieties (this to have each variety tested two times within the village) two of them actually tested them. One lady, Ms K., cultivated four varieties on a clearing in the forest on sloping ground (N 7.19444 W 0.52332 M, asl 255 m) that could be classified between hydromorphic and upland. She was very impressed by the yield of *Sali Fore*, especially as it resembled *BoadekoamO.* She also wanted to keep *Saidou Gbeeli* for the next year. Only *Wansarang* did not differ from *Boadekamo* and therefore she was not that much interested in the variety.

***Table 6**: Farmer experimentation within single plots by a Lolobi farmer in a forest clearing.*

Variety	Botanical group	Sowing date	Plot yield kg/ha
Sali Fore	*glaberrima*	1-08-2008	6333
Saidou Gbeeli	*indica*	1-08-2008	2212
Malaay	*glaberrima*	1-08-2008	1584
Wansarang	*glaberrima*	1-08-2008	4274

When extrapolating the yield this farmer obtained from *Sali Fore*, it was estimated that it would be around 6000 kg/ ha. This is a further indication of the potential of *Sali Fore*. Also *Wansarang* yielded up to 4000 kg/ha (Table 6). This also raises questions on how *glaberrima* might deal with organically fertile soils in relation to fertilised soils. *Glaberrima* is known not to respond well to fertiliser application (Takyi, 1972; Kubota *et al*. (1992) cited in Sumi *et al*. 1998; Dingkuhn *et al*. 1998; Futakuchi *et al*. 2012) but apparently can respond well to soil that is naturally fertile such as land opened from forest fallow. Other farmers took interest in the experiment and Ms K. stated that these other farmers were also impressed with the performance of *Sali Fore*, and she also said she had given *Saidou Gbeeli* to another farmer who wanted to try it.

Two brothers in Lolobi also tried four varieties in the corner of their field. However because of family problems they had to spend considerable time in a distant village and had no time to see to the field until one and half months after sowing, causing the plots to be overgrown with weeds. When they came back, however, they showed high interest in discussing what was left of their experiment, and they were impressed by the high percentage of plants of *Barafita* and *Binta Sambou* still standing (Table 7). Therefore they kept the grains for next year. Although the highest yield came from *Nerica 1* they were less interested in it as they already knew this variety and found that other varieties like *Aqua Blue* suited them better.

***Table 7**: Farmer experimentation within single plots by two young brothers Z. in Lolobi, with no attention until after one and a half months after sowing*

Variety	Botanical group	Sowing date	Percentage of plants left	Plot yield kg/ha
Saidou Gbeeli	*indica*	25-8-2008	33	168
Untufa	hybrid	25-8-2008	54	106
Binta Sambou	hybrid	25-8-2008	83	107
Barafita	hybrid	25-8-2008	74	76
Nerica 1	hybrid	25-8-2008	64	414

In Akpafu Odomi five farmers each evaluated two to four varieties out of 13. Table 8 shows the yield results and the evaluation by the farmers of each variety. Trials were carried out near to N 7.27856 W0.47131, 227 m asl. Sowing was done relatively late to extremely late as farmers gave priority to their other work, which in some cases caused the crop to experience drought at the end of the cycle. Farmers were not really interested in *Nerica 1* as they were already familiar with it, as promoted with little success by the Ministry of Food and Agriculture (MOFA).

***Table 8**: Evaluation of farmer varieties by farmers from Akpafu Odomi*

Farmer	Ecology	Variety	Sowing date	Average height (cm)	Yield/ha	Farmer's evaluation
Gladys B.	upland forest	*Binta Sambou*	11-9-2008	60	1320	Growth very fine and fast, threshing is very easy, generally the yield is very fine
		Malaay		40	2182	Almost the same as *Boadekamo*, duration is good
		Sali Fore		45	740	High percentage was barren because of late sowing.
		Madina Wuleng		45	0	Barren, late sowing.
Hellen A.	upland slope	*Saidou Gbeeli*	20-8-2008	70	1056	Long panicles, good growth, high yield
		Binta Sambou		70	258	Good variety only not drought resistant
		Aqua Blue		80		Flowering when total drought, already familiar with this variety.
Eugène B.	hydromorphic	*Madina Wuleng*	15-9-2008	50	1066	Good variety, high yielding, to be kept for next year.
		Binta Sambou		50	283	Not bad, if sown earlier would do

						very good.
	dry upland	*Malaay*	15-9-2008	45	0	Late sowing, killed by drought
		Nerica 1		40	0	Late sowing, killed by drought
Otilia A.	humid upland forest	*Barafita*	11-8-2008	75	5500	Right from germination plants were very healthy, no shattering, easy to thresh, wants to lodge but this is no disadvantage
		Saidou Gbeeli		95	4337	In beginning plants were dubious but just before flowering stage they did well, normal threshing, wants to lodge but no disadvantage
		Aqua blue		90	3401	Fine, threshing is normal, already familiar with this variety
		Wansarang		85	2066	Faster than *Boadekamo*, early sowing will give bird problems.
Dzigbodi O.	upland/lowland	*Madina Wuleng**	10-8-2008	75	70	Was destroyed by mice otherwise yield would certainly be higher then *Untufa*
		*Untufa**		90	1085	Good variety, is red like our traditional variety but yields higher.

**Plants were uprooted by the farmer from a sloping upland because of drought after 6 to 7 weeks and replanted in the lowland because the plants were dying.*

It was notable that farmers were less motivated than in Lolobi to talk about different varieties. Also farmers had less clear opinions about the varieties, and bringing the growers together in a meeting did not result in common opinions about a certain variety. Although the places where people carried out the farmer experimentation were quite close there was hardly any interest to visit each other's fields, and as can be seen from the sowing dates farmer experimentation was something that was a last priority. However, farmers were clearly open to any variety, although about three quarters of their own rice production was red rice. Remarks about usage in traditional meals or rituals were much less often made than in Lolobi. It was stated, however, that varieties with a red pericarp were preferred, and this has to be taken into account for further evaluation and adoption of varieties. Overall it can be summed up that farmers in Akpafu were in general quite positive about the varieties and only a few varieties were clearly marked as bad ones. This was also partly due to the general lack of interest in the experiment. Notable, however, was the strong motivation of an elderly woman who even uprooted the varieties when they were about to die, to replant them in the lowland.

Discussion

It is only in the Lolobi area that judgment of farmers clearly indicated that *Oryza glaberrima* influenced their variety selection. Particularly the variety *Untufa* was liked because it resembled *Boadekamo* and because it yielded better and did not lodge (like *Boadekamo*). Interestingly three of the farmer hybrids were liked because of their yield and husk colour (*Barafita*), resistance to bird damage (*Barafita*, *Untufa*) and pericarp color (*Madina Wuleng* and *Untufa*). This set of varieties combined two important criteria for these farmers; the need to have rice that can fully represent *Boadekamo* according to its morphology (mainly straight panicles and morphology of the grain and pericarp colour) and rice that is liked for home consumption (rice with a red pericarp and a high yielding white variety for upland conditions). Therefore these varieties can be seen as falling into three categories of use: ritual, consumption and market. Varieties with a white pericarp that seemed promising in yield were well liked and would fall into the category of 'for market only'. Other red varieties that do not resemble *glaberrima* fall in two categories - 'market sale' and 'consumption'. When considering the limited percentage of white rice cultivated by the Lolobi one can conclude that white varieties will only be cultivated when the yield is remarkably good. Because *glaberrima* is mainly cultivated for ritual purposes of connecting with ancestors (and what the ancestors would recognise is an important criterion for planting) no further selection and development within this species is to be expected, even if there is genetic potential for such selection. But *glaberrima* clearly has potential for selection. The Lolobi in fact cultivate a mixture of *glaberrima* varieties as one variety: *Boadekamo.* This facilitates out-crossing between different glaberrimas, and fields of *Boadekamo* within the Ghanaian Togo Hills are potentially genetically rich. The progeny within this landrace group might therefore be worth collection and further study.That the Lolobi cultivate a mixture of *glaberrima* types as a single landrace means that the typical Lolobi farmer is not very interested in trying out unfamiliar *glaberrima* varieties like *Danyi Molni* because they resemble types already present within the local *Boadekamo* mixture. Any of the crossings that might naturally occur in this mixture are not expected to be selected and further differentiated because the mixture itself is already regarded as one variety.

Although farmers in Lolobi and especially in Akpafu were not really motivated to participate in the experiment, perhaps because they themselves are quite satisfied already with their own experimental culture (the Lolobi) and the varieties that are supplied to them by other farmers, ethnic groups (the Akpafu), farmers were generally open to everything that might benefit them and few varieties were discarded directly. Even varieties that did very badly were sometimes evaluated positively as farmers thought that they might have potential if cultivated under different circumstances than the ones encountered in the individual experiments.

On the Danyi Plateau selection by farmers was based on three main criteria: yield, ease of harvest, and size and appearance of the grain. The last criterion was only mentioned for *Nerica 1*, and went together with the qualification of large grains. Farmers indicated that they liked the Nerica because it is easily distinguishable and because, in relation to vegetative parts of the plant, it produced a lot of grains - i.e. it showed a high harvest index - which is in contrast with their local *glaberrima* varieties that produce many leaves. This striking contrast might have contributed to its popularity.

In none of the cases were ritual contexts or cultural factors mentioned. As cited in Chapter 6 (Mokuwa *et al*., 2014) Roy *et al.* (1996) have shown that big grains can be advantageous to developing a larger and deeper initial root system, which can correspond well with the rather poor soils of the Danyi Plateau. Many times farmers also indicated that they would instantly replace the *glaberrima* varieties with any other variety that would yield higher (Teeken *et al*. 2012, Chapter 7). No cultural factors and preferences for seed colour were mentioned and these factors are therefore not narrowing rice diversity here. Only the fact that mostly *glaberrima* types seem to suit the farmers' situation best (no fertiliser input) indicates a narrowing down to *glaberrima* varieties suited to the upland ecologies of the Danyi Plateau. The introduction of new varieties of *glaberrima* or promising hybrids might therefore be successful. That farmers clearly separate and distinguish the different varieties of African rice and use their specific properties (mainly cycle length) shows that genetic diversity within *glaberrima* is not narrowed down. Farmers are open to other varieties of *glaberrima* and the selection of off types within *glaberrima* as a result of crossbreeding between them is more probable than in Ghana.

Because the ecology used for *glaberrima* on the Danyi Plateau more closely resembles the upland ecology to which also the minority groups in Ghana were restricted before they started to use the lowland ecologies, people in the Danyi Plateau probably still select as both they and the Ghanaian groups had been doing at earlier times - for example, selecting on large grains to assure better germination percentages and better resistance to poor top soils, and selecting for early varieties better suited to a more mobile life, with shifts of location to ensure greater security. This would explain the significantly larger grains found among *glaberrima* types from the lower West African coast as compared to the upper coast as described in Mokuwa *et al*. 2013 and 2014. The minorities in Ghana no longer impose such a large grain criterion neither do the use the specific properties of the different varieties of *glaberrima*, as they all appear in a mixture (land race) called *Boadekamo.* This is understandable as their main reference now is lowland rice and upland cultivation on lower slope hydromorphic upland soils (where also varieties such as *Viono* can do well) because no longer does war and danger restrict them to mountain slopes like those around Akpafu Todzi where such upland cultivation is continued in small pockets by elderly women. This explains the motivation of the elderly woman in the farmer experimentation group. She belongs to a generation for which upland rice cultivation was once a major livelihood activity. Akpafu Todzi was the first of the Akpafu villages in the region, and is situated high up on a mountain slope west of Akpafu Meampeasem.

However the high yield of the *glaberrima Sali Fore,* and the hybrids *Untufa* and *Madina Wuleng* immediately made Lolobi farmers think of new opportunities for more lucrative upland farming around their villages, especially for women who, because of their other domestic tasks, are tied tight to that upland environment. In this light the possibly rich genetic reservoir present in the fields of *Bouadekamo* might one day be opened up and used by either farmers themselves, or by researchers, or perhaps ideally through a cooperation between the two.

The relatively large diversity within the *glaberrima* botanical group coming from the Togo Hills (Mokuwa *et al*. 2014) can be understood given the maintenance of a relatively large set of only *glaberrima* rice types as major food source within a tradition of being on the move and having to create spaces of independence and temporary refuge in a complex web of political, economic and therefore cultural diversity.

In general it can be concluded that despite local cultural, religious, political and economic differences, farmers on both sides of the border were alive to the potential of farmer varieties with properties able to serve various market demands, ritual purposes and home consumption needs. No uniform criteria within variety selection could be distinguished. Rather than a barrier to technology development and adoption, culture and social diversity can therefore rather be seen as factors contributing to the long tradition of maintaining diversity within innovation and adoption, reflective of the need for risk spreading and facilitative of various successful and often serendipitous innovations. The findings of this chapter also support Vasavi (1994; 1999) who stresses the importance of agricultural rituals as part of local strategies of adaptation to ecological as well as social challenges, resulting in practices and ideas that directly connect health and well-being to agricultural technologies such as seed.

Interestingly, in the two regions that are most incorporated in the market liberal national economy of Ghana (the Akpafu and the Lolobi in the Ghanaian Togo hills) African rice is explicitly articulated as providing cultural or religious community identity. This also contradicts the idea that the liberal market erases local cultures and values. In this case, it seems more likely that market has helped reinvent tradition, with Akpafu and Lolobi farmers now increasingly meeting demand for red rice by the urbanised middle class in Accra.

Within the long tradition of creating niches within a large field of differentiated economic and political power dictated from outside, the people in the Ghanaian Togo Hills are continuing to reinvent tradition and identity, and seem to connect to a growing national market of local special produce. The situation on the Danyi plateau in Togo is rather different. Here, market integration is much less, and rice cultivation remains especially useful for home consumption. Although it constitutes only a small part of total local agricultural output it is maintained not only because of tradition but because it still constitutes an important variation in a diet otherwise mainly consisting of cassava, yam and maize.

A final, important observation is that the experiment in farmer experimentation described in this chapter took on larger dimensions in a region (Danyi Plateau) where people are more communal in their values, less incorporated into a liberal market economy, and more reliant on local cooperation. This makes the point that the way the variety evaluation and selection is organised has a large influence over the performance of variety evaluation and its outcomes (Richards 2007). But at the same time it is necessary to stress that a higher level of group involvement in a more socially cohesive community does not necessarily imply more innovation and dissemination, since as shown, individual initiatives can also turn into communal effects, as in the Lolobi area, where the outcomes of individual initiative had similar or even larger effects on innovation , adoption and dissemination.

So despite cultural and ecological differences farmers in the Togo Hills are open to many different varieties. This indicates that the shared long term dynamic history of strategising (including migration) and maintaining autonomy within a complex field of political and economic powers has resulted in local ecological *and* cultural differences that both have contributed to the development and maintenance of a diverse set of rice varieties that are robust.

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Annexes

Annex 1 *Average performance of the 14 rice varieties used in the farmer experimentation for yield, number of tillers, plant height, panicle exsertion (scale 0 to 9: 0= highest exsertion)*, acidity damage/brown spots (scale 1 to 7)*, nitrogen status (scale -2 to 2)* and Farmer Evaluation of plant growth and development (scale 1 to 10) on the* ***Danyi Plateau Togo.*** *Variety names are preceded by GLAB, HYBR, IND or JAP respectively indicating the botanical groups glaberrima, Farmer Hybrids, sativa spp. indica and sativa spp. japonica. *See table 2*

Variety	Yield (kg/ha)	sd	Tukey	Nr. of tillers	sd	Tukey	Plant Height	sd	Tukey	Acidity damage	sd	Tukey
GLAB_Sali Fore	863	316	D	8.00	2.62	ABC	108	8.2	D	1.75	1.04	A
GLAB_Danyi Molni	756	158	CD	8.00	2.62	ABC	91	15.2	C	3.00	3.10	AB
GLAB_Malaay	595	337	BCD	6.50	2.73	AB	79	15.1	ABC	3.13	2.17	AB
GLAB_Wansarang	355	342	AB	6.25	1.16	AB	87	14.9	BC	4.50	2.07	BC
HYBR_Untufa	399	311	BC	6.25	1.75	AB	81	11.1	ABC	5.25	2.25	BC
HYBR_Binta Sambou	378	418	ABC	7.50	3.96	ABC	71	23.0	A	5.86	1.57	C
HYBR_Madina Wuleng	378	326	ABC	5.75	2.31	A	93	15.3	C	3.83	2.71	ABC
HYBR_Barafita	470	249	BC	6.63	2.77	AB	88	11.5	C	3.86	2.73	ABC
HYBR_Nerica 1	277	244	AB	5.50	1.31	A	83	12.6	ABC	3.88	3.00	ABC
IND_Saidou Gbeeli	416	186	BC	7.75	3.20	ABC	89	19.2	C	3.75	2.12	ABC
IND_Aworema	0	0	A	11.00	4.90	C	70	28.6	A	3.29	2.43	AB
IND_Viono tall	0	0	A	8.63	2.67	ABC	73	21.6	AB	3.86	1.57	ABC
IND_Zomojo	0	0	A	9.88	2.80	BC	79	13.2	ABC	4.00	2.78	ABC
JAP_Aqua blue	450	74	BC	7.25	2.49	AB	73	11.9	AB	3.71	3.20	ABC

Annex 1 – Trial location: the Danyi Plateau continued

Variety	Panicle exsertion	sd	Tukey	Farmers' evaluation	sd	Tukey	N status	sd	Tukey
GLAB_Sali Fore	1	0.00	A	7.12	1.31	C	1.50	0.93	D
GLAB_Danyi Molni	2.5	1.77	AB	7.21	1.82	C	1.00	1.85	CD
GLAB_Malaay	4	2.45	BC	6.85	1.39	C	0.25	1.49	ABC
GLAB_Wansarang	3.5	1.41	BC	6.48	1.59	C	1.00	0.93	CD
HYBR_Untufa	4.3	2.38	BCD	5.48	1.63	B	0.50	0.53	ABC
HYBR_Binta Sambou	5.3	1.51	CD	5.04	1.58	B	-0.13	0.64	AB
HYBR_Madina Wuleng	3.6	1.90	BC	4.81	1.69	AB	0.63	1.06	BCD
HYBR_Barafita	5.0	2.00	CD	4.69	1.77	AB	-0.38	1.06	A
HYBR_Nerica 1	4.1	1.07	BC	4.75	1.47	AB	1.13	1.13	CD
IND_Saidou Gbeeli	1.5	0.93	A	5.33	1.48	B	0.71	0.49	BCD
IND_Aworema	5	0.00	CD	3.88	1.76	A	0.75	1.16	BCD
IND_Viono tall	5	2.83	CD	5.42	1.83	B	0.00	0.76	AB
IND_Zomojo	6	1.15	D	4.79	1.47	AB	0.63	0.52	BCD
JAP_Aqua blue	4	3.46	BC	5.13	1.91	B	0.00	0.93	AB

Annex 2: *Average performance of the 14 rice varieties used in the farmer experimentation for yield, number of tillers, plant height, panicle exsertion (scale 0 to 9: 0= highest exsertion)*, acidity damage/brown spots (scale 1 to 7)*, nitrogen status (scale -2 to 2)* and Farmer Evaluation of plant growth and development (scale 1 to 10) in* ***Golo Kwati Ghana****. Variety names are preceded by GLAB, HYBR, IND or JAP respectively indicating the botanical groups glaberrima, Farmer Hybrids, Sativa spp. indica and sativa spp. japonica. *See table 2*

Variety	**Yield (kg/ha)**	**sd**	**Tukey**	**Nr. of tillers**	**sd**	**Tukey**	**Plant Height**	**sd**	**Tukey**
GLAB_Sali Fore	1847	55	B	15.00	4.24	C	121	1.41	CDE
GLAB_Malaay	2342	3	B	9.00	1.41	ABC	100	0.00	B
GLAB_Wansarang	1573	269	AB	15.50	2.12	C	93	2.83	B
HYBR_Untufa	2656	82	B	10.50	0.71	ABC	119	4.95	CD
HYBR_Binta Sambou	1972	247	B	10.00	1.41	ABC	90	0.00	B
HYBR_Madina Wuleng	2235	618	B	8.00	0.00	AB	93	4.24	B
HYBR_Barafita	2000	158	B	6.50	0.71	A	113	3.54	C
HYBR_Nerica 1	1189	340	AB	8.00	0.00	AB	97	1.41	B
IND_Saidou Gbeeli	1501	386	AB	13.50	3.54	BC	133	3.54	EF
IND_Aworema	0	0	A	8.00	0.00	AB	78	2.83	A
IND_Viono tall	0	0	A	11.50	0.71	ABC	113	2.83	C
IND_Zomojo	0	0	A	12.00	0.00	ABC	91	0.71	B
JAP_Aqua blue	1956	1302	B	8.00	0.00	AB	139	4.95	F
JAP_Khaki	1389	27	AB	12.50	0.71	ABC	125	0.00	DE

Annex 2 – Trial location: Golo Kwati Ghana continued

Variety	Acidity damage	sd	Tukey	Panicle exsertion	sd	Tukey	Farmers’ evaluation	sd	Tukey
GLAB_Sali Fore	4	1.41	AB	2	1.41	AB	6.1	1.21	ABC
GLAB_Malaay	3	0.00	AB	3	0.00	ABC	6.9	1.46	ABC
GLAB_Wansarang	3	0.00	AB	3	0.00	ABC	4.4	1.40	AB
HYBR_Untufa	3	0.00	AB	4	1.41	ABCD	5.9	1.68	ABC
HYBR_Binta Sambou	6	1.41	BC	4	1.41	ABCD	5.9	1.46	ABC
HYBR_Madina Wuleng	3	0.00	AB	3	0.00	ABC	8.0	2.00	C
HYBR_Barafita	6	1.41	BC	6	1.41	CD	6.6	2.15	ABC
HYBR_Nerica 1	1	0.00	A	3	0.00	ABC	7.3	1.38	BC
IND_Saidou Gbeeli	3	0.00	AB	5	0.00	BCD	5.4	1.62	ABC
IND_Aworema	0		AB	7	0.00	D	4.1	2.41	AB
IND_Viono tall	3	0.00	AB	6	1.41	CD	4.4	1.72	AB
IND_Zomojo	8	1.41	C	5	0.00	BCD	3.7	2.14	A
JAP_Aqua blue	4	1.41	AB	1	0.00	A	8.6	2.07	C
JAP_Khaki	3	0.00	AB	5	0.00	BCD	6.9	1.68	ABC

Annex :3 *Average performance of the 14 rice varieties used in the farmer experimentation for yield, number of tillers, plant height, panicle exsertion (scale 0 to 9: 0= highest exsertion)*, acidity damage/brown spots (scale 1 to 7)*, nitrogen status (scale -2 to 2)* and Farmer Evaluation of plant growth and development (scale 1 to 10) in* ***Ahlon Sassanou Togo.*** *Variety names are preceded by GLAB, HYBR, IND or JAP respectively indicating the botanical groups glaberrima, Farmer Hybrids, Sativa spp. indica and Sativa spp. japonica. *See table 2*

Variety	Yield (kg/ha)	sd	Tukey	Nr. of tillers	sd	Tuckey	Planth height	sd	Tukey
GLAB_Sali Fore	0			5.50	0.71	ABC	126	1.41	DEF
GLAB_Danyi Molni	0			10.00	1.41	E	119	21.92	CDE
GLAB_Malaay	0			7.00	0.00	BCD	121	1.41	DE
GLAB_Wansarang	0			8.00	0.00	CDE	136	1.41	EF
HYBR_Untufa	0			7.50	0.71	CDE	92	0.71	AB
HYBR_Binta Sambou	0			4.50	0.71	AB	116	0.00	CDE
HYBR_Madina Wuleng	0			4.00	0.00	A	96	1.41	ABC
HYBR_Barafita	0			6.50	0.71	ABCD	105	0.71	ABCD
HYBR_Nerica 1	0			6.50	0.71	ABCD	89	0.71	A
IND_Saidou Gbeeli	0			7.50	0.71	CDE	121	0.71	DE
IND_Aworema	0			9.00	1.41	DE	117	0.71	CDE
IND_Viono tall	0			6.50	0.71	ABCD	147	1.41	F
IND_Zomojo	0			8.00	0.00	CDE	84	0.71	A
JAP_Aqua blue	0			8.00	0.00	CDE	113	0.71	BCDE

Annex 3 – Trial location: Ahlon Sassanou continued:

Variety	Acidity damage	sd	Tukey	Panicle exsertion	sd	Tukey	Farmers' evaluation	sd	Tukey
GLAB_Sali Fore	3	0	AB	1	0	A	9.3	0.82	DE
GLAB_Danyi Molni	1	0	A	1	0	A	9.8	0.41	E
GLAB_Malaay	5	0	BC	1	0	A	9.0	1.26	CDE
GLAB_Wansarang	3	0	AB	1	0	A	9.3	0.82	DE
HYBR_Untufa	3	0	AB	1	0	A	8.3	1.21	BCDE
HYBR_Binta Sambou	4	1.41	AB	3	0	AB	6.8	0.98	ABC
HYBR_Madina Wuleng	5	0	BC	1	0	A	7.3	1.21	ABCD
HYBR_Barafita	3	0	AB	1	0	A	6.8	0.98	ABC
HYBR_Nerica 1	8	1.41	C				7.7	1.75	ABCDE
IND_Saidou Gbeeli	6	1.41	BC	3	0	AB	8.5	1.05	BCDE
IND_Aworema	3	0	AB	6	1,41	CD	5.3	1.37	A
IND_Viono tall	5	0	BC	1	0	A	7.5	1.38	ABCDE
IND_Zomojo	1	0	A	7	0	D	6.3	1.37	AB
JAP_Aqua blue	4	1.41	AB	4	1,41	BC	7.7	1.63	ABCDE

CHAPTER FOUR

Evidence for the Emergence of New Rice Types of Interspecific Hybrid Origin in West African Farmers' Fields

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Published as: Nuijten E, van Treuren R, Struik PC, Mokuwa A, Okry F, Teeken B, Richards P (2009) Evidence for the Emergence of New Rice Types of Interspecific Hybrid Origin in West African Farmers' Fields. PLoS ONE 4(10): e7335. doi:10.1371/journal.pone.0007335

Abstract

In West Africa two rice species (*Oryza glaberrima* Steud. and *Oryza sativa* L.) co-exist. Although originally it was thought that interspecific hybridisation is impossible without biotechnological methods, progenies of hybridisation appear to occur in farmer fields. AFLP analysis was used to assess genetic diversity in West Africa (including the countries The Gambia, Senegal, Guinea Bissau, Guinea Conakry, Sierra Leone, Ghana and Togo) using 315 rice samples morphologically classified prior to analysis. We show evidence for farmer interspecific hybrids of African and Asian rice, resulting in a group of novel genotypes, and identify possible mechanisms for in-field hybridisation. Spontaneous back-crossing events play a crucial role, resulting in different groups of genetic diversity in different regions developed by natural and cultural selection, often under adverse conditions. These new groups of genotypes may have potential relevance for exploitation by plant breeders. Future advances in crop development could be achieved through co-operation between scientists and marginalised farmer groups in order to address challenges of rapid adaptation in a world of increasing socio-political and climatic uncertainty.

Keywords: Interspecific hybridisation, *Oryza sativa*, *Oryza glaberrima*, West Africa, farmer varieties

Introduction

Rice (*Oryza* spp.) is one of the two most important grain crops worldwide. Its genetic diversity is a factor in securing local and global food security. West Africa is important for genetic diversity of rice, because, uniquely, two species – African rice (*Oryza glaberrima Steud*.) and Asian rice (*Oryza sativa L.*) – co-exist within the region. African rice was presumably first cultivated in Mali, Senegal and Guinea Conakry, ± 3500 years ago [1,2]. The history of Asian rice in West Africa is still uncertain, with introduction possible via Arab and/or Portuguese trading networks, ± 500–800 years ag*O.* Asian rice has more recently tended to replace African rice, but African rice has persisted or made a modest come-back in some areas, including parts of coastal West Africa.

Several reports claimed that *O. sativa* is completely isolated from *O. glaberrima* by an F1 sterility barrier [3,4]. Hence, the development of the Nericas (New Rice for Africa) based on the hybridisation of *O. sativa* and *O. glaberrima* was considered a technological breakthrough [5,6]. However, some scientists suggested that introgression between the two rice species occurs in the field [7,8]. Based on experiments, Sano [9] argued that pollen flow occurs mainly from *O. sativa* to *O. glaberrima*. Other experimental studies showed that introgression from *O. glaberrima* to *O. sativa* is possible, although at a low frequency [10-13]. Artificial backcrosses produced fertile progenies which resembled the parental phenotypes, indicating that under natural conditions it will be difficult to detect hybrid derivatives [9,14]. This means that, for example, plants belonging to *O. glaberrima* can incorporate *O. sativa* genetic material but remain typically *O. glaberrima* to the eye.

Recent evidence suggests that interspecific hybridisation does occur in farmers’ fields resulting in new varieties [15-18]. Our paper shows that West African farmers have generated their own rices of interspecific background - genetically different from and independent of the scientific initiative leading to Nerica - and suggests possible mechanisms for in-field hybridisation behind this major local genetic development, with spontaneous backcrossing playing a crucial role. Our results strongly suggest that interspecific hybridisation in West Africa farmers’ fields is a recurrent and continuing process, resulting in different groups of genetic diversity in different rice growing areas stimulated by (cultural) differences in selection. Our findings support the hypothesis by Sano *et al*. [14] that hybridisation followed by backcrossing between *O. sativa* and *O. glaberrima* might lead to the development ‘of new variants not belonging to either of the two species’. These findings might have important implications for understanding crop development and human adaptation. For some time, it has been argued that small-scale farmers in the poorest countries should be consulted about crop improvement, to ensure a better fit between scientific innovation and local food security needs [19]. Now, molecular information is available on the importance of farmer agency during the domestication of rice [20]. We suggest that the current relationship between science and African farmers needs change. Our evidence shows that African farmers are active agents in plant improvement and we suggest that their agency may be taken as a starting point for scientific technology development. New lateral forms of cooperation are required to exploit fully the available genetic diversity of rice.

Figure 1*: Geographic overview of the West African study area. Pushpins indicate study areas.*

Materials and Methods

We sampled the coastal West African rice belt, including Senegal, The Gambia, Guinea Bissau, Guinea Conakry and Sierra Leone, and the Togo hills rice cultivation outlier in Ghana and Togo (Figure 1). For demarcation of the upland rice ecology we followed local farmers' definitions. Per country, three or four villages/village clusters were selected, based on ecological and/or cultural contrasts. Per village, as full a set as possible of locally available dryland rice varieties was assembled. Per rice sample, 100–200 panicles were taken at random from the harvest as representative of a variety. Based on farmers' descriptions of the morphological identity of varieties, each rice sample was cleaned carefully. Thus farmer variety samples were morphologically as uniform as formal (released) varieties in the study.

Molecular analysis with AFLP markers, using the EcoRI primer E13 in combination with each of the MseI primers M49 or M51, basically followed the procedures described in Nuijten and Van Treuren[16]. AFLP data from 231 collected samples were combined with those of 84 rice samples analysed previously by Nuijten and Van Treuren [16]. A total number of 176 bands was scored, of which 161 were found to be polymorphic. The programme ‘SplitsTree’ was used to visualise phylogenetic relationships between the samples [21] and version 2.2 of the software package ‘Structure’ was used to analyse genetic population structure and to assign samples to populations [22, 23]. To quantify gene variation within groups of samples, Nei’s gene diversity (H_e) was calculated [24].

Information about trait and variety preferences, and the origin and spread of varieties, was obtained through quantitative and qualitative interviews with farmers from whom the rice samples were collected (in countries listed above).

Information on morphological features was collected in a field trial carried out in Sierra Leone to characterise morphologically the majority of the materials. The trial design and measurement of the traits followed the procedures described in Nuijten and Van Treuren [16].

Definitions

Interspecific hybrids: varieties that result from hybridisation between *O. sativa* and *O. glaberrima*.

Nerica: improved varieties released by the African Rice Center (formerly WARDA) that result from artificial hybridisation between *O. sativa* and *O. glaberrima* followed by two backcrosses to the *O. sativa* parent.

Farmer hybrid: variety that results from spontaneous hybridisation between *O. sativa* and *O. glaberrima* followed by backcrossing in farmers’ fields and subsequent self-pollination.

Off-type: rice plant with a phenotype distinctive from the sown variety and unknown as a variety (including non-cultivated and ‘lost’ varieties). Off-types can result from mixture, genetic mutation or spontaneous hybridisation.

Mixture: a rice stand consisting of various genetically different varieties caused by intentional or unintentional mixing.

Results

An unrooted phylogenetic network of the 315 rice samples is presented in Figure 2. As could be expected, *Oryza sativa* ssp. *indica*, *O. sativa* ssp. *japonica* and *O. glaberrima* form three distinct clusters. Nerica varieties of interspecific origin align along the *japonica* axis, with Nerica 1 and 2 facing the *O. glaberrima* branch. In addition to these three clusters, a fourth distinct cluster, consisting of two sub-clusters, was observed, at the junction of the *O. glaberrima-indica-japonica* axes.

Analyses with the software ‘Structure’ showed that the major structure in the data was captured when four populations were assumed. Three of these populations corresponded with *Oryza sativa* ssp. *indica*, *O. sativa* ssp. *japonica* and *O. glaberrima*, respectively, while the fourth population corresponded with cluster 4 in Figure 2. Of the 315 materials 285 samples were assigned to a cluster with more than 91% probability. All materials in cluster 4 in Figure 2 were assigned to cluster 4 with more than 81% probability in Structure, except two varieties from Senegal that were assigned to cluster 4 with 59% and 46% probability.

Prior to the molecular analysis, all varieties collected from farmers were classified as *O. sativa*, *O. glaberrima*, hybrid or unclear. None of the materials assigned to the two *O. sativa* clusters with more than 81% probability were classified as *O. glaberrima* and vice versa (Table 1). The single sample classified as *O. sativa* that was assigned to *O. glaberrima*, and the single sample classified as *O. glaberrima* that was assigned to *O. sativa*, were most likely caused by interchanging of materials during the experiment.

Cluster 4 comprised two subclusters (Figure 2). All varieties in sub-cluster 4-2 had been taxonomically determined as *O. sativa* prior to the molecular study, while cluster 4-1 consisted of samples that had been determined either as *O. sativa*, *O. glaberrima*, hybrid or unclear (Table 2). The main distinctive features between these two sub-clusters were panicle stature at maturity and pericarp (or seed) colour. Sub-cluster 4-1 consisted of varieties with an erect panicle, typical for *O. glaberrima* (Figure 3), or a semi-erect or slightly drooping panicle, and a red pericarp, except for a single variety from Senegal which had a brown pericarp. Farmers classify particularly the varieties with an erect panicle as *O. glaberrima*, because of the similarity in panicle stature. Farmers do not recognise the varieties of cluster 4 as a separate group. They divide all varieties into two types: those that resemble *O. sativa* and those that resemble *O. glaberrima*. Farmers are not specifically interested in varieties of interspecific origin, but in varieties that perform best under their conditions.

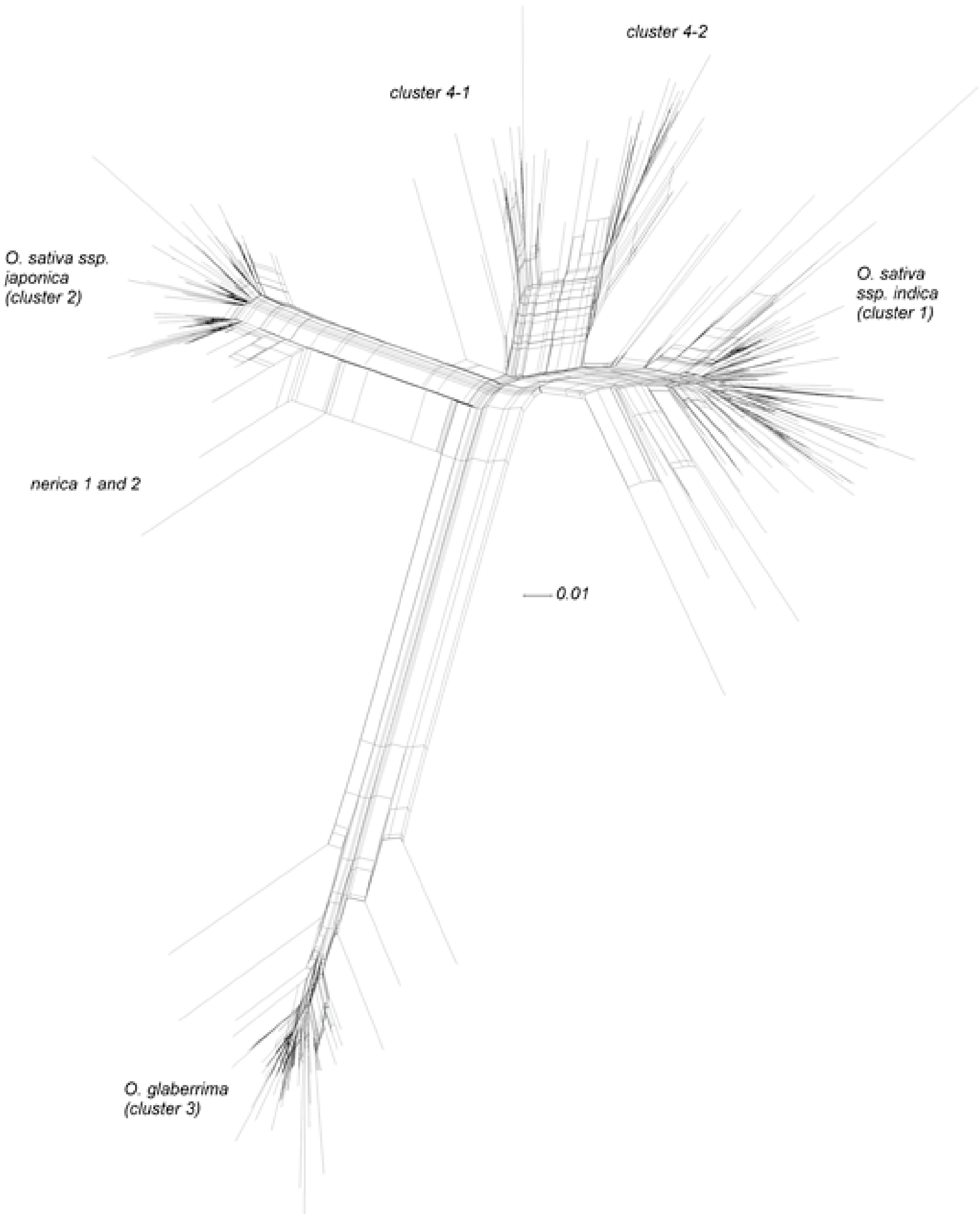

***Figure 2**: Phylogenetic relationships among the 315 samples studied.*

***Table 1**: Presumed taxonomic origin of the 289 farmer varieties in relation to the assignment probabilities to the four observed clusters.*

		O. glaberrima	Hybrid	Unclear	*O. sativa*
P (Gla)*	0.91 - 1.00	56		6	1
	0.81 - 0.90	2			
	0.71 - 0.80				
	0.61 - 0.70				
	0.51 - 0.60				
	0.41 - 0.50				
	0.31 - 0.40				
	0.21 - 0.30				
	0.11 - 0.20		3		
	0.00 - 0.10	8	16	18	179
P (Ind)	0.91 - 1.00	1	2	6	71
	0.81 - 0.90			1	3
	0.71 - 0.80		1		1
	0.61 - 0.70	1	1		2
	0.51 - 0.60			1	2
	0.41 - 0.50				2
	0.31 - 0.40				
	0.21 - 0.30				
	0.11 - 0.20	1	1		
	0.00 - 0.10	63	14	16	99
P (Jap)	0.91 - 1.00		5	5	70
	0.81 - 0.90		2		3
	0.71 - 0.80		1		
	0.61 - 0.70				
	0.51 - 0.60				
	0.41 - 0.50				1
	0.31 - 0.40				
	0.21 - 0.30				
	0.11 - 0.20	1	1		1
	0.00 - 0.10	65	10	19	105
P (Cl4)	0.91 - 1.00	6	6	5	23
	0.81 - 0.90		1		2
	0.71 - 0.80				
	0.61 - 0.70				
	0.51 - 0.60				1
	0.41 - 0.50				2
	0.31 - 0.40			1	2
	0.21 - 0.30	1	1		1
	0.11 - 0.20			1	2
	0.00 - 0.10	59	11	17	147

** Probabilities of the materials assigned to O. glaberrima (Gla), O. sativa ssp. indica (Ind), O. sativa ssp. japonica (Jap) and the fourth cluster (Cl4).*

The three varieties in sub-cluster 4-1 that were classified as *O. sativa* had semi-droopy panicles which made them less distinctive from *O. sativa*. Sub-cluster 4-2 consisted of varieties in which panicles were predominantly strongly drooping, similar to *O. sativa*, and in which the pericarp colour varied from white to brown (90% of the varieties had a brown pericarp colour). Except for pericarp colour, the varieties in sub-cluster 4-2 did not have any clearly distinctive morphological features from *O. sativa* varieties (Table 3). Detailed morphological analysis of some varieties belonging to sub-cluster 4-2 in 2002 showed that when characteristics were aggregated in a Principal Component Analysis these farmer varieties were different from *O. sativa* ssp. *indica* and *O. sativa* ssp. *japonica* [16].

***Table 2**: Presumed taxonomic origin of the farmer hybrid varieties observed in sub-clusters 4-1 and 4-2 in figure 2.*

Presumed taxonomic origin	Sub-cluster 4-1	Sub-cluster 4-2
O. sativa	3	24
O. glaberrima	6	0
Hybrid	7	0
Unclear	5	0
Total	21	24

Genetic diversity within groups (H_e) was calculated for each of the four clusters. For this purpose an assignment probability of 91% was used as cut-off point to define the four clusters. The H_e value for cluster 4 was highest (0.098; n = 40) followed closely by the H_e value for the *O. sativa* ssp. *indica* group (0.089; n = 92). Relatively low values were observed for the *O. sativa* ssp. *japonica* group (0.045; n = 87) and the *O. glaberrima* group (0.034, n= 66).

Varieties in sub-cluster 4-1 not only displayed characteristics typical of *O. glaberrima*, such as the easily observable erect panicle stature (Figure 3), but also characteristics of *O. sativa*, such as the long, pointed ligule typical of *O. sativa* (Figure 4), a less conspicuous feature. The only explanation for this new morphotype is interspecific hybridisation between *O. sativa* and *O. glaberrima*. This was supported by the molecular data, separating cluster 4 from *O. sativa* ssp. and *O. glaberrima*, and showing large within-group diversity.

Cluster 4 consisted of a considerable number of different farmer interspecific hybrids originating from the Upper West African coastal rice belt (Table 4). None of the modern varieties and none of the samples collected in Ghana and Togo were found in cluster 4 in Figure 2, nor were any of these samples assigned to cluster 4 in Table 4 with more than 40% probability. Thirty samples - originating from almost all countries, and including two modern varieties - were assigned with less than 91% probability to one cluster. No samples from Togo were assigned with less than 91% probability to one cluster. Although no samples from Ghana were assigned to cluster 4, five samples were assigned with high probabilities to two clusters. These samples may require further study to know whether they have an interspecific background. But we cannot assume that all such materials have an interspecific nature since one variety from IRRI was assigned to the *O. sativa* ssp. *indica* group with 76% probability (Table S1). Likewise, existence of samples with a very high assignment percentage probability does not rule out an interspecific origin. For example, WAB 450-I-B-P-105-HB, a Nerica that was never officially released was assigned with 100% probability to the *O. sativa* ssp. *japonica* group.

Table 3*: Main distinctive morphological features of 12 varieties from cluster 4**

Variety name	Country	Sub-cluster	Panicle attitude	Ligule shape	Pericarp colour	Days to 80% flowering
Tebeleh	Sierra Leone	4-1	erect	pointed, long	red	105.8
Pa DC	Sierra Leone	4-1	erect	pointed, long	red	103.8
Pa Trimont	Sierra Leone	4-1	semi-droopy	pointed, long	red	92.5
Wonyonwonyon yi	Guinea Conakry	4-1	semi-droopy	pointed, long	red	96.3
Untufa	Guinea Bissau	4-1	erect	pointed, long	red	98.0
Dissi	Guinea Bissau	4-1	erect	pointed, long	red	104.0
Mani Konsunkuto	Guinea Bissau	4-2	strongly droopy	pointed, long	brown	87.5
Kolosar, Mani Wulendingo	Guinea Bissau	4-2	strongly droopy	pointed, long	white	91.8
Mani Wulengo	Gambia	4-2	strongly droopy	pointed, long	brown	88.0
Binta Sambou**	Gambia	4-2	strongly droopy	pointed, long	light brown	103.3
Ablie Mano	Senegal	4-2	droopy	pointed, long	brown	89.5
Madina Wulengo	Senegal	4-2	strongly droopy	pointed, long	brown	90.8

** Varieties of O. glaberrima included in this study had erect panicle, round short ligule and red pericarp colour. Varieties of O. sativa ssp. included in this study had strongly droopy panicle, pointed medium to long ligule, and white or red pericarp colour.*
*** In The Gambia Binta Sambou flowers only a few days later than Ablie Mano.*

To a certain extent, the sub-clusters relate to the countries of collection and local seed colour preferences. The varieties in sub-cluster 4-1 originate from Guinea Bissau (4), Guinea Conakry (2), Senegal (1) and Sierra Leone (14), while the varieties in sub-cluster 4-2 are from The Gambia (9), Guinea Bissau (6) and Senegal (9). Whereas in Guinea Conakry and Sierra Leone farmers commonly cultivate red rice (both African and Asian rice), farmers in The Gambia, Senegal and northern Guinea Bissau predominantly cultivate white rice. Southern Guinea Bissau occupies an intermediate position, as red rice is still cultivated but farmers strongly prefer white rice.

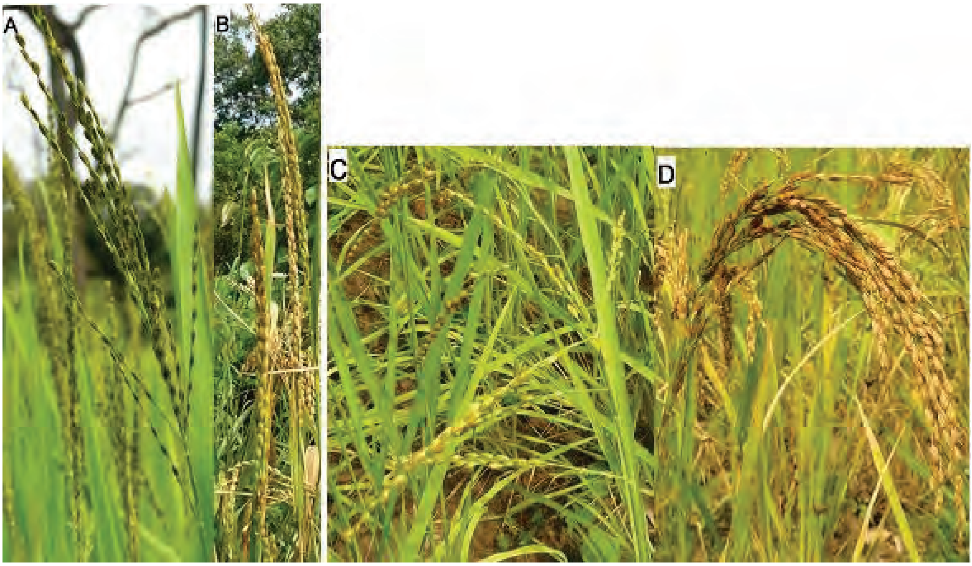

Figure 3*: Main panicle types found in this study. Panicle stature of O. glaberrima (A), interspecific hybrids from sub-cluster 4-1 with erect (B) and intermediate (C) panicles respectively, and O. sativa and interspecific hybrids from sub-cluster 4-2 (D).*

Discussion

Development of interspecific hybrid varieties

The molecular data showed that cluster 4 is more closely related to *O. sativa* than to *O. glaberrima*. This can be explained by the following scenario for the development of interspecific hybrids in farmer fields. The progeny of an F1-hybrid between *O. sativa* and *O. glaberrima* can maintain itself in the gene pool only through backcrossing to either species (*O. sativa* or *O. glaberrima*), because of a high level of sterility of the F1-hybrid. Farmers do not harvest the panicles of an F1-hybrid because (almost) all grains are empty. Hybrids as such are not maintained in a plant population. The event of a flower being pollinated by pollen of the other rice species is not observable. A panicle that carries one seed which is the result of pollination by the other species (and 200 by self-pollination) looks normal. If that panicle is selected for sowing seed, the seed that is produced by the flower pollinated by the other species is sown in the rice field, germinates and produces a hybrid plant. Only after grain filling (usually at harvesting time) can a farmer recognise this plant as an interspecific hybrid because it does not carry any seed and therefore he/she will not harvest it. Backcrossing is the only way for the genes of a hybrid to be incorporated into a new genotype. From this point two sub-scenarios are possible. The first sub-scenario is that a hybrid plant is pollinated by surrounding normal plants and the few seeds produced by the hybrid remain in the field, germinating next season, then to be pollinated by surrounding normal plants, after which fertility is restored and the offspring may be harvested by farmers. This scenario was also suggested by Sano *et al*. [14]. For this scenario to be possible a farmer needs to crop the same field to rice for at least three consecutive growing seasons, as sometimes happens where land is initially fertile and where abandoned plots are then cleared for re-use by members of a household with low labour capacity, such as widows. Work on Nerica [5] and speciation in rice [14] suggests that two backcrosses are sufficient to obtain 'offspring' with good fertility. The second sub-scenario is that during flowering the F1-hybrid may pollinate the surrounding normal plants. A panicle of a normal plant in which one flower is pollinated by the hybrid looks normal and may be included in the seed for next season. Two such backcrossing events to *O. sativa* or *O. glaberrima*, and subsequent replanting of the progeny by farmers should also lead to fertile offspring, given enough time and opportunities. Subsequently, off-types of interspecific origin showing potential may be selected by farmers to be tested, multiplied and grown as new varieties. If other farmers show an interest in such a new variety, it may spread over a wider region. The whole process of the development of interspecific hybrid varieties is a combination of a random process of cross-pollination and backcrossing, followed by a selection process of those off-types that show most potential as new varieties by farmers.

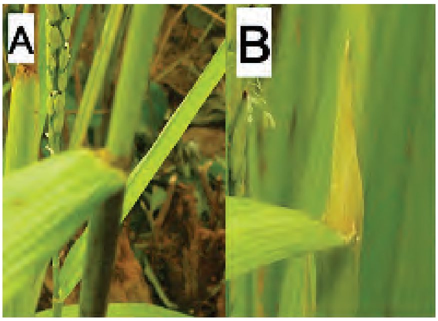

Figure 4*: Main ligule shapes found in this study. Ligule shape of O. glaberrima (A: small, rounded) and O. sativa and interspecific hybrids from cluster 4 (B: long, pointed)*

Field studies suggested that introgression can occur in both directions (from *O. glaberrima* to *O. sativa* and vice versa) [7,8], although some experimental studies have indicated that introgression from *O. sativa* to *O. glaberrima* occurs more often than introgression in the opposite direction [11,12], as confirmed by field observations in 2002 by Nuijten [25]. Artificial backcrosses produced fertile progenies which resembled the parental phenotypes, indicating that under natural conditions it is difficult to detect hybrid derivatives [9,14]. Given that the hybrid group (cluster 4) is closer to *O. sativa* than to *O. glaberrima*, successful backcrossing events in the field to *O. sativa* might be more likely than to *O. glaberrima*. According to Sano [9] the combination of nuclear DNA of *O. glaberrima* with cytoplasmic DNA of *O. sativa* always results in cytoplasmic male sterility. This suggests that the farmer hybrids may be the result of backcrossing to *O. sativa* and carry a combination of cytoplasmic DNA of *O. glaberrima* with nuclear DNA mainly from *O. sativa*. Chloroplast DNA analysis may give more conclusive information on whether the farmer hybrids result from *O. glaberrima* × *O. sativa* hybrids or *O. sativa* × *O. glaberrima* hybrids [26,27]. These results may also clarify which scenario of backcrossing in farmer fields led to the development of the farmer hybrids. But it should also be noted that in both species varieties may exist that are able to overcome the sterility system - so-called Wide Compatibility Varieties [11].

Rice hybridisation in farmer's fields may occur when *O. glaberrima* and *O. sativa* flower side by side. There are various scenarios to explain this co-occurrence at field level. The first possibility is the deliberate sowing of mixtures, which has been reported for several localities in the upper West African coastal zone [15,21,28]. The second, perhaps more common, possibility is the non-deliberate mixing of *O. glaberrima* within *O. sativa* seed stocks.

