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Effects of transformation processes in '*jubraka*' agroforestry systems of the Nuba Mountains, Sudan, on plant diversity

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TRANSFORMING LIVES AND LANDSCAPES

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organicagriculturalsciences **U N I** K A S S E L

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English summary

The global fears of substantial biodiversity losses in human-managed agricultural systems were underpinned by several studies that observed declines in richness and diversity of traditional varieties, landraces, relic crops and rare species due to recent short-term processes termed as commercialization, intensification, simplification, transformation or urbanization as well as the upsetting effect during long-term domestication processes in human managed agricultural systems (the term 'transformation' will be subsequently used). Also the diverse types of agroforestry systems such as homegardens (HG) and their cultivated species are subjected to these kinds of transformation processes.

To enlighten the function, structure and diversity of HGs subjected to ongoing and influencing human-induced transformation as well as domestication process on plant genetic resources, a field study on inter-specific plant and intra-specific indigenous fruit tree diversity was conducted from 2009-2011 in the traditional jubraka HG system in the Nuba Mountains, Kordofan, Sudan. The jubraka represents the most common type of small-scale agroforestry system in the semi-arid zone of Sudan and is distributed from Darfur up to the Kordofan province, southern Sudan. The region is an old settling area with large cultural diversity and is shaped by diverse small and large-scale agricultural cropping systems. Impacting agricultural innovations in this region date back to the beginning of the 19th century with a strong focus on large-scale agriculture to produce mainly cotton as well as staple crops. However, the very one-sided focus on large-scale agriculture and the partly negligence of research hampered the monitoring of recent agronomical changes, which holds in particular true for the existing small-scale jubraka system and its incorporated plant species. The main objective of this study was to assess inter-specific plant species richness and diversity and its driving factors system as well as the intra-specific diversity of two indigenous African fruit tree species (Ziziphus spina-christi and Adansonia digitata) that are both influenced by environmental factors and assumed human interventions.

Firstly, four villages were investigated along an environmental and socio-economic gradient and 61 HGs randomly chosen. In each garden, all useful plant species and individuals were recorded. By means of semi-structured questionnaires household specific socio-economic and garden-related data were assessed. In addition, soil samples were collected and subsequently analyzed for standard soil parameters. Data were subjected to non-parametric statistical tests that allowed comparisons between and among groups (location, level of commercialization and clusters (s. below)), multiple regression analyses to identify influentials on richness and diversity, a cluster analysis (minimum variance) to extract

homogenous groups of HGs and a discriminant analyses to find most explaining species responsible for the underlying clustering.

A surprisingly high plant richness and diversity was found among the villages as well as socio-economic characteristics and soil related parameters. The most remote and the village with the strongest market access harboured a similarly high overall species richness and diversity (excluding ornamentals). Ornamental plant species on the other hand were dominating the villages with the best market access. Key factors affecting plant richness and diversity were commercialization, location, an internally assessed household poverty index as well as soil related factors such as pH. According to the plant composition, four homogeneous clusters of HGs were extracted and described according to their socio-economic factors and main plant use groups: 1. 'traditional-staple', 2. 'transitional-staple', 3. 'pastime-mixed', and 4. 'commercial-vegetable'. Fifteen species contributed much to the explanation of the clusters: *Sorghum bicolor*, *Zea mays*, *Abelmoschus esculentus*, *Arachis hypogeae*, *Balanites aegyptiaca*, *Solanum melongena*, *Solanum lycopersicum*, *Sesamum indicum*, *Cucumis melo*, *Vigna unguiculata*, *Terminalia laxiflora*, *Acacia nubica*, *Physalis angulata* and *Cajanus cajan*.

Secondly, 250 individuals of the indigenous fruit tree (IFT) *Z. spina-christi* from five spatially distant locations were geographically recorded, individual tree and fruit morphometric parameters were assessed and leaf material sampled. Each location was subdivided into HG and adjacent forest sites resulting in 125 individual trees each. General linear models and ANOVAs were used to compare locations and sites. Amplified fragment length polymorphism (AFLP) was applied to study genetic diversity, variation, differentiation and structure among populations.