Roguing off-types requires skill and effort, and is sometimes neglected due to pressure to harvest the crop quickly, resulting in contamination of *O. sativa* seed batches with *O. glaberrima* seeds. Seed contamination can also reflect indebtedness, since farmers harvesting seed intended for loaning to poorer farmers rarely bother to rogue the material [29]. Because the separation of seed types after threshing is a much harder task than panicle roguing at harvest, contamination of *O. sativa* seed batches with *O. glaberrima* may be as high as 30%. These figures boost chances of spontaneous interspecific hybridisation on the farms where seed has been loaned.

Another non-intentional factor is the presence of weedy rice types intermediate between wild African rice (*O. barthii*) and *O. glaberrima* in farmers' fields. Gene flow between weedy types and cultivated Asian rice may also result in some in-field interspecific hybridisation. Weedy rice types like "*ngewobei*" and "*ngafabei*" (as named by Mende-speaking farmers in central Sierra Leone) may be the result of interspecific hybridisation between *O. barthii* and *O. sativa* (Table S1). Such weedy types may provide a bridge between wild and cultivated species for breeders to transfer useful characteristics from wild to cultivated rice.

***Table 4**: Number of farmer varieties, modern varieties and (semi-) wild relatives assigned by the software 'Structure' to the four observed clusters. Data for the farmer varieties are presented separately per country of origin.*

		The Gambia	Senegal	Guinea Bissau	Guinea Conakry	Sierra Leone	Ghana	Togo	Modern	(Semi) wild	Total
P (Gla)*	0.91 - 1.00	4	3	4	25	8	10	9		3	66
	0.81 - 0.90		1	1						1	3
	0.71 - 0.80									1	1
	0.61 - 0.70										
	0.51 - 0.60										
	0.41 - 0.50										
	0.31 - 0.40										
	0.21 - 0.30										
	0.11 - 0.20	2					1				3
	0.00 - 0.10	53	18	36	21	52	35	6	21		242
P (Ind)	0.91 - 1.00	23	7	5	14	8	20	3	12		92
	0.81 - 0.90	1			1	1	1				4
	0.71 - 0.80		1				1		1		3
	0.61 - 0.70	2			1		1				4
	0.51 - 0.60		1	1			1				3
	0.41 - 0.50		1				1				2
	0.31 - 0.40										
	0.21 - 0.30										
	0.11 - 0.20		1		1					1	3
	0.00 - 0.10	33	11	35	29	51	21	12	8	4	204
P (Jap)	0.91 - 1.00	18		18	2	29	10	3	7		87
	0.81 - 0.90	1		2	1		1				5
	0.71 - 0.80	1							1		2
	0.61 - 0.70										
	0.51 - 0.60										
	0.41 - 0.50						1				1
	0.31 - 0.40										
	0.21 - 0.30										
	0.11 - 0.20	1	1	1							3
	0.00 - 0.10	38	21	20	43	31	34	12	13	5	217
P (Cl4)	0.91 - 1.00	8	7	10	2	13					40
	0.81 - 0.90	1	1			1					3
	0.71 - 0.80										
	0.61 - 0.70										
	0.51 - 0.60		1								1
	0.41 - 0.50		1	1							2
	0.31 - 0.40	1					2				3
	0.21 - 0.30		1		1		1		1		4
	0.11 - 0.20	1				1	1		1		4
	0.00 - 0.10	48	11	30	43	45	42	15	19	5	258

** Probabilities of the materials assigned to O. glaberrima (Gla), O. sativa ssp. indica (Ind), O. sativa ssp. japonica (Jap) and the fourth cluster (Cl4).*

Time depth of farmer hybrid-derived rices – historical evidence

Given the release of hybrid-derived interspecific rice varieties in the Nerica series from WARDA (Africa Rice Center) in the late 1990s it is appropriate to provide evidence that the farmer intermediate types analysed in this paper pre-date the Nerica releases. Rice varieties with the name elements 'three month' and '*disi*' (also written as 'DC') and the same morphological features as the collected varieties with the same name elements belonging to cluster 4-1 were collected by Richards and Jusu in Sierra Leone in 1987–88 and 1995–96, respectively.

Farmers from Guinea Bissau provided the following information in the present study. The interspecific farmer hybrids belonging to cluster 4-1 collected in northern Guinea Bissau were reportedly cultivated before 1940. How much earlier they were cultivated is not clear, since precise data from before 1940 are largely absent. Some farmers considered them to have always been there. This gains some support from some of the names. In northern Guinea Bissau farmers referred to these varieties by names also used for *O. glaberrima,* such as '*jangjango*', '*untufa*', and '*wansarang*'. '*Jangjango*' specifically refers to the upright panicle typical of *O. glaberrima.* The meaning of the variety name '*untufa*' is 'rice from here' because it is considered ancient, implying farmers think it is *O. glaberrima,* the rice originally domesticated in West Africa.

The origin of many varieties from cluster 4-2, such as '*mani wulengo*', '*mani wulendingo*', '*mani konsonkuto*', '*ablie mano*', collected in The Gambia, Senegal and Guinea Bissau can be traced back to northern Guinea Bissau. One variety in The Gambia,'*binta sambou*', was developed from an off-type found in a field of '*ablie mano*' around 1990. Except for the variety '*binta sambou*' farmers could not pinpoint place or time of origin. In one village, Pantufa, in northern Guinea Bissau farmers indicated that varieties such as '*mani wulengo*', '*mani konsonkuto*', '*mani wulendingo*' and '*ablie mano*' were cultivated before 1940.

The information available so far suggests the countries where the interspecific farmer varieties were first cultivated were Sierra Leone and Guinea Bissau. No precise dates of origin can be specified, but the aforementioned data suggest that some existed for more than half a century, and thus long before the first release of Nerica varieties.

Spread of interspecific farmer hybrids

Adversity such as war and drought appear to have favoured the selection and spread of spontaneous interspecific rice hybrids among West African farmers. War has forced some farmers into intensively farmed pockets of land without access to fertilisers. Farmer hybrids appear to share the adaptation to poor soils of the *O. glaberrima* parent. Parts of the war zone in Sierra Leone, cut off from aid assistance over several years, appeared to be mainly growing interspecific hybrid varieties (or pure glaberrimas) in the period immediately after fighting ceased [31]. Farmers noted that war reduced the amount of time available for clearing of forest, weeding and careful harvesting new fields, since civilians were reluctant to linger for fear of encountering fighters. In other cases (e.g. as a result of war in Guinea-Bissau and southern Senegal) they fled across borders, taking their hardy varieties with them. Farmer hybrids are particularly frequent in our samples from southern Senegal, Guinea-Bissau and Sierra Leone (Table 4) − all regions affected by recent episodes of armed conflict.

In Senegal and The Gambia the farmer hybrids have probably helped farmers to cope with climatic fluctuation. The farmer hybrids (belonging to sub-cluster 4-2) collected in these two countries tend to flower about one week earlier than the farmer hybrids (belonging to sub-cluster 4-1) collected in Sierra Leone (Table 3). Senegal and The Gambia have been badly affected by drought in recent times. In addition, both countries have faced increased demographic pressure, exacerbated by armed conflict in southern Senegal and Guinea Bissau. Farmer hybrids may embody considerable adaptive plasticity to suboptimal farming conditions associated with such difficulties.

An important reason why in Senegal and The Gambia farmers mainly grow farmer hybrids belonging to sub-cluster 4-2 is that in these two countries farmers do not like a red pericarp colour (the variety belonging to sub-cluster 4-1 and cultivated in Senegal does not have a red pericarp). In addition, some farmers mentioned they do not like an erect panicle when mature. In Sierra Leone and Guinea Conakry the farmer hybrids found belonged to sub-cluster 4-1. In these two countries farmers prefer a red pericarp colour because they claim it is related to slow digestion. Also they do not consider an erect panicle a negative trait. These two traits are the main traits that differentiate sub-clusters 4-1 and 4-2. Both can be considered polygenic traits which may explain why farmer selection practices have resulted in large genetic differences between the two sub-clusters, as is shown by the molecular data. Given the different ecological and climatic conditions in the region, the outcome of farmer selection for traits such as panicle length, tillering, plant height, yield, taste, swelling, and ease of threshing may possibly have contributed to the genetic differences between sub-clusters 4-1 and 4-2.

Why are interspecific farmer hybrids absent or rare in Ghana and Togo?

Farmer interspecific hybrids are less frequent or absent in our samples from Ghana and Togo (Togo Hills), an important region of co-occurrence of *O. glaberrima* and *O. sativa*. Conditions in the Togo Hills may be less favourable to in-field interspecific hybridisation due to cultural and geographical factors. The cultural significance of African rice seems to limit the amount of farmer hybridisation on the Ghana side of the Togo Hills. Rice cultivators in eastern Ghana grow *O. sativa* mainly as a commercial crop under relatively favourable conditions. These farmers maintain a strong interest in African rice, but for cultural reasons. African rice is prominent in traditional ceremonies and as an ethnic marker [32]. In such circumstances, a hybrid would be less suited because of its blurred morphology. Farmers in Togo (the Danyi plateau) grow African rice at higher altitudes, while *O. sativa* is planted at lower altitudes. This imposes a geographical barrier to interspecific hybridisation.

Concluding remarks

Our results strongly suggest that interspecific hybridisation in West African farmers' fields is a recurrent and continuing process, with spontaneous back-crossing events playing a crucial role, resulting in different groups of genetic diversity in different rice growing areas stimulated by differences in selection criteria and selection environments. This clear evidence for the emergence of farmer hybrids of African and Asian rice in West Africa has important implications for understanding crop development and human adaptation. Whether and how such hybridisation and backcrossing events have occurred for other crops may be a useful question to pursue, to achieve a better understanding of crop development and diversity. For example, it may help to identify the most plausible scenario for the development of maize (*Zea mays* L.). Our findings also suggest that adversity, such as dislocation by armed conflict and climatic change, has not hindered, and may have accelerated the rate at which interspecific hybrid rice varieties have spread [31]. Farmer interspecific hybrids of rice may complement those recently developed by formal scientific research. This points to potential value in linking science and local technology development by marginalised groups, better to address challenges of rapid adaptation in a world of increased socio-political and climatic uncertainty.

Supporting Information

Table S1: Overview of the 315 investigated rice samples and their assignment to the four observed clusters by the software Structure (see below).

Acknowledgments

The late Dr Malcolm Sellu Jusu of Rokupr Rice Research Station, Sierra Leone, is recognised for proposing research on farmer interspecific rices during the 1980s. The assistance of Dr. Marina Temudo in the fieldwork in Guinea Bissau is much appreciated. We thank two anonymous reviewers for critical comments that helped improve the manuscript.

Author Contributions

Conceived and designed the experiments: EN RvT PS AM FO BT PR. Performed the experiments: EN RvT AM FO BT. Analysed the data: EN RvT. Contributed reagents/materials/analysis tools: EN RvT AM FO BT. Wrote the paper: EN RvT PS AM FO BT PR.

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Annexes

Table S1: *Overview of the 315 investigated rice samples and their assignment to the four observed clusters by the software Structure.*

Variety name	Origin	Taxonomy	P (Gla)	P (Ind)	P (Jap)	P (Cl4)
A. Farmer varieties						
Kaomo black	Ghana	*O. glaberrima*	1.00	0.00	0.00	0.00
Kaomo black (with awns)	Ghana	*O. glaberrima*	1.00	0.00	0.00	0.00
Kaomo krukutuwa	Ghana	*O. glaberrima*	1.00	0.00	0.00	0.00
Kaomo krukutuwa signaweh	Ghana	*O. glaberrima*	1.00	0.00	0.00	0.00
Kaomo signaweh	Ghana	*O. glaberrima*	1.00	0.00	0.00	0.00
Kaomo signaweh black	Ghana	*O. glaberrima*	1.00	0.00	0.00	0.00
Kaomo white	Ghana	*O. glaberrima*	1.00	0.00	0.00	0.00
Jangjango	Guinea Bissau	*O. glaberrima*	1.00	0.00	0.00	0.00
Jangjango	Guinea Bissau	*O. glaberrima*	1.00	0.00	0.00	0.00
Kurekimbeli	Guinea Bissau	*O. glaberrima*	1.00	0.00	0.00	0.00
Uassolondji	Guinea Bissau	*O. glaberrima*	1.00	0.00	0.00	0.00
Dixi Wansan Lot 1	Guinea Conakry	*O. glaberrima*	1.00	0.00	0.00	0.00
Saali Fire	Guinea Conakry	*O. glaberrima*	1.00	0.00	0.00	0.00
Saali Fore	Guinea Conakry	*O. glaberrima*	1.00	0.00	0.00	0.00
Saali Fore	Guinea Conakry	*O. glaberrima*	1.00	0.00	0.00	0.00
Saali Fore	Guinea Conakry	*O. glaberrima*	1.00	0.00	0.00	0.00
Saali Fore	Guinea Conakry	*O. glaberrima*	1.00	0.00	0.00	0.00
Saali Fore	Guinea Conakry	*O. glaberrima*	1.00	0.00	0.00	0.00
Siiga?	Guinea Conakry	*O. glaberrima*	1.00	0.00	0.00	0.00
Tombo Bokary	Guinea Conakry	*O. glaberrima*	1.00	0.00	0.00	0.00
Tombo Bokary	Guinea Conakry	*O. glaberrima*	1.00	0.00	0.00	0.00
Tombo Bokary	Guinea Conakry	*O. glaberrima*	1.00	0.00	0.00	0.00
Tombo Bokary	Guinea Conakry	*O. glaberrima*	1.00	0.00	0.00	0.00
Tombo Bokary	Guinea Conakry	*O. glaberrima*	1.00	0.00	0.00	0.00
Tombo Bokary	Guinea Conakry	*O. glaberrima*	1.00	0.00	0.00	0.00
Mani Musoo	Senegal	*O. glaberrima*	1.00	0.00	0.00	0.00
Mani Musoo	Senegal	*O. glaberrima*	1.00	0.00	0.00	0.00
Damba	Sierra Leone	*O. glaberrima*	1.00	0.00	0.00	0.00
Saliforeh	Sierra Leone	*O. glaberrima*	1.00	0.00	0.00	0.00
Mani Ba	The Gambia	*O. glaberrima*	1.00	0.00	0.00	0.00
Mani Ba	The Gambia	*O. glaberrima*	1.00	0.00	0.00	0.00
Mani Ba	The Gambia	*O. glaberrima*	1.00	0.00	0.00	0.00
Mani Ba	The Gambia	*O. glaberrima*	1.00	0.00	0.00	0.00
Awinto blanc	Togo	*O. glaberrima*	1.00	0.00	0.00	0.00
Awinto yibo	Togo	*O. glaberrima*	1.00	0.00	0.00	0.00
Danyi moli	Togo	*O. glaberrima*	1.00	0.00	0.00	0.00
Danyi moli	Togo	*O. glaberrima*	1.00	0.00	0.00	0.00
Kpakpalipke	Togo	*O. glaberrima*	1.00	0.00	0.00	0.00
Xleti etoh (three months)	Togo	*O. glaberrima*	1.00	0.00	0.00	0.00
Xleti eve	Togo	*O. glaberrima*	1.00	0.00	0.00	0.00
Yibo riz	Togo	*O. glaberrima*	1.00	0.00	0.00	0.00
Kaomo signaweh white	Ghana	*O. glaberrima*	0.99	0.00	0.00	0.00
Saali Koute	Guinea Conakry	*O. glaberrima*	0.99	0.01	0.00	0.00
Tombo Bokary	Guinea Conakry	*O. glaberrima*	0.99	0.00	0.00	0.00
Mani Musoo	Senegal	*O. glaberrima*	0.99	0.01	0.00	0.00
Sanganyaa	Sierra Leone	*O. glaberrima*	0.99	0.00	0.00	0.01
Dixi Wansan Lot 2	Guinea Conakry	*O. glaberrima*	0.98	0.00	0.01	0.00
Safaary	Guinea Conakry	*O. glaberrima*	0.98	0.00	0.00	0.01

Siiga	Guinea Conakry	*O. glaberrima*	0.98	0.01	0.01	0.01
Tombo Bokary	Guinea Conakry	*O. glaberrima*	0.98	0.00	0.00	0.02
Gbankeyi	Guinea Conakry	*O. glaberrima*	0.97	0.01	0.00	0.02
Safaary	Guinea Conakry	*O. glaberrima*	0.96	0.01	0.02	0.01
Awinto blanc	Togo	*O. glaberrima*	0.93	0.03	0.00	0.03
Maalay	Sierra Leone	*O. glaberrima*	0.92	0.03	0.03	0.02
Saali Fore	Guinea Conakry	*O. glaberrima*	0.91	0.06	0.02	0.01
Saali Fore	Guinea Conakry	*O. glaberrima*	0.91	0.00	0.02	0.07
Mani Musoo	Senegal	*O. glaberrima*	0.82	0.14	0.00	0.04
Wansarang	Guinea Bissau	*O. glaberrima*	0.81	0.02	0.14	0.02
Siiga	Guinea Conakry	*O. glaberrima*	0.01	0.98	0.00	0.01
Dalifode	Guinea Conakry	*O. glaberrima*	0.10	0.67	0.01	0.22
Trimont (white)	Sierra Leone	*O. glaberrima*	0.00	0.00	0.00	1.00
Pa Trimont	Sierra Leone	*O. glaberrima*	0.00	0.00	0.00	0.99
Painy-pain	Sierra Leone	*O. glaberrima*	0.00	0.00	0.00	0.99
Pindie	Sierra Leone	*O. glaberrima*	0.00	0.00	0.00	0.99
Pa Trimont (red)	Sierra Leone	*O. glaberrima*	0.01	0.01	0.00	0.98
Saliforeh	Sierra Leone	*O. glaberrima*	0.00	0.01	0.03	0.96
Samba	Guinea Conakry	*O. sativa*	0.97	0.01	0.02	0.01
Adeisi	Ghana	*O. sativa*	0.00	1.00	0.00	0.00
Akpasseh	Ghana	*O. sativa*	0.00	1.00	0.00	0.00
Red saka	Ghana	*O. sativa*	0.00	1.00	0.00	0.00
Zomojo	Ghana	*O. sativa*	0.00	1.00	0.00	0.00
Bissau	Guinea Bissau	*O. sativa*	0.00	1.00	0.00	0.00
Sajar	Guinea Bissau	*O. sativa*	0.00	1.00	0.00	0.00
Kaniya	Guinea Conakry	*O. sativa*	0.00	1.00	0.00	0.00
Momodou male	Guinea Conakry	*O. sativa*	0.00	1.00	0.00	0.00
Saidou fire (red grain)	Guinea Conakry	*O. sativa*	0.00	1.00	0.00	0.00
Soumaila	Guinea Conakry	*O. sativa*	0.00	1.00	0.00	0.00
Ablie Koyo	Senegal	*O. sativa*	0.00	1.00	0.00	0.00
Fadass	Senegal	*O. sativa*	0.00	1.00	0.00	0.00
Kuboni	Senegal	*O. sativa*	0.00	1.00	0.00	0.00
Madina Koyo	Senegal	*O. sativa*	0.00	1.00	0.00	0.00
Buttercup	Sierra Leone	*O. sativa*	0.00	1.00	0.00	0.00
Yainky-Yanka	Sierra Leone	*O. sativa*	0.00	1.00	0.00	0.00
Akacha	The Gambia	*O. sativa*	0.00	1.00	0.00	0.00
Barafita koyo	The Gambia	*O. sativa*	0.00	1.00	0.00	0.00
Baraso	The Gambia	*O. sativa*	0.00	1.00	0.00	0.00
Bendou	The Gambia	*O. sativa*	0.00	1.00	0.00	0.00
Chinese short	The Gambia	*O. sativa*	0.00	1.00	0.00	0.00
Derisa Mano	The Gambia	*O. sativa*	0.00	1.00	0.00	0.00
Foni Mano	The Gambia	*O. sativa*	0.00	1.00	0.00	0.00
Off-type (in Binta Sambou)	The Gambia	*O. sativa*	0.00	1.00	0.00	0.00
Peking	The Gambia	*O. sativa*	0.00	1.00	0.00	0.00
Peking	The Gambia	*O. sativa*	0.00	1.00	0.00	0.00
Tensi	The Gambia	*O. sativa*	0.00	1.00	0.00	0.00
Tombom	The Gambia	*O. sativa*	0.00	1.00	0.00	0.00
Adeta red rice	Ghana	*O. sativa*	0.00	0.99	0.00	0.01
Awonyo (two months)	Ghana	*O. sativa*	0.00	0.99	0.01	0.01
Bouake	Ghana	*O. sativa*	0.00	0.99	0.00	0.01
James rice	Ghana	*O. sativa*	0.00	0.99	0.00	0.01
Red saka	Ghana	*O. sativa*	0.00	0.99	0.00	0.00
Red saka (off-type?)	Ghana	*O. sativa*	0.00	0.99	0.00	0.01
Red variety	Ghana	*O. sativa*	0.00	0.99	0.00	0.00
Aninha de lugar	Guinea Bissau	*O. sativa*	0.00	0.99	0.00	0.01
Wankarang	Guinea Bissau	*O. sativa*	0.00	0.99	0.00	0.00
Saidou Fire	Guinea Conakry	*O. sativa*	0.00	0.99	0.00	0.00
Saidou Fire	Guinea Conakry	*O. sativa*	0.00	0.99	0.00	0.01

Saidou Gbeeli	Guinea Conakry	*O. sativa*	0.00	0.99	0.00	0.00
Saidou Gbeeli	Guinea Conakry	*O. sativa*	0.00	0.99	0.00	0.00
Jina Mano	Senegal	*O. sativa*	0.00	0.99	0.00	0.00
Kuboni Juuno	Senegal	*O. sativa*	0.00	0.99	0.00	0.00
Rok31	Sierra Leone	*O. sativa*	0.00	0.99	0.00	0.00
Bonti	The Gambia	*O. sativa*	0.00	0.99	0.00	0.01
Kadi Dabo	The Gambia	*O. sativa*	0.00	0.99	0.00	0.00
Mani Suntungo-1	The Gambia	*O. sativa*	0.00	0.99	0.00	0.01
Mani Suntungo-2	The Gambia	*O. sativa*	0.00	0.99	0.00	0.00
Muso Noringo	The Gambia	*O. sativa*	0.00	0.99	0.00	0.01
Peking	The Gambia	*O. sativa*	0.00	0.99	0.00	0.01
Sainey Kolly	The Gambia	*O. sativa*	0.00	0.99	0.01	0.01
Teiba	The Gambia	*O. sativa*	0.00	0.99	0.00	0.01
Awuie red	Togo	*O. sativa*	0.00	0.99	0.00	0.00
Awuie white	Togo	*O. sativa*	0.00	0.99	0.00	0.01
White saka	Ghana	*O. sativa*	0.00	0.98	0.00	0.02
Sambaconcon	Guinea Bissau	*O. sativa*	0.02	0.98	0.00	0.00
CK 21	Guinea Conakry	*O. sativa*	0.01	0.98	0.01	0.01
Pode 1	Guinea Conakry	*O. sativa*	0.00	0.98	0.01	0.01
Sorie Kunde	Sierra Leone	*O. sativa*	0.00	0.98	0.01	0.01
Chinese red	The Gambia	*O. sativa*	0.00	0.98	0.00	0.02
Saidou fire (white grain)	Guinea Conakry	*O. sativa*	0.01	0.97	0.01	0.01
Saidou Gbeeli	Guinea Conakry	*O. sativa*	0.01	0.97	0.02	0.00
Yaka (Rok3)	Sierra Leone	*O. sativa*	0.01	0.97	0.01	0.02
Viotto (off-type?)	Ghana	*O. sativa*	0.00	0.95	0.04	0.01
Zomojo	Ghana	*O. sativa*	0.01	0.95	0.04	0.01
Zomojo (off-type?)	Ghana	*O. sativa*	0.00	0.95	0.00	0.04
Baraso	The Gambia	*O. sativa*	0.00	0.95	0.00	0.04
Sarjo Keeba Mano	The Gambia	*O. sativa*	0.01	0.94	0.04	0.01
Yaka	Sierra Leone	*O. sativa*	0.00	0.93	0.01	0.07
Pa Bad-scent	Sierra Leone	*O. sativa*	0.06	0.92	0.01	0.01
Viono short	Ghana	*O. sativa*	0.00	0.91	0.08	0.00
Wonyonwonyon yi	Guinea Conakry	*O. sativa*	0.02	0.89	0.04	0.05
Terfatch	The Gambia	*O. sativa*	0.01	0.82	0.01	0.16
Damansah 1	Ghana	*O. sativa*	0.00	0.81	0.00	0.18
Mani Koyo	Senegal	*O. sativa*	0.00	0.74	0.01	0.25
Damansah 4	Ghana	*O. sativa*	0.00	0.62	0.06	0.31
Off-type (in Hombo Wulengo)	The Gambia	*O. sativa*	0.00	0.61	0.00	0.38
Bondiyaa Karejang	Senegal	*O. sativa*	0.00	0.54	0.00	0.46
Off-type (in Tabuyaa Mani Koyo)	Guinea Bissau	*O. sativa*	0.00	0.53	0.01	0.46
Aqua blue	Ghana	*O. sativa*	0.00	0.48	0.44	0.07
Aqua blue	Ghana	*O. sativa*	0.00	0.00	1.00	0.00
Aqua blue with awns	Ghana	*O. sativa*	0.00	0.00	1.00	0.00
Gokpui	Ghana	*O. sativa*	0.00	0.00	1.00	0.00
Mateggi	Ghana	*O. sativa*	0.00	0.00	1.00	0.00
Buba Njie	Guinea Bissau	*O. sativa*	0.00	0.00	1.00	0.00
Bumali	Guinea Bissau	*O. sativa*	0.00	0.00	1.00	0.00
Conakry	Guinea Bissau	*O. sativa*	0.00	0.00	1.00	0.00
Demba Ba	Guinea Bissau	*O. sativa*	0.00	0.00	1.00	0.00
Jahuun (sutungo)	Guinea Bissau	*O. sativa*	0.00	0.00	1.00	0.00
Kissidugô	Guinea Bissau	*O. sativa*	0.00	0.00	1.00	0.00
Nahawa	Guinea Bissau	*O. sativa*	0.00	0.00	1.00	0.00
Off-type (in Sefa Fingo)	Guinea Bissau	*O. sativa*	0.00	0.00	1.00	0.00
Sefa Fingo	Guinea Bissau	*O. sativa*	0.00	0.00	1.00	0.00
Senkiliba	Guinea Bissau	*O. sativa*	0.00	0.00	1.00	0.00
Toba	Guinea Bissau	*O. sativa*	0.00	0.00	1.00	0.00
Umobel	Guinea Bissau	*O. sativa*	0.00	0.00	1.00	0.00
Usefa Udjenel	Guinea Bissau	*O. sativa*	0.00	0.00	1.00	0.00

Conakry	Guinea Conakry	*O. sativa*	0.00	0.00	1.00	0.00
Bobordeen	Sierra Leone	*O. sativa*	0.00	0.00	1.00	0.00
Boikortor	Sierra Leone	*O. sativa*	0.00	0.00	1.00	0.00
Gbengben	Sierra Leone	*O. sativa*	0.00	0.00	1.00	0.00
Gbengben	Sierra Leone	*O. sativa*	0.00	0.00	1.00	0.00
Jobboi	Sierra Leone	*O. sativa*	0.00	0.00	1.00	0.00
Jumukui	Sierra Leone	*O. sativa*	0.00	0.00	1.00	0.00
Kondaylah	Sierra Leone	*O. sativa*	0.00	0.00	1.00	0.00
Kortigbongoi	Sierra Leone	*O. sativa*	0.00	0.00	1.00	0.00
Nduluwai	Sierra Leone	*O. sativa*	0.00	0.00	1.00	0.00
Pamanneh	Sierra Leone	*O. sativa*	0.00	0.00	1.00	0.00
Pla Gbon	Sierra Leone	*O. sativa*	0.00	0.00	1.00	0.00
Sembehun nyaha	Sierra Leone	*O. sativa*	0.00	0.00	1.00	0.00
Hombo Wulengo	The Gambia	*O. sativa*	0.00	0.00	1.00	0.00
Kukone	The Gambia	*O. sativa*	0.00	0.00	1.00	0.00
Kukur	The Gambia	*O. sativa*	0.00	0.00	1.00	0.00
Mani Tima	The Gambia	*O. sativa*	0.00	0.00	1.00	0.00
Nerica koyo	The Gambia	*O. sativa*	0.00	0.00	1.00	0.00
off-type (in Hombo Wulengo)	The Gambia	*O. sativa*	0.00	0.00	1.00	0.00
Off-type (in Sefa Koyo)	The Gambia	*O. sativa*	0.00	0.00	1.00	0.00
Off-type (Samano?)	The Gambia	*O. sativa*	0.00	0.00	1.00	0.00
Sefa Fingo	The Gambia	*O. sativa*	0.00	0.00	1.00	0.00
Sefa Fingo (red)	The Gambia	*O. sativa*	0.00	0.00	1.00	0.00
Sefa Koyo	The Gambia	*O. sativa*	0.00	0.00	1.00	0.00
Sonna Mano	The Gambia	*O. sativa*	0.00	0.00	1.00	0.00
Wesiwes	The Gambia	*O. sativa*	0.00	0.00	1.00	0.00
Aquablue	Togo	*O. sativa*	0.00	0.00	1.00	0.00
Ujogade	Guinea Bissau	*O. sativa*	0.01	0.00	0.99	0.00
Uyeey	Guinea Bissau	*O. sativa*	0.00	0.00	0.99	0.00
Bonyaha	Sierra Leone	*O. sativa*	0.01	0.00	0.99	0.00
Coffeegay..	Sierra Leone	*O. sativa*	0.00	0.00	0.99	0.00
Konowanjei	Sierra Leone	*O. sativa*	0.00	0.00	0.99	0.01
Nerica wulengo	The Gambia	*O. sativa*	0.00	0.00	0.99	0.00
Sefa Nunfingo	The Gambia	*O. sativa*	0.00	0.00	0.99	0.00
Sefa Nunfingo (white)	The Gambia	*O. sativa*	0.00	0.01	0.99	0.00
Wab 56-50	The Gambia	*O. sativa*	0.00	0.00	0.99	0.00
Aqua blue	Ghana	*O. sativa*	0.00	0.00	0.98	0.01
Off-type (in Kadidjango)	Guinea Bissau	*O. sativa*	0.00	0.01	0.98	0.01
Otcha	Guinea Bissau	*O. sativa*	0.00	0.01	0.98	0.00
Mabargie	Sierra Leone	*O. sativa*	0.00	0.01	0.98	0.01
Yonnie	Sierra Leone	*O. sativa*	0.01	0.00	0.98	0.01
Berengdinto Koyo	Guinea Bissau	*O. sativa*	0.00	0.01	0.97	0.01
Nerigay	Sierra Leone	*O. sativa*	0.00	0.02	0.97	0.01
Yabasie	Sierra Leone	*O. sativa*	0.01	0.02	0.97	0.00
Gbengben	Sierra Leone	*O. sativa*	0.00	0.00	0.96	0.04
Gbengben	Sierra Leone	*O. sativa*	0.03	0.00	0.96	0.01
Musugomie	Sierra Leone	*O. sativa*	0.02	0.01	0.96	0.01
Jetteh	Sierra Leone	*O. sativa*	0.00	0.04	0.95	0.00
Off-type (lost variety)	The Gambia	*O. sativa*	0.00	0.02	0.95	0.02
Jewule	Sierra Leone	*O. sativa*	0.04	0.01	0.94	0.02
Konko	Guinea Conakry	*O. sativa*	0.00	0.07	0.93	0.00
Ngiligortie	Sierra Leone	*O. sativa*	0.05	0.02	0.93	0.00
Red saka	Ghana	*O. sativa*	0.02	0.00	0.91	0.06
Off-type (lost variety)	The Gambia	*O. sativa*	0.00	0.01	0.90	0.09
Wapu	Guinea Bissau	*O. sativa*	0.00	0.04	0.89	0.07
Off-type (in Uyeeye)	Guinea Bissau	*O. sativa*	0.00	0.06	0.87	0.07
Kolosarr, original	Guinea Bissau	*O. sativa*	0.00	0.00	0.00	1.00
Daakulo Koyo	Senegal	*O. sativa*	0.00	0.00	0.00	1.00

Kumoi	The Gambia	*O. sativa*	0.00	0.00	0.00	1.00
M Mesengo	The Gambia	*O. sativa*	0.00	0.00	0.00	1.00
Mani Wulengo	The Gambia	*O. sativa*	0.00	0.00	0.00	1.00
Kolosarr, Bondiya	Guinea Bissau	*O. sativa*	0.00	0.01	0.00	0.99
Konsonkuto	Guinea Bissau	*O. sativa*	0.00	0.00	0.00	0.99
Maimuna	Guinea Bissau	*O. sativa*	0.00	0.00	0.00	0.99
Kissi Foundeyi	Guinea Conakry	*O. sativa*	0.00	0.00	0.00	0.99
Wonyonwonyon yi	Guinea Conakry	*O. sativa*	0.00	0.01	0.01	0.99
Ablie Mano	Senegal	*O. sativa*	0.00	0.00	0.00	0.99
Einu	Senegal	*O. sativa*	0.00	0.01	0.00	0.99
Madina Wulengo	Senegal	*O. sativa*	0.00	0.01	0.00	0.99
Kari Saba	The Gambia	*O. sativa*	0.00	0.01	0.00	0.99
Mani Mesendingo	The Gambia	*O. sativa*	0.00	0.01	0.00	0.99
Off-type (in Mani Wulendingo)	The Gambia	*O. sativa*	0.00	0.01	0.00	0.99
Kolosarr, M Wulendingo	Guinea Bissau	*O. sativa*	0.00	0.02	0.00	0.98
Mesemese	Guinea Bissau	*O. sativa*	0.00	0.02	0.00	0.98
Off-type (in Madina Wulengo)	Senegal	*O. sativa*	0.00	0.02	0.01	0.98
Binta Sambou	The Gambia	*O. sativa*	0.00	0.02	0.00	0.98
Mani Wulendingo	The Gambia	*O. sativa*	0.00	0.02	0.00	0.98
Off-type (in Madina Wulengo)	Senegal	*O. sativa*	0.00	0.01	0.03	0.95
Kong	Senegal	*O. sativa*	0.00	0.05	0.02	0.93
Moti	The Gambia	*O. sativa*	0.00	0.03	0.08	0.89
Off-type (in Madina Wulengo)	Senegal	*O. sativa*	0.00	0.02	0.11	0.88
Daakulo	Senegal	*O. sativa*	0.00	0.41	0.00	0.59
Trimonte	Guinea Conakry	Hybrid	0.00	1.00	0.00	0.00
Off-type (in Daakulo)	Senegal	Hybrid	0.00	0.99	0.00	0.00
Ataa	Ghana	Hybrid	0.00	0.71	0.00	0.28
Off-type (in WAB 56-50)	The Gambia	Hybrid	0.20	0.64	0.15	0.01
Aquablue awinto	Togo	Hybrid	0.00	0.00	1.00	0.00
Khaki	Togo	Hybrid	0.00	0.00	1.00	0.00
Aqua blue signaweh	Ghana	Hybrid	0.00	0.00	0.99	0.00
Pa Three Month2	Sierra Leone	Hybrid	0.00	0.01	0.99	0.01
Nerica 2 (off-type)	Ghana	Hybrid	0.00	0.01	0.94	0.04
Nerica 2	Ghana	Hybrid	0.12	0.00	0.87	0.00
Sewa	Guinea Conakry	Hybrid	0.00	0.13	0.86	0.00
Off-type (in WAB 56-50)	The Gambia	Hybrid	0.20	0.00	0.80	0.00
Dissi	Guinea Bissau	Hybrid	0.00	0.00	0.00	0.99
Jangjango	Guinea Bissau	Hybrid	0.00	0.00	0.00	0.99
Untufa	Guinea Bissau	Hybrid	0.00	0.00	0.01	0.99
Wansarang	Guinea Bissau	Hybrid	0.00	0.00	0.00	0.99
Tebeleh	Sierra Leone	Hybrid	0.01	0.00	0.01	0.98
Pa Three Month1	Sierra Leone	Hybrid	0.00	0.05	0.01	0.95
Pa Three Month3	Sierra Leone	Hybrid	0.00	0.01	0.10	0.88
Kaomo with awns	Ghana	unclear	1.00	0.00	0.00	0.00
Kolonkalan 1b	Sierra Leone	unclear	1.00	0.00	0.00	0.00
Off-type 1A	Sierra Leone	unclear	1.00	0.00	0.00	0.00
Pindie	Sierra Leone	unclear	1.00	0.00	0.00	0.00
Egomu	Ghana	unclear	0.97	0.01	0.01	0.01
Off-type 1B	Sierra Leone	unclear	0.96	0.02	0.00	0.02
Pugulu undef.	Ghana	unclear	0.00	0.99	0.00	0.01
Pugulu white	Ghana	unclear	0.00	0.99	0.00	0.00
Viono tall	Ghana	unclear	0.00	0.99	0.01	0.00
Pa Follah	Sierra Leone	unclear	0.00	0.99	0.00	0.00
Tema	Togo	unclear	0.00	0.97	0.00	0.03
Pugulu red	Ghana	unclear	0.00	0.95	0.02	0.03
Pla-Camp	Sierra Leone	unclear	0.01	0.87	0.02	0.11
Damansah 3	Ghana	unclear	0.01	0.60	0.03	0.35
Pugulu undef.	Ghana	unclear	0.00	0.00	1.00	0.00

Gbondobai	Sierra Leone	unclear	0.00	0.00	1.00	0.00
Pugulu undef.	Ghana	unclear	0.00	0.00	0.99	0.00
Jebbeh-komie	Sierra Leone	unclear	0.01	0.00	0.98	0.00
Bogootie	Sierra Leone	unclear	0.00	0.02	0.96	0.02
Pindi-pabai 1a red	Sierra Leone	unclear	0.00	0.00	0.00	1.00
Pa DC	Sierra Leone	unclear	0.00	0.00	0.00	0.99
Pa Yariken	Sierra Leone	unclear	0.00	0.00	0.00	0.99
Pa DC	Sierra Leone	unclear	0.01	0.01	0.00	0.98
Trimont (white)	Sierra Leone	unclear	0.01	0.00	0.05	0.95
B. Modern varieties						
I Kong Pao	CIRAD	*O. sativa*	0.00	1.00	0.00	0.00
CCA	NARI	*O. sativa*	0.00	1.00	0.00	0.00
Parasana	NARI	*O. sativa*	0.00	1.00	0.00	0.00
Se 302 G (IRAT 11)	CIRAD	*O. sativa*	0.00	0.99	0.00	0.01
Se 319 G (IRAT 12)	CIRAD	*O. sativa*	0.00	0.99	0.00	0.01
IR66-23	IRRI	*O. sativa*	0.00	0.99	0.00	0.00
DJ 12-519	ISRA	*O. sativa*	0.00	0.99	0.00	0.00
DJ 8-341	ISRA	*O. sativa*	0.00	0.99	0.01	0.00
Off-type (in DJ-11-307)	NARI	*O. sativa*	0.00	0.99	0.00	0.00
RC18-3	IRRI	*O. sativa*	0.00	0.98	0.01	0.01
DJ-11-307	NARI	*O. sativa*	0.00	0.97	0.00	0.03
RC10-43	IRRI	*O. sativa*	0.00	0.94	0.01	0.05
IR36-63	IRRI	*O. sativa*	0.00	0.76	0.01	0.23
IRAT 10	CIRAD	*O. sativa*	0.00	0.00	1.00	0.00
IRAT 110	WARDA	*O. sativa*	0.00	0.00	1.00	0.00
IRAT 112	WARDA	*O. sativa*	0.00	0.00	1.00	0.00
OS 6 (Faro 11)	WARDA	*O. sativa*	0.00	0.00	1.00	0.00
WAB 365-B-2-H3-HB	WARDA	*O. sativa*	0.00	0.00	0.99	0.00
WAB 450-I-B-P-163-4-1	WARDA	Hybrid	0.00	0.00	1.00	0.00
WAB 450-I-B-P-105-HB	WARDA	Hybrid	0.06	0.00	0.93	0.00
Nerica 1	MOFA	Hybrid	0.08	0.02	0.77	0.14
C. Wild and semi-wild material						
*O. barthi*i black	The Gambia	*O. barthi*i	1.00	0.00	0.00	0.00
*O. barthi*i white	The Gambia	*O. barthi*i	1.00	0.00	0.00	0.00
Devil rice	Guinea Conakry	*O. barthi*i	0.97	0.01	0.01	0.01
Ngafa bei	Sierra Leone	*O. barthi*i	0.84	0.10	0.01	0.06
Ngewobei	Sierra Leone	*O. barthi*i	0.75	0.19	0.02	0.04

CHAPTER FIVE

Robustness and Strategies of Adaptation among Farmer Varieties of African Rice (Oryza glaberrima) and Asian Rice (Oryza sativa) across West Africa

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Published as: Mokuwa A, Nuijten E, Okry F, Teeken B, Maat H, Richards P, Struik PC (2013) Robustness and strategies of adaptation among farmer varieties of African rice (*Oryza glaberrima*) and Asian rice (*Oryza sativa*) across West Africa. PLoS ONE 8(3): e34801. doi:10.1371/journal.pone.0034801.

Abstract
This study offers evidence of the robustness of farmer rice varieties (*Oryza glaberrima* and *O. sativa*) in West Africa. Our experiments in five West African countries showed that farmer varieties were tolerant of sub-optimal conditions, but employed a range of strategies to cope with stress. Varieties belonging to the species *Oryza glaberrima* - solely the product of farmer agency - were the most successful in adapting to a range of adverse conditions. Some of the farmer selections from within the *indica* and *japonica* subspecies of *O. sativa* also performed well in a range of conditions, but other farmer selections from within these two subspecies were mainly limited to more specific niches. The results contradict the rather common belief that farmer varieties are only of local value. Farmer varieties should be considered by breeding programmes and used (alongside improved varieties) in dissemination projects for rural food security.

Keywords: *Oryza glaberrima*, *Oryza sativa*, robustness, adaptation, farmer varieties, West Africa

Introduction

It is often supposed that crops should only be grown where conditions are favourable. This is not an option for farmers cultivating food crops with limited resources. They have to grow what they need with the conditions they have been given. In short, they have to cope with sub-optimality. For these farmers, adaptability of varieties under sub-optimal conditions is an essential requirement [1, 2]. Hypothetically, we should expect to find this adaptability among farmer varieties since these are to a large extent the product of farmer selection. This would mean that farmer varieties are the result of interplay between local ecological and social factors.

In large parts of West Africa small-scale farmers rely upon the cultivation of upland rice under low input conditions in a great diversity of micro-environments. The first rice farming in West Africa was based exclusively on African rice (*O. glaberrima* Steud.). The cultivation of African rice is entirely a result of farmer agency as African rice has never been disseminated by extension programmes. Asian rice (*Oryza sativa*) is a more recent introduction, perhaps during the period of the Atlantic Slave trade (beginning c. 1550), or earlier via trans-Saharan trade routes. Asian rice has two main subspecies: *Oryza sativa* var. *japonica* (short-grained, mainly grown as upland rice) and *O. sativa* var. *indica* (long-grained, mainly a lowland type).

Today, farmers in the region mainly grow the two types of Asian rice. Nevertheless in certain areas African rice remains an important crop type [2-6]. These areas all seem to have a shared history of rice cultivation taking place against a background of special difficulty, such as war, population displacement or harsh ecological conditions [7]. This suggests the species may be selected for its greater tolerance to sub-optimal conditions when compared to Asian rice. The logic of the present study, therefore, is to compare African and Asian rice, in farmer conditions, in order to understand the extent to which plasticity and adaptability are factors in farmer varietal choice. The overall aim of the study is to secure a better knowledge base for possible complementary strategies of variety promotion. These complementary strategies would give due consideration both to varieties developed through scientific research and varieties produced by farmer selection. The objective is to assess the case for protecting farmer varieties as an important aspect of local food security, in an environment in which development agencies seek more generally to expand the range of high-yielding cultivars to meet urban rice demand across the region. Our study reports on differences in response to varying environments of a large sample of farmer varieties across five West African countries in the high-rainfall coastal zone.

The study tests the hypothesis that African rice may be more robust than Asian rice in West African farmer conditions. Here robustness is seen as the ability of a variety or group of varieties to perform well in a diversity of cultivation conditions. The following research questions are posed:

1. Are farmer varieties of *O. glaberrima* better suited to sub-optimal agro-ecological conditions than varieties of the two subspecies of *O. sativa*?
2. Do farmer varieties of *O. glaberrima* adapt better to different environmental conditions than varieties of the two subspecies of *O. sativa*?
3. What are the physiological processes and social and eco-regional patterns underlying the adaptation of farmer varieties across environments?

In achieving robustness, varieties can respond to environmental conditions by showing phenotypic plasticity in a range of traits [8, 9]. Different varieties or groups of varieties achieve robustness by combining variability and stability of different traits, thus constituting different physiological strategies. Hence, this study investigates whether different botanical groups of rice, or certain groups of varieties within those botanical groups, have developed different physiological strategies to achieve adaptation.

The hypothesis that African rice might be more robust than Asian rice in West African conditions would make sense of a number of observations already reported. Richards [7] has offered some general evidence that African rice is an important food reserve for communities facing special difficulty (e.g. when displaced by war). Dingkuhn *et al*. [10] and Johnson *et al*. [11] showed evidence that *O. glaberrima* has a vegetative vigour superior to that of *O. sativa*, thus is better able to suppress weeds. Sumi and Katayama [12] provided evidence that African rice has a yield potential similar to Asian counterparts.

Definitions

For a proper understanding of the paper we offer the following definitions of concepts and notions.

Robustness: the persistence of a system's characteristic behaviour under sub-optimal conditions, implying stable performance across environments. In the context of this paper, robustness is taken to be the ability of a variety or a group of varieties to yield well across distinct environments.

Adaptability: the ability of a variety or a group of varieties to be robust. Adaptability implies significant Genotype (G) × Environment (E) interactions.

Plasticity: the physiological process through which varieties adjust their phenotypes in response to different environmental conditions [13]. A plastic response of this nature does not require changes in gene frequencies (i.e. evolution). Such phenotypic shifts can allow varieties to achieve adaptability [9].

Sub-optimal farming: characterised by no or limited mineral fertilisation, no or natural pest and disease control, rain fed moisture conditions, rarely mono cropping, and below an optimal or standard level of output.

Tolerance: the ability of a variety to survive adverse conditions with only a small reduction in performance.

Materials and Methods

Ethics statement

We confirm that no specific permits were required for the locations where the described field trials were conducted, that these locations were not protected in any way, and that none of these field studies involved endangered or protected species. We thank local authorities, NGOs, research institutions and farmers for their support.

Variety collection and selection

From June to December 2007 we carried out field work in seven countries of Coastal West Africa, i.e. The Gambia, Ghana, Guinea, Guinea Bissau, Senegal, Sierra Leone and Togo (Figure 1). The field work aimed at (1) listing rice varieties/accessions used by farmers, (2) observing the development/physiology of these varieties in farmers' fields, and (3) collecting varieties at harvest. A total of 231 accessions were collected in 2007. After seed collection we carried out molecular analysis (AFLP) on the collected varieties in February and March 2008. Output of this molecular analysis was combined with the output of an analysis of 84 accessions performed in 2002 [14]. We used Version 2.2 of the software package 'Structure' to analyse genetic population structure and to assign samples to populations and 'SplitsTree' to visualise phylogenetic relationships between the samples. For further details please refer to [15]. Based on the output of the molecular analysis, 24 commonly cultivated farmer varieties

(*O. glaberrima* and *O. sativa*, including representatives of both the *indica* and *japonica* groups) were selected for further study (Table 1). These 24 varieties reflect the popular varieties grown in different parts of the region and therefore provide a subset of the large set of farmer varieties identified, with good local performance but not necessarily large robustness. All 26 varieties were included in all five experiments described in this paper.

Figure 1: *Geographic overview of the West African study area. Reprinted from [15] under a CC BY license, with permission from Edwin Nuijten, copyright 2009. Original figure generated using Google Maps.*

Results of AFLP analysis suggested several clusters within the various botanical groups. These clusters were more or less coinciding with the regions where the varieties were collected. The *glaberrima* divided into a cluster from the Upper Guinea Coastal region (Glab_UpperCoast) and a cluster from the Lower Guinea Coastal region (Glab_LowerCoast) (Figure 2a). The *indica* divided into *indica* from Ghana (Ind_Gh) and *indica* from Guinea (Ind_Gc) (Figure 2b) and the *japonica* into *japonica* from Ghana and Guinea Bissau (Jap_GbGh) and *japonica* from Sierra Leone (Jap_SL) (Figure 2c). It is possible the differences in the *japonica* group reflect different histories of introduction (Portuguese trading connections linking the Ghana and Guinea Bissau group, and British sources supplying Sierra Leone in the late 18th/early 19th centuries [cf. 16]. We used these molecular clusters in the analysis of robustness and adaptability.

Table 1: *List of varieties used in the study*

Code	Name of variety	Molecular cluster	Country of collection	Ecology of cultivation
O. glaberrima				
333	Saali Firê	Glab_UpperCoast	Guinea	Upland
347	Safaary	Glab_UpperCoast	Guinea	Upland
334	Tombo Bokary	Glab_UpperCoast	Guinea	Upland
318	Saali Forê	Glab_UpperCoast	Guinea	Upland
420	Jangjango	Glab_UpperCoast	Guinea Bissau	Upland/transition
435	Kurekimbeli	Glab_UpperCoast	Guinea Bissau	Upland/transition
113	Kaomo black	Glab_LowerCoast	Ghana (Togo mountain ranges)	Upland
124	Xleti eve	Glab_LowerCoast	Togo (Togo mountain ranges)	Upland
135	Kpakpalipke	Glab_LowerCoast	Togo (Togo mountain ranges)	Upland
272	Saliforeh	Glab_UpperCoast	Sierra Leone	Transition/upland
249	Maalay	Glab_UpperCoast	Sierra Leone	Transition/upland
O. sativa type *indica*				
348	Saidou Firê	Ind_Gc	Guinea	Upland
349	Saidou Gbéli	Ind_Gc	Guinea	Upland
130	Zomojo	Ind_Gh	Ghana (Togo mountain ranges)	Upland/transition/lowland
128	Viono tall	Ind_Gh	Ghana (Togo mountain ranges)	Upland/transition/lowland
163	Ataa	Ind_Gh	Ghana (Togo mountain ranges)	Upland/transition
O. sativa type *japonica*				
407	Demba Ba	Jap_GbGh	Guinea Bissau	Upland
427	Uyeey	Jap_GbGh	Guinea Bissau	Upland
432	Usefa Udjenel	Jap_GbGh	Guinea Bissau	Upland
141	Aqua blue	Jap_GbGh	Ghana (Togo mountain ranges)	Upland/transition
274	Nduliwa	Jap_SL	Sierra Leone	Transition/upland
210	Gbengbeng	Jap_SL	Sierra Leone	Transition/upland
215	Jebbeh-komi	Jap_SL	Sierra Leone	Transition/upland
408	Buba Njie	Jap_GbGh	Guinea Bissau	Upland/transition

Transition: variety cultivated in transitional zone between lowland and upland. Ind_Gc= cluster of *indica* from Guinea. Ind_Gh= cluster of *indica* from Ghana. Jap_GbGh= cluster of *japonica* from Guinea Bissau and Ghana. Jap_SL= cluster of *japonica* from Sierra Leone. Glab_LowerCoast= cluster of *glaberrima* from Lower Guinea coast. Glab_UpperCoast= cluster of *glaberrima* from Upper Guinea coast.