The diversity of dendrometric, fruit morphometric as well as genetic parameters was high and differed significantly among locations. Although statistically not significant mean fruit morphology was continuously larger in HGs compared to the forest. Environmental parameters seemed to affect morphology. The applied multiple regression models were, however, rather of low explanatory power, while a strong partial negative correlation of fruit traits along an increasing altitudinal gradient indicated a large environmental influence. A slightly higher genetic diversity was observed in HG samples. Genetic differentiation showed comparatively high levels of assessed fixation indices that indicated some extent of hampered gene flow among populations, which likely resulted into two distinct gene pools.

Larger dendrometric and fruit morphometric traits are likely to result from better growing conditions in HGs and/or human selection of germplasm. This is in line with the higher genetic diversity in HGs, which is likely explained as a consequence of the admixture of germplasm from different origins planted, one of the first steps of domestication. Resulting

fixation indices showed a moderate differentiation and indicated a hampered gene flow among populations, which likely resulted in the separation into two clusters. It is thus suggested that Z. spina-christi is on a still low level of domestication, but with high potential for future conservation and breeding strategies.

Thirdly, a total of 306 *A. digitata* trees were sampled from seven locations similarly subdivided into HG and forest populations. The availability of already developed simple sequence repeats (SSR) markers for *A. digitata* allowed the analyses of SSR data. Due to the tetraploid fashion of *A. digitata* two approaches were followed by means of a directly derived allele frequency matrix and a transformed binary allele phenotype matrix. Dendrometric tree and morphometric fruit traits were assessed to study the morphological variability.

Genetic diversity was balanced and did not differ between locations or management regimes ($P>0.05$) although tendencies of higher diversity in 'wild' areas were observed. Genetic structure revealed recent introductions of germplasm reflecting migration patterns likely caused by human translocation. A Bayesian cluster approach detected two distinct gene pools in the sample set.

The variability among locations of tree characters was high ($P<0.05$), but low between fruit morphometries. Also HG and wild populations did not show any difference, although slightly larger fruit traits were observed in HG stands.

The morphological and genetic variability shows the potential of the species for future research and breeding. Our study indicates furthermore an urgent need to implement conservation and sustainable management strategies in both genetically distinct units.

Taking into account biodiversity as an integral component of sustainable agroforestry systems, the *jubraka* in the Nuba Mountains showed a surprisingly rich set of plant species richness and diversity parameters. Level of commercialization alone did not seem to be the main factor for variation of richness and diversity as indicated by low differences between subsistence and commercial HGs. However, large differences among villages and plant compositional derived clusters highlighted the complexity of factors influencing plant richness and diversity. The role of IFT species is still important and huge potentials in terms of morphology and adapted alleles are likely present since domestication in the two investigates IFT species was found to be still in its initial steps. Future research and implementation would be beneficial for the inter-specific diversity of the *jubraka* HG system and intra-specific diversity of IFT species to maintain high diversity or increase diversity to assure food security for future generations.

ملخص العربية (*Arabic summary*)

مدعومة المخاوف العالمية من خسائر كبيرة في التنوع البيولوجي في النظم الزراعية التي يديرها الإنسان جاءت والأنواع بالعديد من الدراسات حيث لوحظ إنخفاض في ثراء وتنوع الأصناف التقليدية و السلالات المحلية، و المحاصيل الغابرة النادرة وذلك بسبب ماعرف مؤخراً بالمعالجات قصيرة المدى ويطلق عليها التسويق، والتكثيف، والتبسيط، والتحول أو التحضر، لاحقاً) (سيتم أستخدام مصطلح التحول فضلا عن الأثر المزعج لعمليات التدجين طويلة الأجل في النظم الزراعية التى يديرها البشر والأنواع النباتية المدرجة فيها لهذه الأنواع (HGs)تتعرض أيضا الأنواع المختلفة من النظم الزراعة الغابية مثل الحدائق المنزلية من عمليات التحول.