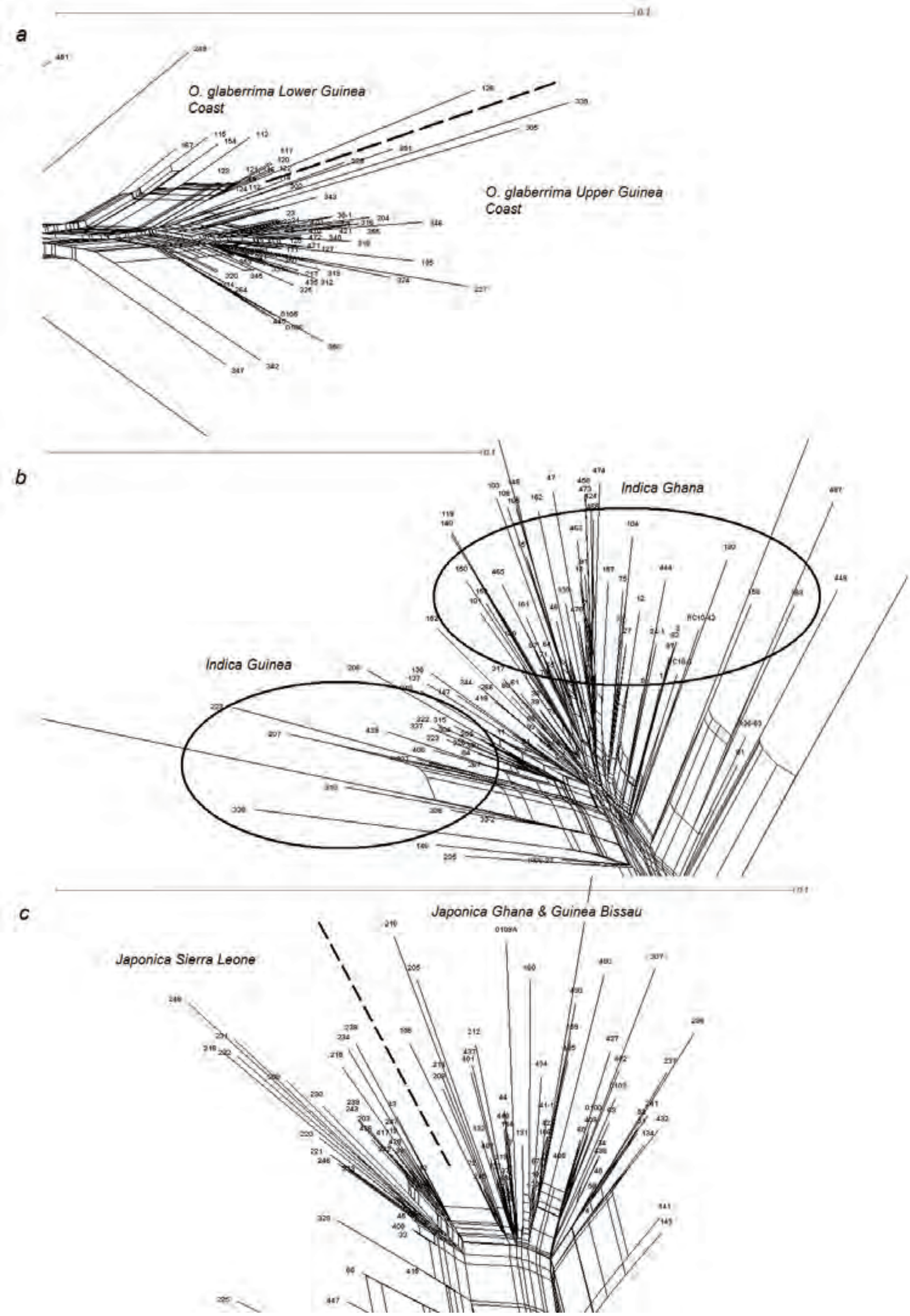


***Figure 2**: Phylogenetic relationships of glaberrima and its sub-clusters (a), indica and its sub-clusters (b), and japonica and its subclusters (c).*

Trials

Locations

Five trials were conducted in Guinea, Guinea Bissau, Ghana, Togo and Sierra Leone from June 2008 to January 2009. Table 2 summarises the characteristics of the experimental sites. Sites were selected to be representative for upland rice production on loamy soils. In all cases the experiments were planted after a fallow period.

Table 2*: Characteristics of the experimental sites*

	Guinea	Guinea Bissau	Ghana	Togo	Sierra Leone
GPS coordinates	10.00275 N 12.91770 W 379 m asl	12.131734 N 15.93607 W 10 m asl	7.26429 N 0.46984 W 213 m asl	7.27028 N 0.71598 W 809 m asl	8.14917 N 11.90806 W 58 m asl
Ecology	Upland	Upland	Upland	Upland	Upland
Soil characteristics					
pH (water)	4.8	4.6	4.6	4.9	4.2
OC%	2.9	1.6	1.9	5.4	4.1
total N g kg^{-1}	0.9	0.2	0.7	0.9	0.6
ppm Meh P	8.1	0.6	7.8	7.0	5.5
sand%	69.0	81.3	63.0	65.0	16.0
clay%	13.7	12.8	8.0	19.0	7.0
silt%	11.1	5.3	28.0	10.0	70.0
soil type	Sandy loam	Loamy sand	Sandy loam	Sandy (clay) loam	Silty loam
Background of experiment sites	- One year fallow - Previous crops (successively): rice, groundnut (*Arachis hypogaea*), cassava (*Manihot esculenta*) - Presence of *Imperata cylindrica*	-At least 5 years of fallow	-5 year fallow -Previous crop: maize (*Zea mays*)	-3 years fallow -Previous crop: maize (*Zea mays*)	24 years fallow. Previous crops: rice mixed cropping (cropped with squash, cucumber (*Cucumis spp.*), eggplant (*Solanum spp.*), pepper (*Capsicum spp.*), sorrel (*Hibiscus spp.*), legumes, *Zea mays*, *Manihot esculenta*, *Ipomoea batatas*, *Arachis hypogaea*, etc. -Presence of *Pennisetum purpureum* -Home for natural pests: rodents, stems borers etc.
Average annual rainfall (mm)	2800-4000	1500	1500	1200	2100-3000
Duration rainfall (months)	6	4 to 5	7	7	6 to 7
General observation	Stress and plant mortality observed during crop establishment phase	Good germination and growth. The late maturing varieties suffered from drought and rodent damage	Most plants showed excellent germination and growth	Most plants showed some traces of acidity damage	-Excellent germination and growth -Low to moderate pest (rodents, termites, cut worms, stem borers) incidences were most specific to *O. sativa* japonica
Trial setup dates					
First sowing	28 June 2008	29 June 2008	16 July 2008	09 July 2008	12 June 2008
Second sowing	16 July 2008	13 July 2008	06 August 2008	30 July 2008	04 July 2008

The experiments were carried out in one growing season. By including different sowing times, we created diverse environmental conditions within each site. The growing seasons allowed normal performance of the crops, although the Guinea experiment experienced some stress during crop establishment and the Guinea Bissau experiment experienced late season drought affecting the late-maturing varieties only.

Experimental design

In each of the five trials, the varieties were sown in a randomised block design with two sowing dates and five replications, resulting in 24 × 2 × 5 = 260 plots. All 24 varieties were included in all experiments. Sowing dates were determined by following the farmers' practices in each region. The time between the first and the second sowing was two to three weeks. Each plot was 1.5 m × 2.1 m and contained 70 pockets, spaced 30 cm between rows and 15 cm within rows. Three to five grains were sown in each pocket and pockets were thinned to one plant within four weeks after sowing.

Measurements

Table 3 summarises the measured variables, the methodology of assessment and the trials in which they were recorded.

The percentage of canopy coverage was determined during the growing cycle using frames of 60 cm × 75 cm (in Togo and Ghana) and 60 cm × 45 cm in Guinea that were put in the plot and photographed from straight above. A series of about 20 photos representing a wide range of canopy cover values was analysed with Matlab 7 and DIP image [17], to allow calculation of the percentage green in a photo. Based on this calibration the percentages of canopy coverage were estimated for all photos.

***Table 3**: Measured parameters and countries of measurement.*

Parameters	*indication on methods of measurement*	*Trials where parameters were measured*
Canopy cover	See below (section: Determination of the canopy cover development)	Ghana, Guinea and Togo
Plant height (cm)*	Measured from the base of the plant to the tip of the panicle of the main tiller	Ghana, Guinea, Guinea Bissau, Sierra Leone, Togo
Number of tillers*	Total number of tillers per plant	Ghana, Guinea, Guinea Bissau, Sierra Leone, Togo
Days to 50% flowering	The number of days between the sowing date and the date 50% of the plants flowered	Ghana, Guinea, Guinea Bissau, Sierra Leone, Togo
Number of panicles*	Total number of panicles per plants	Guinea, Guinea Bissau, Sierra Leone
Panicle length (cm)*	Measured from the base to the tip of the panicle of the main axis	Ghana, Guinea, Guinea Bissau, Sierra Leone, Togo
Panicle weight (g)	Weight of the grains of 14 panicles	Ghana and Togo
200 grain weight (g)	Weight of 200 filled grain. Unfilled and partially filled grains were excluded	Ghana, Guinea, Guinea Bissau, Togo
Plot yield (kg/ha)	Weight of the three inner rows	Ghana, Guinea Bissau, Sierra Leone, Togo

**Measured on 6 plants randomly selected from the inner rows.*

Determination of the canopy cover development

For each plot, canopy coverage curves were made on the basis of 6 to 12 measurements. As curves for the different replications showed a large variation and a block effect was not found we decided to carry out curve fitting on the average values of the five replications.

To describe the canopy development we used a modified version of the model developed by Khan *et al*. [18] for potato. The model of Khan *et al*. distinguishes three development phases for potato: the build-up phase, the phase where the canopy cover remains constant and the decline phase. In our case, possibly because of stress the plants experienced, the canopy never reached 100% coverage, nor did it reach a plateau level maintained for any period of time. This simplified the model because the time that the maximum canopy cover was reached (t_1) and the time it started to decline (t_2) coincided, resulting into a two-phase model:

Phase 1

$$v = v_{max}\left(1 + \frac{t_1 - t}{t_1 - t_{m1}}\right)\left(\frac{t}{t_1}\right)^{\frac{t_1}{t_1 - t_{m1}}} \text{ with } 0 \leq \mathrm{t} \leq t_1 \qquad (1)$$

Phase 2

$$v = v_{max}\left(\frac{t_e - t}{t_e - t_1}\right)\left(\frac{t}{t_1}\right)^{\frac{t_1}{t_e - t_1}} \text{ with } t_1 \le t \le t_e \qquad (2)$$

where:

v = canopy cover (%)

v_{max} = maximum canopy cover (%)

t_{m1} = the inflexion point

t_1 = the time the maximum canopy cover is reached

t_e = the time when the canopy has declined to 0

t_{m1}, t_1, v_{max} and t_e were estimated using SAS.

The accumulated canopy cover A, represented by the sum of surfaces under the curves of phase 1 and 2, was estimated by using the following formulae:

Surface under the curve for phase 1 (A_1):

$$A_1 = v_{max}\left(\frac{2t_1(t_1 - t_{m1})}{3t_1 - 2t_{m1}}\right) \qquad (3)$$

Surface under the curve for phase 2 (A_2):

$$A_2 = \frac{v_{\max}(t_e - t_1)}{2t_e - t_1}\left(t_e\left(\frac{t_e}{t_1}\right)^{\frac{t_1}{t_e - t_1}} - 2t_1\right) \qquad (4)$$

Estimation of the accumulated canopy cover (A):

$$A = A_1 + A_2 \qquad (5)$$

Data analysis

G×E interactions

As different botanical groups and molecular clusters were compared, interactions between genotypes and environment were analysed through ANOVA (analysis of variance) to assess differences in responses to different environments within and between botanical groups.

Significant G×E interactions point to the presence of such a variation in response and indicate that the botanical group or cluster contains varieties that respond differently to different environments, which can be considered an indicator of adaptability within a specific botanical group or cluster. We used the Tukey test to compare means.

Wide sense heritability estimates

$H^2=100\times Vg/(Vg+1/rsVgs+1/rlVgl+1/rslVgls+1/rVe)$

where:

H^2 = wide sense heritability

Vg = genetic variance

Vgs = variance genetic × sowing interactions

Vgl = variance genetic × location interactions

Vgls = variance genetic × location × sowing interactions

Ve = error variance

r = number of replications (5)

s = number of sowings (2)

l = number of locations (2, 3, 5)

Descriptive statistics

Averages and standard deviations were calculated.

Results

In the following sections the parameters are investigated for each botanical group (*glaberrima*, *indica* or *japonica*) and molecular cluster (see section on Materials and Methods). The parameters are dealt with one by one and cross references are made among them to unravel strategies of adaptation. Graphs are used to compare performance of each parameter across environments. ANOVAs provided important information on adaptability, as they provided estimates of G×E interactions (Tables 4-13).

Table 14 shows the average performance of the studied genotypes (grouped into botanical groups and molecular clusters) for ten parameters used to analyse the vegetative growth and yield components: maximum canopy cover (V_{max}; %), accumulated canopy cover (A; %.day), plant height (cm), number of tillers per plant (# tillers), days to 50% flowering (50% flowering), number of panicles per plant (#panicles), panicle length (cm), panicle weight (g), 200 grain weight (g) and grain yield (kg/ha). Table 14 shows the yield and yield components averaged for the five countries, wheras Table 16 shows the estimates of the wide sense heritability for the ten variables listed in Tables 4-14. Tables 17-25 show the Pearson correlations between the yield components.

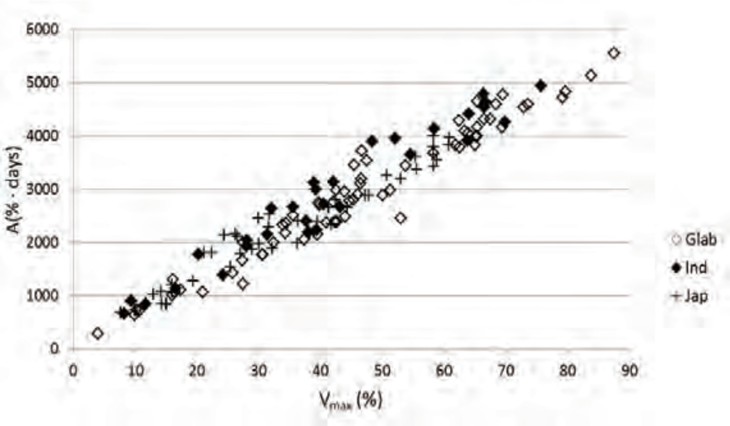


Figure 3*: Relation between the accumulated canopy cover over the whole growing cycle (A; y-axis, in %.days) and the maximum canopy cover (Vmax; x-axis, in %) . Data refer to all combinations of location ×genotype × sowing time, whereas different symbols refer to different botanical groups (glaberrima, indica and japonica).*

Maximum canopy cover (V_{max}) and accumulated canopy cover (A)

V_{max} and A correlated positively (r = 0.984**) at 0.01 level. The same trend was observed for all botanical groups and molecular clusters in all environments (Tables 17-25; Figure 3). Accumulated canopy cover (A) can therefore represent V_{max} and vice versa. In all cases the surface under the canopy curves (A) can be conceived as a triangle with the cycle length (Te) as base and V_{max} as height. Variations in cycle length (Te), inflexion point (Tm1) and the time V_{max} was reached (T1) appear to confirm that A is linearly related to V_{max}.

None of the botanical groups or molecular clusters showed G×E interactions for A or V_{max} (Tables 5-13). This means that within all botanical groups and molecular clusters the varieties responded comparably for A and V_{max} across environments.

***Tables 4-13**: Interaction effects of genotypes, sowing dates and trial locations (location) on maximum canopy development (Vmax), accumulated canopy (A), plant height, number of tillers per plant (#tillers), days to 50% flowering (50% flowering), number of panicles per plant (#panicles), panicle length, panicle weight, 200 grains weight and yield of 24 genotypes grouped according to their botanical groups and further on molecular clusters.*

Table 4: All botanical groups and clusters together

	Genotype	Sowing	Location	Genotype* Sowing	Genotype * Location	Sowing* Location	Genotype* Sowing* Location
V_{max} [d]	0.000***	0.758	0.026*	0.092	0.881	0.029*	-
A [d]	0.000***	0.435	0.027*	0.014*	0.444	0.001***	-
Plant height [f]	0.000***	0.922	0.002**	0.612	0.000***	0.000***	0.264
# Tillers[f]	0.000***	0.533	0.006**	0.043*	0.000***	0.000***	0.986
50% Flowering [f]	0.000***	0.011*	0.000***	0.008**	0.000***	0.003**	0.000***
# Panicles [a]	0.000***	0.334	0.112	0.005**	0.000***	0.000***	0.947
Panicle length [a]	0.000***	0.890	0.003**	0.023*	0.000***	0.000***	0.017*
Panicle weight [e]	0.000***	0.140	0.502	0.236	0.157	0.194	0.012*
200 grains weight [b]	0.000***	0.318	0.006**	0.069	0.018*	0.031*	0.850
Yield [c]	0.000***	0.070	0.042*	0.583	0.873	0.020*	0.000***

*Values in the table are p values (three-way ANOVA). *: Significant at 0.05 level. **: significant at 0.01 level. ***: Significant at 0.001 level. **a**: ANOVA performed for Guinea Bissau, Guinea and Sierra Leone. **b**: ANOVA performed for Guinea Bissau, Guinea, Ghana and Togo. **c**: ANOVA performed for Guinea Bissau, Ghana, Sierra Leone and Togo. **d**: ANOVA performed for Ghana, Guinea and Togo. **e**: ANOVA performed for Ghana and Togo. **f**: ANOVA performed for all five countries. -: not assessed*

Tables 4-13 *continued:*

Table 5: Glaberrima botanical group

	Genotype	Sowing	Location	Genotype* Sowing	Genotype* Location	Sowing* Location	Genotype* Sowing* location
Vmax [d]	0.190	0.373	0.083	0.464	0.319	0.000***	-
A [d]	0.260	0.217	0.055	0.268	0.132	0.000***	-
Plant height [f]	0.000***	0.797	0.009**	0.471	0.001***	0.000***	0.469
# Tillers[f]	0.097	0.246	0.003**	0.268	0.000***	0.014*	0.612
50% Flowering [f]	0.000***	0.007**	0.001***	0.069	0.014*	0.024*	0.000***
# Panicles [a]	0.314	0.267	0.117	0.025*	0.000***	0.000***	0.998
Panicle length [a]	0.000***	0.810	0.001***	0.024*	0.004**	0.009**	0.024*
Panicle weight [e]	0.051	0.255	0.081	0.359	0.088	0.279	0.563
200 grains weight [b]	0.000***	0.457	0.003**	0.584	0.019*	0.103	0.940
Yield [c]	0.000***	0.458	0.254	0.619	0.981	0.002**	0.000***

Table 6: Cluster of Glaberrima from Lower Guinea coast (Glab_Lower Coast)

	Genotype	Sowing	Location	Genotype* Sowing	Genotype* Location	Sowing*L ocation	Genotype* Sowing* location
Vmax [d]	0.137	0.737	0.176	0.330	0.877	0.172	-
A [d]	0.740	0.464	0.082	0.129	0.609	0.053	-
Plant height [f]	0.567	0.566	0.218	0.685	0.665	0.641	0.042*
# Tillers[f]	0.852	0.061	0.002**	0.638	0.026*	0.347	0.935
50% Flowering [f]	0.014*	0.001***	0.004**	0.086	0.061	0.534	0.022*
# Panicles [a]	0.840	0.243	0.086	0.145	0.091	0.008**	0.963
Panicle length [a]	0.582	0.164	0.178	0.144	0.791	0.441	0.393
Panicle weight [e]	0.274	0.081	0.370	0.641	0.330	0.926	0.517
200 grains weight [b]	0.056	0.421	0.119	0.654	0.325	0.258	0.218
Yield [c]	0.099	0.316	-	0.570	0.899	0.604	0.017*

Table 7: Cluster of Glaberrima from Upper Guinea coast (Glab_Upper Coast)

	Genotype	Sowing	Location	Genotype* Sowing	Genotype* Location	Sowing* Location	Genotype* Sowing* Location
Vmax [d]	0.589	0.276	0.076	0.973	0.178	0.001***	-
A [d]	0.545	0.170	0.055	0.667	0.184	0.002**	-
Plant height [f]	0.003**	0.702	0.027*	0.209	0.000***	0.000***	0.956
# Tillers[f]	0.664	0.397	0.031*	0.27	0.008**	0.056	0.145
50% Flowering [f]	0.000***	0.017*	0.005**	0.455	0.29	0.091	0.000***
# Panicles [a]	0.372	0.294	0.144	0.025*	0.000***	0.000***	0.982
Panicle length [a]	0.018*	0.919	0.010**	0.003**	0.000***	0.000***	0.439
Panicle weight [e]	0.309	0.300	0.242	0.322	0.128	0.221	0.454
200 grains weight [b]	0.202	0.581	0.001***	0.464	0.013*	0.329	0.98
Yield [c]	0.000***	0.519	0.412	0.344	0.902	0.001***	0.039*

*Values in the table are p values (three-way ANOVA). *: Significant at 0.05 level. **: significant at 0.01 level. ***: Significant at 0.001 level.* ***a****: ANOVA performed for Guinea Bissau, Guinea and Sierra Leone.* ***b****: ANOVA performed for Guinea Bissau, Guinea, Ghana and Togo.* ***c****: ANOVA performed for Guinea Bissau, Ghana, Sierra Leone and Togo.* ***d****: ANOVA performed for Ghana, Guinea and Togo.* ***e****: ANOVA performed for Ghana and Togo.* ***f****: ANOVA performed for all five countries. -: not assessed*

Tables 4-13 *continued:*

Table 8: Indica botanical group

	Genotype	Sowing.	Location	Genotype* Sowing	Genotype* Location	Sowing*L ocation	Genotype* Sowing* Location
Vmax [d]	0.017*	0.931	0.06	0.16	0.746	0.171	-
A [d]	0.031*	0.588	0.038*	0.177	0.508	0.055	-
Plant height [f]	0.089	0.591	0.000***	0.72	0.000***	0.010**	0.057
# Tillers[f]	0.553	0.998	0.001***	0.022*	0.001***	0.006**	0.979
50% Flowering [f]	0.027*	0.005**	0.000***	0.233	0.003**	0.432	0.120
# Panicles [a]	0.358	0.654	0.149	0.100	0.002**	0.315	0.829
Panicle length [a]	0.162	0.474	0.002**	0.595	0.063	0.377	0.047*
Panicle weight [e]	0.174	0.029*	0.230	0.377	0.271	0.732	0.457
200 grains weight [b]	0.001***	0.053	.	0.339	0.794	0.866	0.365
Yield [c]	0.001***	0.002**	0.358	0.630	0.441	0.916	0.000***

Table 9: Cluster of Indica from Ghana (Ind_Gh)

	Genotype	Sowing.	Location	Genotype* Sowing	Genotype* Location	Sowing* Location	Genotype* Sowing* Location
Vmax [d]	0.057	0.362	estimate.	0.229	0.943	0.756	-
A [d]	0.099	0.762	0.439	0.253	0.891	0.370	-
Plant height [f]	0.385	0.480	0.001 ***	0.798	0.022*	0.124	0.012*
# Tillers[f]	0.361	0.580	0.005 **	0.078	0.055	0.201	0.702
50% Flowering [f]	0.026*	0.026*	0.011*	0.245	0.172	0.539	0.019*
# Panicles [a]	0.448	0.548	0.864	0.222	0.038*	0.644	0.44
Panicle length [a]	0.158	0.872	0.081	0.475	0.170	0.287	0.139
Panicle weight [e]	-	0.119	-	-	-	-	-
200 grains weight [b]	-	-	-	-	-	-	-
Yield [c]	0.016*	0.062	0.061	0.385	0.192	0.342	0.000 ***

Table 10: Cluster of Indica from Guinea (Ind_Gc)

	Genotype	Sowing.	Location	Genotype* Sowing	Genotype* Location	Sowing* Location	Genotype* Sowing* Location
Vmax [d]	0.103	0.657	0.025*	0.242	0.074	0.033*	-
A [d]	0.052	0.439	0.017*	0.122	0.100	0.035*	-
Plant height [f]	0.962	0.957	0.000***	0.829	0.025*	0.008**	0.964
# Tillers[f]	0.634	0.440	0.018*	0.384	0.006**	0.031*	0.973
50% Flowering [f]	0.286	0.003**	0.029*	0.551	0.118	0.823	0.391
# Panicles [a]	0.500	0.189	0.114	0.774	0.038*	0.242	0.876
Panicle length [a]	0.781	0.369	0.021*	0.416	0.180	0.397	0.368
Panicle weight [e]	0.412	0.032*	0.377	0.336	0.358	0.761	0.540
200 grains weight [b]	0.272	0.481	0.350	0.535	0.573	0.494	0.302
Yield [c]	0.598	0.097	0.090	0.112	0.454	0.022*	0.501

*Values in the table are p values (three-way ANOVA). *: Significant at 0.05 level. **: significant at 0.01 level. ***: Significant at 0.001 level.* ***a****: ANOVA performed for Guinea Bissau, Guinea and Sierra Leone.* ***b****: ANOVA performed for Guinea Bissau, Guinea, Ghana and Togo.* ***c****: ANOVA performed for Guinea Bissau, Ghana, Sierra Leone and TogO.* ***d****: ANOVA performed for Ghana, Guinea and Togo.* ***e****: ANOVA performed for Ghana and Togo.* ***f****: ANOVA performed for all five countries. -: not assessed*

Table 4-13 *continued:*

Table 11: Japonica botanical group

	Genotype	Sowing.	Location	Genotype* Sowing	Genotype* Location	Sowing* Location	Genotype* Sowing* Location
Vmax [d]	0.047**	0.178	0.047**	0.703	0.468	0.011**	-
A [d]	0.176	0.318	0.065	0.818	0.285	0.002***	-
Plant height [f]	0.021*	0.562	0.000***	0.846	0.000***	0.001***	0.404
# Tillers[f]	0.000***	0.755	0.033*	0.965	0.008**	0.000***	0.963
50% Flowering [f]	0.001***	0.431	0.005**	0.108	0.007**	0.000***	0.012*
# Panicles [a]	0.010**	0.803	0.653	0.946	0.282	0.020*	0.121
Panicle length [a]	0.000***	0.86	0.038*	0.043*	0.000***	0.000***	0.784
Panicle weight [e]	0.182	0.158	0.405	0.813	0.608	0.368	0.022*
200 grains weight [b]	0.000***	0.197	0.085	0.178	0.936	0.216	0.660
Yield [c]	0.001***	0.006**	estimate.	0.644	0.987	0.884	0.000***

Table 12: Cluster of Japonica from Guinea Bissau and Ghana (Jap_GbGh)

	Genotype	Sowing.	Location	Genotype* Sowing	Genotype* Location	Sowing* Location	Genotype* Sowing* Location
Vmax [d]	0.331	0.116	0.030*	0.637	0.472	0.142	-
A [d]	0.355	0.205	0.028*	0.725	0.347	0.069	-
Plant height [f]	0.080	0.607	0.000***	0.693	0.004**	0.045*	0.229
# Tillers[f]	0.000 ***	0.764	0.035*	0.891	0.714	0.005**	0.661
50% Flowering [f]	0.857	0.574	0.007**	0.851	0.006**	0.000***	0.408
# Panicles [a]	0.027*	0.805	0.466	0.860	0.995	0.106	0.036*
Panicle length [a]	0.005 **	0.808	0.028*	0.014*	0.001***	0.000***	0.835
Panicle weight [e]	0.074	0.188	0.576	0.495	0.547	0.352	0.091
200 grains weight [b]	0.000 ***	0.571	0.129	0.339	0.917	0.278	0.705
Yield [c]	0.856	0.329	0.089	0.442	0.605	0.016*	0.039*

Table 13: Cluster of Japonica from Sierra Leone (Jap_SL)

	Genotype	Sowing.	Location	Genotype* Sowing	Genotype* Location	Sowing* Location	Genotype* Sowing* Location
Vmax [d]	0.433	0.293	0.097	0.526	0.461	0.133	-
A [d]	0.550	0.473	0.128	0.578	0.306	0.044*	-
Plant height [f]	0.072	0.568	0.003**	0.736	0.005**	0.005**	0.845
# Tillers[f]	0.062	0.747	0.049*	0.775	0.072	0.023*	0.949
50% Flowering [f]	0.067	0.305	0.002**	0.044*	0.069	0.037*	0.052
# Panicles [a]	0.199	0.812	0.218	0.88	0.125	0.088	0.816
Panicle length [a]	0.032*	0.988	0.229	0.251	0.006**	0.02*	0.637
Panicle weight [e]	0.977	0.634	-	0.917	0.673	0.728	0.082
200 grains weight [b]	0.328	1.000	-	0.735	0.948	0.925	0.067
Yield [c]	0.114	0.082	0.619	0.516	0.943	0.422	0.000***

*Values in the table 1-10 are p values (three-way ANOVA). *: Significant at 0.05 level. **: significant at 0.01 level. ***: Significant at 0.001 level. a: ANOVA performed for Guinea Bissau, Guinea and Sierra Leone. b: ANOVA performed for Guinea Bissau, Guinea, Ghana and TogO. c: ANOVA performed for Guinea Bissau, Ghana, Sierra Leone and TogO. d: ANOVA performed for Ghana,* *Guinea and Togo. e: ANOVA performed for Ghana and TogO. f: ANOVA performed for all five countries. -: not assessed*

However, for all three botanical groups significant sowing × location interactions were found, in particular for *glaberrima* and *japonica*. Sowing × location interactions were highly significant for the *glaberrima* botanical group and Glab_UpperCoast but not significant for the Glab_LowerCoast cluster. Glab_LowerCoast therefore maintained better A and Vmax across environments, since its genotypes reacted in a similar way to different environments. However, the developed canopy did not turn into a yield increase as Glab_UpperCoast yielded more than Glab_LowerCoast (Table 14).

Of the *indica* group, it was only in the Ind_Gc cluster that significant sowing × location interactions were found for A and V_{max}. The *indica* group showed a significant location effect for A. No significant effects were found for the Ind_Gh cluster. This indicates that the Ind_Gh maintained better V_{max} and A than the Ind_Gc but often failed to yield (Figures 4 and 5).

The *japonica* group showed significant sowing × location interactions, suggesting that (for the two *japonica* clusters) A and V_{max} varied across environments. At cluster level significant sowing × location interactions were found for Jap_SL for V_{max} only, while for the Jap_GbGh cluster the location effects were significant for both A and V_{max}. This suggests that Jap_SL maintained A across environments better than Jap_GbGh. However Jap_SL showed considerable yield variation (Figure 5), suggesting that the relative stability observed for A did not contribute to yield stability.

Generally, the highest A was observed in Ghana followed by Togo and Guinea (Figure 4).

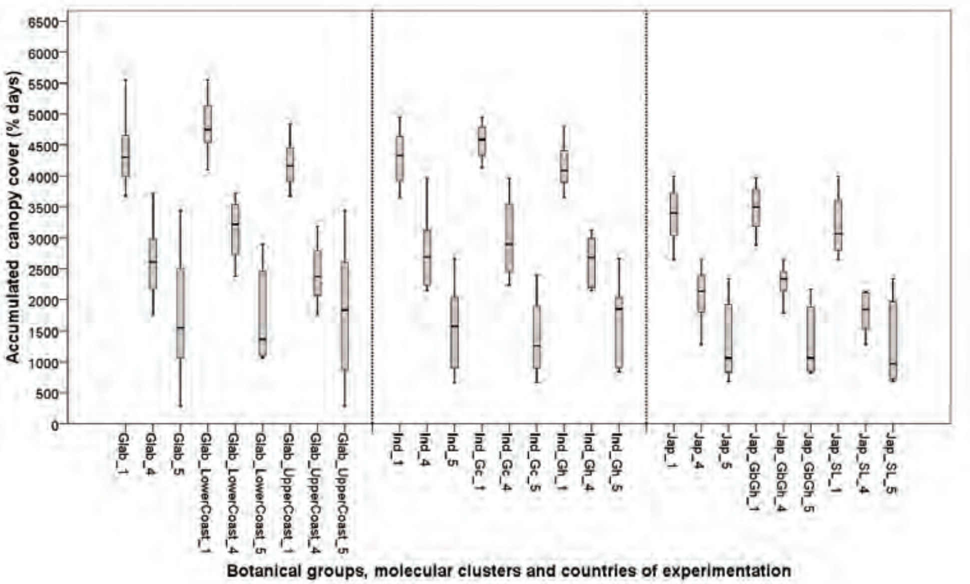


***Figure 4**: Box plots for accumulated canopy cover (A; %.days) of 24 varieties in three experimental sites: Ghana (1); Togo (4) and Guinea (5). See materials and methods section for coding of the botanical groups and molecular clusters.*

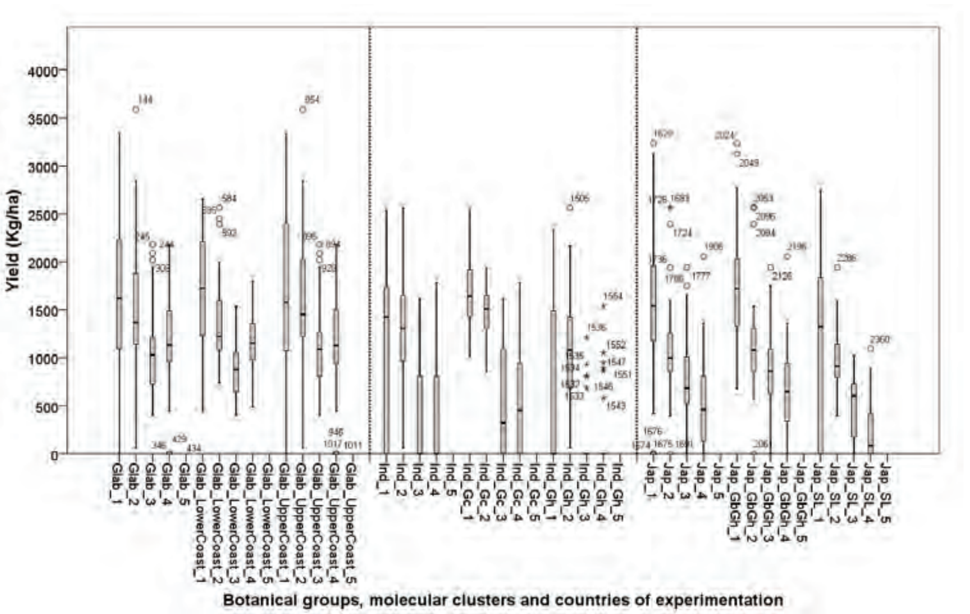


***Figure 5**: Box plots for grain yield (in kg/ha) of 24 varieties in four experimental sites: 1: Ghana; 2: Sierra Leone; 3: Guinea Bissau; and 4: Togo; in 5: Guinea yield was not measured. See materials and methods section for coding of the botanical groups and molecular clusters*

Yield

The analyses of variance performed for all genotypes and at botanical group level showed a highly significant three-way interaction for yield (Tables 4-13). This suggests that the studied rice varieties generally responded differently in yield across environments and sowing dates. The yield variability studied at cluster level also revealed significant G×E interactions (Tables 3,4,6, 9 and 10) with the exception of the *indica* cluster from Guinea (Ind_Gc) (Table 10). The yield therefore varied in a similar manner across environments for genotypes of Ind_Gc.

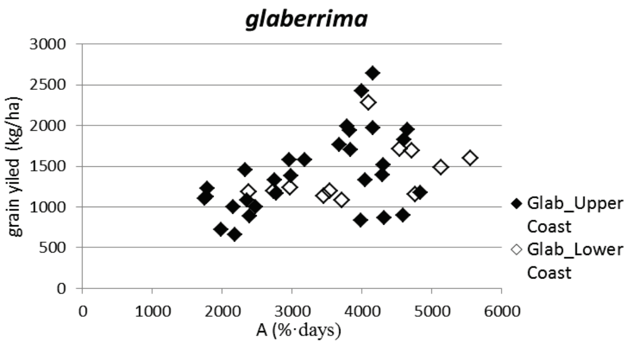
The *glaberrima* botanical group showed the highest yields across all environments (Table 14 and Figure 5). “Zero” yields (complete crop failure) occurred only with *indica* and *japonica*. At cluster level, *glaberrima* from upper Guinea coast (Glab_UpperCoast) showed the highest yield. *Glaberrima* from the Lower Guinea coast (Glab_LowerCoast) had the same yield range as *japonica* from Guinea Bissau and Ghana (Jap_GbGh) and Ind_Gc. Ind_Gh and Jap_SL showed the lowest average yield.

A comparison of the botanical groups on the yield across environments (Figure 5) shows that, within the same environment, *glaberrima* yielded more than *indica* and *japonica*. In Ghana where the average plot yield was generally high, some *indica* varieties showed “zero” yield. Zero yield occurred for *japonica* only in Guinea Bissau and Tog*O.* These are the two countries where the overall yield was generally lowest.

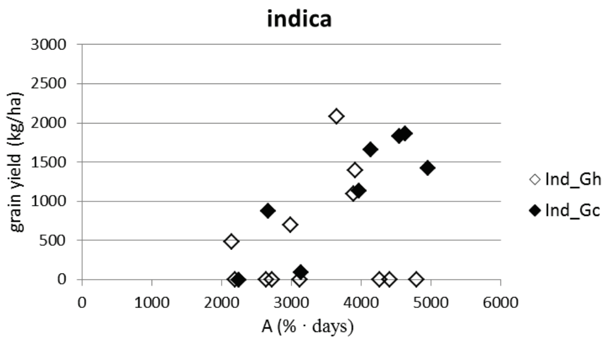
Figures 6a-c show the graphical representations of the relationships between yield and A for each botanical group. At cluster level different relationships were observed. The relation between yield and A was similarly low for Glab_LowerCoast and Glab_UpperCoast (r = 0.451 and r = 0.476** respectively). This shows that *glaberrima* can yield well even when relatively low accumulated canopy cover is produced.

For the *indica* and *japonica* clusters clear differences in the relationship between grain yield and A were found. A significant relationship between yield and A was found for Ind_Gc (r = 0.857**) but not for Ind_Gh (r = 0.137). Also a significant Pearson correlation coefficient was found for Jap_GbGh (r = 0.848**) but not for Jap_ SL (r = 0.497). These findings suggest that Ind_Gc and Jap_GbGh increased their yields by producing a correspondingly dense canopy. The absence of significant correlation values for Ind_Gh and Jap_SL was caused by a number of crop failures that could be related to them being narrowly adapted to Sierra Leone only (Figures 6b and 6c).

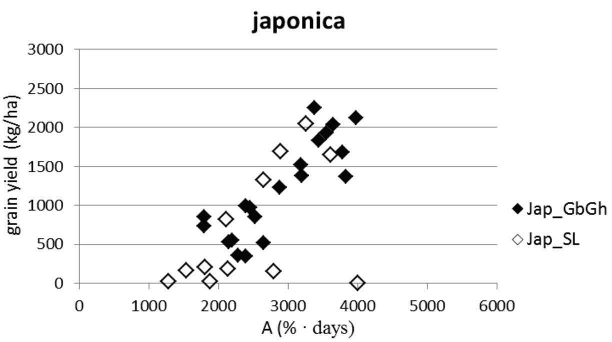
A minimum A is indispensable for yield formation, as shown by the various associations between A and yield observed for the various clusters. But from our observation only the *glaberrima* clusters were able to yield well with low canopy development.



a (r=0.476**)



b (r=0.483*)



c (r=0.706**)

Figure 6*: The relation between yield (in kg/ha; y-axis) and accumulated canopy cover (A in %.days; x-axis) for three botanical groups. Different symbols refer to different molecular clusters. Values presented are averages of 5 replications. Correlation coefficients are: a (varieties belonging to glaberrima): r=0.476 (P<0.01); b (varieties belonging to indica): r=0.483 (P<0.05); c (varieties belonging to japonica): r=0.706 (P<0.01).*

Plant height

Significant G×E interactions for plant height were observed for all botanical groups and their respective clusters. This implies that across environments genotypes within botanical groups and clusters responded differently in plant height, suggesting the existence of varied strategies of adaptation for the different botanical groups and clusters. This finding confirms that plant height is in general sensitive to environmental conditions.

A decreasing trend was observed for plant height from countries with higher yield to countries with lower yield (Figure 7). The *O. glaberrima* group showed significantly greater average plant height than the *indica* and *japonica* groups (Table 14). At cluster level, we found that Glab_UpperCoast had taller plants than Glab_LowerCoast and that Ind_Gc had taller plants than Ind_Gh. The *japonica* clusters did not show significant differences for plant height (Table 14).

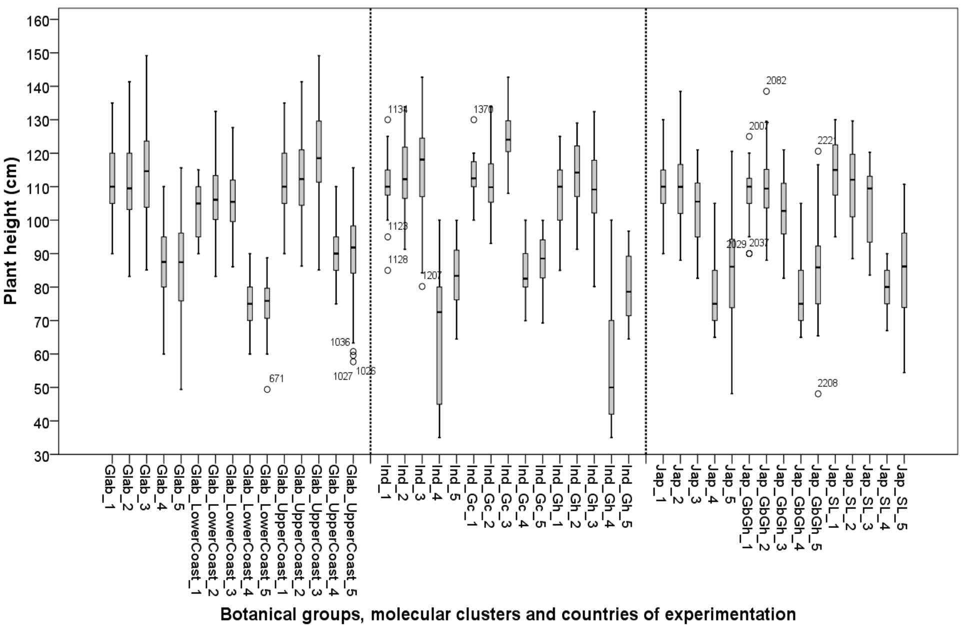


Figure 7*: Box plots for plant height (in cm) of 24 varieties in five experimental sites: 1: Ghana; 2: Sierra Leone; 3: Guinea Bissau; 4: Togo and 5: Guinea. See materials and methods section for coding of the botanical groups and molecular clusters*

The relation between plant height and A is more strongly positive for Glab_UpperCoast (r = 0.826**, Figure 8a) than for Glab_LowerCoast. This difference is, however, absent when considering the relation between plant height and yield (Figure 8b), confirming that when more canopy was produced Glab_LowerCoast no longer invested in its height but rather in the number of its tillers, which was significantly higher for Glab_LowerCoast than for Glab_UpperCoast (Table 14, Figure 9). This suggests two distinct strategies adopted by the Glab_LowerCoast cluster and the Glab_UpperCoast cluster to arrive at similar A, and V_{max}: the second cluster produces higher plants and fewer tillers and the first cluster produces shorter plants but more tillers.

Within *indica*, the cluster Ind_Gc had the tallest plants and showed a highly significant relationship between plant height and A (r = 0.784**). These observations, together with observations of high V_{max} and A for Ind_Gc, imply that Ind_Gc had a better vegetative growth compared to Ind_Gh. Cluster Ind_Gc also displayed the same average plant height as Glab_UpperCoast.

Japonica clusters did not show significant differences for plant height (Table 14) nor for the relationship between plant height and A: r = 0.635** and r = 0.640** for Jap_GbGh and Jap_SL, respectively.

***Table 14**: Average performance of several clusters of rice (including three botanical groups and six related molecular clusters) for main crop characteristics, including maximum canopy development (Vmax), accumulated canopy (A), plant height, number of tillers per plant (# Tillers), days to 50% flowering (50% Flowering), number of panicles per plant (# Panicles), panicle length, panicle weight, 200 grains weight and yield in five West African countries.*

Botanical groups and Clusters*	**V_{max} (%)**	**A (%d)**	**Plant height (cm)**	**# Tillers**	**50% Flowering (d)**	**# Panicles**	**Panicle length (cm)**	**Panicle weight (g)**	**200 grains weight (g)**	**Yield (kg/ha)**
Glaberrima	46.1 C	2908 B	101.1 B	6.8 B	97.1 A	6.4 C	23.4 B	2.0 A	4.3 A	1349 C
Indica	41.7 B	2889 B	97.8 A	7.6 C	108.9 C	5.5 B	22.1 A	1.9 A	4.1 A	757 A
Japonica	35.0 A	2269 A	97.2 A	4.0 A	101.8 B	2.8 A	22.5 A	3.1 B	4.3 A	967 B
Glab_UpperCoast	44.5 bcd	2794 bcd	104.2 de	6.5 c	96.7 b	6.2 cd	23.9 b	2.1 b	4.1 ab	1376 cd
Glab_LowerCoast	50.2 d	3214 d	92.7ab	7.5 d	98.4 bc	7.2 d	21.9 a	1.8 ab	4.9 c	1265 bcd
Jap_GbGh	36.8 ab	2320 ab	97.0 abc	4.4 b	101.9 c	3.1 a	22.7 ab	2.9 c	4.6 bc	1095 bc
Jap_SL	31.1 a	2085 a	98.7 cd	3.3 a	107.8 d	2.2 a	22.0 a	2.9 c	3.9 a	691 a
Ind_Gc	44.2 bcd	2984 cd	104.2 de	7.7 d	110.0 d	6.2 cd	21.6 a	1.7 ab	4.5 bc	1064 b
Ind_Gh	40.0 bc	2826 cd	91.8 a	7.4 d	110.7 d	4.8 b	22.4 a	1.5 a	3.7 a	551 a

Means in a column followed by the same letter are not significantly different from each other at 0.05% (based on Tukey tests for the botanical groups and clusters separately).

** See materials and methods section for coding of the clusters.*

Number of panicles

The *glaberrima* and *indica* groups showed significant G×E interactions for number of panicles, while the *japonica* group did not (Tables 5, 8 and 11). At cluster level Glab_UpperCoast, Ind_Gc Ind_Gh and Jap_GbGh showed significant G×E interactions (Tables 7,9,10,12). There was no such interaction for genotypes of the clusters Glab_LowerCoast and Jap_SL (Tables 6 and 13)

The *glaberrima* group showed the highest average number of panicles. Cluster Ind_Gc showed a significantly higher average number of panicles than Ind_Gh and performed similar to the *glaberrima* group (Table 14). Within the *japonica* group, the highest number of panicles was observed with Jap_SL cluster in Sierra Leone, the origin of the cluster. For all botanical groups and variety clusters, the number of panicles was relatively low in Sierra Leone and Guinea Bissau and highest in Guinea (Figure 10). An opposite trend was observed only with Jap_SL. This cluster showed more panicles in Sierra Leone. This underlines our observation that Jap_SL is specifically adapted to conditions in Sierra Leone.

The *japonica* group showed the lowest numbers of panicles throughout the whole range of A and yield values (Figures 8c and 8d) and across locations (Figure 10). The number of panicles in relation to A and yield hardly overlapped for *glaberrima* and *japonica* (Figures 8c and 8d) and differed significantly (Table 14). The *glaberrima* group showed a decreasing trend in panicle number as yield values increased (r = -0.453**). For the *japonica* and *indica* groups no such decreasing trend was observed. For the *indica* group, the relation between panicle number and yield seemed to be intermediate between the tendencies for the *glaberrima* and *japonica* groups (Figure 8d), thus confirming its group distinctiveness (Table 14).

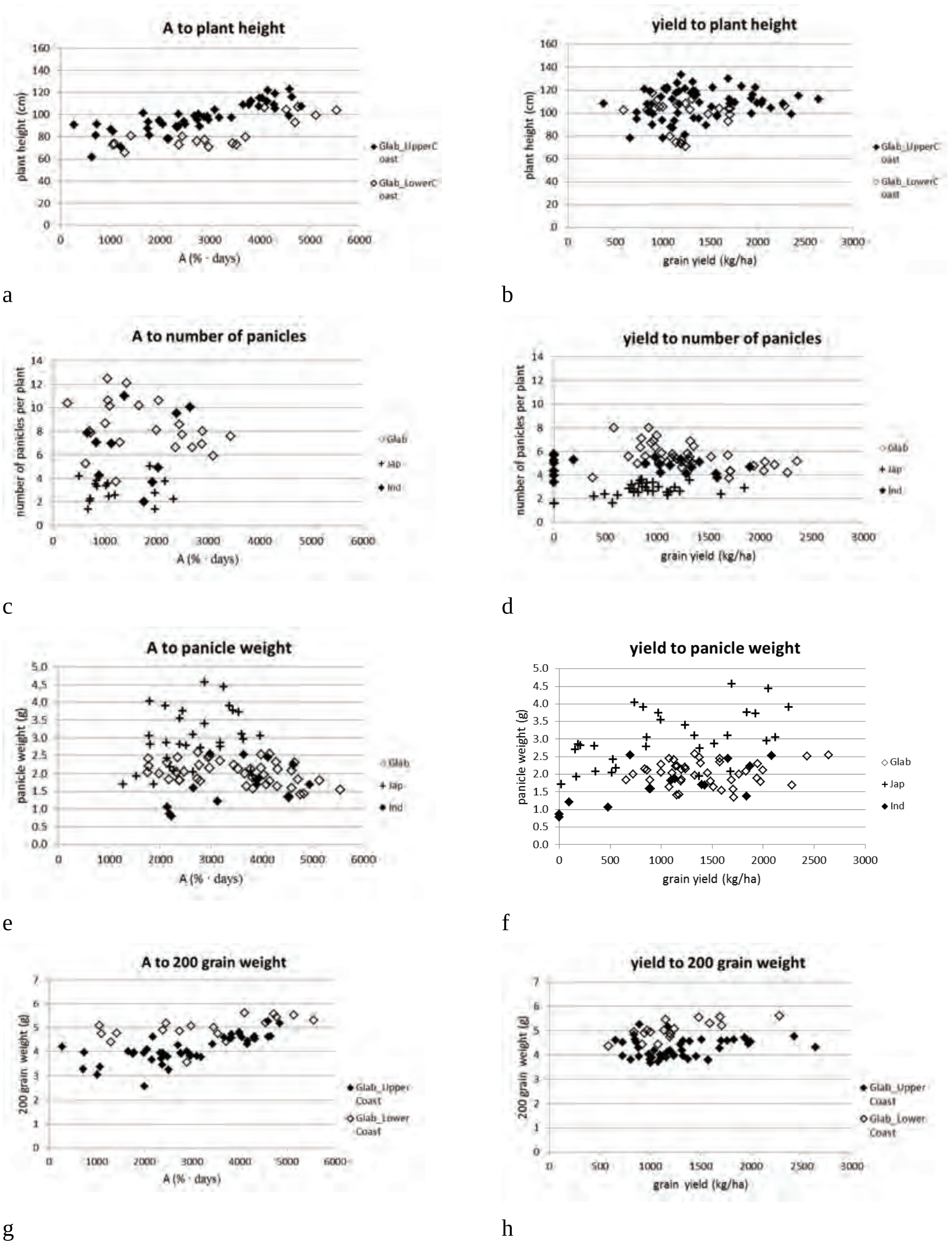


Figure 8: *Relation between accumulated canopy cover (A; in %.days; x-axis of a, c, e, g) or grain yield (in kg/ha; b, d, f, h) and plant height (a, b), number of panicles (c, d), panicle weight (e, f) and 200 grain weight (g, h). Different symbols refer to different botanical groups or molecular clusters within the glaberrima botanical group. Values presented are averages of 5 replications. See materials and methods section for coding of the botanical groups and molecular clusters*

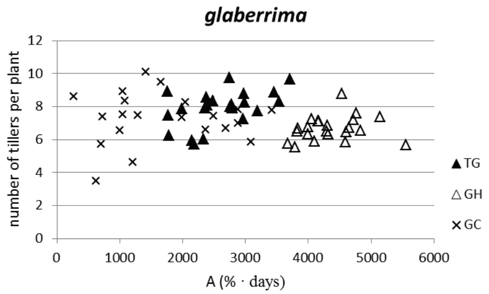
Number of tillers

The three botanical groups showed significant G×E interactions for the number of tillers produced per plant. This means that, in general, genotypes composing the three botanical groups followed different strategies in tiller production across environments (Figure 11). At cluster level, G×E interactions were also found for the two *glaberrima* clusters and for the Ind_Gc cluster, but were absent for the Ind_Gh cluster and the two clusters of *japonica*. This implying that within the *japonica* clusters and the Ind_Gh cluster genotypes all vary tiller production in a similar way across environments.

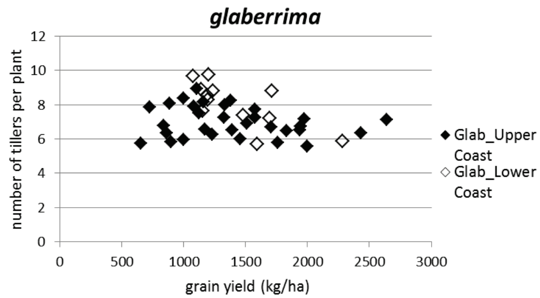
Indica as well as *glaberrima* showed intensive tillering (Table 14). An increase in tiller number was observed from more favourable (Sierra Leone and Ghana) to less favourable environments (Guinea, Togo and Guinea Bissau) for the *indica* cluster (Figure 11). One of the underlying mechanisms facilitating the increase of tillers under less favourable conditions is that generally (for all botanical groups and clusters) under less favourable conditions (Guinea and Togo) the time to flowering is longer than under more favourable conditions (Sierra Leone and Ghana) (Figure 12). It seems particularly the case that the *indica* group uses this time to produce tillers while the *japonica* and *glaberrima* groups responded in various other ways.