م لخص لتسليط الضوء علي وظيفة وتركيبة وتنوع الحدائق المنزلية التي تعرضت للتحول بشكل متواصل بفعل تدخلات الإنسان و بفعل عمليات التدجين على الموارد الوراثية النباتية، تم إجراء دراسة حقلية في منطقة جبال النوبة بأقليم كردفان ال عرب ية والتنوع داخل أشجار الفاكهة (inter-specific) على التنوع بين نباتات معينة 2009 -2011 بجمهورية السودان في الفترة من نظام الجبراكة من .(Jubraka)) في نظم الحدائق المنزلية التقليدية أو ما يعرف محليا بنظام الجبراكة (intra-specificالمحلية (أكثر نظم الحراجة الغابية شيوعا حيث يتواجد في الحيازات الصغيرة أو النطاقات الصغيرة في المنطقة شبه القاحلة من السودان والتى تنتشر المنطقة هي منطقة إستيطان قديمة مع تنوع ثقافي كبير، تشكل من خلال .علي أمتداد إقليمي دارفور و كردفان في جنوب السودان تنوع نظم زراعة المحاصيل في الحيازات الكبيرة والصغيرة. أثر الابتكارات الزراعية في المنطقة يرجع إلى بداية القرن التاسع مع تركيز قوي على زراعة القطن و المحاصيل الأساسية بشكل رئيسي وعلى نطاق واسع. بيد أن التركيز على جانب واحد عشر وهو الزراعة على نطاق واسع والإهمال الجزئي للبحوث أعاق رصد التغيرات الزراعية التي حدثت في الأونة الأخيرة و التي الهدف .القائم على الحيازات الصغيرة و الأنواع النباتية المدرجة فيه تحوي على وجه الخصوص حقيقة وجود نظام الجبراكة والعوامل الدافعة له، وكذلك التنوع داخل أنواع (inter-specific)الرئيسي من الدراسة هو تقييم الثراء و التنوع بين نباتات معينة التي تتأثر على حد سواء بالعوامل البيئية) من أثنين من أشجار الفاكهة الأفريقية المحلية (السدر و التبلدي)intra-specificمحددة (والتدخلات البشرية.

أولاً، تمت الدراسة علي 61 حديقة منزلية تم أختيارها بشكل عشوائي من أربع قري ذات مستوي بيئي وأجتماعي وأقتصادي متجانس ، تم حصر جميع الأنواع والفصائل النباتية المفيدة لكل حديقة. بأستخدام الاستبيانات شبه المنظمة تم تقييم البيانات بالإضافة إلى ذلك، تم أخذ عينات من التربة لكل أسرة الأجتماعية و الأقتصادية و المتعلقة بالنشاط داخل الحدائق تحت الدراسة وتحليلها لمعايير التربة القياسية.

وذلك (non-parametric statistical tests) تم تحليل البيانات أحصائياً أولاً بأستخدام الأحصائيه اللاحدودية تحليل الانحدار المتعدد للمقارنة بين و داخل المجموعات للمحددات الأتية: الموقع، المستوى التجاري والكتل و من ثم تم تطبيق (cluster analysis) لتحديد النافذين على الثراء والتنوع، يليه تحليل الكتله الجماعيه (multiple regression analyses) (discriminant وأخيراً، تم تحليل التمايز الأحصائي (الحد الأدنى للتباين) لأستخلاص مجموعات متجانسة من الحدائق المنزلية للعثور على أكثر الأنواع المسؤولة عن تجميع الكتل (analysis .