Figures 9b and 9e indicate that for the *indica* group there is a positive relationship between canopy cover and tillering in Guinea and Togo, while tillering remains constant at high A in Ghana (Figures 9b). However the positive relation in Guinea and Togo does not match with the relation between number of tillers and yield at low A because tillering remained high even when the crop failed to yield (Figure 9e).

Japonica showed a positive relationship between number of tillers and A ($r = +0.604^{**}$, Figure 9c), but not for number of tillers and yield (Figure 9f). The two *japonica* clusters showed a similar positive relation between A and number of tillers. The Jap_GbGh cluster clearly produced more tillers than the Jap_SL cluster (Table 14). This higher number of tillers contributed to a higher panicle number (although not significantly higher) which in turn might be linked to the significantly higher yield observed for Jap_GbGh.



a



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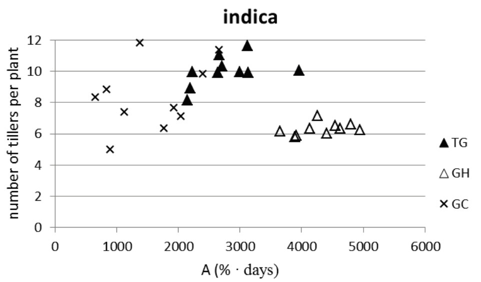

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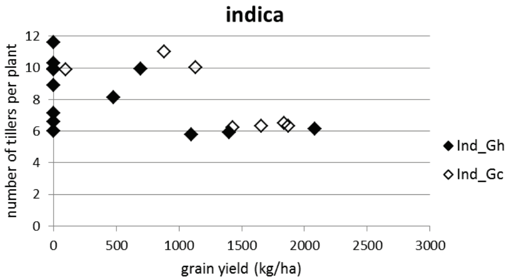

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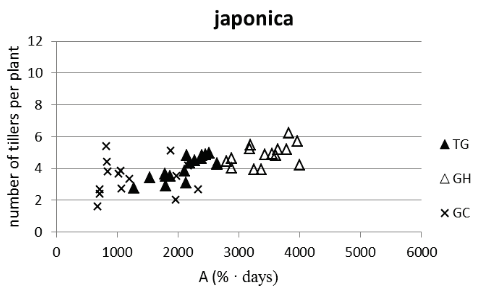

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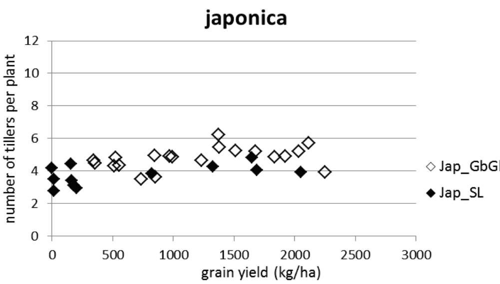

f

Figure 9*: The relation between accumulated canopy cover (A; in %.days; x-axis of a, b, c) or grain yield (in kg/ha; x-axis of d, e, f) and the number of tillers per plant for each of the three botanical groups and their respective molecular clusters. Series TG, GH and GC respectively indicate observations from Togo, Ghana and Guinea. Values presented are averages of 5 replications for each of the two sowing dates. See materials and methods section for coding of the botanical and molecular clusters.*

Time to 50% flowering

We observed that at low yield levels the time to 50% flowering was consistently higher for all genotypes than at higher yield levels (Figure 12). This suggests that under less favourable conditions genotypes generally delayed their flowering.

Panicle weight

Significant G×E interactions were found only for *japonica*. Sowing effects were observed for *japonica* group (as part of the three way interaction between sowing, location and genotype), for the *indica* botanical group, and for the Ind_Gc cluster. Of the clusters only Ind_Gc showed variations of panicles weight by sowing dates. The panicle weight and yield highly correlated positively for Ind_Gc (r = 0.755*) and Jap_SL (r = 0.824**). For other clusters no significant relations were observed between panicle weight and yield. These observations suggest that the *japonica* and *indica* groups were more sensitive to sowing date (less robust) than the *glaberrima* group and its clusters.

Panicle weight for *glaberrima* and *indica* was significantly lower than for *japonica* (Table 14). When yield and A increased, panicle weight also increased, for the *indica* group (0.549*). For the *japonica* group there was no relation between panicle weight and A. However, an increasing trend in panicle weight was observed when yield increased (0.601**) (Figures 8e and 8f). Such trends were not observed for the *glaberrima* group, suggesting that panicle weight of *glaberrima* was more stable. No significant differences or trends were found, for clusters within the *glaberrima*, *japonica* and *indica* groups, for panicle weight, with the exception of Jap_SL, which showed a positive relation with A (r = 0.674*). Panicle weight for cluster Jap_GbGh showed no relation with A.

Panicle length

Significant G×E interactions were found for all botanical groups. The Glab_UpperCoast, Jap_GbGh and Jap_SL clusters all showed significant G×E interactions. There was a tendency towards short panicle production in Ghana and Sierra Leone, the countries where the yields were generally high (Figure 13). The cluster Glab_UpperCoast produced significantly longer panicles than all other clusters except for Jap_GbGh. The fact that the Glab_UpperCoast cluster had a panicle weight similar to that of Glab_LowerCoast implies that Glab_UpperCoast produced more grains of smaller size per panicle than

Glab_LowerCoast. The cluster Glab_UpperCoast also showed a rather slight negative correlation between panicle length and yield (r = -0.332**), A (r = -0.335*) and a somewhat stronger negative correlation with the 200 grain weight (r = -0.427**). This means that for Glab_UpperCoast cluster production of short panicles corresponded with high A, yield and grain weight. This implies that under stress conditions (i.e. low yield and low A) Glab_UpperCoast invested more in panicle length (Figure 13). The negative relation between yield and panicle length was also observed, somewhat more strongly, for Glab_LowerCoast (r = -0.708**), Ind_Gc (r = -0.850**), Ind_Gh (r = -0.664**) and Jap_GbGh (r = -0.450**). Jap_SL did not show any relation between yield and panicle length.

200 grain weight

Significant G×E interactions were found for 200 grain weight for the *glaberrima* group and the Glab_UpperCoast cluster, suggesting that the genotypes composing the Glab_UpperCoast cluster responded differently across environments for 200 grain weight. This might be a factor in observed robustness in yield for this cluster. The absence of G×E interactions within the other botanical groups suggests that the 200 grain weight is genetically determined. The high estimate of wide sense heritability (H^2 = 80%; Table 16) confirms this general trend for *indica*. However, the relatively low wide sense heritability estimate for *japonica* (H^2 = 32%; Table 16) as compared to other botanical groups indicates that environmental conditions might have some considerable impact on the 200 grain weight of *japonica*. However, it is only with the *glaberrima* group, and not for *japonica* or *indica*, that a significant location effect was found.

Significant genotype effects were observed for the *japonica* group and Jap_GbGh cluster. No significant genotype effect was observed for the varieties of the Jap_SL cluster, suggesting little variation for 200 grain weight in the Jap_SL cluster and large genotypic variation in the Jap-GbGh cluster. The *indica* group also showed a significant genotype effect. Not enough data were available for an ANOVA of the Ind_Gh group.

The botanical groups showed little variation for 200 grain weight, but the average 200 grain weight varied significantly among the clusters of each botanical group. Within the *glaberrima* group the Glab_UpperCoast average was lower than that of the Glab_Lower coast cluster. The average 200 grain weight for the Jap_GbGh cluster was higher than that of the Jap_SL cluster and the Ind_Gc cluster average was higher than that of Ind_Gh cluster.

Japonica showed a fairly strong positive correlation between A and 200 grain weight: r = 0.70**, against r = 0.596** and r = 0.581** for the *glaberrima* and *indica* groups, respectively. At low values of A, the Ind_Gh cluster and *japonica* group tended to produce more empty or poorly developed grains, as represented in Figure 14. This is consistent with our summary finding under the section on tillering that extra tillers were produced at lower levels of A and yield contained more empty grains. The trends observed between A and 200 grain weight were also observed between 200 grains weight and yield, but only with the *indica* and *japonica* groups.

A clear divide was observed for the 200 grain values for Glab_UpperCoast and Glab_LowerCoast (Figures 8g, 8h). Figures 8g and 8h show that when canopy cover decreased the 200 grain weight for the Glab_UpperCoast cluster decreased more than the 200 grain weight for the Glab_LowerCoast cluster. Therefore, it can be concluded that the Glab_LowerCoast cluster was less susceptible to variation in environment. The 200 grain weight for clusters within *indica* and *japonica* decreased in a similar way when A and yield decreased. These clusters were similarly sensitive to the environment. In general, all *glaberrima* clusters (and also Ind_Gc) maintained their grain weight across environments even at low yield (Figure 8h, 14). This is contrary to the Ind_Gh and two *japonica* clusters, for which the empty grains increased at lower yield levels. This underscores the claim we make for the robustness of farmer varieties of *glaberrima* and Ind_Gc, and the consequent ability of these types consistently to produce good grains throughout a range of difficult environments.

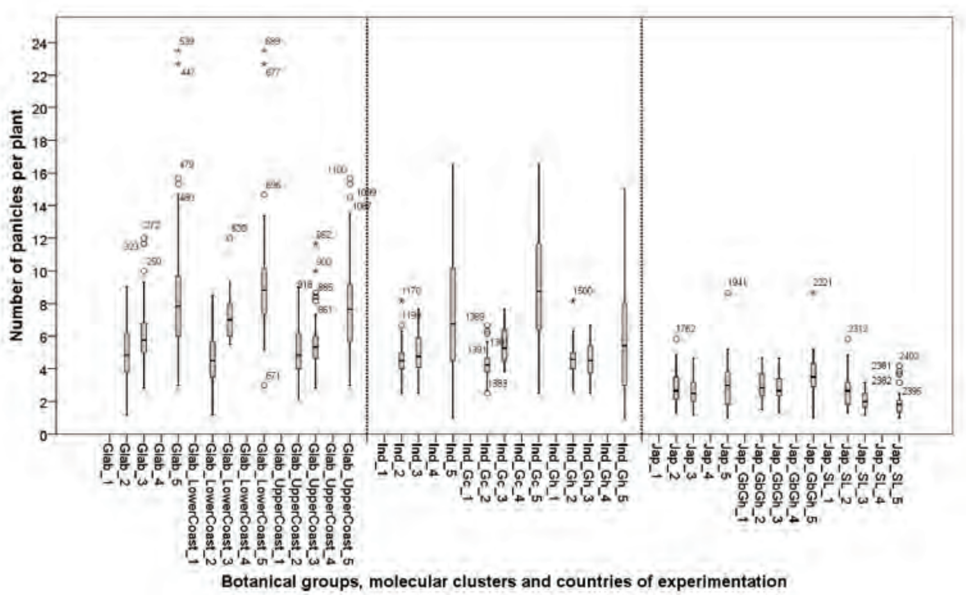

Figure 10: *Box plots for number of panicles of 24 varieties in five experimental sites: 1: Ghana; 2: Sierra Leone; 3: Guinea Bissau; 4: Togo and 5: Guinea. See materials and methods section for coding of the botanical groups and molecular clusters.*

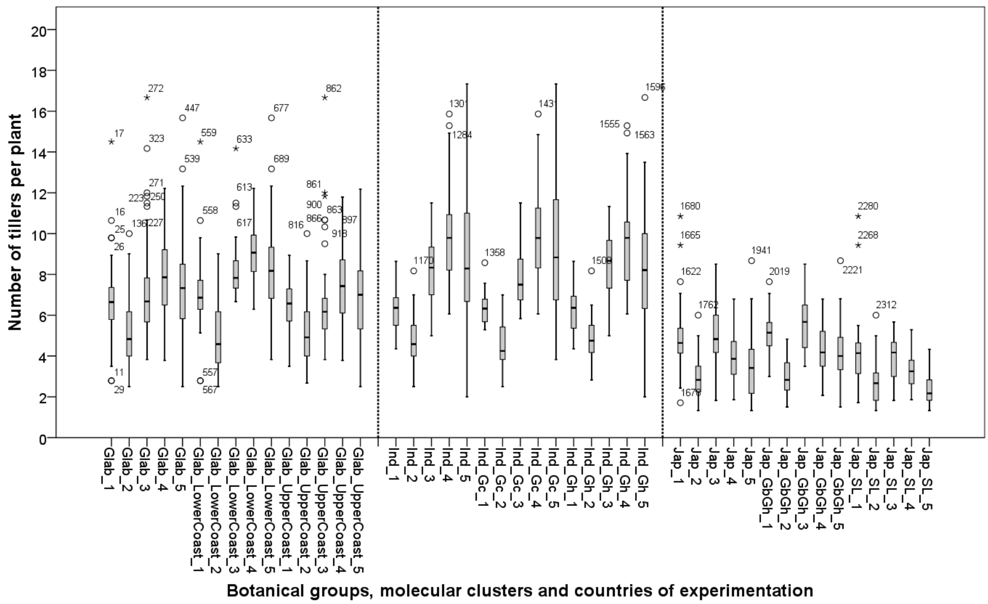

Figure 11: *Box plots of number of tillers per plant of 24 varieties in five experimental sites: 1: Ghana; 2: Sierra Leone; 3: Guinea Bissau; 4: Togo and 5: Guinea. See materials and methods section for coding of the botanical and molecular clusters.*

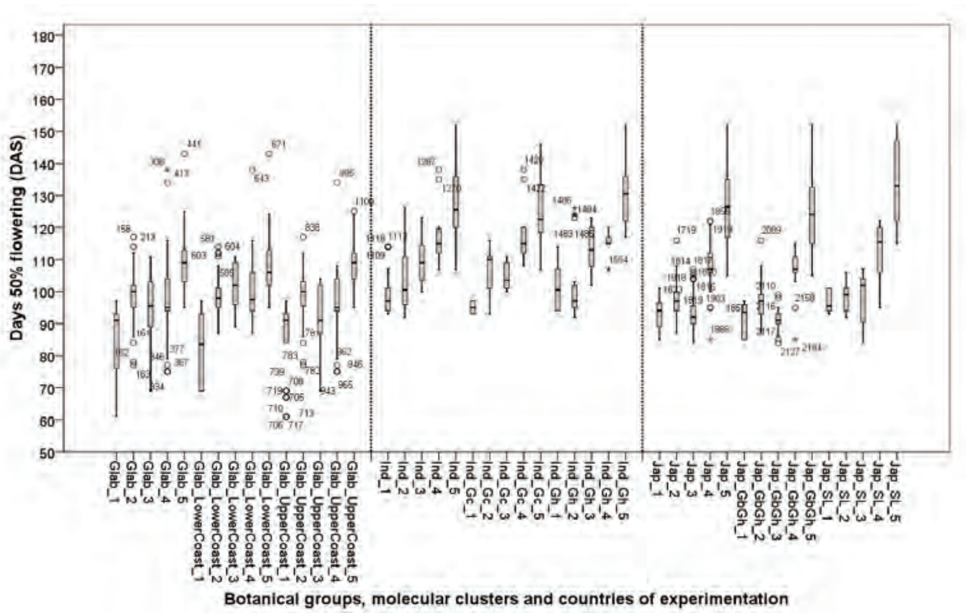

Figure 12: *Box plots for days to 50% flowering of 24 varieties in five experimental sites: 1: Ghana; 2: Sierra Leone; 3: Guinea Bissau; 4: Togo and 5: Guinea. See materials and methods section for coding of the botanical groups and molecular clusters.*

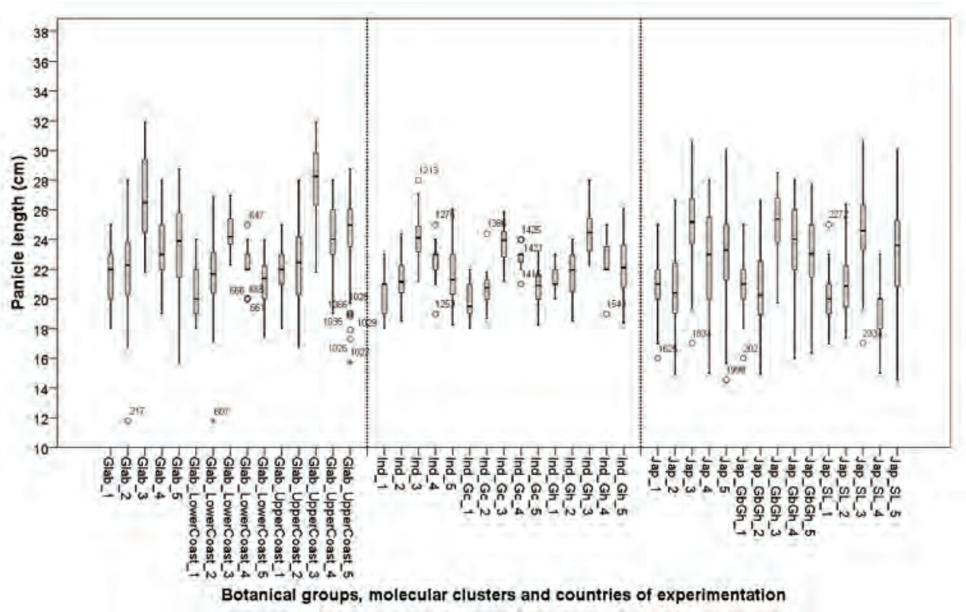

Figure 13: *Box plots for panicle length of 24 varieties in five experimental sites: 1: Ghana; 2: Sierra Leone; 3: Guinea Bissau; 4: Togo and 5: Guinea. See materials and methods section for coding of the botanical groups and molecular clusters.*

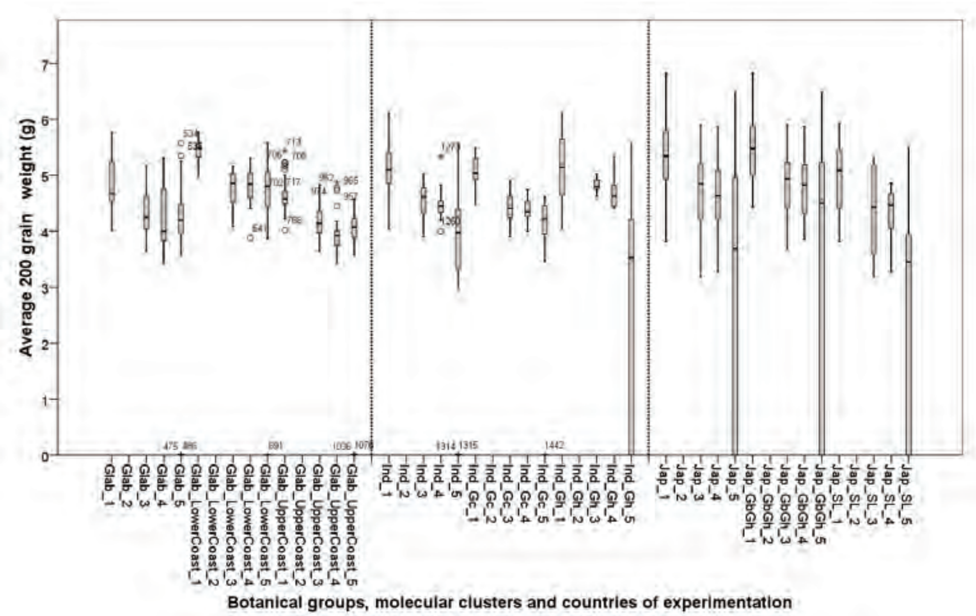

***Figure 14**: Box plots for average 200 grain weight of 24 varieties in five experimental sites: 1: Ghana; 2: Sierra Leone; 3: Guinea Bissau; 4: Togo and 5: Guinea. See materials and methods section for coding of the botanical groups and molecular clusters.*

Discussion

Figure 5 showed that the two clusters of the *glaberrima* group maintained a minimum yield of 660 kg/ha in all environments. We observed that in trials in two countries where yields were relatively high (Ghana and Sierra Leone) the *indica* sourced from Guinea maintained a yield level close to that of *glaberrima*. But in the Guinea Bissau and Togo trials, the likelihood of crop failure was high overall. This might be due to the relatively short rainy season in Guinea Bissau and to the acidity of the soil in Togo. In contrast, varieties in the Ind_Gh cluster yielded only in Sierra Leone and to a lesser extent in Ghana, with a high frequency of zero yield. In Ghana and Sierra Leone Jap_GbGh showed a yield level similar to that of the *glaberrima* clusters. In Guinea Bissau and Togo, Jap_GbGh had a low yield but still reached at least 320 kg/ha.

In contrast, Jap_SL only showed a good yield level (without zero yield) in Sierra Leone. In Guinea Bissau the yield for Jap_SL dropped to 200 kg/ha and the frequency of crop failure increased in Togo and Ghana. Jap_SL thus seemed to be specifically well adapted to the ecology of Sierra Leone. Like Jap_SL, Ind_Gh produced only in Sierra Leone. This might be attributed to the characteristics of the varieties (Viono tall and Zomojo). These varieties from Ghana are mostly cultivated in the lowlands but have proven to suit certain specific upland niches in Ghana for which the conditions were apparently not met in the Ghana trial but were approached best in Sierra Leone. Okry *et al*. [19] also reported on such transfer of varieties across agro-ecologies. They provided a case where farmers were trying CK 21, a typical lowland variety in the upland in the region of Guinea known as Guinea Maritime. Given that farmers have decided, for their own reasons, to shift this variety from the recommended domain, it could be counted as an instance of G×E×S (society) interaction.

These findings on the yield show that clusters differed in yield performance across environments. Glab_Upper coast, Glab_Lower coast, Jap_GbGh and Ind_Gc were best able to maintain their yield across environments. Farmers often look for varieties that assure minimum yield in environments with variable and stressful conditions. These varieties seemingly satisfy such objectives of farmers.

Observations of average performance at cluster level revealed that canopy development and yield scenarios differed between and within botanical groups. Glab_UpperCoast and Glab_LowerCoast showed the highest values for V_{max}, A and yield. The two clusters of *indica*, Ind_Gh and Ind_Gc, showed similar values for V_{max} and A, although the latter significantly outperformed the former in yield. Moreover, Ind_Gc had a canopy development (V_{max} and A) and yield similar to Glab_LowerCoast and Jap_GbGh. Whereas Jap_GbGh and Jap_SL did not significantly differ in V_{max} or A, Jap_GbGh had a significantly higher yield than Jap_SL. Additionally, Jap_GbGh - although displaying low values of V_{max} and A - showed an average yield similar to that of *glaberrima* and Ind_Gc. The clusters Jap_SL and Ind_Gh developed a smaller canopy and also had the lowest yield. From these findings we infer that lower A can be associated with higher yield, and high canopy growth can be associated with lower yields. These associations are strongest for Ind_Gh (lower yield with higher A) and Jap_GbGh (higher yield with lower A).

Looking at the overall averages in Table 14 the ratio number of panicles over number of tillers was highest for *glaberrima* (0.94), followed by *indica* (0.72) and *japonica* (0.70), suggesting that the tillers of *glaberrima* produced more panicles. Particularly under less favourable conditions (e.g. Guinea Bissau) a difference was observed between botanical groups in the ratio of the number of panicles and tillers (Table 15). Of the botanical groups, only the clusters of the *indica* group varied, with tillers of Ind_Gc producing more panicles than those of Ind_Gh (0.8 and 0.65 respectively). However, looking at the averages per country for each botanical group and molecular cluster we observed that the increase in tillering for the *indica* group resulted in increased panicle production: the ratio of number of panicles over number of tillers remained stable or even increased at lower yield (Table 15). The combination of the high number of tillers and panicles for Ind_Gh together with low yield suggests that its panicles have a large percentage of non-formed (i.e. empty) grains.

Table 15: *Yield and yield components for different botanical groups and countries: Average yield (kg/ha) in descending order from left to right, number of panicles per plant, number of tillers per plant and ratio between the number of panicles and the number of tillers across countries. The values for Guinea are put in the uttermost right column as the yield was not assessed.*

Botanical groups and clusters*		Ghana	Sierra Leone	Togo	Guinea Bissau	Guinea
Glaberrima	Yield	1660	1510	1164	1034	-
	Panicles	-	5.0	-	5.9	8.0
	Tillers	6.6	5.0	7.9	6.9	7.2
	Ratio		1.00		0.86	1.11
		Ghana	Sierra Leone	Guinea Bissau	Togo	Guinea
Japonica	Yield	1513	1061	759	504	-
	Panicles	-	2.9	2.6	-	3.0
	Tillers	4.9	2.9	5.1	4.0	3.5
	Ratio		0.98	0.52		0.86
		Sierra Leone	Ghana	Togo	Guinea Bissau	Guinea
Indica	Yield	1248	1132	329	317	-
	Panicles	4.5	-	-	4.9	7.2
	Tillers	4.7	6.3	9.3	8.2	8.3
	Ratio	0.96			0.60	0.88
		Ghana	Sierra Leone	Togo	Guinea Bissau	Guinea
Glab_UpperCoast	Yield	1664	1568	1160	1100	-
	Panicles	-	5.1	-	5.5	7.8
	Tillers	6.5	5.1	7.5	6.4	6.9
	Ratio		1.01		0.86	1.13
		Ghana	Sierra Leone	Togo	Guinea Bissau	Guinea
Glab_LowerCoast	Yield	1651	1356	1174	872	-
	Panicles	-	4.7	-	7.0	8.6
	Tillers	6.7	4.7	9.0	8.1	8.2
	Ratio		1.00		0.87	1.06
		Ghana	Sierra Leone	Guinea Bissau	Togo	Guinea
Jap_SL	Yield	1127	958	525	242	-
	Panicles	-	2.7	2.1	-	2.0
	Tillers	4.4	2.8	4.0	3.3	2.4
	Ratio		0.98	0.51		0.81
		Ghana	Sierra Leone	Guinea Bissau	Togo	Guinea
Jap_GbGh	Yield	1741	1123	869	662	-
	Panicles	-	2.9	2.9	-	3.6
	Tillers	5.1	3.0	5.5	4.4	4.1
	Ratio		0.98	0.52		0.88
		Sierra Leone	Ghana	Togo	Guinea Bissau	Guinea
Ind_Gh	Yield	1096	742	196	153	-
	Panicles	4.6	-	-	4.5	5.7
	Tillers	4.9	6.3	9.2	8.5	7.9
	Ratio	0.95			0.53	0.72
		Ghana	Sierra Leone	Guinea Bissau	Togo	Guinea
Ind_Gc	Yield	1699	1476	553	529	-
	Panicles	-	4.4	5.4	-	8.8
	Tillers	6.4	4.6	7.8	9.4	8.7
	Ratio		0.96	0.69		1.02

- : not measured. *See materials and methods section for coding of the clusters

In general the number of tillers correlated (r = 0.800**) with the number of panicles per plant which in turn correlated with A. The fact that the relationship between the number of tillers and A was not clear for all botanical groups might imply that other variables such as the size of the tillers, leaf width, leaf length and leaf blade angle, which were not measured in these experiments, might account for the overall poor relationships we observed between A and the number of tillers per plant. Vigour-related variables are known to vary between rice species, *O. glaberrima* being often more vigorous than *O. sativa* [10-12].

The longest average period until 50% flowering was observed with the *indica* group. The *glaberrima* group showed the shortest period until 50% flowering, suggesting that this group had a shorter vegetative cycle. The result agrees with farmers' assertions that *glaberrima* (e.g. farmer varieties Malaa and Jangjango) are often earlier than other traditional *sativa* varieties and thus are used to beat the pre-harvest hunger gap [20].

Comparing the negative relationship between time to 50% flowering and A it can be said that this relation is most clear for *japonica* and *indica* (r = -0.880** and r = -0.855** respectively). The same relation was observed at cluster level for these two botanical groups. The *glaberrima* group and its clusters showed lower correlations between 50% flowering and A (r = -0.538** for the botanical group). This might imply that the environmental conditions determining accumulated canopy cover (A) affected 50% flowering of the *glaberrima* and its clusters less than that of the other varieties. This suggests that *glaberrima* is more stable in terms of time to 50% flowering. An advantage of such stability would be that even under high stress conditions farmers do not run the risk that the crop will delay its flowering beyond the scope of the rainy season. This is more likely the case for the varieties from Upper Guinea Coast. Varieties from Lower Guinea Coast usually experience a short dry period 2 to 4 weeks after planting. In such conditions it is important for the rice crop not to flower too early. The stability in flowering time for the *glaberrima* group takes care of that.

When summarising the relation between the yield and yield determining parameters, our study has shown that a large number of farmer varieties are able to adapt to large variations in environment. Our findings on tillering, yield, A, flowering and number of panicles suggest the existence of three different physiological strategies of adaptability for each of the botanical groups, which we now attempt to summarise.

Glaberrima

Across environments *O. glaberrima* consistently showed the highest values for maximum canopy, plant height, number of panicles and yield. Also remarkable was the absence of crop failure for the *glaberrima* group; this helps explain why it makes a more reliable and secure choice for sub-optimal farming or situations of special difficulty. In addition, the *glaberrima* group showed the shortest time to 50% flowering, a useful property for farmers affected by a pre-harvest hunger gap [20].

Overall, accumulated canopy, maximum canopy cover and yield were similar for Glab_LowerCoast and Glab_Upper coast clusters. But the two clusters differed in their strategy of canopy building: Glab_LowerCoast invested more in tiller production while Glab_UpperCoast produced taller plants. When A decreased, Glab_LowerCoast was better able to maintain its grain weight than Glab_UpperCoast and therefore appears to be more stable in grain weight. Under stress conditions (i.e. low yield and low A) Glab_UpperCoast invested more in panicle length. Also *glaberrima* from the lower coast showed higher values for 200 grain weight and the decrease of the 200 grain weight at lower yield levels was also less. However, the panicle weight for Glab_LowerCoast was less than that of the cluster Glab_UpperCoast. This also applies to panicle length and plant height. The Glab_LowerCoast varieties thus tended to invest more in grain weight, whereas Glab_UpperCoast varieties produced more grains per panicle. These two distinct strategies led to similar yields for these two clusters.

In sum, among the studied genotypes, those of *O. glaberrima* developed different strategies of adaptation, but interestingly, these strategies led to similar performance throughout the range of environments tested, demonstrating the robustness of this group of rices when compared to other botanical groups. These strategies relate to the area of collection of the varieties and also coincide with molecular groupings [15].

The *glaberrima* showed more G×E interactions than *indica* and *japonica*. This is worthy of note, since it is sometimes assumed that *O. glaberrima* is genetically less diverse than *indica* and *japonica*. Molecular analysis conducted by Nuijten *et al*. [15] showed that *glaberrima* and *japonica* were roughly similar in terms of genetic diversity: (H_e = 0.034; n = 66) and (H_e = 0.045; n = 87), respectively).

Indica

In less favourable environments varieties of the *indica* group produced more tillers than in the more favourable environments. The underlying mechanism seems to be that under less favourable conditions flowering is delayed and at the same time the tillering period is prolonged. The result is that at higher yield levels *indica* produced fewer tillers. At lower yield levels *indica* seemed less vigorous, as the increase in number of tillers did not lead to an increase in A. These tillers were, however, productive because an increase in tillering led to an increase in panicle production. The fact that an increase in panicle production did not lead to an increase in yield is a product of the crop failure observed for many plots in the less favourable environments, and the many panicles with unfilled grains.

The cluster Ind_Gc showed the highest plant height. This observation together with observations of high V_{max} and A for Ind_Gc implies that Ind_Gc is more vigorous compared to Ind_Gh. This vigour tuned into higher yield for Ind_Gc. The Ind_Gc cluster also displayed the same average plant height as the Glab_Upper coast cluster.

This shows that the Ind_Gc cluster, like *glaberrima,* is able to maintain its yield. At lower yield levels, however, it follows a different physiological strategy of adaptation than *glaberrima,* as it produced the largest number of tillers. But compared to *glaberrima*, these tillers contributed less to A and contributed also less to yield maintenance, as there were high numbers of unfilled grains.

In sum, the *indica* from Guinea resembled the *glaberrima* group in several ways. Like *glaberrima* it was able to maintain its number of tillers and also increased its number of panicles at low yield levels. Like *glaberrima*, it showed significant G×E interactions that helped to stabilise A and V_{max}.

Japonica

Low canopy cover and limited tiller and panicle production seem typical for the *japonica* group. At a high level of A, *japonica* consistently produced more tillers. This relation seemed linear, as was the relation between yield and accumulated canopy, thus suggesting that an increase in tillering contributes to canopy formation and yield. In addition, *japonica* slightly increased its panicle number while tillering, A and V_{max} were not maintained at low yield levels. Instead of investing in high tiller number *japonica* invested more in panicle weight:

when compared with *glaberrima* and *indica* panicle weight was approximately 50% to 100% higher.

The Jap_GbGh cluster maintained a yield across environments similar to that of the *glaberrima* group and *indica* cluster from Guinea, although it failed to maintain A at lower yield level. In contrast, varieties in the Jap_SL cluster only yielded well in Sierra Leone. This might suggest that these *japonica* varieties were highly adapted to a specific niche. In Sierra Leone, however, varieties in the *japonica* group are often found bridging an ecological gradient from lowland to upland [20].

Observed behaviour of the studied genotypes in relation to the area of collection

Glab_LowerCoast: Farmers in the Togo Hills (Togo mountain ranges) in Ghana and Togo traditionally used these varieties mainly on stony hills and slopes with poor soil because political conflict and war drove them into mountainous areas, since life on the plains was too dangerous. Reliability of yield was very important in these conditions and rice was probably once the main carbohydrate crop. The data for this cluster indeed show that they are highly reliable in relation to yield. Nowadays these varieties are cultivated on the Ghanaian slopes of the Togo Hills only for ceremonial reasons, because lowland farming has been added to the local farming repertoire since the 1960s, and other crops like cassava and maize are now more important than previously [21]. Occasionally African rice is used on the Ghanaian slopes and in the lowlands of the Togo Hills when farmers are very late with sowing rice. African rice is used because of its short cycle. Farmers in the Togo Hills (Danyi Plateau) grow only African rice, which is an important secondary crop. They said they have tried other varieties but nothing works as well in the hills as the rices of the Glab_LowerCoast cluster.

Glab_UpperCoast: The upper West African coast includes two secondary centres of domestication and diversity for *O. glaberrima* [22], so we might not expect a great deal of similarity in the behaviour of genotypes collected from this region (on a transect from Senegal to Sierra Leone). When comparing the Glab_LowerCoast to Glab_UpperCoast in our experiments the differences observed within and between clusters appear to reflect the fact that rice farmers on the Upper Coast grow rice as their main staple, and work a much broader range of environments (and thus exercise a larger range of selection pressures) than the farmers in the Togo Hills. Farmers experience quite different constraints in their farming systems. In the semi-arid zone of the upper coast (Senegal, Gambia and Guinea Bissau), a short rainy seasons (3 to 4 months) may have forced farmers to select for short duration *glaberrima* types better adapted to their conditions. In these conditions, farmers appear to have selected taller plants with longer panicles and fewer tillers.

In the forest belt of Sierra Leone and Guinea, with a much longer rainfall period (6 to 7 months) the environment is favourable for longer duration crops. However, farmers still cultivate *O. glaberrima* to some extent because of its adaptability to poor, eroded soils and tolerance to drought at the beginning and end of the rainy season. In the forest belt farmers report many weed problems [20], particularly in areas with short fallow periods. Selecting for tall plants could also help in suppressing weed. In addition farmers seem to have selected *glaberrima* types that were less photoperiod sensitive, facilitating the planting of short-duration types to be sown in late April and used as hunger breaker crops.

Ind_Gc: These varieties appeared to be stable in yield and in that way resemble *O. glaberrima* and Jap_GbGh. The Ind_Gc types are widely cultivated in the area of collection, under typical upland conditions on poor soils. Farmers state that rices in the Ind_Gc cluster resemble *O. glaberrima* in being well adapted to poor soils. They are also drought tolerant when compared to other *O. sativa* varieties (e.g. Samba, Dalifodé, Podê) and also yield well under good conditions (as well as well enough, under poor conditions). They dominate upland rice cultivation in their area of collection because, as farmers state, *O. glaberrima* lodges at complete maturity, as frequently mentioned as a drawback by a number of rice researchers [7, 23, 24]. Farmers claim this results in low yields, especially when they lack sufficient labour for a timely harvest.

Ind_Gh: These are varieties that performed relatively poorly in our experiments, except in Sierra Leone. In addition to cultivation under upland conditions (in the Ghanaian Togo Hills) these varieties are also cultivated very successfully in the adjacent lowlands. Since the 1960s lowland cultivation has been added to the farming systems of the different minority groups living at the foot of the Togo Hills. Ever since that time farmers have been experimenting with lowland varieties in the upland area and vice versa. The varieties in the Ind_Gh cluster are probably adapted to very specific upland conditions in the Ghanaian Togo mountain ranges, conditions apparently replicated in experimental conditions at the foot of the Sierra Leonean escarpment (Kamajei Chiefdom).

Jap_GbGh: These varieties are commonly planted under upland conditions. They are equal in yield to the two *O. glaberrima* clusters and the Ind_Gc cluster. Farmers grow them for their white pericarp, good taste and the fact that they fit the rainy season calendar very well, being not too short, and not too long. Farmers visiting the trial in Guinea Bissau were very impressed with the growth of some varieties of this *japonica* cluster, and indicated they would like to grow these varieties in the following season. However, upon realising the pericarp colour was red these farmers lost interest, as they have a strong preference for white seed colour. Elsewhere (in Ghana and Sierra Leone, for example) farmers actually prefer varieties with red pericarp. This underlines the importance of taking into account cultural factors in crop development [4].

Jap_SL: These varieties seem to be very specifically adapted to Sierra Leonean conditions. They are widely cultivated in this area of collection. Farmers who are conversant with them typically look for toposequences to allow flexible planting up and down slopes, taking account of the stage of the season. They are thus adapted to a mid-slope planting scenario, between wetland and upland varieties. The mid-slope niche is very common in an undulating, well-watered country such as Sierra Leone, but is less common in the other areas in which we carried out experiments. This may explain why this particular group only seemed to do well in its zone of collection. It has been selected for robustness in a niche.

Conclusion

It can be concluded, that the *glaberrima* group as a whole, and the *indica* cluster from Guinea and *japonica* from Guinea Bissau and Ghana, were more plastic than other rices in the study, allowing them to be more constant in yield, A, and in number of tillers and panicles. Seemingly, farmer selection in Guinea has created a group of Asian rices that resemble in performance the highly adapted African rices of the region.

This paper has presented evidence that farmer rice varieties in coastal West Africa are, for the most part, highly robust, and well-adapted to a range of sub-optimal farming conditions. A case has been made that much of this robustness is a product of adaptation. An implication is that many farmer varieties will maintain their performance across a range of low-input conditions, and thus might be very useful to farmers in neighbouring countries. More efforts should be made to conserve, evaluate and distribute farmer-selected rice planting materials in the region. Farmers themselves should be consulted about the best way to develop relevant modalities of dissemination, and involved directly in any such activity.

***Table 16**: Wide sense heritability estimates (for all genotypes together and per botanical group).*

	V_{max}	A	Plant height	# Tillers	50% Flowering	# Panicles	Panicle length	Panicle weight	200 grains weight	Yield/ha
All genotypes	60	45	60	79	86	77	67	75	49	76
Glaberrima	35	12	68	17	86	1	61	48	65	43
Indica	50	55	61	0	64	5	30	56	80	90
Japonica	76	63	45	62	59	56	69	48	32	59

***Table 17**: Pearson correlations between yield components and days to 50% flowering*

Cluster	Plant height (cm)	Panicle length (cm)	Number of tillers	Number of panicles	Panicle weight (g)	200 grain weight (g)	Plot yield (kg/ha)	Canopy cover A (%)
All	- 0.390**	0.073	- 0.018	0.045	0.101	-0.581**	-0.298**	-0.661**
Glab	- 0.194*	0.211*	0.111	0.304*	0.464**	- 0.515**	0.080	- 0.538**
Ind	- 0.693**	0.115	0.413**	0.355	- 0.306	- 0.839**	-0.316	- 0.855**
Jap	- 0.593**	0.138	- 0.432**	- 0.029	- 0.237	- 0.716**	-0.511**	- 0.880**
Glab_Upper Coast	- 0.113	0.272*	0.043	0.385**	0.641**	- 0.705**	0.266*	- 0.482**
Glab_Lower Coast	- 0.335	0.189	0.193	0.099	0.245	- 0.714**	-0.428*	- 0.668**
Ind_Gc	- 0.751**	0.119	0.497*	0.589*	- 0.416	- 0.878**	-0.403	- 0.854**
Ind_Gh	- 0.649**	0.073	0.370	0.262	- 0.221	- 0.862**	-0.273	- 0.873**
Jap_GbGh	- 0.699**	0.058	- 0.274	0.459*	- 0.054	- 0.685**	-0.559**	- 0.896**
Jap_SL	- 0.548**	0.289	- 0.619**	- 0.449	- 0.611	- 0.702**	-0.342	- 0.877**

***Table 18**: Pearson correlations between yield components and plant height (cm)*

Cluster	Days to 50% flowering	Panicle length (cm)	Number of tillers	Number of panicles	Panicle weight (g)	200 grain weight (g)	Plot yield (kg/ha)	Canopy cover A (%)
All	- 0.390**	0.225**	- 0.206**	- 0.168*	0.179	0.301**	0.346**	0.596**
Glab	- 0.194*	0.337**	- 0.384**	- 0.530**	- 0.067	0.051	0.168	0.671**
Ind	- 0.693**	0.274	- 0.495**	- 0.113	0.580*	0.631**	0.392*	0.555**
Jap	- 0.593**	0.034	0.093	- 0.017	0.442*	0.348**	0.420**	0.621**
Glab_UpperCoast	- 0.113	0.290**	- 0.191	- 0.408**	- 0.098	0.438**	0.181	0.826**
Glab_LowerCoast	- 0.335	0.152	- 0.550**	- 0.677**	- 0.788**	0.359	0.020	0.796**
Ind_Gh	- 0.649**	0.450*	- 0.520**	0.143	0.674	0.682*	0.393	0.485
Ind_Gc	- 0.751**	0.123	- 0.583**	- 0.673*	0.670	0.615*	0.228	0.784**
Jap_GbGh	- 0.699**	- 0.139	0.061	- 0.134	0.229	0.359*	0.482**	0.635**
Jap_SL	- 0.548**	0.323	0.300	0.254	0.727*	0.368	0.452*	0.640**

***Table 19**: Pearson correlations between yield components and panicle length (cm)*

Cluster	Days to 50% flowering	Plant height (cm)	Number of tillers	Number of panicles	Panicle weight (g)	200 grain weight (g)	Plot yield (kg/ha)	Canopy cover A (%)
All	0.073	0.225**	0.182**	0.120	0.102	- 0.187*	- 0.293**	- 0.256**
Glab	0.211*	0.337**	0.107	0.023	0.731**	- 0.542**	- 0.338**	- 0.355**
Ind	0.115	0.274	0.484**	0.124	-0.128	0.240	- 0.767**	- 0.132
Jap	0.138	0.034	0.192	- 0.085	0.065	- 0.159	- 0.338**	- 0.317*
Glab_Upper Coast	0.272*	0.290**	0.220	0.130	0.728**	- 0.427**	- 0.332**	- 0.335*
Glab_Lower Coast	0.189	0.152	0.338	0.099	0.525	- 0.319	- 0.708**	- 0.362
Ind_Gc	0.119	0.123	0.463*	- 0.145	-0.488	- 0.328	- 0.850**	- 0.227
Ind_Gh	0.073	0.450*	0.600**	0.485*	0.868	0.511	- 0.664**	0.040
Jap_GbGh	0.058	-0.139	0.335*	0.091	0.087	- 0.136	- 0.450**	- 0.319
Jap_SL	0.289	0.323	-0.142	- 0.353	0.465	- 0.379	- 0.313	- 0.479

***Table 20**: Pearson correlations between yield components and number of tillers*

Cluster	Days to 50% flowering	Plant height (cm)	Panicle length (cm)	Number of panicles	Panicle weight (g)	200 grain weight (g)	Plot yield (kg/ha)	Canopy cover A (%)
All	- 0.018	- 0.206**	0.182**	0.800**	- 0.562**	0.147	- 0.125	0.165*
Glab	0.111	- 0.384**	0.107	0.815**	0.025	0.145	- 0.328**	- 0.130
Ind	0.413**	- 0.495**	0.484**	0.677**	- 0.361	0.089	- 0.573**	- 0.314
Jap	- 0.432**	0.093	0.192	0.518**	- 0.018	0.564**	0.239	0.604**
Glab_Upper Coast	0.043	- 0.191	0.220	0.768**	0.232	-0.137	- 0.272*	- 0.087
Glab_Lower Coast	0.193	- 0.550**	0.338	0.857**	0.296	-0.389	- 0.446*	- 0.512*
Ind_Gc	0.497*	- 0.583**	0.463*	0.895**	- 0.527	-0.488	- 0.616*	- 0.532
Ind_Gh	0.370	- 0.520**	0.600**	0.525*	- 0.110	0.211	- 0.594**	- 0.170
Jap_GbGh	- 0.274	0.061	0.335*	0.301	- 0.357	0.394*	0.042	0.608**
Jap_SL	- 0.619**	0.300	- 0.142	0.420	0.446	0.705**	0.236	0.784**

***Table 21**: Pearson correlations between yield components and number of panicles*

Cluster	Days to 50% flowering	Plant height (cm)	Panicle length (cm)	Number of tillers	Panicle weight (g)	200 grain weight (g)	Plot yield (kg/ha)	Canopy cover A (%)
All	0.045	-0.168*	0.120	0.800**	.[a]	0.282*	0.150	0.122
Glab	0.304*	- 0.530**	0.023	0.815**	.[a]	0.083	- 0.453**	- 0.280
Ind	0.355	- 0.113	0.124	0.677**	.[a]	0.638*	- 0.201	0.137
Jap	- 0.029	- 0.017	- 0.085	0.518**	.[a]	0.207	0.474**	- 0.009
Glab_Lower Coast	0.099	- 0.677**	0.099	0.857**	.[a]	0.159	- 0.824**	- 0.521
Glab_Upper Coast	0.385**	- 0.408**	0.130	0.768**	.[a]	-0.335	- 0.281	- 0.228
Ind_Gc	0.589*	- 0.673*	- 0.145	0.895**	.[a]	-0.002	- 0.677	0.478
Ind_Gh	0.262	0.143	0.485*	0.525*	.[a]	0.707	- 0.022	0.314
Jap_GbGh	0.459*	- 0.134	0.091	0.301	.[a]	-0.116	0.038	0.076
Jap_SL	- 0.449	0.254	- 0.353	0.420	.[a]	0.321	0.717**	- 0.034

[a]: non estimated

***Table 22**: Pearson correlations between yield components and panicle weight (g)*

Cluster	Days to 50% flowering	Plant height (cm)	Panicle length (cm)	Number of tillers	Number of panicles	200 grain weight (g)	Plot yield (kg/ha)	Canopy cover A (%)
All	0.101	0.179	0.102	-0.562**	.[a]	0.231*	0.228*	- 0.225*
Glab	0.464**	- 0.067	0.731**	0.025	.[a]	- 0.625**	0.109	- 0.417**
Ind	- 0.306	0.580*	- 0.128	-0.361	.[a]	0.716**	0.701**	0.503
Jap	- 0.237	0.442*	0.065	-0.018	.[a]	0.379*	0.563**	0.251
Glab_Upper Coast	0.641**	- 0.098	0.728**	0.232	.[a]	- 0.553**	0.243	- 0.268
Glab_Lower Coast	0.245	- 0.788**	0.525	0.296	.[a]	- 0.299	- 0.347	- 0.551
Ind_Gc	- 0.416	0.670	- 0.488	- 0.527	.[a]	0.778*	0.755*	0.623
Ind_Gh	- 0.221	0.674	0.868	- 0.110	.[a]	0.617	0.702	0.574
Jap_GbGh	- 0.054	0.229	0.087	- 0.357	.[a]	0.563**	0.382	- 0.046
Jap_SL	- 0.611	0.727*	0.465	0.446	.[a]	0.320	0.824**	0.674*

[a]: non estimated

***Table 23**: Pearson correlations between yield components and 200 grain weight (g)*

Cluster	Days to 50% flowering	Plant height (cm)	Panicle length (cm)	Number of tillers	Number of panicles	Panicle weight (g)	Plot yield ($kg.ha^{-1}$)	Canopy cover A (%)
All	- 0.581**	0.301**	- 0.187*	0.147	0.282*	0.231*	0.369**	0.568**
Glab	- 0.515**	0.051	- 0.542**	0.145	0.083	- 0.625**	0.218	0.596**
Ind	- 0.839**	0.631**	0.240	0.089	0.638*	0.716**	0.809**	0.581**
Jap	- 0.716**	0.348**	- 0.159	0.564**	0.207	0.379*	0.621**	0.692**
Glab_Upper Coast	- 0.705**	0.438**	- 0.427**	- 0.137	- 0.335	- 0.553**	0.223	0.725**
Glab_Lower Coast	- 0.714**	0.359	- 0.319	- 0.389	0.159	- 0.299	0.766**	0.499*
Ind_Gc	- 0.878**	0.615*	- 0.328	- 0.488	- 0.002	0.778*	0.902**	0.834**
Ind_Gh	- 0.862**	0.682*	0.511	0.211	0.707	0.617	0.861*	0.612*
Jap_GbGh	- 0.685**	0.359*	- 0.136	0.394*	- 0.116	0.563**	0.600**	0.708**
Jap_SL	- 0.702**	0.368	- 0.379	0.705**	0.321	0.320	0.599*	0.628*

***Table 24**: Pearson correlations between yield components and plot yield (kg/ha)*

Cluster	Days to 50% flowering	Plant height (cm)	Panicle length (cm)	Number of tillers	Number of panicles	Panicle weight (g)	200 grain weight (g)	Canopy cover A (%)
All	- 0.298**	0.346**	- 0.293**	- 0.125	0.150	0.228*	0.369**	0.478**
Glab	0.080	0.168	- 0.338**	- 0.328**	- 0.453**	0.109	0.218	0.450**
Ind	- 0.316	0.392*	- 0.767**	- 0.573**	- 0.201	0.701**	0.809**	0.483*
Jap	- 0.511**	0.420**	- 0.338**	0.239	0.474**	0.563**	0.621**	0.706**
Glab_Upper Coast	0.266*	0.181	- 0.332**	- 0.272*	- 0.281	0.243	0.223	0.476**
Glab_Lower Coast	- 0.428*	0.020	- 0.708**	- 0.446*	- 0.824**	- 0.347	0.766**	0.451
Ind_Gc	- 0.403	0.228	- 0.850**	- 0.616*	- 0.677	0.755*	0.902**	0.857**
Ind_Gh	- 0.273	0.393	- 0.664**	- 0.594**	- 0.022	0.702	0.861*	0.137
Jap_GbGh	- 0.559**	0.482**	- 0.450**	0.042	0.038	0.382	0.600**	0.848**
Jap_SL	- 0.342	0.452*	- 0.313	0.236	0.717**	0.824**	0.599*	0.497

***Table 25**: Pearson correlations between yield components and canopy cover A (%)*

Cluster	Days to 50% flowering	Plant height (cm)	Panicle length (cm)	Number of tillers	Number of panicles	Panicle weight (g)	200 grain weight (g)	Plot yield (kg/ha)
All	- 0.661**	0.596**	- 0.256**	0.165*	0.122	- 0.225*	0.568**	0.478**
Glab	- 0.538**	0.671**	- 0.355**	- 0.130	- 0.280	-0.417**	0.596**	0.450**
Ind	- 0.855**	0.555**	- 0.132	- 0.314	0.137	0.503	0.581**	0.483*
Jap	- 0.880**	0.621**	- 0.317*	0.604**	- 0.009	0.251	0.692**	0.706**
Glab_Lower Coast	- 0.668**	0.796**	- 0.362	- 0.512*	- 0.521	- 0.551	0.499*	0.451
Glab_Upper Coast	- 0.482**	0.826**	- 0.335*	- 0.087	- 0.228	- 0.268	0.725**	0.476**
Ind_Gc	- 0.854**	0.784**	- 0.227	- 0.532	0.478	0.623	0.834**	0.857**
Ind_Gh	- 0.873**	0.485	0.040	- 0.170	0.314	0.574	0.612*	0.137
Jap_GbGh	- 0.896**	0.635**	- 0.319	0.608**	0.076	- 0.046	0.708**	0.848**
Jap_SL	- 0.877**	0.640**	- 0.479	0.784**	- 0.034	0.674*	0.628*	0.497

Acknowledgements

The authors would like to acknowledge the contributions of all those involved in the research, in particular the staff of the research stations and universities in the countries involved, the farmers in the different countries and the research assistants at the different trial sites.