علي غير المتوقع وجد تباين نباتي عالي الثراء والتنوع بين القري كما في الخصائص الاجتماعية والاقتصادية والمعايير القري النائية والقري التي لديها سبل وصول ممتازة للأسواق تأوي بالمثل ثراء وتنوع عالي من الأنواع النباتية المتعلقة بالتربة. أثبتت الدراسة أن.التي من ناحية أخرى كانت تسيطر على القرى التي لديها سبل وصول جيدة إلى الأسواق باستثناء نباتات الزينة العوامل الرئيسية التي تؤثر في ثراء وتنوع النباتات هي التسويق، الموقع، التقييم الداخلي لمؤشر الفقر المنزلي للأسر، فضلا عن وفقا للتكوين الغذائي من النبات، أستخلصت أربع كتل متجانسة من الحدائق المنزلية. العوامل المتصلة بالتربة مثل درجة الحموضة كتل تعتمد غذاء 2/كتل تعتمد غذاء أساسي تقليدي، : ال/1الأ قتصادية، و الغذاء الأساسي و هي وصفت وفقا للعوامل الأجتماعية و الخضر التجارية كتل تعتمد 4// كتل لمجرد الهواية والترويح ، 3أساسي وتتنقل مابين الهواية والتجارة ،

خمسة عشر نوع وهي: الأنواع النباتية التي ساهمت بقدر كبير في شرح وتفسير الكتل المستخلصة حصرت في

، (*Abelmoschus esculentus*)، البامية (Zea mays) الذرة الشامية، (*Sorghum bicolor*) الذرة الرفيعة

Solanum)، الباذنجان الأسود (*Balanites aegyptiaca*)، الهجليج(*Arachis hypogeae*) الفول السوداني

Cucumis)، العجور (*Sesamum (indicum*)، السمسم (Solanum lycopersicum)، الطماطم (melongena

، الطماطم (Acacia nubica)، السنط(*Terminalia laxiflora*)، داروت (*Vigna unguiculata*)، الورق(*melo*

(*Cajan cajanus*) و اللوبيا عدس (*Physalis angulata*)البري

شجرة من أشجار الفاكهة المحلية 250 ثانيا، تم عمل حصر جغرافي في خمسة أماكن بعيدة من الناحية المكانية لعدد

للأ شجار و الثمار كلٍ علي حدي مع أخذ عينات من (morphometric) السدر) تم تقييم المعايير المظهرية- المترية(IFT)

وغابات متاخمة و نتج الحصر عن 125 شجرة للحدائق المنزلية تم تقسيم كل من الأماكن الخمس إلي حدائق منزلية الأوراق.

لمقارنة الأماكن الخمسة المختارة ANOVAs و (general liner models) أستخدمت النماذج الخطية العامة .ومثلها للغابات

(amplified fragment length) المتضخمة تم تطبيق تعدد أشكال أطوال الشدف وتقسيماتها (حدائق منزلية وغابات).

polymorphism, AFLP (والهيكلة بين السكان) لدراسة التنوع الوراثي، والتباين، والتمايز.

(dendrometric)للثمار و الصفات المترية للأغصان(morphometric) التنوع في الصفات المظهرية-المترية

وكذلك في المعايير الوراثية كان كبيرا و يختلف معنوياً بين المواقع. على الرغم من عدم وجود فروق معنوية إلا أنه مظهرياً حجم

نماذج الانحدار . مقارنة مع الغابة فمما يبدو فأن المعايير البيئية قد تؤثر علي الشكل الظاهري الثمار كان أكبر في الحدائق المنزلية

ضعيفة، بينما أفاد وجود أرتباط جزئي التي تم تطبيقها، كانت ذات مقدرة تفسيرية(multiple regression models)المتعدد

لوحظ وجود تنوع جيني عالى قليلا في .سلبي قوي في صفات الثمار على طول الزيادة في تدرج المرتفعات علي الأثر البيئي الكبير

أظهر التمايز الوراثي مستويات عالية نسبيا عند تقييم الأرقام القياسية المثبتة التي الأوراق النباتية المأخوذة من الحدائق النباتية كما

أشارت إلى حد ما إلي إعاقة في التدفق الجيني بين السكان، والتي من المرجح أنها أدت إلى اثنين من تجمعات الجينات المميزة.