Author contributions

Supervised the research: EN HM PR PCS. Conceived and designed the experiments: AM EN FO BT HM PR PCS. Performed the experiments: AM EN FO BT. Analysed the data: AM EN FO BT. Contributed reagents/materials/analysis tools: AM EN FO BT. Wrote the paper: AM EN FO BT HM PR PCS.

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CHAPTER SIX

Processes Underpinning Development and Maintenance of Diversity in Rice in West Africa: Evidence from Combining Morphological and Molecular Markers

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Published as: Mokuwa A, Nuijten E, Okry F, Teeken B, Maat H, Richards P, Struik PC (2014) Processes Underpinning Development and Maintenance of Diversity in Rice in West Africa: Evidence from Combining Morphological and Molecular Markers. PLoS ONE 9(1): e85953. doi:10.1371/journal.pone.0085953

Abstract

We assessed the interplay of artificial and natural selection in rice adaptation in low-input farming systems in West Africa. Using 20 morphological traits and 176 molecular markers, 182 farmer varieties of rice (*Oryza* spp.) from 6 West African countries were characterised. Principal component analysis showed that the four botanical groups (*Oryza sativa* ssp. *indica*, *O. sativa* ssp. *japonica*, *O. glaberrima*, and interspecific farmer hybrids) exhibited different patterns of morphological diversity. Regarding *O. glaberrima*, morphological and molecular data were in greater conformity than for the other botanical groups. A clear difference in morphological features was observed between *O. glaberrima* rices from the Togo hills and those from the Upper Guinea Coast, and among *O. glaberrima* rices from the Upper Guinea Coast. For the other three groups such clear patterns were not observed. We argue that this is because genetic diversity is shaped by different environmental and socio-cultural selection pressures. For *O. glaberrima*, recent socio-cultural selection pressures seemed to restrict genetic diversity while this was not observed for the other botanical groups. We also show that *O. glaberrima* still plays an important role in the selection practices of farmers and resulting variety development pathways. This is particularly apparent in the case of interspecific farmer hybrids where a relationship was found between pericarp colour, panicle attitude and genetic diversity. Farmer varieties are the product of long and complex trajectories of selection governed by local human agency. In effect, rice varieties have emerged that are adapted to West African farming conditions through genotype × environment × society interactions. The diversity farmers maintain in their rice varieties is understood to be part of a risk-spreading strategy that also facilitates successful and often serendipitous variety innovations. We advocate, therefore, that farmers and farmer varieties should be more effectively involved in crop development.

Key words: adaptation, farmer varieties, genetic diversity, morphological characterisation, *Oryza*, rice, seed systems

Introduction

West African farmers have cultivated two species of rice *Oryza sativa* (Asian rice) and *Oryza glaberrima* (African rice) for several centuries. Over much of the West African coastal zone, resource-poor farmers cultivate the two species as rainfed varieties in a range of ecologies, from lowland to upland. According to one view, Asian rice was introduced into coastal West Africa by Portuguese traders in the 16th century [1]. Another view is that it may have arrived earlier (perhaps around the beginning of the Common Era) via trans-Saharan trade routes and trade links between East Africa and India [2]. African rice (*O. glaberrima*) is thought to have been first domesticated in the swampy basins of the upper Niger River delta 3000-4000 years ago [3, 4]. Since its introduction into West Africa, Asian rice has tended to replace African rice, particularly in wetland cultivation. From the late 18th century onwards a second wave of introductions occurred from Asia and America, including both *O. sativa* ssp. *indica* and *O. sativa* ssp. *japonica*. This boosted the rate at which *O. sativa* replaced *O. glaberrima* [3], now including in dryland rice farming conditions. This accelerated replacement, alongside the enduring cultivation of *O. glaberrima* in certain pockets, is often explained as resulting from local variations in socio-cultural, political, ecological and geographical factors influencing farmers and their work [5-9]. *O. glaberrima* is widely believed to be well adapted to low-input farming conditions [10].

Oryza glaberrima has never been improved by agronomists or plant breeders. Professional opinion has been that the species has little to offer and that yields are invariably low. More recently, *O. glaberrima* has been seen as a useful genetic resource to improve *O. sativa* varieties [11, 12]. The two rice species are genetically isolated from each other by an F1 sterility barrier [13-17, amongst others], although gene exchange can occur in the field [15, 17-21]. Recent research confirms that varieties with an interspecific background, resulting from introgressions, are regularly to be found in farmer fields along the Upper Guinea Coast from The Gambia down to Sierra Leone [22, 23]. Because backcrossing to either parent (to produces fertile progeny) results in parental phenotypical resemblance, it is difficult to detect hybrid derivatives; they look like either *sativa* or *glaberrima* [17, 23]. This means that four botanical clusters can be identified as co-existing in West Africa: these are *O. sativa* ssp. *indica*, *O. sativa* ssp. *japonica*, *O. glaberrima* and interspecific farmer varieties [23].

A recurrent idea in the literature is that although farmer varieties look very diverse morphologically, they are actually genetically rather uniform at gene pool level because of continuous selection on qualitative traits in the same gene pool [24] and because most farmer varieties are the result of recombination of existing farmer varieties [25]. A common, different view is that farmer varieties are made up of different genotypes, making them genetically quite diverse. Both views do not seem to apply to rice in West Africa. The first idea is countered by a study conducted by Nuijten *et al*. [23], and the second view may apply to other crops, but not to rice [6]. In West Africa the coexistence of Asian and African rice has resulted in an enlarged gene pool and the development of interspecific farmer varieties [23, 26, 27]. The main underlying factors are farmer selection and gene flow through cross pollination and seed exchange [6]. From seemingly isolated hamlets seed can travel long distances, through informal seeds networks, mostly based on extended family ties, and can diffuse across countries [7, 28]. These processes of seed diffusion have been traced over several centuries [29]. The time-depth and durability of this process prepares us to understand the finding that farmer varieties can embody greater levels of genetic diversity than formal varieties [30], challenging an assumption often made by plant breeders that the reverse is true on account of the access enjoyed by breeders to a world-wide spectrum of genetic resources [31]. The existence of farmer varieties with an interspecific background clearly shows that farmer crop development has more potential value as a complement to scientific breeding than is often assumed [23]. The value of these activities, by farmers in West African conditions, is further reinforced by recent research showing that farmer rice varieties can be adapted to a wide range of agro-ecological conditions [10].

Country-specific studies have been conducted to unravel the genetic variability of rice in West Africa (e.g. for Sierra Leone, Guinea and The Gambia, see [22, 30, 32, 33]). Nuijten *et al*. [23] then offered a regional perspective by analysing a large set of farmer varieties collected from seven countries across coastal West Africa, using molecular markers. To obtain a more complete understanding of the processes underlying the development and maintenance of genetic diversity, the present study now combines molecular and morphological characterisation with socio-economic information concerning four botanical groups of rice from six West African countries. The aim is to explain how farmer practices have combined with environmental pressures to shape rice diversity in the case study countries. Reference to historical and socio-cultural data is made in order to better understand region-specific morphological traits.

Analysis directs attention to underlying processes regulating the development of genetic diversity in crops in low-input farming systems - processes not yet well understood. An important issue is to grasp the scope of the interplay of artificial and natural selection in crop adaptation. Our findings suggest (Figure 1) that there are multiple pathways for natural and artificial (farmer) selection to influence molecular and morphological markers. Correlations between morphological and molecular data may also vary among the botanical groups because of differences in genetic background, robustness and differential response to human or environmental selection pressures.

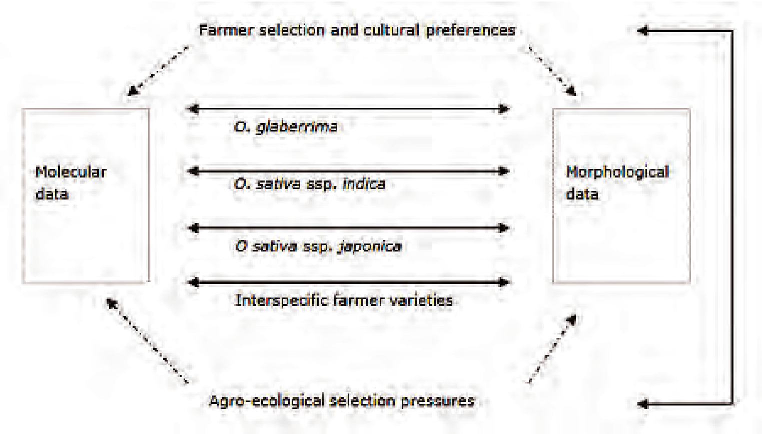

Figure 1*: Schematic representation of the main aspects of our research and their interlinkages.*

Our analysis confirms that rice varieties in West Africa are adapted to their conditions as a result of genotype × environment × society interactions. The rice diversity farmers appeared to maintain is probably part of a risk-spreading strategy that facilitates innovations in variety development.

Materials and Methods

Ethics statement

We confirm that no specific permit was required for using the location where the field trial was conducted. The location was not protected in any way. The field study never involved endangered or protected species. Approval for the collection of socio-economic data using in-depth interviews and questionnaires was obtained from the Social Sciences Ethical Committee (SSEC) of Wageningen University. The research was carried out by researchers living in the country for at least several years and approved by village elders and farmer communities. Individual participants provided their verbal informed consent to participate in the interviews as part of the interview protocol. Written consent was not possible as most of the interviewees were illiterate. The SSEC approved this consent procedure. We thank the village elders, farmers and the land holding family at Fala Junction Kowa Chiefdom, Sierra Leone.

Variety collection and molecular analysis

Variety collection was carried out from June to December 2007 in seven countries of Coastal West Africa: The Gambia, Ghana, Guinea, Guinea Bissau, Senegal, Sierra Leone and Togo (Figure 2). The purpose was to collect varieties of *O. glaberrima* and *O. sativa* cultivated by farmers in regions where *O. glaberrima* was known to be cultivated. In each country varieties were collected in a number of case study villages. In exceptional cases, varieties in other villages were collected if they had a clear relationship to the main case study villages, if there was an important 'story' related to them, or if they were morphologically intermediate between *O. sativa* and *O. glaberrima*. At harvest time a total of 231 accessions were collected. In February and March 2008 these accessions were analysed molecularly using AFLP markers. In the research by Nuijten *et al*. [23] these data were then added to the 84 accessions analysed by Nuijten and Van Treuren [30]. With the software package 'Structure' (version 2.2), materials with a probability equal to or higher than 91% were assigned to four clusters (*glaberrima*, *indica*, *japonica* and farmer hybrids (see Table 1). Materials assigned with a value lower than p = 0.91 were considered outliers. Farmer hybrids are farmer varieties of interspecific origin [23].

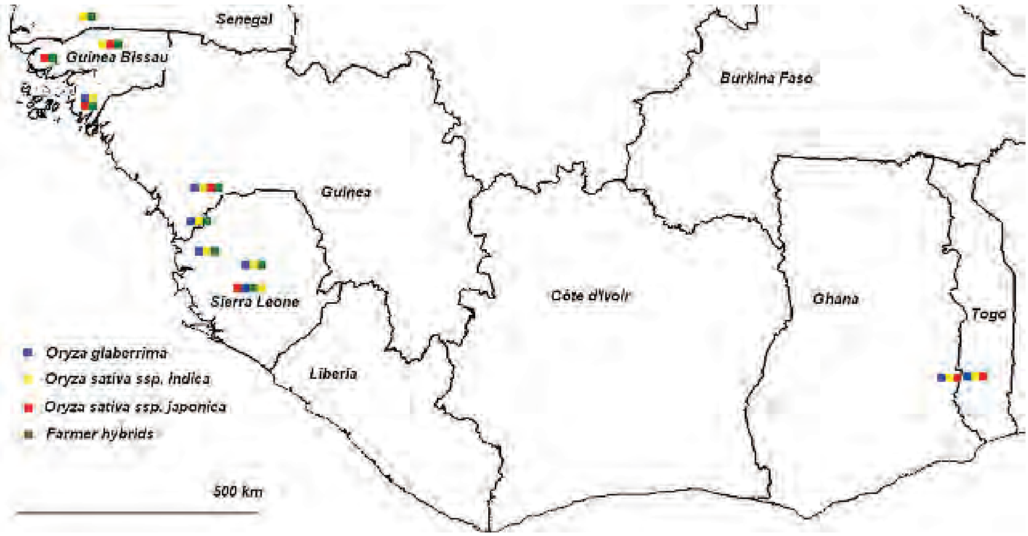

Figure 2*: Case study areas are indicated by colours representing the most commonly cultivated botanical groups in those areas.*

Choice and types of farmer varieties

In this paper we consider only the materials that were assigned with a probability equal to or larger than 91% to the botanical groups *O. glaberrima*, *O. sativa* ssp. *japonica*, *O. sativa* ssp. *indica* and the farmer interspecific hybrids (Cluster 4). The focus of this study was on upland varieties. Apart from pure upland varieties also varieties from the upper part of the lowland-upland continuum were included. Typical lowland varieties were left out.

In addition, the number of materials collected from The Gambia in 2007 was too limited for a meaningful comparison and were left out. Because for some materials not enough seeds were available for the morphological analysis, we worked with a total of 182 varieties.

***Table 1**: Number of materials used in the molecular and morphological analysis according to their botanical group and their areas of collection.*

Botanical group	Senegal (Casamance)	Guinea Bissau	Guinea (Kindia and Forecariah)	Sierra Leone (Central-N/West)	Ghana (Togo Hills, Volta region)	Togo (Togo Hills, Danyi plateau)	Total
O. glaberrima	3	4	19	6	8	9	49
O. sativa ssp. *indica*	7	4	13	5	15	2	46
O. sativa ssp. *japonica*	0	18	2	28	5	3	56
Farmer hybrids*	7	10	2	12	0	0	31
Total	17	36	36	51	28	14	182

*Interspecific farmer varieties with a combined background of *O. glaberrima* and *O. sativa*

Trial set-up

Field evaluations were carried out in Sierra Leone from June to December 2008. The trial was set up under upland rain-fed conditions at Fala Junction, Kowa Chiefdom (8.14917 N, 11.90806 E, 58 m asl), in Moyamba District. The period of field evaluation corresponded to the cropping season. The average annual rainfall is between 2100-3000 mm and the rainy season lasts for 6 to 7 months. The selected site was flat. The soil was cleared and deeply plowed after 24 years of bush fallow. The soil was silt loam (Mende: *tumui*).

The seeds of each accession were sown in a randomised block design. Each plot was 1.5 m × 2.1 m and contained 70 pockets, spaced 30 cm between rows and 15 cm within rows. Three grains were sown in each pocket and pockets were thinned to one plant within four weeks after sowing. Sowing date was determined by following the farmer practices in the region. Excellent germination and growth were observed with low to moderate pest (rodent, termites, cut worms, stem borers) incidences, mostly with *O. sativa* ssp. *japonica* varieties. Traditional fencing and mesh wire were used to prevent damage by rodents. No fertiliser was applied.

Measurements

A total of 20 traits were measured (Table 2). Most traits were measured in all four replications, except a few qualitative traits which were measured only on the first replication, as these traits were not influenced by microenvironment. Measurements were done on five plants chosen randomly in each plot excluding the border rows. The accessions were characterised according to the descriptor list by Bioversity International (2007) [34] with the exception of rattooning potential.

***Table 2**: The 20 traits measured on the rice genotypes in a field trial in Sierra Leone in 2008. Ratings were based on five at randomly chosen plants per plot.*

Characteristic	Description and scale or unit	Type of determination	Stage of measurement
Agronomic traits			
Culm length	Average length, from ground level to the base of the panicle, in cm	Numerical	Physiological maturity
Plant height	Average height, from soil surface up to the tip of the tallest panicle, in cm	Numerical	Physiological maturity
Leaf length	Average length of peninsulate leaf (leaf below flag leaf), from collar to tip of leaf, in cm	Numerical	Physiological maturity
Leaf width	Average width of peninsulate leaf (leaf below flag leaf), widest portion of the leaf, in cm	Numerical	Physiological maturity
Panicle length	Average length, of main panicle, from panicle base to tip, in cm,	Numerical	Physiological maturity
Panicle number	Average number of panicles per plant	Numerical	Physiological maturity
Number of tillers	Average number of tiller(s) per plant	Numerical	Physiological maturity
Rattoon potential	Assessed after harvests: 0 = None; 1 = Low; 3 = Medium; 5 = Vigorous; 7 = Very vigorous	Scale.	After harvest
Grain length	Average length of grain length, from base of lowermost sterile lemma to tip of fertile lemma or palea, in mm.	Numerical	Post-harvest
Grain width	Average width, measured at the widest portion, in mm.	Numerical	Post-harvest
100-grain weight	Average weight of 100 filled seeds at 13% moisture content.	Numerical	Post-harvest
Botanical traits			
Leaf blade colour	0 = No green visible due to anthocyanin; 3 = Light green; 5 = Medium green; 7 = Dark green	Visual assessment	Physiological maturity
Leaf blade pubescence	1 = Glabrous (smooth); 2 = Intermediate; 3 = Pubescent	Ocular inspection and then fingertip rub to class hairiness	Physiological maturity
Ligule length	Average length, on peninsulate leaf of main stem, from the base of the collar to the tip, in mm	Numerical	Physiological maturity
Ligule shape	0 = Absent; 1 = Truncate; 2 = Acute to acuminate; 3 = 2-cleft	Visual assessment	Physiological maturity
Panicle attitude of main axis (PAMA)	1 = Upright; 2 = Semi-upright; 3 = Slightly drooping; 4 = Strongly drooping	Visual assessment of the main axis of the panicle	Physiological maturity
Panicle attitude of primary branches (PAB)	1 = Erect (compact panicle); 3 = Semi erect, semi-compact panicle; 5 = Spreading (open panicle); 7 = Horizontal; 9 = Drooping	Visual assessment	Physiological maturity
Awn length	0 = None (awn less); 1 = Very short (<5 mm); 3 = Short (~8 mm); 5 = Intermediate (~15 mm); 7 = Long (~30 mm); 9 = Very long (>40 mm)	The awn was measured from base to the tip, then translated in scales	Post-harvest
Husk (lemma and palea) colour	1 = White; 2 = Straw; 3 = Gold and gold furrows; 4 = Brown (tawny); 5 = Brown spots; 6 = Brown furrows; 7 = Purple; 8 = Reddish to light purple; 9 = Purple spots; 10 = Purple furrows; 11 = Black	Visual assessment	Post-harvest
Seed coat colour / pericarp colour	1= White; 2 = Light brown; 3 = Speckled brown; 4 = Brown; 5 = Red; 6 = Variable purple; 7 = Purple	Visual assessment	Post-harvest

Socio-economic data collection

Besides the collection of farmer accessions, socio-economic data were collected on all 182 varieties using in-depth interviews and questionnaires which mainly covered (i) household data, (ii) number of varieties grown, (iii) ecology of cultivation, (iv) the area under cultivation, (v) farmer reasons for growing the variety, (vi) seed source, (vii) on-farm seed management practices from harvest to sowing and farmer knowledge related to variety use.

Data analysis

Principal component analysis (PCA) was used to describe the morphological data measured through a reduced number of variables shown in biplot as vectors. The genetic implications can be assessed from the eigenvalues ascribed to the different traits [35]. The values of the principal components per genotype correspond to a combination of traits explaining the variability. The closer the distance between genotypes in the biplots with the different principal components the closer the genotypes are related with respect to the traits represented by the principal components. PCA was conducted using SPSS/ PASW Statistics 18.

The morphological data were also analysed with the software Splitstree [36]. The measured data were translated into dummy variables. For the data with ordinal scales: for each value a column was created. For the numerical data, the number of categories was determined based on the difference between the maximum and minimum value divided by the standard deviation. The width of a category was determined by dividing the range by the number of categories multiplied with the factor 1.5. These data and the molecular data were analysed with the software Splitstree using the same method followed by Nuijten *et al*. [23].

Results and Discussion

Rice diversity in West Africa at the molecular level

Figure 3 illustrates the phylogenetic relationships of materials studied in the field trial, as assessed during molecular analysis [cf. 23]. Four clusters are shown in detail. Three of these clusters correspond to the botanical groups *O. glaberrima*, *O. sativa* ssp. *japonica* and *O. sativa* ssp. *indica*. In between *O. glaberrima* and *O. sativa* ssp. *indica* is situated the group of interspecific farmer varieties sharing the genetic background of both *O. glaberrima* and *O. sativa* (see [23], hereafter referred to as Cluster 4).

The genotypes comprising each cluster also tend to separate in sub-clusters (Figure 3). The genotypes of the *O. glaberrima* cluster split into *O. glaberrima* from the lower Guinea Coast and *O. glaberrima* from the upper Guinea Coast. The *indica* group splits into several sub-clusters in a complex way. Some sub-clusters only consist of genotypes from one country (*indica* from Ghana), while other sub-clusters are constituted by materials from different countries. The *japonica* cluster splits into one sub-cluster with *japonica* mainly from Sierra Leone and a sub-cluster with *japonica* mainly from Ghana and Guinea Bissau. The cluster of the farmer hybrids splits into one sub-cluster with genotypes that display erect and semi-erect panicles and a second sub-cluster with droopy panicles. Genotypes of the first sub-cluster (Cluster 4-1) were found in Sierra Leone, Guinea and Guinea Bissau while genotypes of the second sub-cluster were found in Guinea Bissau and Senegal (Cluster 4-2). The following sections explore the morphological diversity of the respective sub-clusters to see how they are related to the observations at molecular level and farming system level. Various historical and contextual explanations for these clusterings are discussed in Nuijten *et al*. [23] and Mouser *et al*. [29]. For example, the Ghana-Guinea Bissau *japonica* cluster could be interpreted as indicating a pathway of rice introduction from the East Indies via the important and long-established Portuguese coastal trading stations at Elmina (Ghana) and Cacheu (Guinea Bissau).

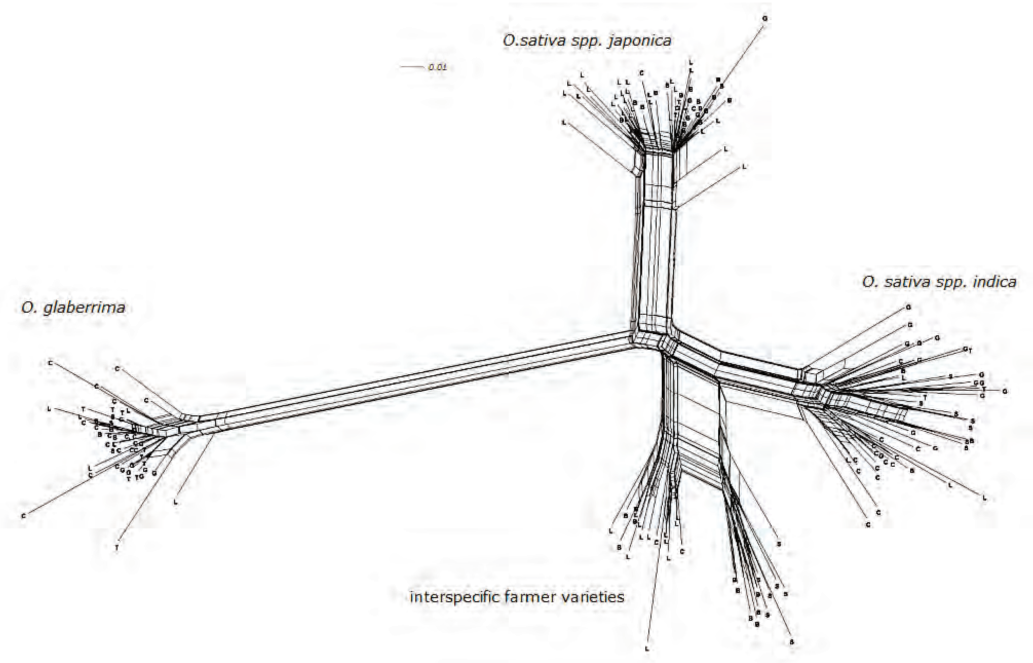

Figure 3*: Phylogenetic relationships based on molecular markers of the 182 materials included in the morphological analysis. Country of collection is indicated by letters: B = Guinea Bissau, C = Guinea Conakry, G = Ghana, L = Sierra Leone, S = Senegal, T = Togo.*

Morphological diversity

Out of 17 principal components (PCs), the first four accounted for 73.57% of the variance among the traits studied (Table 3). The fifth component was not used in the biplots (Figures 4, 5, 6, 7, 8, and 9) because it had very little explanatory value for most traits. Table 4 presents the rotated principal components matrix and shows how traits contributed to the PCs. Traits commonly used to distinguish *O. glaberrima* from *O. sativa* contributed most to PC 1: ligule shape and length, panicle attitude of main axis (PAMA), and leaf blade pubescence. Traits that contributed most to PC 2 were leaf width, seed width, number of tillers and number of panicles. Traits that contributed most to PC 3 were culm length, plant height, panicle length and leaf length. Seed length contributed clearly to PC 4. Tables 5 and 6 show average values, standard deviations and coefficients of variation for 10 agronomic traits, by botanical groups and sub-groups.

***Table 3**: Initial eigenvalues and rotation sums of squared loadings of 17 principal components based on 17 morphological traits measured on 182 rice accessions.*

Principal	Initial eigenvalues			Rotation sums of squared loadings		
Component	Total	% of variance	Cumulative %	Total	% of variance	Cumulative %
1	5.98	35.17	35.17	5.51	32.38	32.38
2	3.13	18.38	53.55	2.98	17.51	49.90
3	2.20	12.94	66.49	2.65	15.57	65.47
4	1.20	7.08	73.57	1.29	7.58	73.04
5	1.00	5.90	79.47	1.09	6.43	79.47
6	0.88	5.16	84.63			
7	0.64	3.79	88.42			
8	0.58	3.42	91.84			
9	0.36	2.09	93.93			
10	0.29	1.70	95.63			
11	0.23	1.38	97.01			
12	0.21	1.22	98.23			
13	0.12	0.71	98.94			
14	0.08	0.47	99.41			
15	0.06	0.34	99.76			
16	0.04	0.24	100.00			
17	0.00	0.00	100.00			

Extraction Method: Principal Component Analysis.

***Table 4**: Rotated Principal Components (PCs) of 17 morphological rice traits.*

Trait	Components				
	1	2	3	4	5
Leaf blade colour	0.65	0.50	-0.04	-0.10	-0.05
Leaf blade pubescence	0.90	0.02	0.01	-0.16	0.07
Culm length	-0.09	0.05	0.88	-0.15	0.24
Plant height	-0.09	0.02	0.95	-0.10	0.12
Panicle length	-0.04	-0.09	0.70	0.17	-0.40
Leaf length	0.25	0.37	0.60	0.14	0.20
Leaf width	-0.37	0.80	0.25	0.05	0.12
Ligule length	0.90	-0.22	0.05	-0.02	-0.01
Ligule shape	0.97	0.07	-0.07	-0.00	0.02
# tillers / plant	-0.42	-0.79	-0.05	-0.07	0.11
# panicles / plant	-0.44	-0.79	-0.00	-0.08	0.07
Panicle attitude of main axis (PAMA)	0.88	0.16	-0.09	0.28	-0.07
Panicle attitude of branches (PAB)	0.77	0.28	-0.07	0.17	-0.04
Seed length	0.10	-0.07	-0.05	0.93	0.09
Seed width	-0.05	0.71	-0.05	-0.36	0.19
Collar colour	0.05	0.03	0.17	0.09	0.81
Rattoon potential	0.74	0.15	0.08	0.23	0.27

* Extraction Method: Principal Component Analysis; Rotation Method: Varimax with Kaiser Normalization.

Comparison between botanical groups

Figures 4, 5, 6, 7, 8, and 9 represent the morphological diversity using different combinations of PC 1, 2, 3 and 4. The graphical representation of genotypes using PC 1 and 2 (53.6%) shows two clouds of genotypes (Figure 4), separating *glaberrima* distinctly from the other three groups. *O. glaberrima* has a rounded and short ligule, erect panicle, erect primary branches, generally displays little leaf blade pubescence and tends to have a rather light leaf blade colour. This separation agrees with separations achieved through the molecular analysis.

By contrast, the three other botanical groups are not as clearly separated as they are in the molecular analysis. The clusters *japonica,* and *indica* form two connected clouds distributed along PC 2. The japonicas produce fewer tillers and panicles, and wider leaves and seed compared to the indicas. The farmer hybrids overlap mostly with the indicas. The molecular analysis also suggested that farmer hybrids are more closely related to indicas than to japonicas (see Figure 3). Most of the farmer hybrids that are clearly separate from the indicas belong to Sub-cluster 4-1 (Sierra Leone and Guinea Bissau) and only a few to Sub-cluster 4-2 (Guinea Bissau).

The combination of PC 1 and 3 (Figure 5) shows a larger overlap between japonicas, indicas and the farmer hybrids along the third component while the *glaberrima* cluster is pulled apart along the third component. The genotypes of *glaberrima* studied here are thus highly differentiated from each other on traits represented by PC 3 (plant height, culm length, panicle length and leaf length). The genotypes from Togo and Ghana tend to sit toward the lower part of the cloud and those from Guinea and Sierra Leone sit in the upper part.

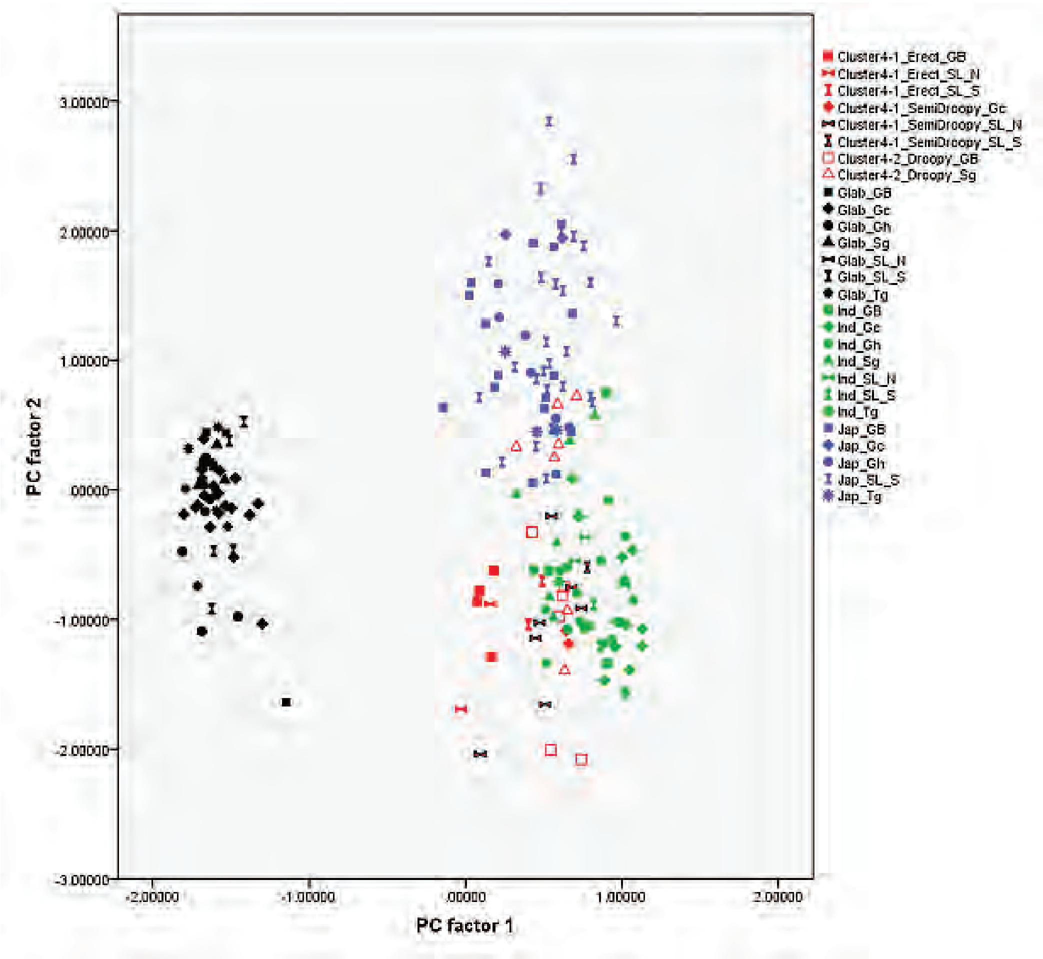

Figure 4*: Graphical repartition of materials based on morphological data of PC 1 and 2.*
Component 1*: Ligule shape (0.97)*, Leaf blade pubescence (0.90), Ligule length (0.90), PAMA** (0.88), PAB*** (0.77), Rattoon potential (0.74), Leaf blade colour (0.65)*
Component 2*: Leaf width (0.80), # tillers per plant (-0.79), # panicles per plant (-0.79), Seed width (0.71), Leaf blade colour (0.50) Glab: glaberrima, Ind: indica, Jap: japonica, Clusters 4-1 and 4-2: farmer hybrids, GB: Guinea Bissau, SL: Sierra Leone (north: N south: S), Gc: Guinea Conakry, Sg: Senegal, Gh: Ghana, Tg: Togo.*
**(): value of the correlation of the trait with the component*
***: Panicle Attitude of Main Axis*
****: Panicle Attitude of Branches*

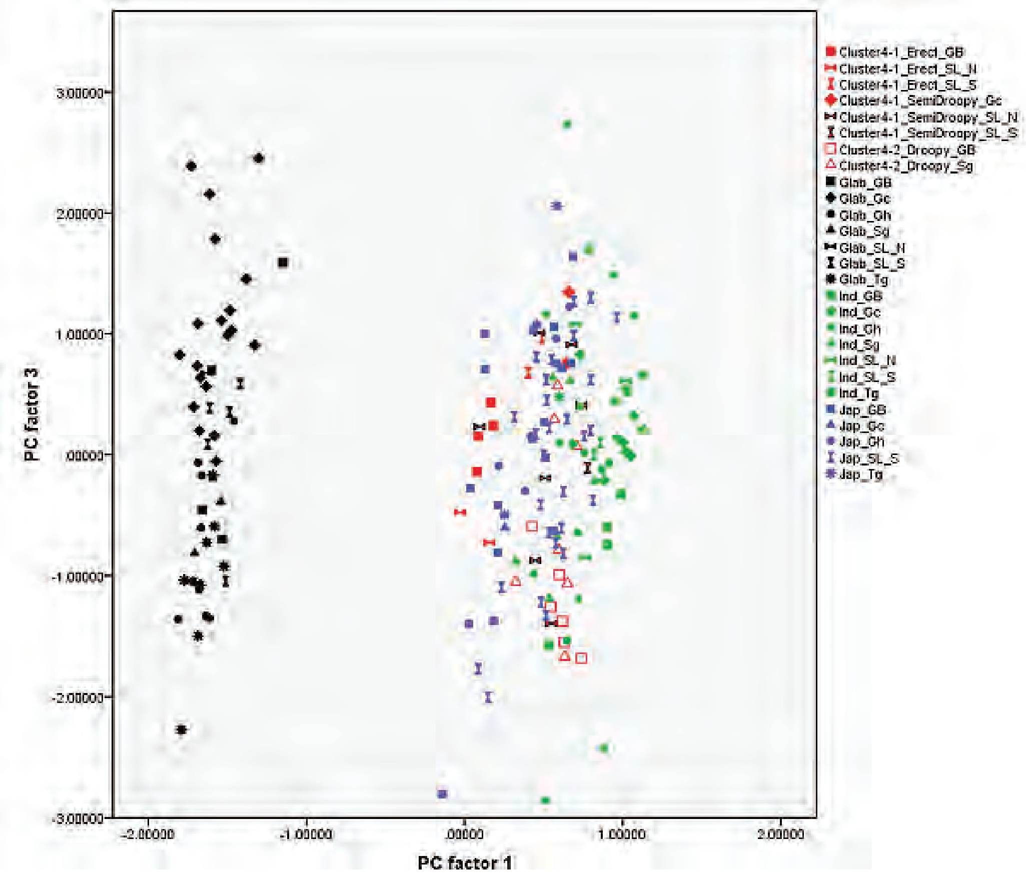

Figure 5: *Graphical repartition of materials based on morphological data of PC 1 and 3*
Component 1: *Ligule Shape (0.97)*, Leaf blade pubescence (0.90), Ligule length (0.90), PAMA** (0.88), PAB*** (0.77), Rattoon potential (0.74), Leaf blade colour (0.65)*
Component 3: *Plant height (0.95), Culm length (0.88), Panicle length (0.70), Leaf length (0.60)*
GB: Guinea Bissau, SL: Sierra Leone (north: N south: S), Gc: Guinea Conakry, Sg: Senegal, Gh: Ghana, Tg: Togo.
**(): value of the correlation of the trait with the component*
***: Panicle Attitude of Main Axis*
****: Panicle Attitude of Branches*

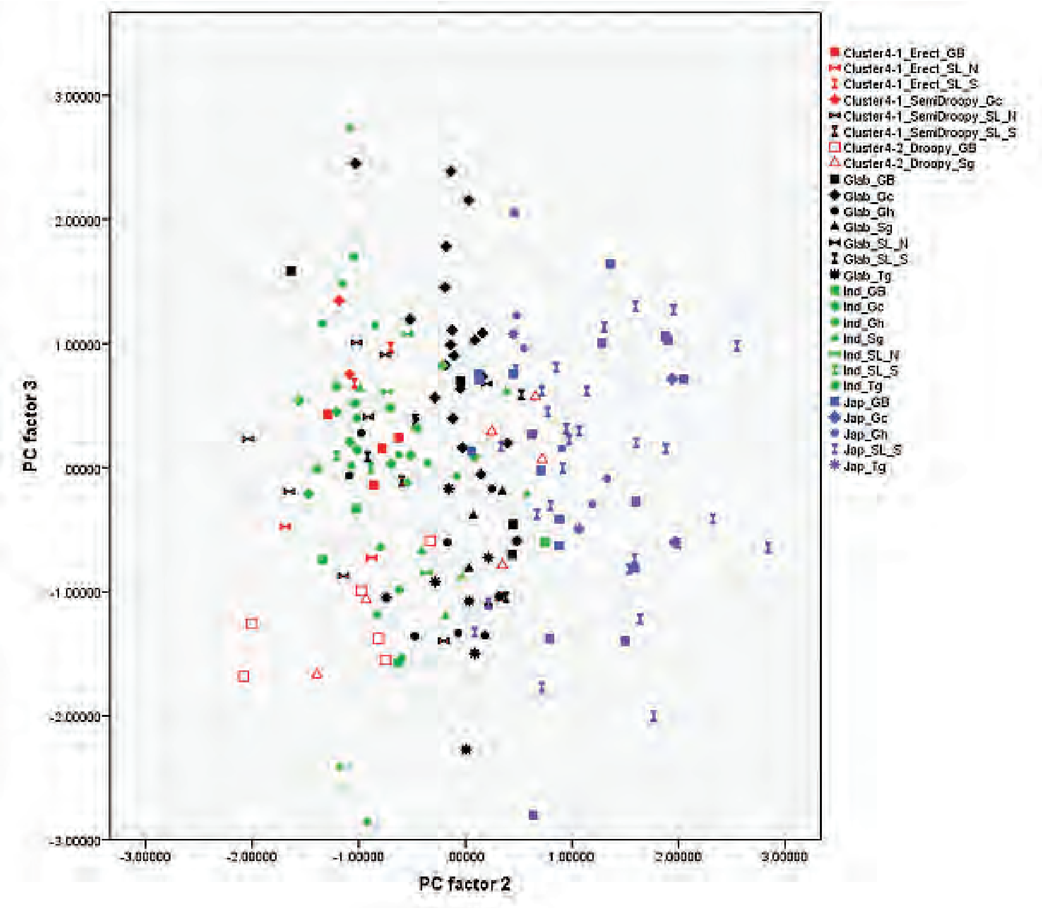

***Figure 6**: Graphically repartition of materials based on morphological data of PC 2 and 3*
***Component 2**: Leaf width (0.80)*, # tillers / plant (-0.79), # panicles/plant (-0.79), Seed width (0.71), Leaf blade colour (0.50)*
***Component 3**: Plant height (0.95), Culm length (0.88), Panicle length (0.70), Leaf length (0.60)*
GB: Guinea Bissau, SL: Sierra Leone (north: N south: S), Gc: Guinea Conakry, Sg: Senegal, Gh: Ghana, Tg: Togo.
**(): value of the correlation of the trait with the component*

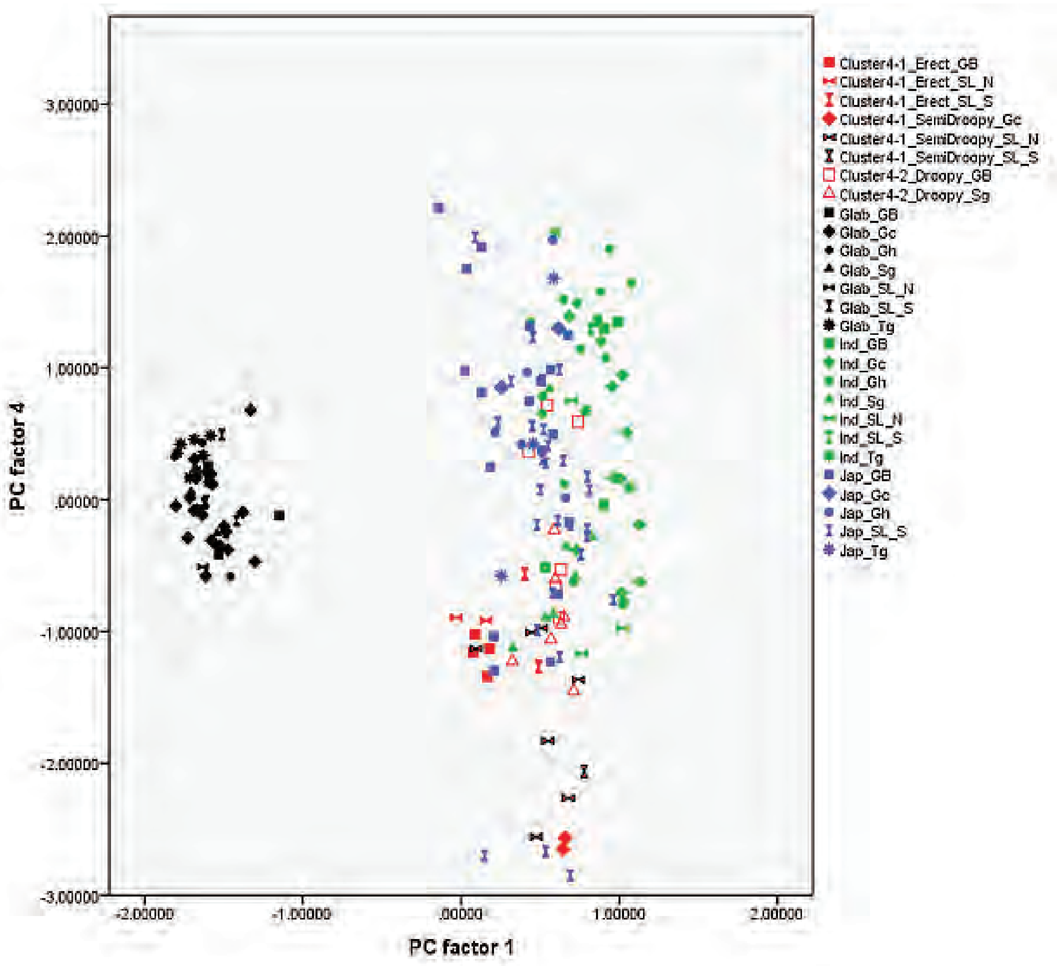

***Figure 7**: Graphically repartition of materials based on morphological data of PC 1 and 4*
Component 1**: Ligule Shape (0.97)*, Leaf blade pubescence (0.90), Ligule length (0.90), PAMA** (0.88), PAB (0.77), Rattoon potential (0.74), Leaf blade colour (0.65)*
***Component 4**: Seed length (0.93), Seed width (-0.36)*
GB: Guinea Bissau, SL: Sierra Leone (north: N south: S), Gc: Guinea Conakry, Sg: Senegal, Gh: Ghana, Tg: Togo.
(): value of the correlation of the trait with the component
**: Panicle Attitude of Main Axis*
***: Panicle Attitude of Branches*

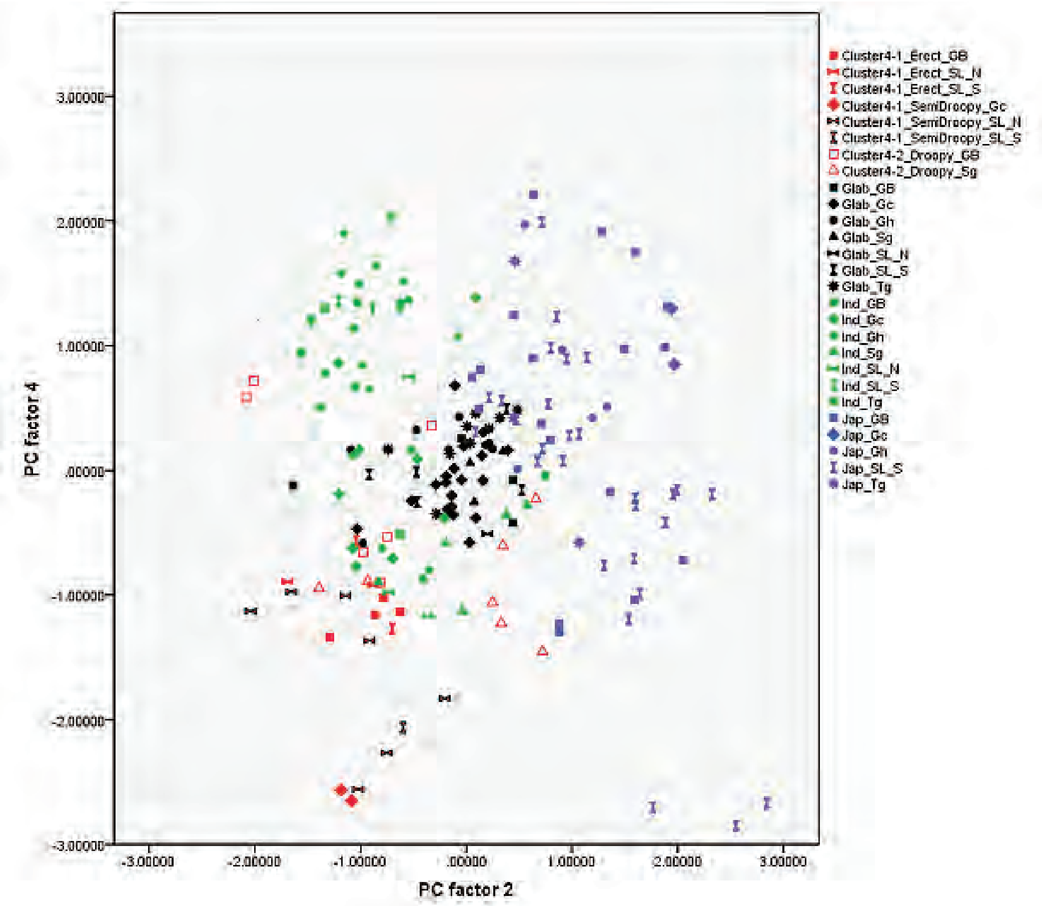

***Figure 8**: Graphically repartition of materials based on morphological data of PC 2 and 4*
***Component 2**: Leaf width (0.80)*, # tillers / plant(-0.79), # panicles/plant (-0.79), Seed width (0.71), Leaf Blade Colour (0.50)*
***Component 4**: Seed length (0.93), Seed width (-0.36) GB: Guinea Bissau, SL: Sierra Leone (north:N south: S), Gc: Guinea Conakry, Sg: Senegal, Gh: Ghana, Tg: Togo.*
.(): value of the correlation of the trait with the component*

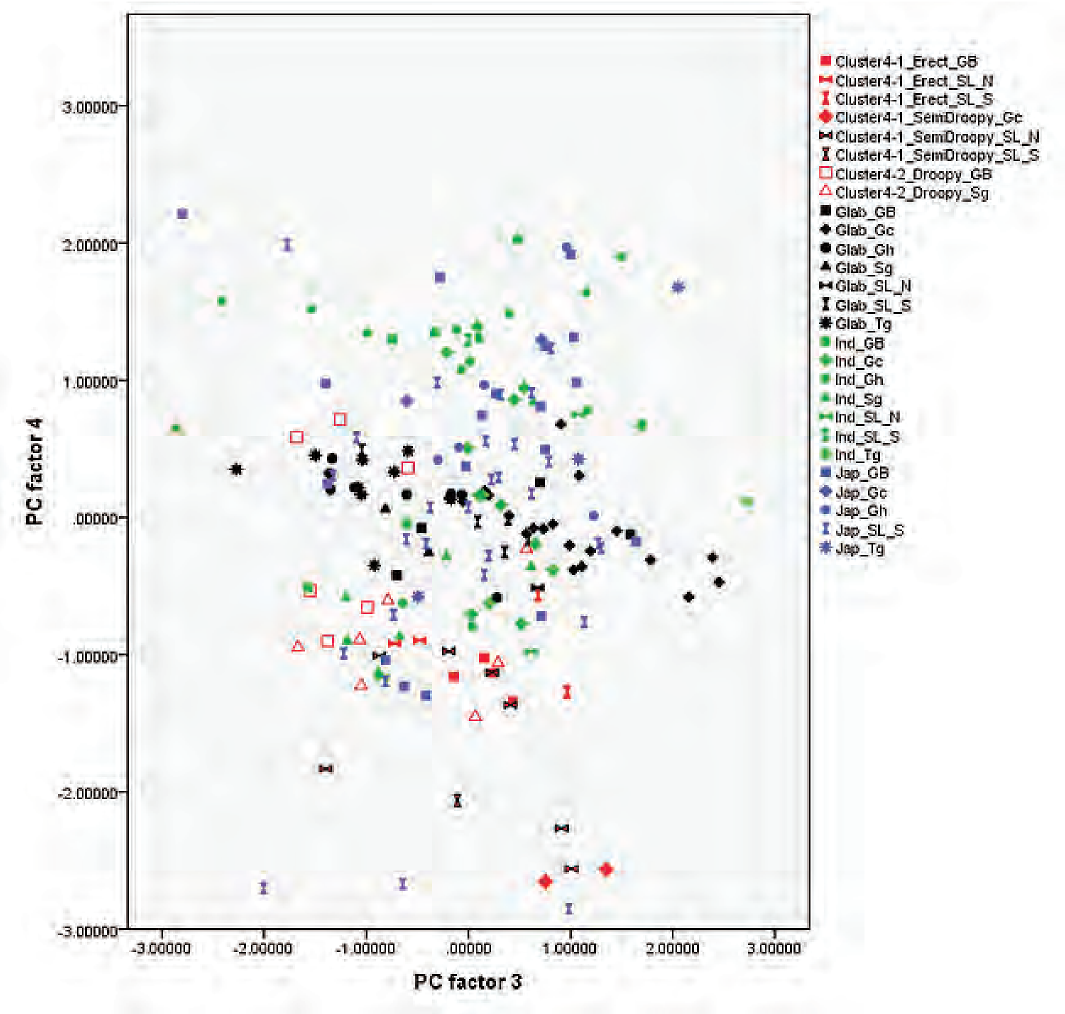

***Figure 9**: Graphically repartition of materials based on morphological data of PC 3 and 4*
***Component 3**: Plant height (0.95)*, Culm length (0.88), Panicle length (0.70), Leaf length (0.60)*
***Component 4**: Seed length (0.93), Seed width (-0.36)*
GB: Guinea Bissau, SL: Sierra Leone (north: N, south: S), Gc: Guinea Conakry, Sg: Senegal, Gh: Ghana, Tg: Togo.
**(): value of the correlation of the trait with the component*

When combining PC 2 and 3 (31.3%) all botanical groups form a single cloud (Figure 6). Whereas PC 1 is based on traits that separate *glaberrima* from the other botanical groups, PC 2 and 3 are based on a majority of the agronomic traits included in this study. The glaberrimas, indicas and most of the farmer hybrids, except for most of those from Senegal, are situated towards the left of the scatter, while the japonicas are positioned towards the right. Also, Figure 6 shows that *glaberrima* varieties differ more in height-related traits and panicle length than in number of panicles and tillers and leaf and seed width.

Through combination of PC 1 and 4 (Figure 7) the *glaberrima* group is bunched into a concentrated cluster showing a large degree of uniformity in related traits. The *indica* and *japonica* genotypes, however, show an equally large range for seed length. The farmer hybrids (mostly the erect and semi-droopy types) are situated at the lower part of the shared cloud with indicas and japonicas, showing relatively short grain length.

Comparison within botanical groups.