ذات الحجم (dendrometric) للثمار و الصفات المترية للاغصان (morphometric) الصفات المظهرية- المترية

وهذا يتماشى مع .الكبير من المحتمل أن تنجم عن ظروف زراعة أفضل في الحدائق المنزلية / أو بالأنتخاب من الأصول الوراثية

والذي من الممكن تفسيره كنتيجة للخلط في المادة الوراثية عند زراعة أصول نباتية التنوع الجيني العالي في الحدائق المنزلية

مختلفة كخطوة أولى نحو التدجين وعليه فقد أقترحت الدراسة أن أشجار السدر لا تزال علي مستوي تدجين محدود مع أمكانيات عالية

للحفظ والتربية في ظل أستراتيجية مستقبلية.

أتاح توفر علامات الأقمار .ثالثا، أخذت عينات من 306 من أشجار التبلدي من سبع مواقع وزعت لحدائق منزلية وغابات

الصناعية الصغري المطورة بالفعل أو ما يعرف أيضاً بتكرار التسلسل البسيط لأشجار التبلدي بتحليل معلومات الأقمار الصناعية

بسبب مظهر التبلدي رباعي الصيغة الصبغية تم أتباع منهجين عن طريق الأستخلاص المباشر لقوالب تواتر الأليل وعن .الصغري

بغرض دراسة التنوع في الصفات المظهرية تم أيضاً تقييم الصفات .طريق أستخلاص قوالب أليل ثنائية النمط الظاهري المحوله

للثمار (morphometric) والصفات المظهرية- المترية (dendrometric)المترية للأغصان.

) على الرغم من أنه لوحظ 0.05 > Pالتنوع الجيني كان متوازن مع عدم وجود أختلاف بين المواقع أو أنظمة الأدارة (

كشفت التركيبة الجينية إدخالات حديثة علي المادة الوراثية تعكس أنماط هجرة من .وجود نزوع لتنوع عالي في المناطق البرية

النهج العنقودي للنظرية الافتراضية كشف عن اثنين من التجمعات الجينية المميزة المحتمل أن يكون سببها حركة وتنقلات الإنسان.

في مجموعة العينات المأخوذة.

، ولكنه منخفض بين الصفات المظهرية- المترية (0.05 > P)التباين في صفات الاشجار بين المواقع كان عاليا

الحدائق المنزلية البرية لم تظهر أي اختلاف، على الرغم من أنه قد لوحظ وجود ثمار أكبر قليلا في للثمار.(morphometric)

أثبتت الدراسة الحوجة الملحة لتفعيل وتنفيذ أستراتيجيات للأدارة والحفظ والأستدامة للصفات المظهرية والوراثية.الحدائق المنزلية .

مع الأخذ بعين الاعتبار التنوع البيولوجي كجزء لا يتجزأ من نظم الزراعة المختلطة بالغابات المستدامة، أظهرت الجبراكة مستوي التسويق وحده ليس سبب رئيسي للتنوع والثراء النباتي بدليل وجود أختلافات بسيطة. في جبال النوبة ثراء وتنوع نباتى عالى ومع ذلك، أبرزت الاختلافات الكبيرة بين القرى و التركيبية. بين الحدائق المنزلية التجارية و الحدائق المنزلية للألستهلاك الذاتي أشجار الفاكهة المحلية. النباتية المستمدة من التجمعات المعرفة في هذه الدراسة تعقيد العوامل المؤثرة في الثراء والتنوع النباتي لها دور مهم وأمكانات ضخمة من حيث المظهر وأما من حيث تكيف الأليل فمن المرجح أنه وجد منذ التدجين في الصنفين (IFT) الذي لا يزال في مراحله الأولى تحت الدراسة.