When combining PC 1 and 3 (Figure 5) the *O. glaberrima* varieties from the Upper Guinea Coast are found in the upper part of the cloud, with those from Guinea right at the top, and those from the Lower Guinea Coast further down. The glaberrimas from the Upper Guinea Coast are taller and have longer culms and panicles but have similar leaf length and ligule length, when compared to the glaberrimas from the Lower Guinea Coast (Table 5). Among the Upper Guinea Coast glaberrimas, the varieties from Guinea seem to constitute a special group, being taller, with longer culms, panicles and leaves (Table 6). This was also observed in several trials conducted in five countries by Mokuwa *et al*. [29]. That some *glaberrima* varieties from Senegal and Guinea Bissau sit with those from Ghana and Togo when combining PC1 and 2 (Figure 4) might imply a process of adaptation to agro-ecological conditions, such as amount of rainfall, since this is comparable in the two regions.

Table 5 shows that glaberrimas from the Lower Guinea Coast have longer and heavier seeds than those from the Upper Guinea Coast. The differences in seed and plant height-related traits might be ascribed to a process of adaptation to specific ecological and/or socio-cultural factors. Farmers on the Danyi Plateau in the Togo Hills stated that glaberrimas used to thrive well on relatively poor and acid soils, in which the availability of vital nutrients is restricted. The cultivation of rice under these acid conditions might have led to selection for shorter plants that produce heavier and longer grains. Roy *et al*. [37] showed that larger seeds germinate better and produce more vigorous seedlings than smaller seeds and are able to produce a deeper initial root system. Also farmers on the Danyi plateau indicated that larger seed is clearly preferred for culinary reasons (B. Teeken, unpublished data: Chapter 3).

A few *glaberrima* varieties from Ghana, Sierra Leone, Guinea and Guinea Bissau separate (downwards) from the core *glaberrima* cluster (Figure 4). These varieties have more tillers and panicles but have narrower leaves and smaller seed width compared to the other glaberrimas. For these traits, these *glaberrima* varieties resemble the *indica* group.

Unlike the case for *O. glaberrima*, no separate clustering can be observed for *O. sativa* ssp. *indica* from the Upper and Lower Guinea Coast (Figures 4, 5, 6, 7, 8, and 9), nor are significant differences observed for the agronomic traits (Table 5). At molecular level, some indicas from Sierra Leone and the Maritime region of Guinea tend to cluster together. Likewise, the materials from Senegal and the Togo hills cluster. However, at the morphological level a different tendency can be observed. Within the *indica* group (Figure 4) those from Guinea are situated towards the right, and those from Senegal are situated in the upper part, of a cloud. The indicas from Togo, Ghana, Sierra Leone and Guinea Bissau sit together in the centre of the cloud. The indicas show similarity with the farmer hybrids, particularly the semi-droopy hybrids from Sierra Leone and Guinea, and the droopy hybrids from Guinea Bissau.

Within Figures 4, 5, and 6, the indicas from Guinea closely bunch together whereas those from Ghana and other countries are very scattered. One explanation is that the materials collected in Guinea represent a small range of *indica* varieties, whereas a wide range of *indica* varieties was collected from rather diverse ecologies (ranging from hydromorphic soils to pure upland ecologies) in Ghana. Only when combining PC 1 and 4 (Figure 7) and PC 2 and 4 (Figure 8) is the Guinea material pulled apart, reflecting diversity on seed width and length, but not on other traits. The Guinea materials do not differ from the other *indica* varieties from the upper Guinea Coast on agronomic traits, except slightly for leaf length (Table 6).

***Table 5**: Means, standard deviation (SD), coefficient of variation (CV) and t-test results (P, in bold) for the agronomic morphological traits for the different botanical groups from the Lower Guinea Coast (Lower) and the Upper Guinea Coast (Upper).*

Botanical group		*Glaberrima*		*Indica*		*Japonica*		Average
Region		Lower	Upper	Lower	Upper	Lower	Upper	all groups
Trait	N	17	32	29	17	8	48	151
Culm length (cm)	Mean	79.1	86.3	81.0	82.5	89.2	82.4	83.4
	SD	5.10	6.52	8.37	6.25	5.09	5.72	6.18
	CV (%)	6.45	7.55	10.33	7.57	5.71	6.94	7.43
	P		**0.000**		**0.528**		**0.003**	
Plant height (cm)	Mean	99.1	109.7	103.3	104.7	110.2	103.9	105.2
	SD	5.22	7.09	9.21	6.17	6.27	6.52	6.75
	CV (%)	5.27	6.46	8.91	5.89	5.68	6.27	6.41
	P		**0.000**		**0.561**		**0.014**	
Panicle length (cm)	Mean	20.1	23.4	22.3	22.2	21.1	21.5	21.8
	SD	1.01	1.29	1.44	1.01	1.95	2.23	1.49
	CV (%)	5.03	5.50	6.46	4.55	9.24	10.37	6.86
	P		**0.000**		**0.800**		**0.611**	
Leaf length (cm)	Mean	41.4	42.3	43.1	42.8	48.7	46.3	44.1
	SD	2.80	2.52	4.17	2.65	3.22	3.91	3.21
	CV (%)	6.77	5.96	9.66	6.19	6.62	8.45	7.28
	P		**0.234**		**0.761**		**0.107**	
Leaf width	Mean	1.44	1.46	1.04	1.06	1.50	1.58	1.34
	SD	0.07	0.12	0.10	0.14	0.08	0.20	0.12
	CV (%)	5.04	8.14	9.62	13.17	5.62	12.57	9.03
	P		**0.140**		**0.572**		**0.261**	
# tillers / plant	Mean	5.2	4.8	4.3	4.6	3.3	3.1	4.2
	SD	0.80	0.80	0.58	0.64	0.46	0.59	0.65
	CV (%)	15.48	16.46	13.32	14.05	14.11	19.12	15.42
	P		**0.599**		**0.208**		**0.485**	
# panicles / plant	Mean	4.5	4.4	3.8	4.0	2.7	2.7	3.7
	SD	0.56	0.70	0.52	0.60	0.30	0.47	0.53
	CV (%)	12.51	16.19	13.98	15.05	10.89	17.39	14.34
	P		**0.621**		**0.123**		**0.738**	
Average 200 seed weight (g)	Mean	4.63	4.17	4.67	4.77	5.29	4.82	4.73
	SD	0.19	0.41	0.38	0.44	0.33	0.73	0.41
	CV (%)	4.10	9.83	8.07	9.12	6.29	15.08	8.75
	P		**0.000**		**0.421**		**0.082**	
Seed length (mm)	Mean	8.69	8.40	9.13	9.03	9.25	8.66	8.86
	SD	0.16	0.29	0.68	0.60	0.49	0.82	0.51
	CV (%)	1.84	3.45	7.47	6.68	5.28	9.51	5.71
	P		**0.001**		**0.629**		**0.058**	
Seed width (mm)	Mean	3.07	3.03	2.93	2.96	3.18	3.25	3.07
	SD	0.07	0.13	0.30	0.19	0.24	0.31	0.21
	CV (%)	2.28	4.29	10.27	6.26	7.50	9.52	6.69
	P		**0.112**		**0.651**		**0.545**	
Average CV (%)		5.9	7.6	8.9	8.0	7.0	10.5	

Table 6: *Means, standard deviations (SD), coefficients of variation (CV) and t-test results (P, in bold) for the agronomic morphological traits for the four different sub-groups within the Upper Guinea Coast. UpperSL = material from Sierra Leone; UpperGB = material from Guinea Bissau; UpperGc = material from Guinea; Cluster 4-1 = material belonging to the sub-cluster of Cluster 4 with erect and semi-droopy panicles; Cluster 4-2 = material belonging to the sub-cluster of Cluster 4 with droopy panicles; 4-1 Erect = material of Cluster 4-1 with erect panicle; 4-1 semi droopy = material belonging to Cluster 4-1 with semi-droopy panicle.*

Botanical group		*Glaberrima*		*Indica*		*Japonica*		Cluster 4		Cluster 4-1	
Region / sub-cluster		Upper Gc	Upper-Other	Upper Gc	Upper-Other	Upper GB	Upper SL	Cluster 4-2	Cluster 4-1	4-1 Erect	4-1 Semi-droopy
Trait	N	19	13	13	12	18	28	13	18	8	10
Culm length (cm)	Mean	89.3	82.1	84.9	82.6	83.9	81.6	76.3	83.3	83.6	83.0
	SD	5.66	5.32	4.76	5.39	6.83	4.98	5.23	5.32	4.13	6.33
	CV (%)	6.34	6.48	5.61	6.53	8.14	6.11	6.86	6.39	4.94	7.63
	P		**0.001**		**0.260**		**0.198**		**0.001**		**0.826**
Plant height (cm)	Mean	112.8	105.2	107.1	104.3	105.1	103.2	97.9	104.6	104.3	104.9
	SD	6.25	5.80	4.70	5.84	7.95	5.68	5.76	6.04	4.51	7.28
	CV (%)	5.54	5.52	4.39	5.60	7.57	5.50	5.89	5.77	4.32	6.94
	P		**0.001**		**0.192**		**0.349**		**0.004**		**0.834**
Panicle length (cm)	Mean	23.6	23.3	22.2	21.7	21.1	21.6	21.6	21.4	20.7	22.0
	SD	1.08	1.57	1.05	1.17	2.06	2.23	0.98	1.43	1.13	1.44
	CV (%)	4.59	6.75	4.76	5.38	9.75	10.32	4.55	6.68	5.47	6.57
	P		**0.543**		**0.352**		**0.479**		**0.642**		**0.060**
Leaf length (cm)	Mean	43.1	41.1	43.6	41.5	46.1	46.3	38.5	45.6	48.2	43.6
	SD	1.77	3.01	2.04	2.82	4.05	4.03	4.21	3.45	3.34	1.84
	CV (%)	4.10	7.32	4.68	6.79	8.77	8.70	10.93	7.55	6.94	4.22
	P		**0.043**		**0.041**		**0.892**		**0.000**		**0.002**
Leaf width	Mean	1.49	1.40	1.08	1.05	1.51	1.62	1.04	1.01	1.05	0.98
	SD	0.13	0.07	0.15	0.14	0.23	0.18	0.18	0.09	0.09	0.09
	CV (%)	8.92	4.72	13.99	13.76	15.08	10.85	17.11	9.22	8.26	9.13
	P		**0.030**		**0.633**		**0.087**		**0.672**		**0.104**
# tillers / plant	Mean	4.7	5.0	4.7	4.3	3.2	3.1	4.2	4.7	4.9	4.6
	SD	0.66	0.97	0.63	0.66	0.61	0.56	1.02	0.63	0.47	0.74
	CV (%)	13.85	19.51	13.62	15.31	19.32	18.05	24.44	13.45	9.73	16.14
	P		**0.367**		**0.240**		**0.874**		**0.101**		**0.391**
# panicles / plant	Mean	4.3	4.4	4.1	3.8	2.7	2.7	3.6	4.2	4.3	4.1
	SD	0.43	1.00	0.57	0.54	0.48	0.44	0.92	0.72	0.57	0.84
	CV (%)	9.91	22.79	13.90	14.38	17.83	16.42	25.84	17.44	13.32	20.83
	P		**0.808**		**0.128**		**0.819**		**0.049**		**0.529**
Average 200 seed weight (g)	Mean	4.04	4.35	4.73	4.93	5.03	4.58	3.73	3.59	4.37	2.96
	SD	0.20	0.54	0.49	0.21	0.67	0.61	0.61	0.79	0.30	0.39
	CV (%)	4.95	12.41	10.29	4.28	13.36	13.31	16.27	22.16	6.81	13.14
	P		**0.064**		**0.196**		**0.024**		**0.580**		**0.000**
Seed length (mm)	Mean	8.37	8.45	8.98	8.78	8.95	8.43	8.13	7.51	8.20	6.96
	SD	0.32	0.25	0.54	0.66	0.72	0.84	0.51	0.82	0.25	0.68
	CV (%)	3.82	2.96	6.00	7.51	8.01	9.92	6.28	10.90	3.05	9.78
	P		**0.469**		**0.425**		**0.035**		**0.015**		**0.000**
Seed width (mm)	Mean	2.96	3.12	2.96	3.15	3.20	3.27	2.84	2.90	3.09	2.74
	SD	0.08	0.14	0.15	0.28	0.31	0.32	0.40	0.21	0.04	0.16
	CV (%)	2.70	4.49	4.92	9.01	9.69	9.71	14.07	7.36	1.26	5.98
	P		**0.002**		**0.062**		**0.469**		**0.632**		**0.000**
Average CV (%)		5.9	8.5	7.5	8.0	10.7	9.9	12.0	9.7	5.8	9.1

Our findings at morphological level suggest that farmers in Ghana, Guinea Bissau, Sierra Leone and Senegal tend to select *indica* varieties with a range of morphological features while farmers in Guinea have been selecting narrowly, favouring a particular group of indicas. In the rather difficult upland conditions of the Guinea case-study areas (adjacent to the Bena hills) only a limited range of *indica* varieties has proven to be locally well adapted.

As is the case with *O. glaberrima*, *O. sativa* ssp. *japonica* from the Togo hills tends to have heavier seeds than the *japonica* from the Upper Guinea Coast region, but unlike *glaberrima* the *japonica* from the Togo hills are taller plants (Table 5). Considering PC 1 and 2 (Figure 4) the genotypes from the Upper Guinea Coast (mostly from Sierra Leone and Guinea Bissau) are found throughout the whole of the *japonica* cluster, while genotypes from the Lower Guinea Coast (materials from Ghana and Togo) are only found in the lower part of the cluster. *Japonica* varieties situated in the upper part of the cluster have broader leaves, fewer panicles and tillers, broader seeds and darker leaves. Materials from Sierra Leone and Guinea Bissau showed equal (high) levels of variation for these traits (see also Table 6). The japonicas from Sierra Leone were only collected from the south of the country meaning that farmers in a specific area deal with a highly diverse set of japonicas. At molecular level the japonicas from Sierra Leone tend to cluster separately from those from the other countries. Such separation does not show clearly in Figures 4, 5, 6, 7, 8, and 9.

Mokuwa *et al*. [10] found that a group of japonicas from Sierra Leone were more niche adapted, whereas a group of japonicas from Guinea Bissau showed wide adaptation. Both the Sierra Leone materials and most of the materials from Guinea Bissau used in the experiments by Mokuwa *et al*. [10] are among the genotypes sitting in the upper part of the *japonica* cluster (PC 1 and 2; Figure 4). At molecular level one Sierra Leone variety (Nduluwai) clusters with the Guinea Bissau varieties. In Figures 10 and 11 these varieties are found in different sub-groups, clustering in idiosyncratic ways. What this suggests is that farmers in both regions have selected morphologically similar materials responsive to different agro-ecological conditions. This might reflect histories of adaptation and introduction for these japonicas [29]. Evidence supporting a different process of introduction and adaptation is the similarity of the varieties Aqua Blue (‘blue water’) from Ghana and Sefa Fingo (meaning ‘black type’ in Mandinka) from Guinea Bissau at molecular and morphological levels, perhaps indicating common origins via Portuguese trading networks. It is thought that Portuguese traders brought japonicas from Indonesia to Guinea Bissau from where they spread to other West African countries [38]. To emphasise the distinctiveness of this case, both varieties have a distinct colouration during flowering and maturation not observed in other varieties.

Farmers from the Ghana side of the Togo hills have been selecting japonicas with relatively narrow leaves, high tillering and panicle production, slender and long grains similar to some indicas. (Figures 6 and 7). The long grain size could be explained by the large demand for long grained rice in the market.

In Figures 4, 5, 6, 7, and 8, farmer hybrids (Cluster 4) in general formed a large cloud suggesting they are diverse, confirming the molecular findings. Based on the panicle architecture (PAMA) most widely used to distinguish *O. glaberrima* from *O. sativa* varieties, the farmer hybrids were assigned to three sub groups: erect panicles, semi-droopy panicles and droopy panicles. In Figures 4, 5, 6, 7, and 8 the farmer hybrids with erect panicles did not clearly separate from the farmer hybrids with semi-droopy and droopy panicles, although they did in Figures 10 and 11. Table 6 shows statistically significant differences in seed weight, length and width between farmer hybrids with erect and semi-droopy panicles. For these two groups no clear difference was observed in the clustering based on molecular data.

Figure 5 (PC 1 and 3) shows that the farmer hybrids with erect panicles from Guinea Bissau cluster closely together, whereas those from Sierra Leone are more scattered. This agrees with the molecular analysis. Particularly, erect farmer hybrids from Northern Guinea Bissau sit together. These varieties were considered weeds by Mandinka farmers from northern Guinea Bissau; they referred to these interspecific varieties by names they also used for *glaberrima*. The one from Southern Guinea Bissau was brought from Guinea and sits somewhat separated. The scattering of the farmer hybrids with erect and semi-droopy panicles from Sierra Leone in Figure 4 points to active selection by farmers.

The erect farmer hybrids of Guinea Bissau and Sierra Leone are known to be four months in duration from germination to ripening. The semi-droopy farmer hybrids from Sierra Leone and Guinea are three months in duration. These semi-droopy farmer hybrids can be further divided into those with small and slender grains and those with short and bold grains. The latter are visible in Figure 7 down among the semi-droopy farmer hybrids from Sub-cluster 4-1. Farmers have been selecting 'three month' varieties as hunger breakers because they ripen about one and half or two month(s) before the major rice harvesting time. In this respect the three-month group of farmer hybrids has been replacing some of the short cycle *glaberrima* traditionally used as hunger breakers. Compared to the erect farmer hybrids these 'three months' interspecific farmer varieties vary more for husk colour and seed size (see also Table 6).

Compared to the limited diversity represented by the erect farmer hybrids from Guinea Bissau, the larger diversity in droopy farmer hybrids from Guinea Bissau and Senegal (Sub-cluster 4-2 in Table 6) agrees with interview data that farmers actively select for droopy farmer hybrids in these regions. The farmer hybrids with droopy panicles split into two groups largely reflecting their area of collection. Figure 4 (PC 1 and 2) shows that only farmer hybrids with droopy panicles from Senegal are found in the area where *indica* and *japonica* overlap. Interviews with farmers indicated that the farmer hybrids in Senegal have their origin in Guinea Bissau. The droopy varieties spread to Senegal particularly during the independence war in Guinea Bissau from 1963 to 1974. However, the farmer hybrids with droopy panicles collected in Guinea Bissau are situated in the lower part of the cloud of farmer hybrids. This suggests that over a period of approximately 40-50 years a selection process has taken place, and that farmers in the case study areas in Senegal and Guinea Bissau prefer farmer hybrids with area-specific morphological characteristics. Overall, morphological characterisation of farmer hybrids underlines a conclusion that Cluster 4-2 is highly variable and shares characteristics with *japonica* and *indica*. At the molecular level, however, the farmer hybrids are all closer to *indica* than to *japonica*.

Geographical and climatic clustering

Figure 10 shows an unrooted tree based on 20 morphological traits, and Figure 11 based on agronomic traits only (see Table 2). The clustering in Figure 10 is largely according to botanical groups, with *glaberrima* and *japonica* making well-defined clusters and *indica* and the farmer hybrids consisting of several clusters. The *glaberrima* clearly forms three sub-clusters for Guinea and Sierra Leone, Ghana and Togo, and north Guinea Bissau and Senegal. For the other botanical groups some country based clustering patterns can also be observed, although less clearly. Some clusters contain material from several botanical groups. In the case of *japonica*, two clusters hold mostly material from Sierra Leone, and another cluster groups material from various countries. In the case of *indica* from the Upper Guinea Coast some clustering based on seed colour can be observed, but not for the Lower Guinea Coast. Some white seeded indicas cluster with light-coloured droopy farmer hybrids from Guinea Bissau, and some red seeded indicas cluster with red-coloured semi-droopy farmer hybrids from Sierra Leone and Guinea.

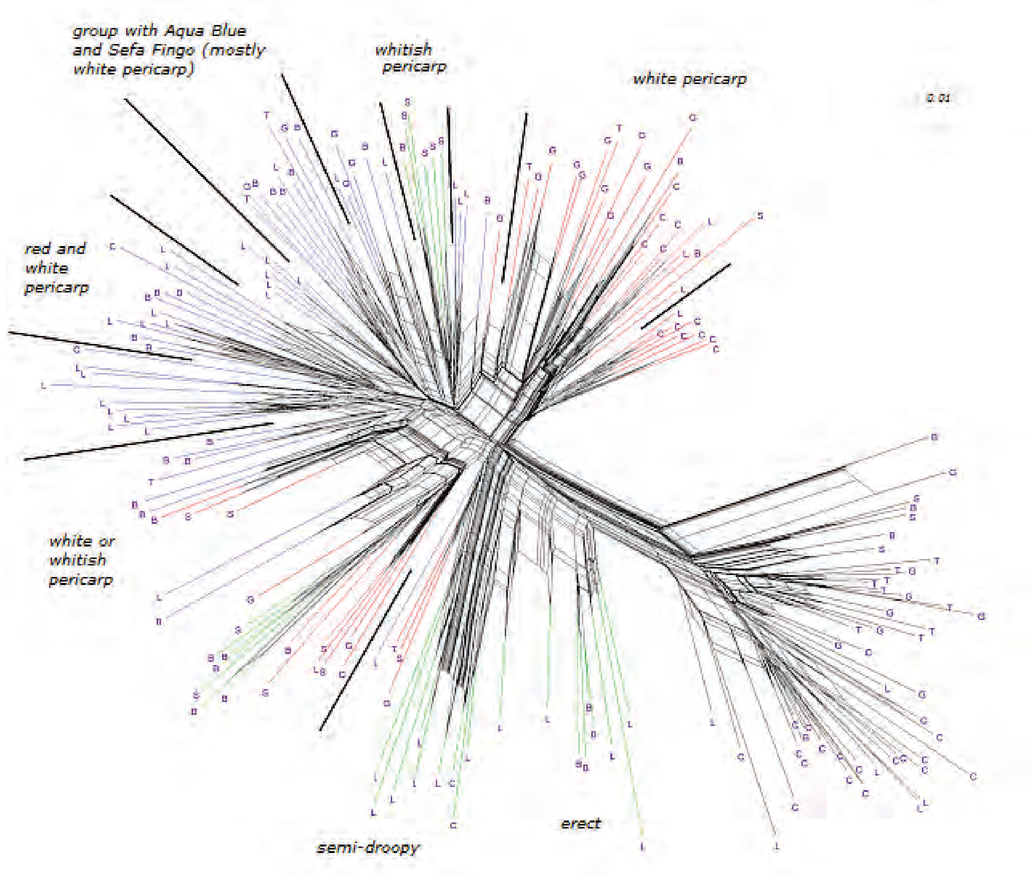

***Figure 10**: Phylogenetic relationships of 182 rice genotypes based on all morphological traits converted into dummy variables. Botanical groups are indicated by colours: Black = O. glaberrima, red = O. sativa ssp. indica, blue = O. sativa ssp. japonica and green = interspecific farmer varieties. Country of collection is* indicat*ed by letters: B = Guinea **B**issau, C = Guinea **C**onakry, G = **G**hana, L = Sierra **L**eone, S = **S**enegal, **T** = Togo.*

The clustering in Figure 11 is complex, with material from the four botanical groups clustering in various ways. To some extent the patterns may reflect agro-ecological selection pressures. This is perhaps particularly true for the glaberrimas, where grouping reflects geographical factors. The glaberrimas from Senegal and northern Guinea Bissau, for instance, cluster more closely with the glaberrimas from Togo and Ghana, with both areas having similar amounts of rainfall. For the other botanical groups no such clear separation is apparent. Another apparent indicator of agro-ecological selection pressures is the extent to which material from various botanical groups from one country, or two neighbouring countries, clusters together. For example, the erect farmer hybrids, most coming from Sierra Leone, and the indicas from Guinea cluster closely with the glaberrimas from Guinea and Sierra Leone. However, clusters can also be found grouping material from all countries, as applies to subsets of indicas and japonicas. Also the droopy farmer hybrids from Senegal form several small independent clusters.

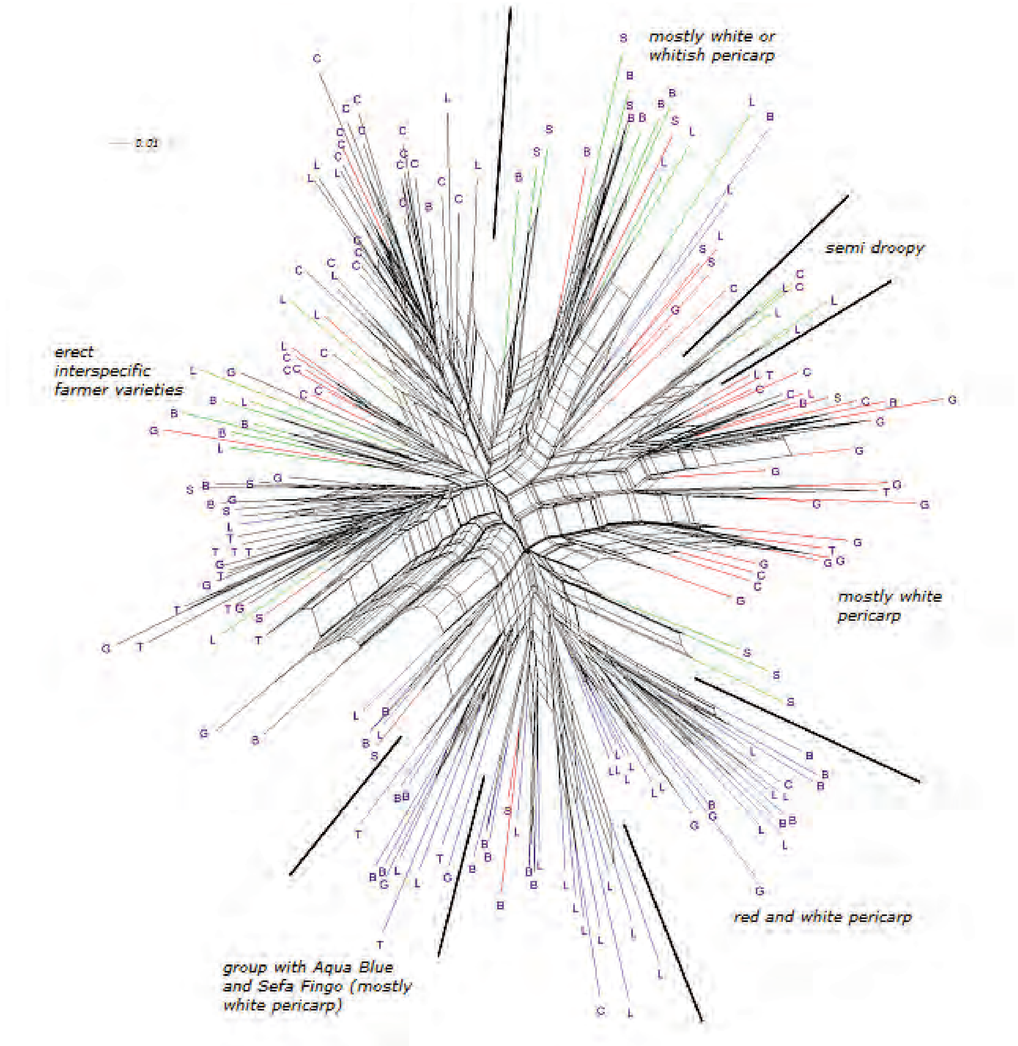

Figure 11: *Phylogenetic relationships of 182 rice genotypes based on the agronomic traits converted into dummy variables. Botanical groups are indicated by colours: Black = O. glaberrima, red = O. sativa ssp. indica, blue = O. sativa ssp. japonica and green = interspecific farmer varieties. Country of collection is indicated by letters: B = Guinea **B**issau, C = Guinea **C**onakry, G = **G**hana, L = Sierra **L**eone, S = **S**enegal, T = **T**ogo.*

Pericarp colour as a selection factor

Seed colour (pericarp) is an important characteristic often mentioned by farmers [9]. Depending on the farming system and social context, pericarp colour is a nutritional, gender, religious or cultural marker, and plays a role in the selection and acceptance of rice varieties [9]. Seed colour was not incorporated in the PCA because it could not be converted into a linear scale. Instead we labelled the materials of this study according to seed colour. Figure 12, 13 and 14 respectively show the combination of factor PC 1 and 2, 1 and 3 and 2 and 3 marked according to seed colour, country of collection and botanical group. Only a few relationships between pericarp colour, molecular, and morphological data were found. The clearest relationship was among the farmer hybrids, where varieties with erect and semi-droopy panicles have a red pericarp, and those with a droopy panicle have a white or light brown pericarp. The varieties Pugulu 'white' and 'red' from Ghana were found in neighbouring clusters in Figure 10 (B. Teeken, unpublished). This is a case of farmers using the same name with the addition 'white' or 'red' for varieties that are genetically different.

Farmers from whom we collected material have no fixed ideas about the 'correct' morphological traits of rice varieties [39]. Rather than focusing on a particular ideotype they sustain what might be termed a broad flexset (combining a range of ideotypes depending on the conditions). Seemingly, this is a way to optimise benefits of cognitive flexibility, to be understood in relation to a long history of in situ domestication. Gross *et al*. [40] indicate that pericarp colour might be a phenomenon rather independent of trajectory of domestication. In Ghana preference for white and red varieties was modulated by other traits, such as robustness, yield and intended usage. In the Ghanaian Togo hills, as well as in Sierra Leone, rice with a red pericarp is considered 'heavier' in the stomach (i.e. it digests more slowly than white rice, a valuable characteristic where sustained hard work has to be attempted). To make a meal last longer, white rice is sometimes mixed with some red rice before eating and in some cases (e.g. in Sierra Leone) it is sometimes mixed before sowing to allow easy milling. In Mandinka-dominated areas of Upper West Africa, red rice is regarded as "outmoded" and white rice is now preferred. There is also high demand for white rice in urban areas where people, because of their different labour pattern, tend to prefer rice that is more easily prepared.

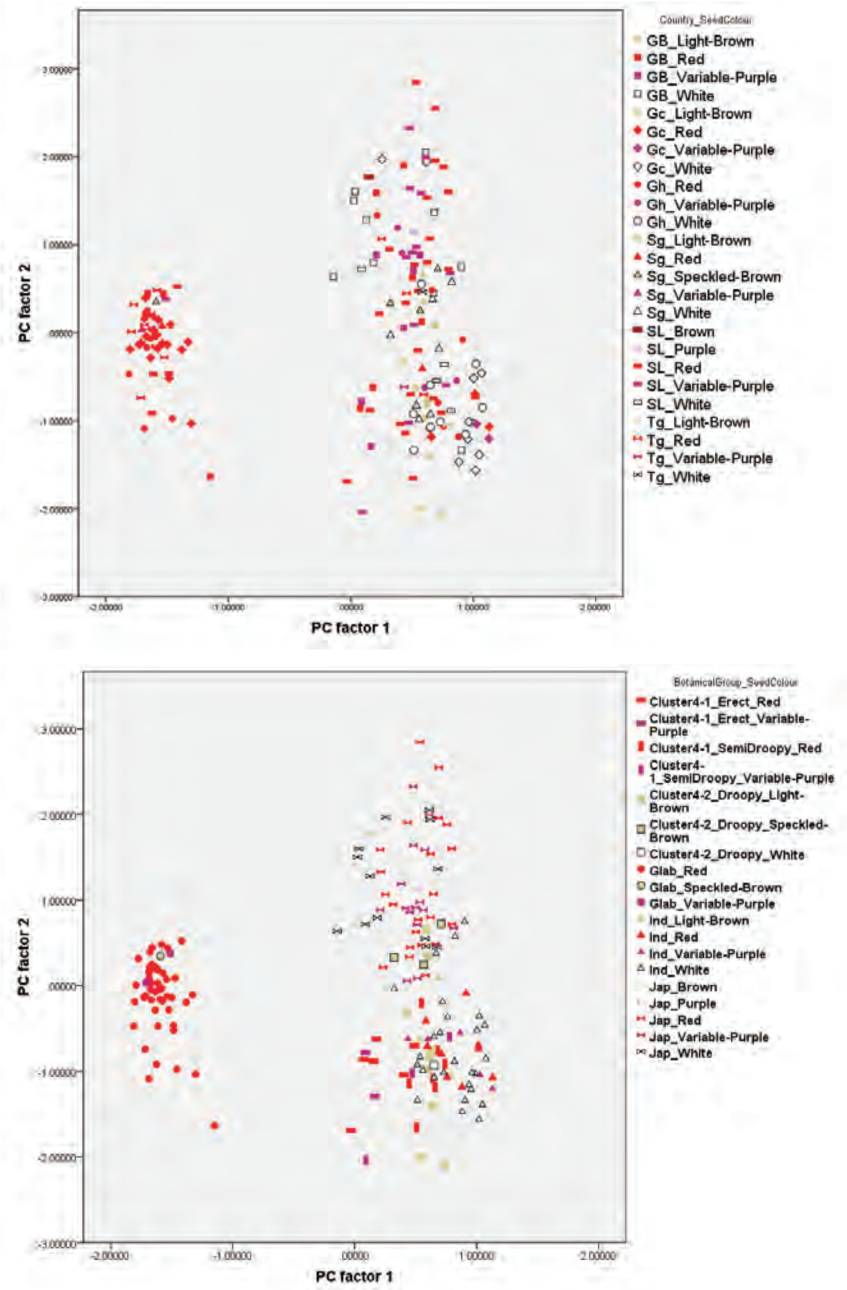

***Figure 12**: Graphically repartition of materials based on morphological data of PC 1&2 marked according to country of collection and seed colour* as well as botanical group and seed colour. Country of collection is indicated by letters: Gc = Guinea Conakry, GB = Guinea Bissau, Gh = Ghana, Sg = Senegal, SL = Sierra Leone, Tg = Togo.*

** According to the seed colour chart of the Bioversity rice descriptor version 2007 [34]*

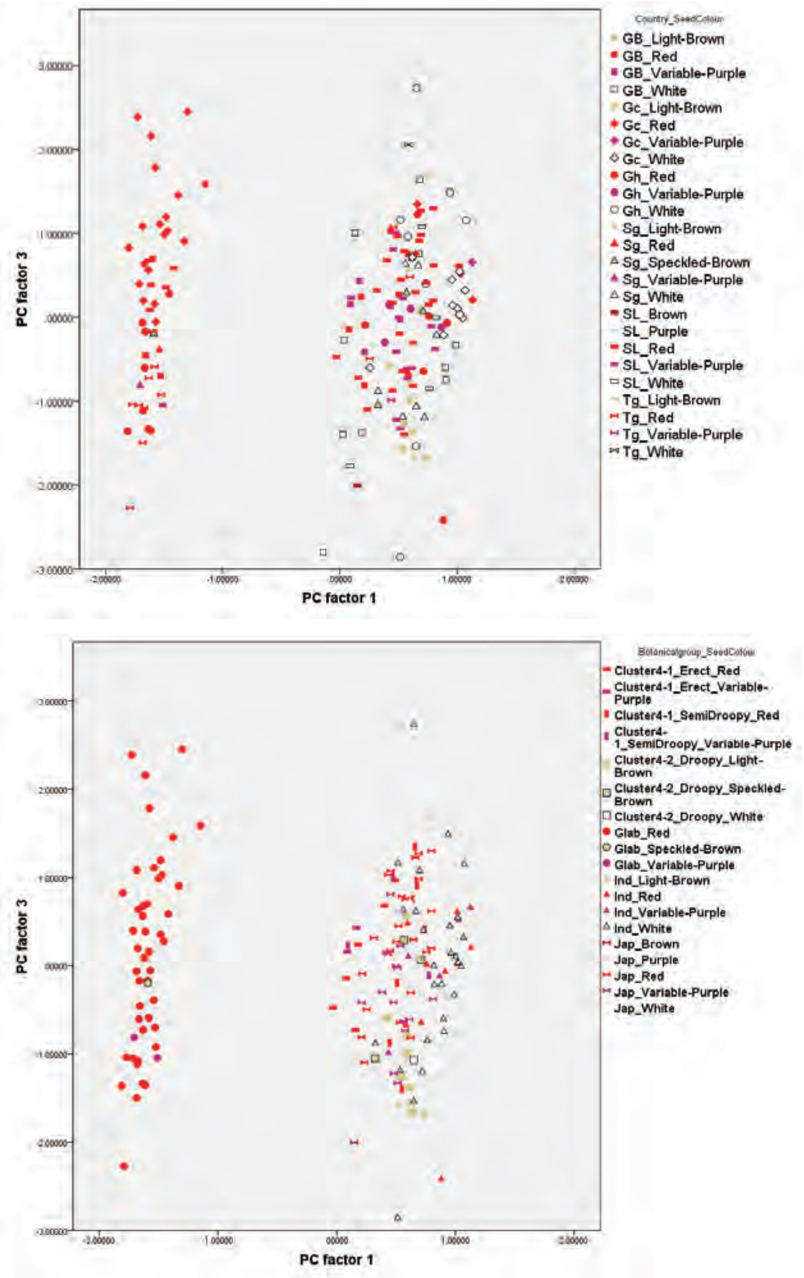

Figure 13*: Graphically repartition of materials based on morphological data of PC 1&3 marked according to country of collection and seed colour* as well as botanical group and seed colour. Country of collection is indicated by letters: Gc = Guinea Conakry, GB = Guinea Bissau, Gh = Ghana, Sg = Senegal, SL = Sierra Leone, Tg = Togo.*

** According to the seed colour chart of the Bioversity rice descriptor version 2007 [34]*

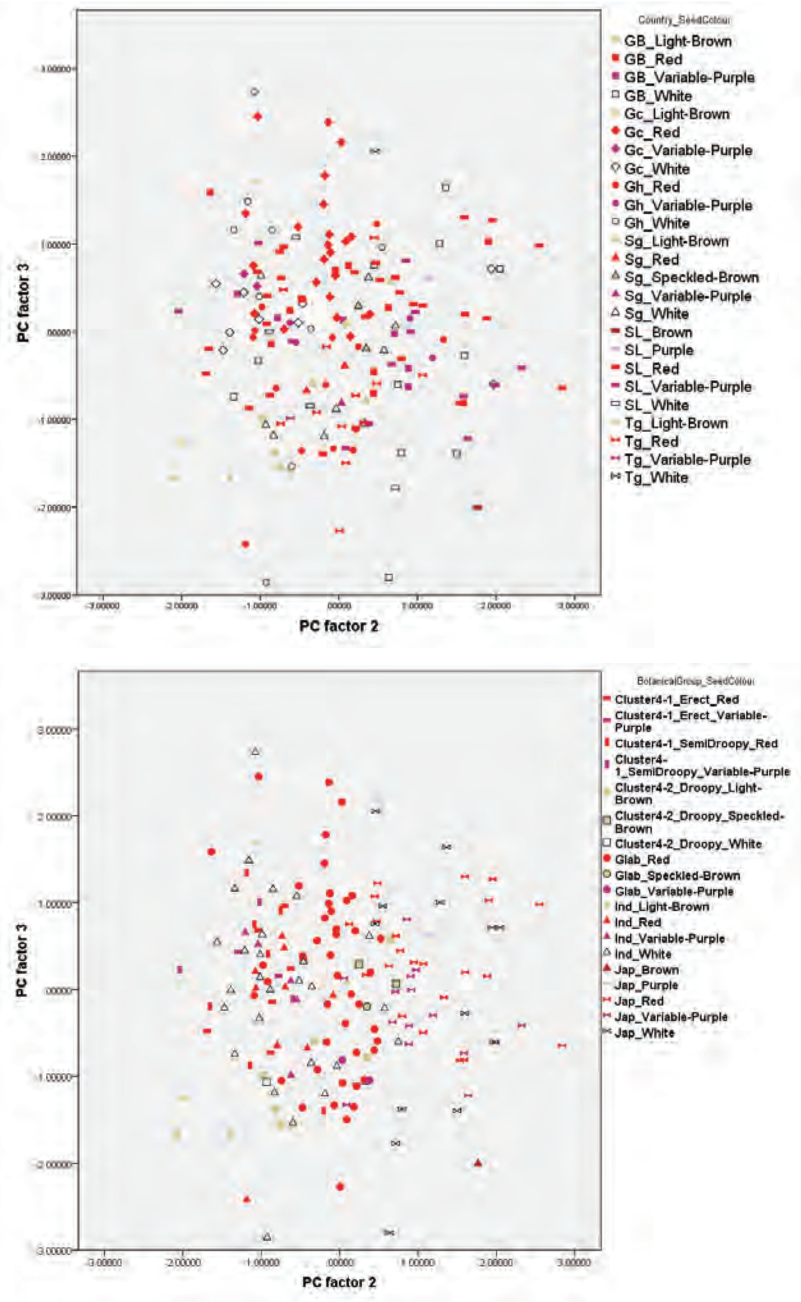

***Figure 14**: Graphically repartition of materials based on morphological data of PC 1&3 marked according to country of collection and seed colour* as well as botanical group and seed colour. Country of collection is indicated by letters: Gc = Guinea Conakry, GB = Guinea Bissau, Gh = Ghana, Sg = Senegal, SL = Sierra Leone, Tg = Togo.*

** According to the seed colour chart of the Bioversity rice descriptor version 2007 [34]*

Development of genetic diversity

Whereas the molecular data suggested that the *indica* group and farmer hybrids had greater genetic diversity than the *japonica* and *glaberrima* groups (see Table 7), Figures 4, 5, 6, 7, 8, and 9 suggest the differences in genetic diversity between the groups might be smaller than represented by the molecular analysis. Particularly for *japonica*, Figures 5, 6, 7, 8, and 9 and Figure 12, 13 and 14 show a large dispersion, similar to *indica*, for all components. For *glaberrima* only Figures 5, 6, and 9 show a large dispersion. Calculations of genetic diversity based on morphological traits (Table 7) confirm that *glaberrima* have less diversity, but that *japonica* has a higher level of diversity (see also Tables 5 and 6).

There seems to exist a relationship between the level of farmer selection and seed exchange and the level of diversity in botanical groups. Farmer accounts of the introduction or in situ development of new varieties related mainly to farmer hybrids, *indica* and to a lesser extent *japonica*. No such account related to *glaberrima*. In recent years farmers in Ghana have developed an idea that the morphology of *glaberrima* is fixed, and Mandinka people in Senegal and northern Guinea Bissau consider *glaberrima* to be a rice belonging to history. Only in a few areas (e.g. southern Guinea Bissau) are farmers actively re-introducing varieties of *glaberrima* [9]. This suggests there is little current active farmer variety development for *glaberrima*. By contrast, accounts concerning introductions and further development of farmer hybrids and/or *indica* are especially numerous in all countries where the research took place [6, 9, 39; A. Mokuwa, unpublished data).

***Table 7**: Level of genetic diversity of four botanical groups of rice in West Africa, calculated with Nei's index (He) and the fraction of polymorphic markers (P-value), based on molecular markers and morphological traits converted into dummy variables.*

Botanical group	N	Molecular markers		Morphological traits	
		He	P-value	He	P-value
O. glaberrima	49	0.042	0.430	0.189	0.762
Lower Guinea Coast	17	0.027	0.181	0.131	0.438
Upper Guinea Coast	32	0.047	0.362	0.185	0.724
Guinea	19	0.052	0.305	0.154	0.610
Other	13	0.035	0.152	0.190	0.552
O. sativa ssp. *indica*	46	0.099	0.653	0.218	0.800
Lower Guinea Coast	17	0.102	0.410	0.195	0.619
Upper Guinea Coast	29	0.070	0.429	0.208	0.733
Guinea	13	0.055	0.276	0.173	0.581
Other	16	0.072	0.333	0.208	0.590
O. sativa ssp. *japonica*	56	0.054	0.481	0.238	0.819
Lower Guinea Coast	8	0.033	0.143	0.173	0.476
Upper Guinea Coast	48	0.053	0.400	0.240	0.810
Guinea Bissau	18	0.035	0.200	0.236	0.676
Sierra Leone	28	0.056	0.371	0.225	0.705
Cluster 4	31	0.102	0.444	0.257	0.752
Cluster 4-1	18	0.060	0.274	0.223	0.629
Cluster 4-1 erect	8	0.038	0.143	0.149	0.400
Cluster 4-1 semi-droopy	10	0.065	0.219	0.169	0.495
Cluster 4-2	13	0.078	0.281	0.204	0.581

Country-specific findings

Sierra Leone. In Sierra Leone *japonica* varieties are extensively cultivated only in the southern half of the country while almost all upland varieties in the north are mainly farmer hybrids and *indica*, with a few *glaberrima*. This suggests that diversity of climate and agro-ecological conditions (upland and hydromorphic ecologies) is the main driver for selection of botanical groups [41]. The *japonica* in southern Sierra Leone and the farmer hybrids in northern Sierra Leone show considerable variation, suggesting that active cultivation plays a role in maintaining and developing genetic diversity. Close to the border with Guinea more extensive cultivation of *glaberrima* occurs with varieties that resemble varieties from Guinea, an area where *glaberrima* is still widely cultivated [7, 9]. An ethnic factor plays a part - the *glaberrima* were collected mainly among the Susu people who live on both sides of the border, linked by strong family ties and seed networking relationships.

Guinea. It is important to mention that in the Guinea case study area almost no *japonica* varieties are cultivated. In these conditions (soils of low pH) farmers mainly cultivate *glaberrima* and *indica* varieties. Among rice scientists it is thought that West African upland varieties are generally *japonica* rather than *indica* [38, 42, 43]. As a result, and in contrast to *japonica, indica* cultivars have yet to be fully evaluated regarding their adaptation to upland conditions in West Africa [44; 45, cited in 46].

The *indica* varieties collected in Guinea showed less diversity compared to varieties collected from the other study countries. This limited diversity partly relates to a fieldwork circumstance - varieties were collected from an ethnically homogenous group (Susu) growing essentially the same set of varieties along a 120 km transect from the Sierra-Leone borders (Bassia) to Kindia. These Guinean indicas are morphologically strongly differentiated from both *glaberrima* as well as from *japonica*. This is despite the fact that in Guinea *indica* and *glaberrima* are cultivated in the same upland conditions. For Susu farmers, selecting morphologically distinct genotypes helps avoid variety mixtures in the field. This part of Guinea (the Benna region in particular) was historically involved in an international rice trade to Freetown when local slave-manned plantations replaced the Atlantic slave trade. The Freetown rice trade demanded white rice [29]. Keeping field homogeneity (a relic of this long-dormant trade) is a cultural and managerial value lingering for nearly two centuries in some of these Susu farming communities [7]. That indicas with white and red seed colour cluster differently helps to confirm the significance of these socio-economic and cultural selection preferences in influencing genetic make-up of rice.

That the *glaberrima* from Guinea also show much diversity, points to active selection of African rice in this region. Mouser *et al*. [29] suggest that this may be linked to the food security needs of newly founded maroon communities of self-emancipated slaves fleeing Susu rice plantations.

Senegal. Senegalese *indica* (and hybrid) varieties resemble *japonica* in having fewer tillers and panicles, broader leaves and seeds than the *indica* from the other countries in the study. The land farmers work in Senegal mostly comprises hydromorphic soils, but also some uplands. The low tiller number is probably related to the relative earliness of local varieties. All farmer hybrids collected in Senegal had a light coloured pericarp as farmers strongly selected against red pericarp. A few off-types (representing old varieties) rogued from collected samples clustered with red seeded varieties from Guinea and Sierra Leone. This can be taken as an indicator that localised farmer preferences changing over time can influence the genetic make-up represented by the varieties cultivated.

Guinea Bissau. The collected farmer hybrids cluster with indicas and have low similarity to *japonica* from Guinea Bissau. Japonicas were cultivated under upland conditions and the farmer hybrids tended to be more frequently cultivated in hydromorphic zones. However, respondents said that in the past, when more labour was available for bird scaring, farmer hybrids were also cultivated in the uplands. The droopy farmer hybrids are genetically different from the erect farmer hybrids. One reason is seed colour. Mandinka farmers are unlikely to select an off-type with an erect panicle to develop it into a variety since they associate erectness of the panicle with (undesirable) red pericarp. The *glaberrima* from northern Guinea Bissau clustered with those from Senegal while those from southern Guinea Bissau clustered with those from Guinea and Sierra Leone. Climatic conditions are clearly different between the case study villages in the north and south of the country, but account should also be taken of the fact that historical relationships differ. The north is oriented towards Senegal (Casamance) and the south is oriented towards Guinea.

Togo Hills (Ghana and Togo). The relatively large diversity within the *indica*, *japonica* and *glaberrima* groups in the Togo Hills can be partly ascribed to the many different ecological niches found in a forested landscape that ranges from lowland to mountain where farmers take considerable advantage of intra-mountain basins for rice cultivation. These mountain basins offered the double advantage of more fertile soils and security. Rice diversity can thus be related to a history of refuge, displacement and enclaved social life in a region characterised by war and political instability. Seeking security, farmers strove to intensify farming on stony, acid and often sloping soils by emphasising *O. glaberrima*, the only rice available at that time. More recent factors include the developments in farming over the past 50 years. Until the 1960s, the main rice producing ecology was upland, where mainly *glaberrima* varieties were cultivated.
On the Ghana side of the range, farmers started to cultivate *indica* varieties in lowland areas from the 1960s onwards, while in the Togolese Togo Hills (mainly the Danyi Plateau) farmers continued - to this day- to cultivate solely *glaberrima* varieties, as no lowland ecologies were available to them. Lowland rice farming in the foothills of the Ghanaian Togo Hills has meanwhile become a major activity. It has also resulted in farmers introducing some *indica* varieties to hydromorphic and upland conditions. The cultivation of *glaberrima* is still maintained today, especially for its role in customary rites, and as a significant part upland cultivation clearly continues to set criteria for the selection and development of *indica* rice varieties [9]. This also helps explain why no farmer hybrids are found in the Togo hills. Here *O. glaberrima* and *O. sativa* are separated in the landscape by altitude, not grown side by side, as they have been for centuries, in Upper West Africa. It should also be noted that local customary rites demand use of pure *glaberrima* for feeding and sacrifice. This

acts as a disincentive to any farmer inclined to select off-types intermediate between *O. glaberrima* and *O. sativa*.

Conclusions and Implications

Main conclusions

This paper has combined morphological and molecular data with socio-economic and cultural information to provide a better understanding of how cultivation practices combine with environmental pressures to shape rice diversity in six case study areas in coastal West Africa. Examples have been provided of how, per botanical group and case study area, these integrated data offer novel insights into the potential of neglected crop resources. The paper points both to the complexity of farmer rice genetic diversity management and to the significance of farmer innovation.

For *O. glaberrima* the molecular and morphological data largely agree with each other (see Figure 1). The morphological data showed clear differences in morphological features between *glaberrima* varieties from the Togo hills and the Upper Guinea Coast region, and between Guinea and the other countries of the Upper Guinea Coast. A relationship between genetic diversity and agro-ecology emerges. Farmers did not exchange *glaberrima* varieties over large distances, and we did not receive information about the development of new *glaberrima* varieties (the Guinea case excluded). What seems now to be true is that ethnic groups either stress the true-to-type maintenance of specific varieties or have abandoned the cultivation of *glaberrima* altogether.

For the other botanical groups a different picture emerges. Molecular and morphological data do not always agree. Particularly for the *japonica* group more diversity was observed at the morphological than at the molecular level. This could be caused by the possibility that the molecular markers used were more informative on other botanical groupings than on the japonicas. Taken in conjunction with the findings on differences in adaptation within *japonica* reported by Mokuwa *et al*. [10] the question arises about whether the *japonica* harbour more genetic diversity than observed.

At the morphological level the three non-*glaberrima* botanical groups did not group geographically (by country, or groups of neighbouring countries). Particularly for indicas and the farmer hybrids, much evidence of recently introduced or newly developed varieties was recorded. Particularly with the farmer hybrids, seed colour has a clear relationship with the genetic make-up of rice varieties. Such a relationship is non-existent (or less clear) for the *japonica* group.

Apart from *glaberrima*, farmers seem ready to cultivate any variety of the other three botanical groups that meets a certain minimum set of criteria, such as plant height, time of ripening, seed colour and digestibility. Even these criteria are used flexibly, depending on the other advantages a variety may possess. For example, in general farmers prefer tall varieties. In Ghana this is because a long stem is considered easier for threshing. In southern Sierra Leone farmers mostly harvest by panicle and seek to avoid too much stooping and an aching back. Short plants, however, may not always be selected against if they have compensating advantages such as earliness [39].

For *glaberrima*, socio-cultural selection pressures seem to reduce diversity, particularly at a more local scale, while for the other botanical groups they seem to have an enhancing effect on genetic diversity. However, *glaberrima* still plays an important role in determining the selection criteria of farmers and shaping variety development pathways. For instance, farmers in northern Sierra Leone select farmer hybrids with erect panicles. This implies these farmer hybrids are selected according to standards established for *glaberrima* cultivation. Most japonicas in southern Sierra Leone have a red pericarp. This results from historically-specific socio-cultural selection pressures [29]. The farmer hybrids from Senegal and Guinea Bissau show much overlap with, respectively, the japonicas and the indicas in the PCA analysis. This is apparently related in part to shared agro-ecological conditions. The droopy panicle and light seed colour of farmer hybrids in this region also reflect a history of *O. sativa* cultivation. In sum, at a regional level, farmer hybrids combine (advantageous) traits from different botanical groups by embodying responses to different local cultural and ecological considerations.

Because farmers in West Africa embark on risk spreading practices - e.g. growing varieties mixed-in with other varieties and assigning sections of their fields to different varieties [47] – ‘in-situ’ experimentation and on-farm hybridisation is facilitated. In Sierra Leone farmer hybrids are generally popular; they are said to perform well under low field management and when consumed enable farmers to sustain longer hours of work without hunger, and are thus similar to *glaberrima*. In Senegal, the farmer hybrids also perform well under low field management, but do not have a red pericarp and in that respect are regarded as being similar to the *O. sativa* varieties commonly planted. The farmer hybrids are a welcome enrichment of local planting resources since they are genetically rich and diverse and can be considered products of long trajectories of interaction between botanical groups, ecological, socio-cultural and economic factors.

Wider societal context and implications

The present paper belongs to a group of three that report an interconnected set of findings: we first described the emergence of a new rice type of interspecific hybrid origin in West African farmers’ fields [23], then we analysed robustness and strategies of physiological adaptation within a large set of farmer varieties of African rice and Asian rice across West Africa [10] and third, this paper has compared morphological and molecular data with information on socio-economic seed selection factors, in order better to show how farmer practices and culture combine with environmental selection pressures to shape diversity in rice across coastal West Africa.

All three papers provide evidence that West African small-scale food-crop farmers conserve and develop valuable rice varieties, despite limitations of poverty, isolation, and formal education. A major implication of this result is that farmer practices and culture strengthen the conservation and development of genetic diversity. Modern varieties of many crops have little or no genetic disparity within cultivars. It has been estimated that as little as 20% [48] of the total diversity contained within the wild ancestors of rice, cassava, and soybeans is maintained through breeding of ‘modern elite’ varieties [49-51]. Our work shows, by contrast, that farmer innovation helps to protect this diversity and keep it ‘in play’ for future adaptation. Sustaining crop genetic diversity in situ is an especially important topic in an era of rapid climatic change. Our results, therefore, support calls for the protection and valorisation of farmer crop innovation processes, as a basis for addressing issues of rural food security in Africa.

Acknowledgements

The authors would like to acknowledge the contributions of all those involved in the research, in particular the staff of the research stations and universities in the countries involved, the farmers in the different countries, the research assistants at the different trial sites, and Rob van Treuren of the Centre for Genetic Resources, the Netherlands for contributing to the molecular analysis.

Author contributions

Supervised the research: EN HM PR PCS. Conceived and designed the experiments: AM EN FO BT HM PR PCS. Performed the experiments: AM EN FO BT. Analysed the data: AM EN FO BT. Contributed reagents/materials/analysis tools: AM EN FO BT. Wrote the paper: AM EN FO BT HM PR PCS.

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CHAPTER SEVEN

Maintaining or abandoning African rice: Lessons for understanding processes of seed innovation

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Published as: Teeken B, Nuijten E, Temudo MP, Okry F, Mokuwa A, Struik PC, Richards P. (2012) Maintaining or Abandoning African Rice: lessons for Understanding Processes of Seed Innovation. Human ecology 40: 879–892. DOI 10.1007/s10745-012-9528-x.

Chapter seven

Abstract

Rice breeding and crop research predominantly emphasise adaptation to ecological conditions. Based on qualitative and quantitative research conducted between 2000 and 2012 we show how ecological factors, combined with socio- economic variables, cultural norms and values, shape the use and development of local technologies related to the cultiva- tion of African rice (*Oryza glaberrima Steud.*) in seven West African countries (Ghana, Guinea, Guinea-Bissau, Senegal, Sierra Leone, The Gambia and Togo). In this region the role of African rice is diverse across ethnic groups. Findings suggest that farmers, through various pathways, are active in the development of promising new varieties based on genetic resources of Asian rice, African rice, or both, as well as in the adoption of modern varieties. These findings require fur- ther research into interactions among ecological, genetic, so- cioeconomic and cultural factors within farmers' innovation systems and recognition of emergent knowledge and technol- ogies resulting from such interactions.

Keywords: *Oryza glaberrima*; West Africa; Technology development; Farmer interspecific rice hybrids

Introduction

West African agriculture is characterised by high agro-ecological and cultural diversity, limited labor availability and access to agrochemicals, and a strong tradition of selfsufficiency. Consequently, farmers in many areas of West Africa have rejected “modern” varieties of rice developed by formal, science-based institutions for use with inputs such as fertiliser and irrigation water since their local vari- eties often outperform them (Sall *et al.*,1998).

Farmer participatory research stresses that technology development should connect to the needs and priorities of local communities (e.g. Farrington, 1988). This approach has led to the formation of institutions such as Farmer Field Schools (FFS). Although the aim of FFS was that farmers would learn optimally from field observations and experi- mentation, FFS have failed to properly address cultural and social dynamics (Isubikalu, 2007; Richards, 2007).

The “farmer first” paradigm (Chambers *et al.*,1989) associated with the rejection of the “transfer of technology” approach was also responsible for new approaches to seed development and dissemination, such as participatory vari ety selection (PVS) and participatory plant breeding (PPB) (Almekinders and Elings, 2001). A role for farmers in varietal development and selection was recognised particularly in PPB. While in PVS farmers select among finished or almost finished breeding products (Gridley *et al*., 2007), in PPB most of the breeding process is transferred to farmers’ fields (Ceccarelli and Grando, 2007). PPB has much poten- tial to valorise farmer varieties, but plays only a minor role compared to PVS. Farmers’ varieties are the outcome of a long breeding process shaped by ecological and social factors, but this legacy tends to be neglected in existing partic- ipatory seed improvement approaches. This is perhaps because farmer varieties are seen as the product of more or less static ‘traditional’ technologies and suitable only for local conditions, where they are still used only because of lack of better, scientifically developed, alternatives.

Farmers’ processes of innovation and variety development continue to remain almost invisible to research and develop ment organisations in the formal seed improvement sector. In the rare cases where it is acknowledged that farmers produce valuable seeds, these are thought to be adopted only on a local scale and thus unsuitable for use together with scientifically developed varieties (Mokuwa *et al*., 2012). There have been no releases of improved African rice varieties.

Although the Consultative Group for International Agri- cultural Research (CGIAR) and national agricultural research centers have been increasingly integrating participatory approaches in the development and dissemination of new technologies, these approaches are insufficiently informed by recent findings from interdisciplinary research involving social scientists. Cernea (2005) argued that social scientists are still fighting an ‘uphill battle’ against ‘institutional barriers, scholarly biases from other researchers or some centers’ man- agers, and virtually suffering from constant underfunding’ (2005: 73). Additionally, as Davidson (2010) has highlighted, access to farmers’ technical capacity can be particularly tricky in societies where this knowledge is deeply bound up with complex communicative strategies. Consequently, local cultural and social determinants of farmer development of seed varieties and acceptance of new varieties remain barely acknowledged in many research and development initiatives (Richards, 1996; Okry *et al*., 2011; Temudo, 2011). To rectify this it is essential to assess the cultural, social and historical factors that along with ecological factors have shaped local seed technologies and preferences.

The cultivation of African rice (*Oryza glaberrima Steud.*) by many farmers today is a good example of the complex dynamics behind the development and adoption of new local seed technologies, particularly because, to date, scientists have rejected this species as a candidate for improvement. All cultivated varieties of *Oryza glaberrima* are entirely the prod- uct of farmer agency. Understanding these processes is given renewed significance by the recent discovery of West African farmer rice varieties with an interspecific background that are the outcome of the crossbreeding of African and Asian rice in farmers’ fields in response to agro-ecological and sociocultural selection pressures (Nuijten *et al.*, 2009). They are distinct from the well-known Nerica rices (*O. glaberrima* × *O. sativa* crosses produced by modern breeding techniques).

There is general agreement that *O. glaberrima* was domesticated in West Africa around 3,000 years ago while Asian rice was introduced to the region by European Atlan- tic traders from the sixteenth century onwards if not earlier through trans-Saharan trade routes. The grains of African rice are generally more glabrous (hence *glaberrima*) and have a red/brownish pericarp. The plant has a particular round and short ligule and its panicles stand upright unlike Asian rice, which has a longer and more pointed ligule and panicles that droop after flowering. Across West Africa, African rice plays an important role in the ritual life of farming communities (Brydon, 1981; Linares, 2002; Tanzibul *et al*. 2004) and it retains a deep cultural significance among some African dias- pora groups in South America (van Andel, 2010).

This article analyses why farmers in different parts of the West African coastal zone either continue to grow or have abandoned *O. glaberrima* as an illustration of local agency in seed technology and innovation adoption in rice farming, in particular in relation to variety development. Five case studies are presented: (1) a detailed comparison among three ethnic groups in the Togo Hills in Ghana and Togo, (2) the Mandinka rice farming system in The Gambia, Senegal and Guinea- Bissau, (3) the Balanta mangrove rice farming system in Guinea-Bissau, (4) the Susu farming system in

Maritime Guinea, and (5) a comparison of the Temne and Mende ethnic groups in Sierra Leone (Figure 1). The results illustrate how farmers' history, culture and organisation coproduce and shape impor- tant and successful seed technologies in different ways.

We argue that farmers can and should be regarded as research partners in the production of seed technologies with considerable potential to be disseminated and promoted more widely. This would imply that farmers' varieties developed in different places of the world can be transferred successfully to other regions. To support this aim we argue, further, that the epistemological context and the historical trajectories within which farmer varieties have arisen should be more fully researched (See, for example, Mouser *et al.,* 2012)

Figure 1*: Case study areas are indicated by pushpins*

Methods

The Togo Hills of Ghana and Togo: the Akpafu, the Lolobi and the Ewe

We conducted research in 2007 and 2008 in two areas in the Volta Region of Ghana, Akpafu and Lolobi, and one in Togo, the Danyi Plateau. In Akpafu, Lolobi and on the Danyi Plateau, 150, 103 and 148 households were interviewed, respectively, using questionnaires. An additional 18 farmers on the Danyi Plateau were interviewed in depth on rice cultivation practices and all their fields were visited. In-depth interviewing was combined with participant observa- tion and evaluation of different rice varieties in farmers' fields. In Ghana, research was carried out mainly in the villages Akpafu Odomi and Lolobi Kumasi, 10 and 8 km north of Hohoe, respectively. A few households from the neighboring villages of Lolobi Ashambi and Akpafu Mempeasem were also included. These villages were selected because of their extensive involvement in both lowland and upland rice cultivation and their representativeness for the Akpafu (3 villages) and Lolobi (4 villages) areas.

The Akpafu and Lolobi are minority groups that share languages belonging to the "Togorestsprachen" (Westermann, 1954), with little relationship to the regionally dominant Ewe language. These groups all share some history as refugees (Nugent, 2002). The Lolobi and the Akpafu were divided during a war with the Ashanti. The Lolobi managed to resist while the Akpafu, located on the other side of a mountain, surrendered. A German Protestant mission from Bremen converted the Akpafu to Christianity around 1800. The missionaries were keen to eliminate local beliefs and were rejected by the Lolobi, who later (1903) converted to Catholicism since the Catholic missionaries showed respect and interest in their local religion and allowed them to continue their traditional practices.

In Togo, approximately 40 km from the Ghana case study villages, data were collected in four Ewe-speaking villages on the Danyi plateau: Elevagno, Xexatro, Mempeasem, and Dafor. The inhabitants are active in upland rice cultivation on poor and acid soils. African rice is the main rice species on the Danyi Plateau. Although the Ewe are a distinct linguistic group they share a history as refugees in the area (Quarcoopome, 1993).

The Gambia, Senegal and Guinea Bissau: the Mandinka farmers

Research was carried out in eight Mandinka villages and one Jola village in The Gambia, southern Senegal (Casamance) and northern Guinea-Bissau. Case studies were conducted in Western Division (from 2000 to 2003, 2007 and 2008), Region de Sedhiou (2007 and 2008) and Oio Region (2007 and 2008). In Western Division, The Gambia, in-depth research was conducted in four villages (Tujereng as principle site and Faraba, Janack and Kitti as additional sites), where in total 104 households were interviewed using a diversity of methods. These villages are populated mainly by Mandinka farmers, but also contain considerable numbers of Muslim Jola who fled from the conflict in Casamance that started in 1981 (Linares, 1992). Janack is a Jola village. All were selected because farmers in these villages actively cultivate both upland rice and late millet. The villages in Region de Sedhiou (Bunjadu and Dar Silame) in Casamance and in Oio Region (Kolosar and Djendur) in Northern Guinea-Bissau were selected because they are connected through seed and variety exchange networks with the Gambian villages. In Region de Sedhiou and in Oio Region, 20 and 22 households respectively were interviewed using questionnaires.

Guinea Bissau: Balanta farmers

Extensive ethnographic research (a total of 36 months of field work) was conducted in the Cubucaré peninsula of southern Guinea-Bissau (the heart of rice production), not far from the border with the Republic of Guinea. Between 1994 and 2003 up to 244 household heads were interviewed on rice variety selection and innovation processes using semi-structured interviews (Temudo, 2011). During this period a total of 1420 interviews were conducted with mangrove swamp rice farmers living in 59 different villages evenly distributed across the region, of which 71% were Balanta (who practice tradi- tional religion). The remainder (29 %) belonged to other ethnic groups (with a majority of Muslims). In addition, focus group discussions were conducted in 2001, 2009, 2011 and 2012 with farmers from 156 villages across the entire country practicing mangrove swamp rice cultivation to understand variety naming and selection criteria, and to assess the persis- tence or abandonment of *O. glaberrima*.

Guinea: Susu farmers

Data were collected in Maritime Guinea. Field research covered three sub-prefectures (local levels of government): Molota, Friguiagbé and Moussayah, located in the prefectures of Kindia and Forecariah. Ten villages were selected and, based on their proximity to each other, were grouped into three research sites. Site 1 villages (Bokariya and Sangaran) were chosen because of their remoteness (about 90 km from Kindia, the regional capital) in order to learn about farmers' seed strategies and varietal selection practices in a situation of poor infrastructure, limited interventions of development organisations and absence of important nearby markets. Site 2 villages (Seifan and Dentègueya) were selected because of their proximity to the rice seed center at Kilissi and the Centre de Recherche Agronomique de Kilissi (CRAK), the national rice breeding unit. Site 3 villages (Kinyaya, Hononkhouré, Tour, Yaya, Dandakhouré and Sinta) were selected because of their proximity to Kindia. The dominant ethnic group is Susu, and the dominant religion is Islam.

Data were collected using focus group discussions, ques- tionnaires and informal interviews. Interviews took place in 2007 and 2008 and covered 91 rice-growing households (32, 24 and 35 selected from sites 1, 2 and 3 respectively).

Sierra Leone: the Mende, Temne, Limba and Susu farmers

Between 2007 and 2009 extensive ethnographic and botanical data collection was undertaken in six chiefdoms: Kamajei, Kholifa, Rowalla, Magbema, Tonko Limba and Bramaia in a transect from central to northwestern Sierra Leone. In 2007, 287 household heads living in six villages were interviewed using questionnaires. Between 2008 and 2009, the sample size was enlarged to 1,575 households. The selection of interviewed households was based on proximity and access to farmland.

Four ethnic groups were represented: Mende, Temne, Limba and Susu. The Susu are mainly found in the Kambia district in the northwest of the country along the international border with Maritime Guinea. The Limba and Temne were predominantly sampled in the northwestern and north-central part of the country. The Temne share boundaries with the Kpa-Mende, who occupy the central portion of Sierra Leone. The villages were selected in order to analyse how agro-ecological and sociocultural factors impact in village rice variety portfolios and genetic diversity, and to explore the role of African rice under extreme conditions. Islam is the main religion among all ethnic groups, but there is a large Christian minority among the Mende, the Temne and the Limba.

Results

African rice is still actively cultivated in Guinea-Bissau, Guinea, Sierra Leone and the Togo Hills in Ghana and Togo, but was mostly found as a weed in farmers' fields in Casamance (south Senegal) and The Gambia. This section summarises the different reasons, and the combinations of factors that determine whether African rice is maintained as a crop or is abandoned.

The Togo Hills of Ghana and Togo: Akpafu, Lolobi and Ewe farmers

African rice used to be the staple food of the Akpafu and Lolobi in Ghana and the Ewe on the Danyi Plateau in Togo, at a time when war and uncertainty forced them to seek refuge in mountainous areas. African rice grows well on hillsides and in the poor soils on the Danyi Plateau and it is usually intercropped with cassava. Its rich nutritive value is mentioned by all farmers, who in general state that African rice and other red farmer varieties are "heavier." The rice is said to stay in the stomach longer and therefore enables one to work longer without getting hungry.

Besides rice production, farmers in the Ghanaian foothills of the Togo Hills massif have incomes from cocoa farming and from non-agricultural activities. Farmers on the Togolese side of the Togo Hills (in the hills proper and on the Danyi plateau) do not have many economic opportunities outside agriculture. Coffee tree production, which used to generate income, is no longer lucrative since coffee prices dropped. Farmers grow vegetables for the local market and rice, cassava, yams and maize mainly for subsistence.

For the Lolobi in Ghana African rice is a religious asset. Although most of the rice cultivated in Lolobi and Akpafu now is Asian rice (*O. sativa* L.), African rice (*Boadekamo* in Siwu) is still grown in small quantities for customary rites, marriages and funerals. *Boadekamo* is not a single variety but a mixture of seven different varieties of *O. glaberrima* (Figure 2).

The Lolobi and the Akpafu cultivate African rice in mixture since they regard the varieties as being the same ancient rice that was cultivated by their ancestors. Asian rice dominates in the form of the variety *Viono* and this actually resembles African rice especially in pericarp color, taste, cooking characteristics and "heaviness."

Figure 2*: Panicles of Boadekamo. This variety is constituted of several varieties of African rice (O. glaberrima).*

White (Asian) rice is also grown (mainly for sale) both by the Akpafu but especially by the Lolobi. It is often consumed mixed with some *Viono*, as red-skinned rice is greatly preferred over white rice. The pericarp of all red rice, be it Asian or African rice, is only partly (about 75%) removed in preparation. When red rice is used for porridge or to make a thick paste called *fufu*, none of the pericarp is removed. Porridge and *fufu* are considered very nutritious and often used as baby food, as food for pregnant women, and as the basis of meals for special occasions.

According to informants, a farmer discovered *Viono* within another red variety around 1990, and since then this variety is said to have spread all over the lower Volta region. At the Kpong research institute (University of Ghana) researchers were not able to classify this variety. Dr. Kofi Dartey (personal communication, Hohoe, 2007) , who runs a rice program at the Crop Research Institute in Kumasi, stated that this variety was certainly not introduced by any research institute and belonged to the interesting local varieties found in the Hohoe area. It seems certain that *Viono* has a farmer origin, since scientific research has only very recently been directed towards developing red-skinned varieties (e.g., Nerica 14 and 18). *Aworema* is a second promising red Asian rice variety that was discovered within *Viono*, and is very similar to it. The main difference lies in its erect leaves that protect the panicle against birds (the name *Aworema* means ‘hiding from the enemy’ in Siwu). *Aworema* was discovered in Lolobi around 2006. This also accounts for the small proportion of *Aworema* in Akpafu (Table 1). The preference for red pericarp varieties explains why the farmer hybrid *Untufa* from Guinea Bissau with an interspecific origin (Nuijten *et al*., 2009) was so positively evaluated by Lolobi farmers in comparative trials (chapter 3, this thesis) ; the variety resembles *Boadekamo* in grain and panicle shape and yields very well. Farmers stated that it can therefore be used for customary rites.

Table 1 shows the role of African rice (*Boadekamo*), *Viono* and *Aworema* in rice production in Lolobi Kumasi and Akpafu Odomi. The importance of African rice among the Lolobi is illustrated by the following statement by a farmer (2007):

> ‘The *Boadekamo* is like the chariot of the queen of England, until today they have not replaced the chariot with a car […] we change varieties all the time and we abandon varieties all the time so we have to have something that stays the same, something that [would be] recognised by our forefathers’.

In Lolobi Kumasi, *Boadekamo* plays a very important role in offerings to the ancestors and to local gods. Viono and other food crops cannot be used. Offerings are made in the home at the household shrine and to the seven local gods through their priests (Mabia), who are consulted by clients seeking prosperity and solutions to pressing problems (Figure 3). African rice is, in short, an important component of the community’s moral and physical well-being, a link between the domains of production and religion.

In contrast to the Lolobi, African rice is more a cultural than religious asset among the Akpafu, who have largely abandoned family rituals and local gods and are strongly hostile to traditional religion. People who still perform rituals related to these gods are openly stigmatised as ‘pagans’. However, African rice is still cultivated for cultural reasons (Table 1), such as libations and offerings to the ancestors and gods which are legitimised by the Akpafu when done explicitly out of respect for local culture and tradition; to do so in the name of religion would be considered a sin. African rice remains part of funeral and marriage ceremonies and an important ingredient for dishes eaten on all special occasions. Interestingly one of those dishes, *Kamokra*, can today be made with the Asian rice variety

Viono. African rice is thus a marker of cultural identity but no longer connects religion to the domain of production.

***Table 1**: Estimated proportion (%) of rice production within agro-ecology in the Lolobi and Akpafu areas in Ghana in 2007 and 2008 (Survey 2008).*

Area	Lolobi				Akpafu			
Agro-ecology	Upland		Lowland		Upland		Lowland	
Year	2007	2008	2007	2008	2007	2008	2007	2008
Nr. of farmers	20	36	54	75	10	19	57	82
Red rice	**92**	**100**	**61**	**65**	**93**	**70**	**83**	**85**
Boadekamo (African rice)	*39*	*76*	*9*	*4*	*24*	*13*	*2*	*2*
Viono	30	10	35	32	69	28	70	81
Aworema	23	14	13	25		5		1
Damansah			4	4		17	4	1
Mateggi							1	
Saka						7	6	
White rice	**8**	**0**	**39**	**35**	**7**	**30**	**17**	**15**
Adeisi	8		21	12	7	6		
Akpesse			10	10				
Aqua blue						<0.5		
Kabila						18	4	3
Longgrain				3				
Nerica			2	4				
Perfume			6	7		6	13	12

Among the Akpafu, *Boadekamo* is assessed as having good taste, high nutritional value, and as a mark of community identity. In interviews, farmers frequently stated that *Boadekamo* has not vanished completely because the older farmers are familiar with cultivating it, and also because outsiders had told them that it was very good rice[1]

[1] Researchers from the University of Reading, England were mentioned several times (see Dorward *et al*., 2007).

For the Ewe on the Danyi Plateau of Togo, African rice remains an important food crop but is used purely for subsistence. Apart from some very small fields of Asian rice in the scarce humid backlands, only African rice varieties are cultivated. Farmers do not have means to acquire fertilisers, and African rice seems to be the only rice that thrives well in the poor soils typical of the plateau. The seven African rice varieties making up *Boadekamo* in Akpafu and Lolobi are cultivated separately here, since by respecting differences in cycle length farmers can get higher yields. Optimal cycle length can be achieved by planting some varieties earlier and others later. Sowing a short duration variety too early will result in larger vegetative growth, to the detriment of productive growth. The advantage of respecting the optimal cycle length is no longer valued by the Lolobi and Akpafu farmers, probably because they are no longer dependent on African rice as a basic staple.

Figure 3*: Offering to a village god in Lolobi Kumasi Ghana in which African rice flour is compulsory.*

Perhaps rather surprisingly, the Ewe of the Danyi plateau do not depend exclusively on African rice for ceremonies and rituals for ancestors. Other crops such as maize, cassava and yams are also used in these contexts. Almost all farmers (146 out of 148) stated that it does not matter what kind of rice variety is used in ceremonies as long as it has been cultivated on their own land. Six interviewees (a fetish priest and other people familiar with performing funeral and marriage rites) all stated that the local rice (*O. glaberrima*) is necessary. They indicated later, however, that it was not the morphology of the plant that was important but that the rice was cultivated on their land. In detailed semi-structured interviews on rice cultivation with 18 farmers all stated that they would readily abandon the traditional African rice variety should they find a higher yielding one. Such rice could then, without any problem, also be used in ceremonies. African rice, with its specific plant and seed characteristics, has not taken on religious significance as it has for the Lolobi. Although in relation to other crops the area cultivated is relatively small, rice is nevertheless regarded as a key food crop, offering important nutritional value in a diet otherwise consisting mainly of cassava, yams and maize.

Figure 4*: A field of the African rice variety Danyi Molni on the Danyi Plateau, just before harvest. Notice the straight panicles.*

The Gambia, Senegal and Guinea Bissau: the Mandinka

In The Gambia, in the south of Senegal (Casamance) and in the north of Guinea-Bissau, Mandinka farmers have stopped growing African rice. The main reasons given are the red bran or "pericarp" and the difficulty of milling by hand. It is the removal of the red pericarp that makes the pounding difficult. Mandinka farmers (but also farmers from other ethnic backgrounds living in the same region) have a strong preference for white rice. Women indicated that they preferred a white grain color even in the past when they still cultivated Asian rice varieties with a red pericarp.

Another disadvantage of African rice is that its taste is considered good only for certain dishes, like porridge and munkoo (small balls made of flour, traditionally made with the first harvested rice, and used for various ceremonies). Other disadvantages mentioned by only a few farmers were low yield, lodging, earliness and tillering among others (Table 2). Yield trials conducted in The Gambia in 2001 and 2002 suggest that African rice does not seem to perform less well than Asian rice (Nuijten, 2005). A survey conducted in the three case study areas in 2007 showed that an increasing number of Mandinka farmers consider African rice to be something bad, unrelated to agronomic or culinary aspects. The negative traits they men- tioned included the erect panicle (8 out of 63 farmers) and “they just do not like it” (7 out of 63 farmers) (Table 2). These answers were particularly given by younger women who have never cultivated African rice themselves.

Table 2*: Disadvantages of African rice (O. glaberrima) mentioned by Mandinka female farmers in three case study areas in 2007*

Nr of farmers	**The Gambia** 21	**Casamance** 20	**Guinea Bissau** 22	**Total** 63
seed colour	7	9	13	29
difficult pounding	4	7	8	19
panicle does not bend	2	2	4	8
‘I do not like it’	1	3	3	7
bad taste	3	2	1	6
too early	0	1	0	1
low yield	0	1	0	1
needs rain	0	1	0	1
shatters	0	0	1	1
itches	0	0	1	1
few grains / panicle	0	0	1	1
lodges	0	0	1	1
does not swell when cooked	0	1	0	1
does not tiller	0	1	0	1
unpounded grains remain in mortar	1	0	0	1
difficult threshing	1	0	0	1
dominates the seed if not rogued	1	0	0	1
no disadvantage	0	1	1	2
no answer	1	0	0	1

In the past, the main advantage of African rice was its earliness. Another advantage was the taste of its porridge. In The Gambia older women say African rice was cultivated up to the 1970s. In Casamance women stopped its cultivation only very recently. In most cases they sowed it mixed in fields of Asian rice, because farmers said the African rice does not yield much and it would be a waste of land to sow it in pure stands. Some women, however, say ‘it is just a saying that it does not yield much’.

Until the 1950s women of the village of Tujereng in the western part of The Gambia preferred pounding African rice instead of “findo” (Digitaris exilis), which is even more difficult to mill. However, when men stopped growing findo because of lack of labor and children started going to school, the cultivation of African rice also decreased. Increased turnover reduced the mouldy smell associated with rice sold in shops. A sharp increase in rice imports around 1970 was another reason for women to stop growing African rice. This coincided with the introduction of the first early maturing Asian rice variety, Kari Saba, in Tujereng, one of the first farmer hybrids introduced in The Gambia. The availability of early maturing varieties with a white or brown pericarp color was another reason for women to stop cultivating African rice and it is likely that the availability of these newer varieties, mostly with an interspecific origin, led to a sharp decline in the cultivation of African rice. Nowadays, only a few, predominantly older, farmers grow African rice as a mixture in the field. In The Gambia older farmers say the first rice cultivated was African rice, called Mani ba in Mandinka (Nuijten, 2005). *Mani ba* means ‘old rice’ and *ba* is also used to indicate ‘respect’. Some older women know it is older than all other rice varieties, and that it originates in the faro (lowland):

> ‘When there was a drought in the faro, all rice died and people did not have any seed. The next year *Mani ba* was the only rice to germinate in the field. So people harvested the *Mani ba* and used that as seed again the next year, and so on. That is why *Mani ba* is the oldest rice. This happened a very long time ago’.

These women say they only mix *Mani ba* in the seed planted in the upland but not for faro (lowland), where it originates and germinates naturally. Nowadays, *Mani ba* is mostly present as a weed in farmers’ fields, particularly in the lowlands and transitional zones. In the lowland areas of the villages of Kitti and Faraba *Mani ba* is much more common than in the uplands of Tujereng and farmers seemed to rather dislike it in their fields. In Kitti and Faraba women call African rice ‘*Lola,’* which means ‘standing straight up,’ because its panicle stands straight unlike the bending panicle of Asian rice. Many of the older women of Tujereng say they are happy if they see it in their rice field, and some say they mix a few panicles of *Mani ba* in the seed for the sake of tradition. Some older women also said that if you see *Mani ba* in your field, you know you will have a good harvest, it will bring you luck.

Changing beliefs and attitudes may also play a role in the sharp decline in African rice cultivation. In the Region de Sedhiou in Casamance women still maintain some cultural notions related to rice cultivation, such as the idea that mixtures in the field can be sown by 'other beings' and should not be removed as this may cause problems in the future when the 'other being' wants to collect his/her rice. It is only in recent years that woman in the Region de Sedhiou stopped the cultivation of African rice. This contrasts with The Gambia and northern Guinea Bissau, where African rice was abandoned several or many decades ago. Interestingly, the men of the Region de Sedhiou are considered very learned in the Koran, and their wives seem to maintain traditional cultural ideas more tenaciously than rural women in The Gambia or in Guinea Bissau. It might therefore be suggested that Islam has played a part in the complex decisions among the Mandinka to abandon African rice cultivation (Linares, 2002).

Guinea Bissau: the Balanta

In Guinea Bissau four different varieties of *O. glaberrima,* each with a slightly different cycle, are cultivated in the uplands and in both inland fresh-water and mangrove swamps but by only a few farmers, mostly Balanta and Jola (or Felupe, one of the smallest ethnic groups in Guinea-Bissau). In terms of husk (not pericarp) color, two varieties have a whitish husk, one has a black husk, and the fourth has a brownish-black husk. At present, only Jola farmers are still using the white husked *O. glaberrima* varieties in propitiatory agricultural rituals, but both the Balanta and the Manjako acknowledge that in former times only African rice varieties could be used in these rituals.

The white husked African rice varieties are said to be the 'first rice'[2] and labeled by Jola, Balanta, and Manjako as either "primordial rice" or rice belonging to that particular ethnic group (e.g., *Malu brasa* meaning Balanta rice). The Balanta have a general name – *N'conton* – for all *O. glaberrima* varieties. This reflects their eating characteristics. Usually the term designates the leaves of edible plants (such as baobab, cassava, sweet potato) when they are old and hard to digest. *N'conton* are eaten during the "hungry gap" before the beginning of the main Asian rice harvest. Any surplus is then set aside to feed laborers, when a very nutritious food that is digested slowly is needed. It is also said that it cannot be eaten at night (the belly swells and hurts), especially by old people or young children, unless it is parboiled and subsequently cooked in a mixture with other varieties.

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[2] The black husk African rice varieties are reported by Jola and Balanta farmers as being adventitious plants that appeared in the white husks varieties' fields and that afterwards were selected and propagated.

The majority of the farmers interviewed attribute the origin of African rice to God or the spirits, and only a few could trace any domestication pathway. The following statements of two Balanta farmers encapsulate the folk history that describes decentralised domestication in West Africa[3]:

> 'In old times people discovered *N'conton* in the swamps. They harvested the seeds, [and] brought them home. Then they sowed it and had a huge output".
>
> *"N'thante* (*O. barthii* [wild rice]) is *N'conton* (*O. glaberrima*). It was from *N'thante* that all *N'conton* varieties came. When you cultivate *N'conton* [for]many years on the same parcel [of land]it turns again into *N'thanthe*'.

The Balanta are the main ethnic group in demographic terms in Guinea Bissau, and they are also the sole producers of rice surplus in the country. Oral and written sources locate the Balanta homeland in a region in northern Guinea Bissau, between Rio Geba and Rio Casamance (Hawthorne, 2003). They later settled the coastal wetland zone, and developed more intensive mangrove rice farming from perhaps the sixteenth century.

In the northern Oio province they today practice upland, freshwater and mangrove swamp rice cultivation according to the mix of agro-ecological conditions found in each village. However, around 1900 when some Balanta migrated to the southern regions of Quinara and Tombali, driven by land scarcity and a desire to escape colonial forced labor, they concentrated exclusively on mangrove swamp rice and related technologies (Temudo, 2011). They brought an African rice, *Mal-mon* (black rice), which due to its high salt tolerance is the first to be cultivated in newly created mangrove swamp fields. The seeds are also used as a medicine for hepatitis. The southern Balanta are considered the most skilled mangrove swamp rice producers in Guinea-Bissau, and perhaps on the whole of the West African coast.

Balanta farmers describe *N'conton* varieties of rice as having the shortest growing cycle until recent introduction of modern varieties, well adapted to poor and hard soils (its many roots are said to soften the soil), high tillering capacity, sufficient weed competitiveness to allow direct sowing and to limit weeding required and are drought tolerant and tolerant to pre- and post-harvest pests. They have erect panicles and the seeds shatter and germinate the following year, and plants can be uprooted and transplanted very early. They have hard grains that are difficult to cook and digest that only slightly

[3] This history contradicts Portères' (1962) version of a domestication centre in the inland delta of the Niger and two secondary centers of diversification.

expand (due to high amylose content (Futakuchi and Sie, 2009)) and have an unpleasant taste. These last qualities can be advantageous in times of scarcity when people would not complain if less than the usual quantity is served and when hard labor demands an especially filling meal. Old women also cultivate it on the dykes for medicinal purposes or to sell. According to other ethnic groups, today, the kinds of varieties that are hard to chew and difficult to swallow are said to be varieties associated with "[formerly] enslaved people".

The red or brownish pericarp of African rice and some Asian varieties is considered a negative trait by women of all ethnic groups most of whom still dehusk and polish their rice with a pestle and mortar. Both women and men state that people have always preferred to eat rice varieties with a white pericarp, or varieties from which the red/brownish pericarp has already been removed. Today, women say that varieties with a red pericarp are "dirty", and those who do not polish the rice until almost all the red pericarp is removed are considered lazy by their peers. However, while non-Balanta (mainly Muslim) women prefer varieties with a thin, white pericarp (known as "one mortar," because they only need to be dehusked and slightly polished), Balanta women favor varieties with a thick (usually red) pericarp because the bran is important as pig food. Nevertheless hunger is a great leveler of preferences, and all ethnic groups eat the whole pericarp during the end of the hungry season, when the first panicles have matured and the grain must be parboiled to be dehusked. Until the 1970s varieties of African rice had the shortest growing cycle and during the hungry season could be eaten as whole grain flour mixed with some water and honey or sugar (a practice still observed among the Jola and somewhat similar to *munkoo* eaten by Mandinka). An advantageous characteristic of *N'conton* varieties reported by those farmers who still harvest rice panicle by panicle with a knife as it matures (a practice frequent among the Jola, but now rare among the Balanta) is that if the rains persist the plants ratoon (that is, they produce new tillers with panicles), thus prolonging the harvest for a further three months.

After independence, climatic instability increased, and people also began to travel a lot, regularly bringing back new rice varieties. *Mal-mon,* highly praised by southern Balanta farmers, began to be replaced, until only a few farmers still cultivated it. *Caublak* was the main variety adopted by Balanta farmers after independence due to its early maturation (less than four months), moderate salt tolerance, fairly stable productivity in different ecologies and climatic conditions and its relatively good eating and cooking qualities (Temudo, 2011). In the Cubucaré peninsula, 10.6% of Balanta (107 of 1008) cultivated *Mal-mon* versus only 0.5% of non-Balanta farmers, although there were marked variations over the years (Figure 5). In 1997, irregular rains led to a bad harvest and in 1998 an 11-month civil war began and southern farmers hosted internally displaced relatives and friends.

This long period of rice scarcity led to an increase of *Mal-mon* cultivation among the Balanta in 1998 and 1999. In 2001 (and in 2005) exceptionally high tides destroyed many dykes, resulting in food insecurity and an increase in soil salinity leading to the second resurgence in *Mal-mon* cultivation in 2002 (Figure 5).

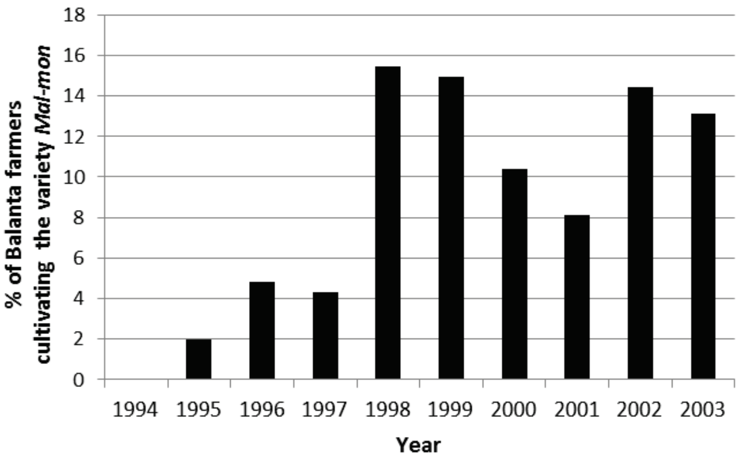

Figure 5*: Percentage of Balanta farmers cultivating the African rice variety Mal-mon in the Cubucaré peninsula, Guinea-Bissau, from 1994 to 2003. Source: M.P. Temudo and R. Figueira (unpublished data).*

Contrary to the situation in Tombali province, which has the highest rainfall in Guinea-Bissau, in the North and in the southern province of Quinara, Balanta farmers prefer the shortest cycle white husked *N'conton* variety, which is drought tolerant and has a high amylose content. This is cultivated in the upper part of the valley side soil catena where the soils dry quickly. Although many prefer the tastier short cycle rice belonging to the *Abulai* varietal complex, or the recently introduced modern variety *Culhi néme*, the extent of African rice production is reported by farmers to be increasing due to its drought resistance and its slow digestive properties.

These facts call for a need to closely monitor the rate of cultivation of *N'conton* varieties and the factors influencing this rate as an indicator for the stability of rice production in the region in particular and in general of adaptation to climate change.

Guinea: the Susu

As in Akpafu Odomi (Ghana), there are few if any ceremonies associated with rice farming in the Susu area of Maritime Guinea because Islamic religious practices not related to rice cultivation are now dominant. However, there is still a strong folk belief that "rice yield" can be stolen by witches, or that the entire harvest might be stolen in the night by thieves. Specifically the African rice variety

Sali Fore is mixed at sowing with other varieties (African or Asian rice) to prevent theft and crop failure caused by witchcraft since it is well known in the area that one should never approach *Sali Fore* by night, even when stored at home. No other variety of African rice is regarded as having this property. Farmers mixed on average three rice varieties per field (Okry, 2011). These mixtures, called *Sumbu*, are made before sowing and should contain at least one African rice variety. However, 10% of the mixed fields surveyed in 2007 were mixtures of only Asian rice varieties (Okry, 2011). In the other 90%, African rice represented on average 50% (min. 25%, max. 75%) of the mixture. A mixture of only African rice varieties was not observed in the study area. Farmers reported preparing *Sumbu* for different purposes:

- To protect the field against witches, for which only the variety *Sali Fore* is used.
- To assure a stable yield and prevent crop failure. Farmers expect that at least one variety will survive unpredictable rainfall and decreasing soil fertility.
- To reduce the quick consumption of certain Asian rice varieties such as *Samba*, *Pode*, *Dalifode* which are very light but tasty, farmers purposely mix them with African rice varieties, most often *Sali Fore* and *Tombo Bokary*. Some upland African rice varieties (*Siiga* and *Saafary*, for example) were not used to make up *Sumbu* but cultivated as stand-alone varieties, as were some of those used in *Sumbu*.

Table 3 quantifies the cultivation of African rice in Southern Lower Guinea from 2004 to 2007. African rice accounts for 15% of the cultivated area. It is also important to note that the size of fields planted with African rice is comparable to those with Asian rice.

***Table 3**: Characteristics of the use of African rice (O. glaberrima) in variety number, percentage of total cultivated area and average field size, in upland rice cultivation in Southern Lower Guinea (survey 2007 and 2008).*

Year	Number of fields measured (N)	Total number of Asian rice varieties	Total number of African rice varieties	Percentage African rice (of total area)	Average field size with Asian rice (ha)	Average field size with African rice (ha)
2004	66	9	4	15	0.61	0.80
2005	86	5	5	18	0.54	0.53
2006	105	10	2	13	0.76	0.86
2007	170	13	5	15	0.69	0.67

Sierra Leone: the Mende, the Temne, the Limba and the Susu

Findings from fieldwork in 2007 and 2008 show that communities within the chiefdoms in the north have fewer rice varieties per farmer compared to those in the south (Table 4). Gravelly and rocky soil may be a partial reason why farmers in the north grow predominantly African rice and farmer hybrids, as both seem to be well adapted to poor soils. For all studied ethnic groups rice with a red pericarp has a positive connotation. Additional research points to an increase in the cultivation of farmer hybrids in northern Sierra Leone during the war, possibly because they require low level of field management and are adapted to poor soils.

The case study areas in the southern part of the country are located within the interior lowland plateau (below 100 m) at the foot of the escarpment, with undulating lowlands. The vegetation is secondary forest 'oil palm' bush and derived savanna. There is a strong preference for Asian rice varieties with a red pericarp (Table 5), perhaps because the soils are more suitable for Asian varieties. Traditionally, farmers in this region consider African rice as hunger-gap stand-by, sown early (in mid-April) and harvested late August to early September. These were non-photoperiod sensitive African rice varieties. These have now often been replaced with short cycle Asian rice varieties and farmer hybrids (Jusu, 1999), with the advantage that the Asian and hybrid types are easier to thresh and mill. Rice with a red pericarp is also important in ceremonies for community gods of river, streams and trees and ancestral spirits that are performed by ’traditional societies, which are not considered in conflict with Islam or Christianity and are present within all ethnic groups.

Additional research conducted in Susu communities along the international borders with Maritime Guinea shows similar findings to those in Guinea. It is claimed that the African rice variety *Sali fore* has certain protective powers against witchcraft. Among Limba and Susu farmers *Sali fore* is considered to be one of the oldest rice types and thought to have existed before the early settlers arrived. A widely known story among Susu farmers tells that at the time the original settlers made farms in the area, *Sali fore* germinated a spot where a black (spitting) cobra had been burnt accidentally during the preparation of the field, before the farmers had even broadcasted any seed. *Sali fore* is said to attract (cobra) snakes and caution must be exercised for all on-farm activities involving this variety. It is forbidden to take seeds from the barn during the night for fear of confrontations with the cobra.

***Table 4**: Average number of varieties cultivated by farmers in case study areas1 in Sierra Leone in 2007 (survey 2008)*

Region	Chiefdom	Average number of varieties	Standard deviation	Number of farmers (N)
North	Bramayia	1.15	0.36	112
	Kholifarowalla	1.85	0.63	476
	Magbema	1.76	0.59	235
	TonkoLimba	1.37	0.57	263
South	Kamajei	2.74	0.88	628

***Table 5**: Dominant pericarp colour and average field size per rice type for each of the Sierra Leone case study villages (survey 2007)*

Region	Village	(Sub) species	Dominant pericarp Colour	Average field size (ha)	Number of fields	Std. deviation
North	Bumban	unclear	white	0.611	22	0.329
		Asian rice	white	0.336	9	0.090
		farmer hybrids	red/brown	0.631	47	0.401
	Mayemberie	unclear	white	0.393	8	0.412
		African rice	red/brown	0.271	32	0.177
		Asian rice	white	0.174	32	0.108
		farmer hybrids	red/brown	0.299	25	0.207
South	Mobai	Asian rice	red/brown	0.328	125	0.222
	Mogbuama	unclear	white	0.053	1	
		Asian rice	red/brown	0.312	162	0.271
		farmer hybrids	red/brown	0.069	5	0.052
	Njagbema	Asian rice	red/brown	0.255	202	0.245

Discussion

This paper offers a regional comparison of how socioeconomic, cultural, religious and ecological factors shape the cultivation of African rice, based on a number of case studies in West Africa. The data show a range of complex interactions between ecological and cultural factors (Table 6). As a consequence of social and natural factors each region has developed preferences for different rice varieties, different combinations of variety characteristics and different assessments of the value of current and future value of African rice.

In certain areas (e.g., Danyi plateau) the most important factors in the continued cultivation of African rice are ecological, while in others (e.g., Akpafu and Lolobi in Ghana) maintenance of African rice is almost entirely explained by cultural and religious factors. In yet other cases, such as in Guinea Bissau, Guinea and Sierra Leone, ecological, socioeconomic and cultural factors interact. Among the Mandinka in The Gambia, Casamance and northern Guinea Bissau, African rice is gaining a new but negative significance. In the case of the Mandinka in The Gambia reduced rainfall during the 1970s in combination with the availability of good-tasting imported white-skinned rice and alternative varieties of short duration with interspecific origin led to a gradual abandonment of African rice.

The reasons given by farmers in Guinea for the cultivation and mixing of African rice indicate the influence in more or less equal measures of ecological, religious and/or sociocultural factors. In southern Guinea Bissau the use of African rice is mainly determined by ecological (salt tolerance and poor soils), cultural and social factors (especially war). The robustness and short maturation period of African rice may have been a factor recommending it to farmers in war-affected northern Sierra Leone. Interestingly, a rice with alleged poor digestibility may be abandoned in some areas but become a preferred variety in others. In Guinea, farmers add the more slowly digested African rice to supplies of Asian rice to slow consumption and safeguard food security. In the Togo Hills partly removing the pericarp is not considered a problem as petrol-fed mills are available in most cases. In Sierra Leone and Guinea, farmers very much prefer unpolished red rice and the labor required for polishing seems not to be an issue. However, in Guinea Bissau not polishing the red rice seems to be a social marker for laziness.

***Table 6**: Main characteristics of the region concerning rice cultivation in the case study areas.*

Case study area	Region and country	Latitude	Specific soil conditions	Rainfall (mm)	Ethnic group	Crop cycle length African rice	Way of milling/ polishing	Preferred polishing of red varieties	Preferred pericarp colour	Preferred rice species	Dominant factor in cultivating or abandoning African rice
1	Togo Hills Togo (Danyi Plateau)	7° 08’	poor & acid	1500	Ewe / Ahlon	2 months 3 months 4 months	hand	partly/full	red	African	ecology
1	Togo Hills Ghana (Siwu speaking)	7° 08’	rich forest	1200	Lolobi / Akpafu	3-4 months	machine	partly	red	Asian / African	culture
2	Gambia	13° 10’	sandy	<1000	Mandinka	3 months	hand	not cultivated	white	Asian / farmer hybrids	ecology / sociology / economy
2	Casamance	12° 50’	sandy	1000	Mandinka	3 months	hand	not cultivated	white	Asian / farmer hybrids	ecology / sociology / economy
2	Guinea Bissau (Madinka)	12° 20’	rich forest	>1000	Mandinka	3 months	hand	not cultivated	white	Asian / farmer hybrids	ecology / sociology / economy
3	Guinea Bissau (Balanta)	11° 12’	salty (coast)	>2000	Various	3 months 4 months	hand	full	white	Asian / African / farmer hybrids	ecology / sociology / economy
4	Guinea West	9° 40’		>2000	Susu	4 months	machine	partly	red	Asian / African / farmer hybrids	ecology/culture
5	Sierra Leone North	9° 10’		>1000	Various	3 months 4 months	hand	partly	red	Asian / African / farmer hybrids	ecology /sociology
5	Sierra Leone Central/South	8° 12’		>2000	Mende	3 months 4 months	hand	partly	red	Asian / African / farmer hybrids	Ecology / sociology

Across the region farmers commonly describe African rice as filling the stomach for a long time and as “heavier” than Asian rice. This may reflect the fact that African rice varieties in general have a relatively high amylose content, which slows its digestion. Rice varieties can be classified as high (25-32%), medium (20-25%) and low (10-20%) in amylose content. The average amylose content of African rice varieties lies around 27% (Futakuchi and Sié, 2009). Bao *et al*. (2006) have shown that the amylose content of landraces is high when compared to modern varieties. This suggests that some local red and white Asian rice varieties may resemble African rice in terms of slow digestibility. This is in line with the assertion of Guinea farmers that *Saidou Gbeli,* a local red Asian rice, resembles African rice as far as digestibility is concerned. However, further research on amylose content needs to be conducted to provide more information.

In the Togo Hills the red pericarp is left on the seed when the rice is used to make rice flour that is then made into porridge or rice *fufu*, which consequently becomes reddish. When the whole grain is cooked, farmers consider the rice too fibrous to eat if the pericarp is not partly removed, although this rice is always preferred over white or fully polished red rice. This is similar to the preferences in Sierra Leone, although in Guinea Bissau varieties with red pericarp are often disliked for human consumption among the Balanta, the bran is highly valued as fodder for pigs. Both in the Togo hills and among the Balanta of Guinea-Bissau African rice is said to have curative properties.

There is also variability in the acceptability of farmer varieties of hybrid origin in which pericarp color plays a part. Whereas farmer hybrids with red pericarp developed in the Upper Guinea Coast region are accepted in Ghana because they have red pericarp and look like African rice, they are not accepted by the Mandinka of Guinea Bissau, The Gambia and Senegal, for precisely the same reason.

Regional differences in the appreciation of African rice can explain farmer responses to new technologies. The cultural and religious factors that maintain African rice within the Lolobi and Akpafu areas have resulted in recently developed Asian rice varieties *Viono* and *Aworema*, both with a red pericarp. This is an important finding as it is often thought that varieties with a red pericarp are “historical” while varieties with a white pericarp are of more recent origins. In Lolobi and Akpafu, religion and culture have opened up specific opportunities for a particular path of technology development.

In Sierra Leone red rice is preferred and African rice is still very much appreciated, although perhaps reduced in cultivation. The farmer hybrids that have become an essential part of rice farming are very similar in morphology and performance to African rice, which may explain their success as well as the abandonment of African rice in certain areas where many hybrids were found (Nuijten *et al.*, 2009).

Among the Mandinka in The Gambia, Senegal and northern Guinea Bissau, farmer hybrids with white or light-brown pericarp, resembling Asian rice, are very popular (see Nuijten *et al*., 2009). However, like African rice, the farmer hybrids seem to perform very well on poor soils. The Mandinka in northern Guinea Bissau consider both the erect farmer hybrid type (very much appreciated in Sierra Leone) and African rice weeds.

A better insight into the cultural values and practices impacting the cultivation of African rice also allows us to better understand why farmer hybrids developed along the Upper Guinea Coast but not in the Togo Hills (Nuijten *et al*., 2009). The mixing of African rice and Asian rice remains a common practice along the Upper Guinea Coast but is not practiced in the Togo Hills because of political factors that have caused people to 'isolate' themselves in the mountains during times of slave raiding and war (and thus have no access to lowland cultivation). As African rice still is an important identity marker for the people on the Ghanaian side of the Togo Hills, the mixing of African with Asian varieties is still uncommon even though Asian rice is grown in the uplands and lowland farming has been added to their cropping system.

Conclusions

This paper shows that the epistemology present in farmer innovations and preferences is determined by trajectories of interaction between ecological as well as social factors (see also Rana *et al*. 2007) that have resulted in specific preferences as well as tailor-made technologies for resource poor farmers. The need to acknowledge such trajectories implies arguing in favor of an endogenous, bottom-up food security revolution. Indeed, there are systemic alternatives to a top- down Green Revolution in Africa (Richards, 2006; Offei *et al.*2010). Together with ecological factors, sociocultural and religious factors all deserve attention in models of technology development and dissemination (Nuijten *et al*. 2012). African rice, across West Africa, embodies important values of historical consciousness and therefore is part of the social structure and order. The case studies presented show that African rice is maintained or abandoned because of different interactions between social and ecological factors. An important and challenging task for future research is to categorise and document and thus validate farmer material while not disconnecting cultural and historic data and data concerning preferences among varieties (Linares, 2002; Temudo, 2011). In doing so farmer varieties can be tested and disseminated just as has been done with the New Rice for

Africa series (NERICA)[1] , probably achieving more successful adoption. West African history and culture have produced valuable mechanisms that have resulted in a great range of valuable farmer varieties and technologies. Doing justice to the "laboratories" of African farmers requires a new approach that takes advantage of subtle interactions between social and ecological factors at the local level to develop a whole new range of opportunities to increase rice production and improve food security.

[1] A set of varieties produced by AfricaRice by crossbreeding African and Asian rice

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CHAPTER EIGHT

General discussion and conclusions: the importance of interactions between socio-cultural dynamics, ecologies and varieties

Béla Teeken

1. A summary of findings for each chapter and how they relate to research questions

Chapter 1 formulated the subject matter and research questions of this thesis. It also shortly sketched the socio-historical background of the area of study and illustrated the cultural diversity and the dynamic history of the Togo hill minority groups and highlighted how cultural diversification can be understood as a strategy to maintain group autonomy in a region characterised by a history of contestation between larger political and economic powers.

The thesis inquired into the role African rice plays within the cropping systems and farming communities of the Togo hills, so it was deemed necessary to give an overview of what was locally present in this landscape, in socio-economic and cultural terms as well as in agronomic, biological and genetic terms. This firstly required a local description of the differences in configuration of social as well as natural factors for the different micro-regions within the Togo Hills, as well as a description on how these factors relate to each other, and how they constitute rice cultivation and the lives of the communities within the Togo hills region. This description was made in Chapter 2 and it showed that farmers in the Togo hills mostly rely on farmer varieties, and that different communities have different reasons to cultivate African rice. It also showed that the cultivation of African rice is related to local traditional practices - ceremonial – in the Akpafu and to a lesser extent the Ahlon case, religious in the Lolobi case, and mainly ecological in the case of the Ewe on the Danyi plateau. In Ghana - among the Akpafu and the Lolobi - the cultivation of African rice seems closely linked to the assertion of identity and social structure. The chapter also showed that the tradition of cultivating African rice steered a preference for equally red Asian rice varieties said to have culinary as well as stomach filling capacities similar to African rice. Here, however, other Asian (white) rice varieties are also part of the local variety portfolio. By strong contrast, African rice is grown on the Danyi Plateau because it is the only rice that seems to thrive well in this challenging niche. The presence of white Asian rice in a few marshy places on the plateau, and the statement of farmers that they have recurrently tried other varieties on the Plateau, suggests that they are open to any variety that grows well in this environment. So, preference for other non-*glaberrima* varieties has never been an issue, since they cannot be grown. Although in some areas in West Africa rice with a red pericarp is not liked - in the Gambia for example - , this is not an issue for the Ewe on the Danyi Plateau because they grow what they can.

In general, it can be concluded that cultural and social factors have steered and directed variety choice, adoption and innovation but are in no sense an absolute barrier to change. Reasons for low adoption of modern upland varieties were not addressed in this chapter but were explored later in Chapter 4, as part of a discussion of the specific physiological traits of farmer varieties.

So, the reason why farmers cultivate African rice is connected to ecology, especially the Danyi Plateau in Togo, but also to local culture, especially among the Lolobi and Akpafu in the Ghanaian Togo hills region. This points to the potential importance of a mutual interaction between the cultural and biological factors, at least in some cases. To further investigate farmers' variety choice in relation to African rice it was necessary to compare such variety selection processes in the different case study areas within the Togo hills. This is the topic dealt with in Chapter 3.

In Chapter 3, a set of farmer varieties from different West African countries was evaluated by field trials in two communities in the Ghanaian Togo hills and two communities in the Togolese Togo hills. All the varieties evaluated were chosen because they had genetic, morphological, or culinary properties directly comparable with African rice. There was a clear difference between the Ghanaian and Togolese communities in the way they organised the field trials. In Togo the trials were communally managed, while this was done individually in Ghana, perhaps reflecting the two countries larger political and economic characteristics. Ghana is a liberal market economy while Togo has an economy in which the state plays a greater controlling part. Farmers in Ghana selected material clearly based on criteria related to African rice: morphology of the plant, and grain and pericarp colour. These varieties were mainly selected for home consumption, and for incorporation in ritual practices, as well as for market sale. Ghanaian farmers, however, also selected varieties that were very different from African rice and these were mainly selected for market sale or to be prepared mixed with African rice or other red Asian rice varieties. In Togo, farmers selected several varieties no matter how they related or did not relate to African rice. They also selected varieties that did not do well but were liked mainly because of their large grains. The last might be explained by the security large grains might offer as seed: varieties with large seeds can build up a larger initial root system and can therefore reach deeper into the soil, making use of the reserves of energy and nutrients stored in the grain.

It can be concluded that despite the different roles of culture and ecology in each of the regions within the Togo Hills, farmers in all regions do not look for one specific ideotype of rice but prefer a set of different varieties to be used for various purposes. Differently from the Ewe on the Danyi Plateau, but similarly to the Lolobi and Akpafu in Ghana, the Ahlon community in the Togolese Togo hills placed a special emphasis on African (red) rice traditionally because an important clan in Ahlon Sassanou must only eat red African rice.

An interesting choice of varieties was made by the Ahlon. They followed the same selection criteria as the Ewe people on the Danyi Plateau, including sharing their appreciation for large grains. But because their ecology more resembles the Ghanaian Togo hills' ecology, being more fertile and humid, they selected the Asian rice variety *Viono* partly because it is red, like African rice, but mainly because it did well in their ecology. Moreover, Ahlon farmers also selected the farmer hybrid variety *Binta Sambou* which has very small grains, as it was found perfect for home consumption. This also shows the diverse selection criteria held by farmers in the Togo hills. Instead of restricting or narrowing down selection - creating a genetic bottleneck - cultural factors seem to contribute, in the cases just cited, to maintaining genetic diversity because the cultural factors provide additional reasons to select varieties apart from only those of pragmatic agronomic or economic evaluation.

Very interesting is also that these cultural factors are most strongly present in the Ghanaian regions much more incorporated into a liberal market economy, where farmers also benefit from cash crops, mainly cacao. This can be understood in the light of a continuing felt need to formulate community identity and cooperation, thereby assuring a certain degree of independence from the more individualistic market economy in which the Ghanaian Togo hills have become incorporated. A region that once sought to differentiate itself from the cultures of the Ashanti Empire now seeks, perhaps, to assert its identity free of the nostrums of the global financial institutions, much as (say) modern France uses farming and cuisine to resist the same set of globalising tendencies towards cultural homogenisation.

Chapter 4 turns to a broader, comparative topic by investigating the genetic diversity of farmer varieties in West Africa using molecular markers. The chapter shows that farmers maintain a high diversity of rice varieties and have even created a diverse set of inter-specific hybrids between African and Asian rice, long before the introduction of such hybrids by the West African Rice Development Association that were the result of the cross-breeding between one *sativa* variety and one *glaberrima* variety. These natural inter-specific farmer hybrids occurred in farmers' fields and were then developed further by farmer selection. They seem to be able to grow and produce under sub-optimal conditions. For example just after and during the war in Sierra Leone many farmers grew these farmer hybrids as well as *glaberrima* varieties. Many of these hybrids therefore probably incorporate glaberrimas capacity to grow under sub-optimal, low input conditions. This particularly illustrates the active role of farmer agency in relation to variety development.

On the other hand it is interesting that farmer interspecific hybrids were not found in the Togo hills. This might be due to the fact that *glaberrima* and *sativa* varieties have only been grown next to each other in this region only since the 1960s, whereas they have been adjacent in Upper West Africa for many decades, and perhaps even centuries. But the cultural and religious status of African rice also plays a part. The Lolobi case is instructive, since it is known in the region that this group is the most active in rice variety development. For the Lolobi it is culturally mandated that African rice should remain recognisable to the ancestors, and hybrid offtypes are therefore less likely to be selected.

The chapter also showed a broad taxonomic divide between glaberrimas from the Togo hills and those from the Upper Guinea Coast, thereby pointing in general terms to a different trajectory of farmer selection and adaptation.

Chapter 5 provided an important answer to the question why farmers with a dynamic long term or short term history of farming within suboptimal conditions continue to appreciate African rice. This chapter investigated the crop physiological differences between Asian and African rice with regard to their capability to adapt to different ecologies. Sets of farmer varieties of Asian and African rice were compared by evaluating their growth, development and yield in field trials under farmer conditions, replicated in five different West African countries. African rice appeared to be the most robust, and showed the largest G × E interactions for the measured parameters and was able to adapt best to the different ecologies, as it was best able to maintain its yield. An important mechanism here seems to lie in the tillering that seems to increase or at least remain constant when conditions become less favourable. The high yield observed within the farmer experimentation trials on forest ground for the *glaberrima* varieties Sali Fore and Wansarang (Chapter 3) also brought forward the possibility that *glaberrima* has a specific nutrient uptake mechanism related to the physical, chemical and biological properties of the soil. Further research is needed to clarify this. The specific tillering strategy followed by *glaberrima* varieties is also followed by the Asian *indica* rices but the *indica* produced fewer panicles and suffered from several cases of empty grains and zero yields. Importantly one *indica* group, and also one *japonica* group appeared to be quite robust. These data provide an important reason why farmers continue to use and appreciate African rice, and farmer varieties in general, under dynamic and adverse conditions. The chapter provides evidence that selection in farmers' dynamic conditions, governed by social as well as ecological factors, has resulted in varieties well suited to such conditions. It therefore makes a lot of sense that these varieties have become part of customary rites and traditional religion, conferring identity on groups of people, especially where these groups try to achieve a level of independence from larger political economic powers. Farmer hybrids were not incorporated in this physiological research as these were not identified and classified as such at the time the field trials were sown. An important follow-up research would therefore be to investigate the robustness of the farmer hybrids as well. This might provide further evidence on the achievements of West African rice farmers, and the importance of farmer agency in crop selection and adaptation more generally.

Chapter 6 offered an analysis of West African farmer varieties based on traits that are visible to farmers: namely, the morphological traits of the plant. It investigates if certain communities of farmers select specific morphological traits, and if so how this relates to social and ecological factors. Very few specific morphological farmer traits could be distinguished, and in correspondence with Chapter 3 it appears that farmers in different communities and regions select for sets of varieties with varied morphological traits. It however appeared that current socio-cultural selection pressures may be limiting genetic diversity within African rice, while this was not observed for Asian rice and the farmer hybrids. The tradition of African rice cultivation has nevertheless resulted in diverse development pathways: hybrids with a red pericarp and straight panicle attitude can be seen as continuing the cultivation of the main ideotype of AfricanAfrican, while hybrids with a white pericarp and a droopy panicle attitude and can be regarded as a continuation of a tradition of cultivating Asian rice, though with types of clear inter-specific genetic derivation.

Farmer hybrids combine (advantageous) traits from different botanical groups by embodying responses to different local cultural and ecological considerations. Similarly, the cultivation of Asian *indica* rice varieties with a red pericarp in the Togo Hills, sharing culinary and stomach filling properties with African rice, can be seen as the continuation of the African rice tradition in an upgraded and diversified form better adapted to the new social-economic conditions of the farmers - in this case, incorporation in a liberal market economy but where farmers still seek to maintain some degree of autonomy within this sphere – and to new ecological opportunities, such as the opening up of lowland and hydromorphic areas to farming by Togo hills communities.

Chapter 6, supported by data from the trials performed in Chapter 5, and by molecular analysis described in Chapter 4, also showed that there was a clear difference between the African rice varieties from the upper Guinea Coast and the lower Guinea Coast. The African rice from the lower coast, i.e., the Togo hills, has smaller plants and heavier grains. This can be understood as an indication of local adaptation to the challenges of cultivation in a mountainous region with many infertile slopes, where people may have favoured the security of larger grains able to produce a larger initial root system on basis of the nutrients stored in the grain only.

As African rice is generally believed to have a single origin of domestication (Portères, 1976; Li *et al.*, 2011) this shows again the role of farmer agency in the selection and development of locally adapted varieties of (African) rice.

Chapter 7 puts the case of the Togo hills in a wider West African perspective and compared it with other pockets where African rice cultivation persists. The chapter showed that different combinations of socio-cultural, economic and ecological factors determine the continuation as well as abandonment of African rice. In the Ghanaian Togo hills it is mainly cultural factors that maintain African rice and importantly set criteria for the development and selection of Asian rice varieties. In the Togolese Togo hills it is mainly ecological factors which are the controlling factors under farmer conditions, since no other rice than African rice seems to grow well on the Danyi Plateau.

2. Discussion and conclusion: farmer selection in broader context

If we then look to other parts of the region the Sierra Leone case seems important for comparison. Here there is little or no attachment of cultural factors to African rice, other than a general preference for red rice for ceremonial meals. Here African rice seems largely to have been replaced by farm hybrid selections with a general similarity in their morphology to African rice. The adoption of these hardy hybrids is clearly determined by a mix of ecological factors (low input upland farming conditions) and social factors such as labour availability and insecurity. Some African rice varieties of short duration are still retained specifically to spread harvesting labour and to fill the hunger gap when other varieties are not ripe yet and stocks are finished. Nowadays many farmer hybrids are also used for these buffering purposes, indicating again the role that farmer agency and farmer innovation have played in exploiting genetic and morphological features of African rice in new contexts, equivalent to the science-based inter-specific rice hybrids.

Among the Susu in Guinea African rice is maintained for a balance of cultural and ecological reasons (Okry 2011; Teeken 2009). This is similar to the situation among the Balanta in Guinea Bissau reasons, where in periods of climate instability farmers fall back on African rice because it still keeps producing under harsh conditions and with little external input (Temudo, 2011; Teeken 2012). Among the Madinka in The Gambia, Senegal and Guinea Bissau the abandonment of African rice cultivation is mostly determined by the high labour demands to mill the African rice, and by the modern availability of other short cycle varieties such as the farmer hybrids as well as by the availability of cheap imported rice (Nuijten, 2005; Teeken 2012).

All these examples show the active role farmers have in variety development and selection and that the results of farmer selection are highly diverse and the product of an interaction between the ecological and social factors; *emergent* innovations sprout from such interactions, linked to the concept of performance (Richards, 1993; Janssen & Vellema, 2012). Performance is situated action.

In upland rice farming this situated action comprises sequential adjustment to a range of unpredictable and contingent societal factors as well as natural factors (ecological/climatic/genetic) that facilitate important serendipitous discoveries, such as the farmer varieties shown in Chapter 5 to be especially robust.

The chapters on the genetic analysis (Chapter 4), the crop physiology of farmer varieties (Chapter 5) and morphology of farmer varieties (Chapter 6) have shown that through farmer selection a large diversity of farmer varieties have emerged that are well able to adapt to various ecologies. The maintenance of this diversity appears to be part of a risk spreading farmer strategy that facilitates important serendipitous innovations. The chapter on maintaining and abandoning African rice in various places in West Africa (Chapter 7) shows the importance of socio economic and cultural factors in the maintenance or abandonment of African rice and shows the diverse influences that the cultivation of African rice, as a pure product of farmer agency, has on variety selection and development. This demonstrates the expression of social as well as ecological factors in farmer varieties, whereby the various sociological as well as ecological conditions that farmers have experienced, have materialised in the varieties that farmers develop. Moreover the chapter on farmer experimentation and selection (Chapter 3) shows that cultural differences also result in different preferences. Nevertheless farmers are interested in other farmer varieties with various characteristics and do not hold uniform criteria and are generally open to adoption of a set of various varieties rather than one specific “best” variety. This in turn rests on the discovery (chapter 5) that African rice and farmer varieties are not only ecologically robust but are also suitable across a range of socio-cultural contexts. This supports the general argument of this thesis that genetic, environmental and societal components are all part of the story of variety development, especially in marginal societies able to develop survival strategies and some sort of independence from larger political bodies. Here, in short, is a template for development of successful, robust and scalable seed technologies capable of tackling food security issues for many smallholder farmers in West Africa. These seed technologies should therefore be included in any approach aimed at tackling food security issues, technology dissemination and agricultural development in risk prone areas in West Africa and beyond.

In West Africa where pre-colonial states were traditionally predatory and strongly associated with the Saharan and Atlantic slave trade, a system for dodging larger political powers and remaining “uncaptured” (Hydén, 1980) and autonomous was a key to survival as a “free” peasantry. The retention and development of African rice should be seen as an important tool and product of this system. Farmers in the Togo hills embraced the crop as an integral part of their resilient culture, and even today African rice continues to set a standard for the varieties farmers select and develop.

The issue of why there are few inter-specific crosses in the Togo Hills is one that demands explanatory attention. Here, it has been suggested that the cultural and religious significance of African rice, and its attachment to identity and minority status in the Akpafu and Lolobi areas in Ghana, might be seen as a factor that has tended to isolate African rice from Asian rice, thereby disfavouring rather than facilitating the emergence of natural crosses, in strong contrast to the situation on the upper Guinea Coast, where rice is the predominant staple among all ethno-linguistic groups, and thus of no salience in terms of culinary marking of ethnic boundaries, and where any and all varieties are tried and welcomed, with the result that neighbouring fields (and sometimes even the same field) will contain both Asian and African rice types, and where in consequence farmers have developed a large diversity of natural hybrids. This does not mean that this cultural and religious significance hampers farmer innovation, because it has resulted in the development of Asian rice varieties that resemble African rice in nutritional and dietary properties. From an ecological perspective innovating upon Asian rice is also more logical for the Lolobi and Akpafu as they now have access to much more lowland and hydromorphic ecologies than their forefathers forced to stay in the hills.

But in areas where African rice has been cultivated along with Asian rice for a long period, as is the case in Sierra Leone popular hybrids between the two rice types have emerged. On the Danyi Plateau African rice has no explicit or obvious cultural value, but the area hardly favours the cultivation of any other rice than the African species. Clearly, in this case the tough hill environment is the reason why there are no inter-specific hybrids. Here, the maximum of different varieties of African rice is maintained and whereas crosses between different African rice varieties might be selected no farmer ever mentioned such selection processes. Farmers here also stated that the number of African rice varieties available to them is small (about seven) and no other kinds of rice are available. The farmer experimentation study brought out, however, that farmers on the Danyi Plateau took great interest in a *glaberrima* variety like *Sali Fore* from Upper West Africa, and even in some hybrid material from the research centre 'AfricaRice', as well as some natural farmer hybrid material, suggesting that these farmers may have something to gain from the further introduction of farmer varieties from elsewhere in the region, and beyond.

This thesis has provided important evidence for the argument that crop development should pay more attention to the analysis of the interaction between genetics, environment and society. The particular history of the Togo hill minorities has influenced variety choice and development in different ways in different micro regions within the Togo hills. The genetic makeup of the current varieties is therefore a result of the interaction between genetics, environment and society. Varieties like *Viono* and *Aworema* are not only the result of shifting to a new ecology but are also the result of the continuation of a culture of *glaberrima* cultivation because *glaberrima* retains its important role because of agronomical and physiological robustness, and cultural identity construction via the elaboration of religion and tradition. Although *Viono* was found not to be very robust it appeared to do best in an environment where it did not originate: the trial in Sierra Leone. This indicates its suitability to be transferred and disseminated to the more humid upland environments outside of its locality. Similar G×E×S interaction trends can be observed in Sierra Leone where the cultivation of several farmer hybrids also reflect the continuation of the cultivation of African rice, or the further development of a tradition of rice cultivating Asian rice with genetic input from African rice. The robustness of a specific group of *indica* varieties in Guinea also shows that farmers have selected important varieties not only related to African rice but also to Asian rice, as these *indica* varieties appeared to be robust and well fitted for many upland conditions. This is especially interesting as *indica* varieties are generally believed to be only suited for lowland cultivation (Khush, 1997; de Kochko, 1987; WARDA 2003-2005). The same applies to a group of japonicas that were also found to be robust. Interestingly the group of japonicas (from Sierra Leone) found to be more niche adapted, are possibly the result of the introduction of Carolina rice varieties by European traders in the late 18th century (Mouser *et al*., 2015).

What general lessons, then, can be drawn from this thesis about rice development? Participatory Variety Selection (PVS) trials have shown that farmers can select according to cultural preferences (Almekinders & Elings, 2001), and breeding can be adjusted to that (Ceccarelli & Grando, 2007). This study has suggested that many of the complications of the performance of PVS trials and farmer participatory approaches in general might be avoided by hoping in farmer innovations and farmer varieties, and testing these for broader dissemination. More especially as the evidence suggests they appear to be physiologically robust as well as suitable for many cultural contexts facing peasant farmers working in suboptimal farming conditions.

This in turn implies paying more explicit attention to “genealogies” of farmer varieties (and technology in general), and making an institutional shift towards an epistemology capable of apprehending long trajectories of G × E × S and acknowledging this as the domain of farmer practices, so that ecological and cultural contexts do not become objectified, with the danger of defining and fixing them in time on the basis of the scientific culture studying them. To avoid this classical anthropological problem of creating a “museum” model of culture there is need to acknowledge farmer selection as an innovating and knowledge generating institution in which performance, serendipitous discovery and unsupervised learning are of major epistemological importance. Serendipity, performance and unsupervised learning are important emergent properties resulting from unanticipated and unpredictable interactions between G, E and S, in what might be termed evolutionary real-time. But if this model could be implemented to build on the capacity of African peasant farmers as collaborating subjects then a successful Green Revolution for Africa might yet be possible, and offer a real systemic alternative to the still predominant top-down approach to rural transformation in Africa and beyond. This notion corresponds with the framework formulated in Helen Tilley's work on Africa as a living laboratory (2001); in a similar vein one might state that the laboratory of African farmers has produced innovations in which the ecological has never been separated from the societal.

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Appendices

English Summary

Rice is an important crop for small-scale farmers in West Africa. Besides the wetland rice cultivation, upland rice cultivation is also important in this region. Various research- and agricultural extension programmes are focused on developing and distributing new varieties. Given the very limited adoption of new rice varieties by West African small-scale farmers, the question arises what varieties farmers grow, select and develop themselves and how they do this. The answer to that question may be very relevant in the context of agricultural improvement and in strengthening food security for small-scale farmers in West Africa. This thesis tackles this question. In addition to ecological and biological factors it is assumed that socio-cultural and economic factors are important in the development and selection of suitable farmer rice varieties. The cultivation of African rice (*Oryza glaberrima*) is taken as an entry point, because African rice was traditionally grown by West African farmers and was never scientifically or commercially improved or promoted, but only used as a genetic resource for the improvement of Asian rice (*Oryza sativa*). The cultivation of African rice and related practices are therefore very suitable to study farmer variety development and selection as it is fully the product of farmer agency. Although much of the African rice in West Africa is replaced by Asian rice it is still grown in some regions which are characterized by a recent or earlier dynamic history of resistance of minority groups against greater economic and political powers. The Togo Hills on either side of the border between Ghana and Togo, is one such region and includes not only a great ecological diversity but also a large cultural and political diversity. The case study areas of this research are situated in both the Ghanaian and the Togolese Togo Hills.

This diversity exists not only because the Togo Hills are situated on the border in both Ghana and in Togo, but also because they are home to many different minorities within a relatively small area. All these differences within a relatively small geographic area make the Togo Hills an ideal research area to obtain insight in the different forms of interaction between genetic and environmental variation and social aspects of farmers' innovation of rice seed. From a technographical approach it is studied why African rice is still grown in the Togo Hills and to what extent and how cultural, political-economic and environmental factors play a role. Instead of working within one scientific discipline, the rice cultivation in the Togo Hills is contextualized using different scientific disciplines. This was done to avoid “reduction”: explaining social processes with natural science or vice versa. The result is an interdisciplinary study that examines both biological and social aspects of the culitvation of African rice in the Togo Hills. The aim of this thesis is to illustrate the need to study the local trajectories of interaction between social and biological aspects and varieties /

technologies that sprout from it. These processes are essential in any project that aims to improve agriculture and food security of farmers in West Africa.

Chapter 2 provides the reader with the agronomic as well as historical and socio-cultural context of rice cultivation for the different case study areas within the Togo Hills. It deals with the present cropping systems and rice variety portfolios. Importantly it shows that farmers mainly use farmer varieties and it illustrates the different entanglements of African rice with socio-cultural and ecological factors and puts them in a historical perspective. The different ethnic groups in the Togo Hills all seem to have had a certain earlier history of migration, refugees and conflict or war in their strategy to retain autonomy in relation to larger political powers such as the Ashanti Empire and the Dahomey Empire and later on the various colonial powers: first the Germans, then the British and the French, and then the more liberal state model of Ghana and the more centrally planned model in Togo.

Chapter 3 continues with an evaluation with farmers of a set of different farmer varieties from 7 West African countries. The role of socio-cultural and ecological factors within the organisation of rice cultivation, farmer selection and variety development of the Togo Hills is studied. The same set of varieties was evaluated within all the three case study areas. Reflecting the different political economic regimes of the two countries, Ghanaian farmers set up individual trials while in Togo farmers formed groups. Despite this difference the social effects on variety dissemination should not be considered necessarily different.

Farmers in all regions appear to select a set of different varieties rather than one or two ideotypes. Rather than limiting and narrowing rice diversity, cultural factors seem to contribute to the diversity as they determine additional variety development pathways. Importantly, the different political, economic backgrounds of the Ghanaian and Togolese Togo Hills result in the different articulation of the cultivation of African rice. In the Ghanaian Togo Hills, African rice has become explicitly part of a cult that provides identity and union and is especially cultivated for that reason. In the Togolese Togo Hills, African rice cultivation is maintained for food security and variance of diet.

Chapter 4 presents the genetic diversity, using molecular AFLP (Amplified Fragment Length Polymorphism) markers, among the collected farmer varieties in seven countries of West Africa. An important finding of this chapter is that farmers appear to have developed a new rice type that also shows high diversity: a group of varieties that are the result of interspecific hybridisation between Asian and African rice. These interspecific farmer varieties could be divided up into two groups: one group with red pericarps (red rice) and upright panicles and another group with white pericarp (white rice) and droopy panicles. The first group can be seen as a continuation of a tradition of cultivating African rice, while the second can be seen as a continuation of a tradition of cultivating Asian rice. The first type is mainly grown in Sierra Leone where red rice is preferred, just like in the Togo Hills, and the second type especially in The Gambia and Senegal where white rice is clearly preferred. These interspecific farmer varieties clearly illustrate the importance of the various pathways of farmer selection. It was striking that such varieties were not present in the Togo Hills, probably because people here only started cultivating Asian rice since the sixties and because African rice and its particular morphology is a distinct cultural entity and is mainly cultivated for ritual and cultural purposes on the Ghana side, which makes the selection of off types less probable. On the Togo side African rice is not planted in the proximity of Asian rice because almost no other rice than African rice is cultivated there.

Chapter 5 tries to find out how the physiological and agronomic characteristics of the African varieties relate to those of farmer varieties of Asian rice. A set of both botanical groups was sown in five different locations in West Africa. Results show that a large group of the collected farmer varieties are robust: they are able to perform well within different ecologies, contrary to the received wisdom that farmer varieties are only adapted to a specific locality. Varieties of African rice and several other farmer varieties appear to be robust and this robustness is the result of adaptation to dynamic conditions and farmer selection. This chapter therefore provides important insight in the biological reasons why certain groups of farmers continue to grow African rice and farmer varieties related to African rice. An important physiological mechanism behind this robustness seems the tillering strategy. African rice combines strong tillering with a dense canopy cover. However one group of japonica varieties from Sierra Leone was not robust and did only well in the area of origin were it was adapted to upland as well as lowland cultivation. Probably this is a group of varieties based on varieties that have been introduced by the British and further developed by farmers in Sierra Leone in a particular niche. These varieties thus seem the result of a specific trajectory of selection and development by West African farmers.

Chapter 6 presents results from combined morphological and molecular (Chapter 4) analysis, showing the large genetic diversity of *O. glaberrima*, *O. sativa* (japonica as well as indica) and a group of natural farmer hybrids that farmers maintain. The chapter gives further insight in what farmers have genetically achieved looking at genetic characteristics visible to farmers: the plant morphology. It studies whether morphological and molecular analysis reveal patterns of selection according to morphological similarity in relation to ecology and/or socio-cultural factors and shows that farmers in each area maintain a wide variety of varieties and do not spot a uniform ideal type or validate one specific morphological trait. It also shows that recent human selection pressures limit the diversity within African rice while this is not the case for the other rice species. African rice however is still important in determining diversity enhancing development pathways within the other rice species. This is particularly the case within the interspecific farmer varieties for which - in accordance with the results presented in Chapter 4 - a relationship was found between the local culture, the farming system, pericarp colour, panicle attitude and genetic diversity. Analysis also showed a difference between African rice from the upper Guinea Coast and the Togo Hills, indicating different pathways of selection and adaptation because African rice is believed to have one centre of origin. African rice from the Togo Hills produced heavier seed and shorter plants. The heavier seed may be associated with better germination necessary in a mountainous area as the Togo Hills with highly weathered and stony soils and a farming history of migration and conflict. Chapter 3 also showed that farmers in Togolese Togo Hills were also fond of varieties with large seeds.

Chapter 7 compares the African rice cultivation in the Togo Hills with its cultivation by other ethnic groups in West Africa: the Mandinka in The Gambia, Senegal and Guinea-Bissau, the Balanta in Guinea-Bissau, the Susu in Guinea and the Mende, the Temne, Limba and the Susu in Sierra Leone. Results show how in different regions in West Africa, the interplay between ecological, economic and socio-cultural factors determine the continuation or abandonment of African rice and illustrates that in each region these type of factors are all determinative in different proportions. Together with ecological factors, socio-cultural and economic factors set selection criteria within the adoption abandonment and development of rice varieties of African, Asian rice as well as interspecific farmer varieties; and farmer agency has a prominent role herein. The difference between the African rice varieties from the upper Guinea coast and the Togo Hills as observed in Chapter 6 seem to be explained by the relatively longer isolation of African rice within the Togo Hills. These comparisons between regions in West Africa once again show that the epistemology present in farmers' innovations and preferences are determined by the processes of the interaction between genetic, ecological and social factors that have led to specific preferences, as well as customised technology for resource poor farmers with few resources.

Chapter 8 gives a discussion of results and draws the overall conclusions of this thesis. The different chapters provide insight in how social factors and natural factors articulate the cultivation of African rice and shows important emergent innovations that result from such articulations. In the Ghanaian Togo Hills cultural factors set additional and rice diversity enhancing criteria for selection while in Togo selection criteria are mostly pragmatically agronomic. This can be understood by the higher necessity in Ghana to construct identity and autonomy within the larger and more dynamic economic and political powers of competition and individualization. African rice has become a tool to shape such identity. Despite cultural differences, farmers in all the case studies in the Togo Hills select a set of different varieties used for different purposes rather than a uniform type. This can be seen as a continuation of their earlier dynamic history in which the maintenance of diversity is part of a risk spreading strategy facilitating emergent innovations that suit such dynamics. Other examples from West Africa also show different combinations of social and natural factors within the maintenance of rice diversity.

This thesis therefore asks for full attention for the “genealogies” between the genetic, the ecological and the social within variety development and food security issues. Therefore, it is the task of science to take an evolutionary perspective. These genealogies and their products should be made visible and need juxtaposition to formal scientific breeding strategies, strategies to tackle food security and agricultural and societal development issues in general. The need to recognize such pathways implies an argument in favour of an endogenous, bottom-up approach. This indicates that there is a systemic alternative next to a top-down Green Revolution in Africa. Trajectories of interaction between the social and the natural have produced a large variety of versatile resources and are crucial within tackling development issues in such areas where such trajectories took place: there where farmer conditions are dynamic and suboptimal. Instead of mapping local cultural preferences (these can change quickly over time and can vary over small distances) it is much more fruitful to emanate from and also disseminate the varieties farmers have already developed themselves.

Dutch Summary (Samenvatting)

Rijst is een belangrijk gewas voor kleinschalige boeren in West-Afrika. Naast de natte rijstteelt, is de droge rijstteelt ook belangrijk in deze regio. Diverse onderzoeks- en landbouwvoorlichtingsprogramma's zijn gericht op het ontwikkelen en verspreiden van nieuwe rassen. Gezien de zeer beperkte adoptie van nieuwe veredelde rijstrassen door West-Afrikaanse kleinschalige boeren, rijst de vraag welke rassen boeren verbouwen, selecteren en ontwikkelen en hoe ze dit doen. Het antwoord op die vraag is wellicht zeer relevant in het kader van landbouwverbetering en het vergroten van de voedselzekerheid voor kleinschalige boeren in West-Afrika. In dit proefschrift wordt dit onderzocht. Naast ecologische en biologische factoren wordt verondersteld dat ook sociaal-culturele en economische factoren belangrijk zijn bij het ontwikkelen van geschikte rijstrassen. Als uitgangspunt wordt hier de teelt van Afrikaanse rijst (*Oryza glaberrima*) genomen omdat Afrikaanse rijst van oudsher door West-Afrikaanse boeren verbouwd werd en nooit wetenschappelijk of commercieel verbeterd is, maar enkel is gebruikt als genetische bron voor het verbeteren van Aziatische rijst (*Oryza sativa*). Hoewel veel van de Afrikaanse rijst in West- Afrika vervangen is door Aziatische rijst wordt deze wel nog steeds verbouwd in enkele regio's die gekenmerkt worden door een recente of eerdere geschiedenis van oorlog en verzet van minderheidsgroepen tegen grotere economische en politieke machten. Het onderzoeksgebied van dit proefschrift, de Togo Hills aan weerszijde van de grens tussen Ghana en Togo, is zo'n regio en kent naast een grote ecologische diversiteit ook een grote culturele en politieke diversiteit. De case studies van dit onderzoek liggen in zowel de Ghanese als de Togolese Togo Hills.

Deze diversiteit bestaat niet alleen omdat de Togo Hills zich zowel in Ghana als in Togo bevinden maar ook omdat er in dit relatief kleine gebied veel verschillende minderheden wonen. Al deze verschillen binnen een relatief kleine geografische ruimte maken van de Togo Hills een ideaal onderzoeksgebied om een beeld te krijgen van de verschillende vormen van interactie tussen de genetische, ecologische en sociale aspecten die resulteren in boeren innovatie van rijstrassen. Vanuit een technografische benadering wordt onderzocht waarom Afrikaanse rijst nog steeds in de Togo Hills verbouwd wordt en in welke mate en hoe culturele, politieke, economische en ecologische factoren hierin een rol spelen. In plaats van te werken binnen één wetenschappelijke discipline, is de rijstteelt in de Togo Hills gecontextualiseerd met behulp van verschillende wetenschappelijke disciplines. Dit werd gedaan om "reductie" te vermijden: het verklaren van sociale processen met natuurwetenschappen of vice versa. Het resultaat is een interdisciplinaire studie die zowel natuurwetenschappelijke aspecten als sociale aspecten van de teelt van Afrikaanse rijst in de Togo Hills onderzoekt. Doel van dit proefschrift is om de interactie tussen sociale en biologische processen te illustreren en zo te pleiten voor de noodzaak om de lokale trajecten van interactie tussen de sociale en biologische aspecten en de rijstrassen / technologieën die deze trajecten opleveren te onderzoeken. Deze trajecten zijn essentieel binnen elk project dat de landbouw en voedselzekerheid van boeren in West- Afrika wil verbeteren.

Hoofdstuk 2 schetst de agronomische, evenals historische en socio-culturele context van de rijstteelt voor de verschillende case studie gebieden binnen de Togo Hills. Het behandelt de huidige teeltsystemen en de diversiteit aan rijst die verbouwd wordt. Het laat zien dat boeren voornamelijk boeren rassen verbouwen en het illustreert de verschillende verstrengelingen van Afrikaanse rijst met sociaal-culturele en ecologische factoren en zet deze in een historisch perspectief. De verschillende etnische groepen in de Togo Hills hebben allemaal een zekere geschiedenis van vluchten, migratie en / of oorlogsconflict: door de geschiedenis heen hebben ze altijd een zekere autonomie weten te behouden en op te bouwen ten opzichte van de grotere politieke machten zoals het Ashanti en Dahomey Rijk en later de verschillende koloniale machten: eerst de Engelsen en de Duitsers en vervolgens de Engelsen en de Fransen en daarop het meer vrije markt gerichte staatsmodel van Ghana en het meer centraal geleide staatsmodel in Togo.

Hoofdstuk 3 evalueert een set verschillende boerenrassen uit zeven West-Afrikaanse landen samen met boeren. De rol van de sociaal-culturele en ecologische factoren binnen de organisatie van de rijstteelt, de selectie en ontwikkeling van rassen door boeren in de Togo Hills wordt bestudeerd via veldproeven. Dezelfde set rijstrassen werd in de verschillende gebieden van de case studies geëvalueerd. De organisatie van de veldproeven weerspiegelde de verschillende politiek-economische regimes van de twee landen. Ghanese boeren voerden individuele veldproeven uit terwijl in Togo boeren in groepen werkten. Ondanks dit verschil, is het maatschappelijke effect op de verspreiding en adoptie van rassen niet noodzakelijkerwijs verschillend.

Boeren in alle regio's lijken een set van geheel verschillende rassen te kiezen in plaats van één of twee ideotypen of een set van op elkaar lijkende rassen. In plaats van het verkleinen van diversiteit, dragen culturele factoren eerder bij aan de diversiteit omdat zij extra redenen aanvoeren om bepaalde rassen te selecteren en in stand te houden. Zo zorgen culturele factoren dus voor additionele trajecten van rasontwikkeling. Belangrijk is dat de verschillende ecologische en politiek-economische achtergronden van de Ghanese en Togolese Togo Hills resulteren in het verschillend vorm geven van de teelt van Afrikaanse rijst. In de Ghanese Togo Hills is de Afrikaanse rijst expliciet onderdeel geworden van een cultus die identiteit en solidariteit biedt en Afrikaanse rijst wordt speciaal om die reden verbouwd. In de Togolese Togo Hills, is de Afrikaanse rijstteelt hoofdzakelijk belangrijk voor de voedselzekerheid en als variatie op de hoofdgewassen cassave en yam.

Hoofdstuk 4 onderzoekt de genetische diversiteit van zaadmonsters van boerenrassen die in zeven verschillende West-Afrikaanse landen werden verzameld. Dit werd gedaan met behulp van de moleculaire AFLP (Amplified Fragment Length Polymorphism) methode. Een belangrijke bevinding van dit hoofdstuk is dat de boeren een nieuw rijsttype hebben ontwikkeld met een hoge diversiteit: een groep van rassen die het gevolg is van interspecifieke hybridisatie tussen Aziatische en Afrikaanse rijst. Deze interspecifieke boerenrassen kunnen worden onderverdeeld in twee groepen: een groep met een rode zaadhuid (rode rijst) en rechtopstaande aren en een andere groep met witte zaadhuid (witte rijst) en hangende aren. De eerste groep kan worden beschouwd als een voortzetting van de traditie van het verbouwen van Afrikaanse rijst, terwijl de tweede kan worden gezien als een voortzetting van een traditie van het verbouwen van Aziatische rijst. Het eerste type wordt voornamelijk geteeld in Sierra Leone, waar rode rijst de voorkeur heeft, net als in de Togo Hills, en het tweede type vooral in Gambia en Senegal, waar witte rijst duidelijk de voorkeur heeft. Deze boerenrassen met interspecifieke oorsprong illustreren duidelijk het belang van de verschillende trajecten van boeren selectie. Opvallend was dat dergelijke rassen niet in de Togo Hills gevonden werden, waarschijnlijk omdat men hier pas rond de jaren zestig ook Aziatische rijst is gaan verbouwen en omdat Afrikaanse rijst met zijn bijzondere morfologie (o.a. rechtopstaande aren en rood zaad) apart verbouwd wordt: aan de Ghanese zijde hoofdzakelijk voor rituele en culturele doeleinden - waardoor afwijkende planten niet gauw geselecteerd zullen worden - en aan de Togolese zijde omdat er bijna geen enkele andere rijst dan de Afrikaanse rijst wordt geteeld.

Hoofdstuk 5 probeert erachter te komen hoe de fysiologische en agronomische kenmerken van rassen van Afrikaanse rijst zich verhouden tot die van boeren rassen van Aziatische rijst. Een set van beide soorten werd gezaaid in vijf verschillende locaties in West-Afrika. De resultaten laten zien dat een grote groep van de verzamelde boerenrassen robuust is: de rassen doen het goed in verschillende ecologieën in tegenstelling tot het gangbare idee dat boerenrassen het enkel goed doen in één specifieke lokale ecologie. Vooral Afrikaanse rijst maar ook verschillende boerenrassen van Aziatische rijst blijken robuust en dit is het gevolg van aanpassingen aan dynamische omstandigheden en selectie door boeren. Dit hoofdstuk geeft daarom belangrijk inzicht in de biologische redenen waarom bepaalde groepen boeren Afrikaanse rijst en boerenrassen blijven verbouwen. Een belangrijke fysiologische mechanisme achter deze robuustheid moet gezocht worden in de strategie van uitstoeling. Afrikaanse rijst combineert sterke uitstoeling met een dicht bladerdek. Een groep van *japonica* rassen uit Sierra Leone echter deed het alleen goed in het gebied van herkomst waar deze groep zowel aan droge als natte rijstteelt aangepast is. Waarschijnlijk is dit een groep van rassen gebaseerd op Aziatische rijstrassen die door de Britten geïntroduceerd werden en daarna in een bepaalde niche verder ontwikkeld zijn door boeren in Sierra Leone. In dat geval zijn deze rassen dus het resultaat van een specifiek traject van selectie en ontwikkeling door West-Afrikaanse boeren.

Hoofdstuk 6 presenteert de resultaten van een gecombineerde morfologische en moleculaire (hoofdstuk 4) analyse. Hieruit blijkt een grote genetische diversiteit van *O. glaberrima*, *O. sativa* (*japonica* evenals *indica*) en een groep van natuurlijke interspecifieke boerenrassen die boeren gebruiken. Het hoofdstuk geeft verder inzicht in wat boeren genetisch hebben bereikt door te kijken naar genetische kenmerken die voor boeren zichtbaar zijn: de morfologie van de rijstplant. Gekeken wordt of de morfologische en moleculaire analyse trends laten zien die overeenkomen met ecologie en / of sociaal-culturele factoren. Het blijkt echter dat overal in West-Afrika boeren allerlei verschillende rassen tegelijk op het oog hebben, in stand houden en waarderen en niet een uniform ideaal type of één specifieke morfologische eigenschap. Ook blijkt dat recente menselijke selectiedruk de diversiteit van Afrikaanse rijst beperkt terwijl dit niet het geval is voor de andere soorten rijst. Afrikaanse rijst is echter nog steeds belangrijk bij het bepalen van diversiteit bevorderende trajecten van boeren selectie binnen de andere soorten rijst. Dit is met name het geval voor de boeren hybriden waar - in overeenstemming met de resultaten van hoofdstuk 4 - een relatie gevonden is tussen de lokale cultuur, het teeltsysteem, de kleur van de zaadhuid, de positie van de aar en de genetische diversiteit. Analyse toonde ook een verschil aan tussen Afrikaanse rijst uit de Upper Guinea Coast (de kustlanden van Senegal t/m Sierra Leone) en de Togo Hills. Afrikaanse rijst uit de Togo Hills heeft zwaarder zaad en minder hoge planten wat wijst op verschillende trajecten van selectie en aanpassing, omdat wordt aangenomen dat Afrikaanse rijst één enkel oorsprongscentrum van domesticatie heeft. Het zwaardere zaad kan in verband gebracht worden met een betere kieming noodzakelijk in een berggebied als de Togo Hills met sterk verweerde en steenachtige gronden en een geschiedenis van migratie en conflict. In hoofdstuk 3 kwam ook naar voren dat boeren in de Togolese Togo Hills erg gesteld zijn op rassen met grote zaden.

Hoofdstuk 7 vergelijkt de teelt van Afrikaanse rijst in de Togo Hills met die door andere etnische groepen in West-Afrika: de Mandinka in Gambia, Senegal en Guinee-Bissau; de Balanta in Guinee-Bissau; de Susu in Guinee en de Mende, de Temne, Limba en de Susu in Sierra Leone. De resultaten laten zien hoe in verschillende regio's in West-Afrika, het samenspel tussen ecologische, economische en sociaal-culturele factoren het behouden of het verdwijnen van de Afrikaanse rijst bepaalt en hoe deze factoren in de verschillende regio’s in verschillende verhoudingen bepalend zijn. Samen met ecologische factoren, bepalen sociaal-culturele en economische factoren de criteria bij het adopteren, het afstand doen van en het ontwikkelen van rijstrassen van Afrikaanse en Aziatische rijst en boerenrassen met interspecifieke oorsprong. Boeren hebben hierin een belangrijke actieve rol.

De verschillen tussen de Afrikaanse rijstrassen uit de Upper Guinea Coast en de Togo Hills zoals geconstateerd in hoofdstuk 6 kunnen worden verklaard door de relatief lang geïsoleerde teelt van alleen Afrikaanse rijst in de Togo Hills. Deze vergelijkingen tussen regio's in West-Afrika laten wederom zien dat de epistemologie aanwezig in boeren innovaties en -voorkeuren wordt bepaald door processen van wisselwerking tussen genetische, ecologische en sociale factoren. Deze interacties hebben geleid tot specifieke voorkeuren en aangepaste technologieën voor kleinschalige arme boeren met weinig middelen.

Hoofdstuk 8 is een bespreking van de resultaten en trekt de algemene conclusies van dit proefschrift. De verschillende hoofdstukken geven inzicht in hoe sociale en natuurlijke factoren het gebruik van Afrikaanse rijst vormgeven en laten belangrijke innovaties zien die het gevolg zijn van dit verschillend vormgeven. In de Ghanese Togo Hills zorgen culturele factoren voor extra criteria bij de selectie van rijstzaad, terwijl in Togo het vooral pragmatische agronomische factoren zijn die zulke criteria bepalen. Dit kan worden begrepen door de hogere noodzaak in Ghana om identiteit en autonomie te scheppen binnen de grotere en meer dynamische economische en politieke macht van de concurrentie en individualisering. Afrikaanse rijst is uitgegroeid tot een instrument om dergelijke identiteit mede vorm te geven. Boeren in ieder van de case studies in de Togo Hills selecteren een set van verschillende rassen die voor verschillende doeleinden gebruikt worden in plaats van een uniform type. Dit kan worden beschouwd als een voortzetting van hun eerdere dynamische geschiedenis waarin het behouden van diversiteit van rijstrassen deel is van een strategie van risicospreiding die innovaties mogelijk maakt die goed aansluiten bij zo’n dynamische geschiedenis. Andere voorbeelden uit West-Afrika tonen ook verschillende combinaties van sociale en natuurlijke factoren binnen het behoud van de diversiteit van rijst.

Dit proefschrift vraagt daarom volle aandacht voor de "genealogieën" tussen het genetische, het ecologische en het sociale bij het ontwikkelen van rassen en binnen vraagstukken rond voedselzekerheid. Daarom is het de taak van de wetenschap om een evolutionair standpunt in te nemen. Deze “genealogieën" en hun producten moeten zichtbaar worden gemaakt en moeten op hetzelfde niveau geplaatst worden als formele wetenschappelijke strategieën van veredeling die gericht zijn op voedselzekerheid en agrarische- en maatschappelijke ontwikkelingsvraagstukken in het algemeen. De noodzaak om deze trajecten te erkennen impliceert het ondersteunen van een endogene benadering van onderaf, een ‘bottom-up approach’. Dit geeft aan dat er meer ruimte moet komen voor een systematisch alternatief naast een Groene Revolutie in Afrika van bovenaf (‘top-down’). Trajecten van interactie tussen het sociale en het natuurlijke hebben een grote verscheidenheid aan veelzijdige rijstrassen geproduceerd en zijn cruciaal binnen de aanpak van ontwikkelingsvraagstukken in gebieden waar dergelijke trajecten hebben plaatsgevonden: daar waar de omstandigheden van boeren dynamisch en suboptimaal zijn. In plaats van het in kaart brengen van de lokale culturele voorkeuren (deze kunnen snel veranderen en binnen kleine afstanden variëren) is het vruchtbaarder om uit te gaan van rassen die boeren zelf al hebben ontwikkeld en om deze ook te promoten en te verspreiden in andere gebieden.

PhD Education Certificate

Béla Teeken
Completed Training and Supervision Plan
Wageningen School of Social Sciences (WASS)

Name of the learning activity	Department/Institute	Year	ECTS*
A) Project related competences			
Language Course Ewe	Centre for Linguistics Leiden University (LUCL)	2006, 2007	3
Tailor made workshops to use software: Matlab, Dip Image, SAS curve fitting, PASW	Centre for Crop Systems Analysis WUR	2009-2011	2
Technography: Researching Technology and Development	Technology and Agrarian Development (TAD) WUR	2007	6
Complexity in and between eco- and social systems	CERES, WUR	2007	3
Research Proposal Development	TAD and Centre for Crop Analysis	2006, 2007	4
Analysing farming systems and rural livelihoods in a changing world: Vulnerability and Adaptation	University of Zimbabwe and WUR.	2008	2.8
B) General research related competences			
Introduction course (partly, Including full attendance of the presentation tutorials)	CERES	2007	3
Two-day Lecture & PhD master class prof. Nick Tilley and prof. Perri 6	CERES	2006	1
Tailor made workshops to use software: Matlab, Dip Image, SAS curve fitting, PASW	Centre for Crop Systems Analysis WUR	2009-2011	2
Participation in a series of 20 workshop-seminars on sociological theory and method	Rural Develop Sociology	2006-2007	2
Participation in TAD seminars		2006-2015	3
C) Career related competences/personal development			
'*African Rice (Oryza glaberrima) and community identity - environment, culture and history in southern Ghana'* Corsage Winter Meeting "Genomics in Society, from intentions to implementations"	WUR; VU Amsterdam; Genomics Network for young Scientists (GeNeYouS)	2006	0.5
Writing Summery on the "Sociology after Durkheim conference" at the University of Surrey England. *'Sociology after Durkheim conference in Surrey 21st June 2006: a summary'*	TAD, WUR	2006	2
Registration on film and rerun of the lectures by Nick Telly / Perry 6	TAD, WUR	2006	0.5
Presentation on the fieldwork results of the WOTRO project Biology and Anthropology of African rice	University of Ghana, Legon and WUR	2009	1

'Improving rice-based technology development and dissemination through a better understanding of local innovation systems'	2nd Africa Rice Congress, Bamako, Mali	2010	1
'The maintenance of African rice (Oryzaglaberrima) in the Togo mountain ranges: ecology, culture and food security'	Young Research Seminar Agropolis, Montpellier France	2010	1
'Advocating the integration of socio-cultural factors in models for variety dissemination'	International Rice Research Conference, Hanoi, Vietnam	2010	1
Pitch presentation at 95th Dies Natalis Alumni Awards celebration	WASS	2013	0.5
Total			**39.3**

*One credit according to ECTS is on average equivalent to 28 hours of study load

About the author

Béla Teeken was born on Februari 10, 1975 in Maastricht, the Netherlands. He studied Tropical land use at Wageningen University. After completing an MSc thesis in plant physiology, studying the drought resistance of a crossbreeding between African and Asian rice at the West African Development Association in Ivory Coast, he became more interested in the societal context of rice cultivation and continued with an MSc thesis in rural sociology with fieldwork in the Office du Niger rice production area in Mali, pleading for a development sociology based on the communication with local actors.

After his graduation he worked shortly as a journalist photographer for the Amsterdam Fund for the Arts (AFK) for which he reported cultural events organised by minority groups in the Netherlands and funded by the AFK. Then he continued to work as a research fellow at the Indian NGO 'SRISTI'(Society for Research & Initiatives for Sustainable Technologies & Institutions) to help shape a new academy in cooperation with the Indian Institute of Management Ahmadabad (IIMA) with the objective to critically reflect on the process of up-scaling local innovations and to trigger horizontal connections between local innovators. The 'Honey Bee network' that was initiated by SRISTI is a horizontal network that connects grassroots innovators.

After having been granted an opportunity to take part in an NWO-WOTRO financed project on the biology and anthropology of African rice he pursued an interdisciplinary PhD study at Wageningen University, combining genetics and plant physiology with social science. This thesis is the result.

He is especially interested in how agricultural technology development is related to the local ecology, community and society: how do the natural environment, local institutions and culture shape and determine local innovations and agricultural practices and how do these innovations and practices relate to those of formal scientific research. This implies understanding and tackling agrarian development in an interdisciplinary way without making the error of reduction: tackling natural science issues with social science tools or vice versa. In this way food security issues might be tackled more accurately as such a perspective does not exclude elements that constitute social organisation, identity and the motivation to cooperate.

Publications

Peer reviewed in a scientific journal:

First author and shared first author:

Teeken B, Nuijten E, Temudo MP, Okry F, Mokuwa A, Struik PC, Richards P (2012) Maintaining or Abandoning African Rice: Lessons for Understanding Processes of Seed Innovation. Human Ecology 40(6) 879-892. doi: 10.1007/s10745-012-9528-x

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As co-author:

Nuijten E, van Treuren R, Struik P.C., Mokuwa, A., Okry, F., Teeken, B., Richards, P. (2009). Evidence for the Emergence of New Rice Types of Interspecific Hybrid Origin in West African Farmers' Fields. PLoS ONE 4(10): e7335. doi:10.1371/journal.pone.0007335

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