تنفيذ بحوث في المستقبل علي التنوع بين الحدائق المنزلية أو مايعرف بنظام الجبراكة والتنوع داخل أشجار الفاكهة المحلية لحفظ وزيادة التنوع النباتي من شأنه أن يساهم في ضمان الأمن الغذائي للأجيال القادمة(IFT).

Deutsche Zusammenfassung

Die Befürchtung erhebliche Verluste biologischer Diversität in anthropogen beeinflussten Agrar-Ökoystemen zu erfahren, wurde durch mehrere Studien weltweit bestätigt, welche einen Rückgang des Artenreichtums und der Diversität von traditionellen Sorten, Landrassen, Reliktarten und seltenen Arten feststellten. Ursachen dafür sind jüngste und kurzfristige Prozesse welche unter die Begriffe Kommerzialisierung, Intensivierung, Simplifikation, Transformation (wird im folgenden stellvertretend verwendet) oder Urbanisierung fallen als auch langfristige Domestikationprozesse in landwirtschaftlichen Produktionssystemen. Auch die verschiedenen Typen von Agroforstsystemen wie Hausgärten (HG) und deren kultivierte Pflanzenarten sind diesen Prozessen unterworfen.

Um die Funktion, Struktur und Vielfalt von HG und die fortlaufenden und beeinflussenden Transformations- und Domestikationsprozesse auf pflanzengenetische Ressourcen zu erleuchten, wurde eine Feldstudie zur inter-spezifischen Pflanzen- und intra-spezifischen indigenen Obstbaumdiversität in den Jahren 2009-2011 im traditionellen *jubraka* HG-System in den Nuba Bergen, Kordofan, Sudan durchgeführt. Der *jubraka* stellt die häufigste Form kleinskalierter Agroforstsysteme in der semi-ariden Zone des Sudan dar und erstreckt sich von Darfur bis zur Provinz Kordofan, im Süden des Sudan. Die Region ist ein altes Siedlungsgebiet mit großer kulturellen Vielfalt und wird durch diverse kleine bis große landwirtschaftliche Anbausysteme geprägt. Einschneidende landwirtschaftliche Neuerungen in den Nuba Bergen reichen bis zum Anfang des 19. Jahrhunderts zurück und sind gekennzeichnet durch einem starken Fokus auf groß angelegte Landwirtschaft, um Baumwollproduktion voranzutreiben. Dieser einseitige Fokus behinderte gleichzeitig die Beachtung und die Erforschung anderer Produktionssysteme, was insbesondere für das bestehende kleinräumige *jubraka* system und deren Nutzpflanzen zutrifft.

Das Hauptziel dieser Studie war inter-spezifische Pflanzendiversitätsparameter als auch die intra-spezifische Formenvielfalt von zwei einheimischen afrikanischen Obstbaumarten (*Ziziphus spina-christi* und *Adansonia digitata*) in *jubraka*s und deren beeinflussende anthropogene Faktoren und Umweltparameter zu untersuchen.

Zunächst wurden vier Dörfer entlang eines Umwelt- und sozio-ökonomischen Gradienten untersucht und 61 HG zufällig ausgewählt. In jedem Garten wurden alle Nutzpflanzenarten und Individuen erfasst. Mittels semi-strukturierter Fragebögen wurden haushaltsspezifische sozio-ökonomische und gartenbezogenen Daten erfasst. Darüber hinaus wurden Bodenproben aus Gemüse- und Getreideflächen genommen und anschließend auf Standardbodenparameter hin analysiert. Die Daten wurden nicht-parametrischen statistischen Tests unterworfen, um Vergleiche zwischen Gruppen (Standort,

Grad der HG-Kommerzilisierung und Cluster (s. unten)) zu ermöglichen. Es wurden Regressionsanalysen durchgeführt, um Einflussfaktoren auf Pflanzenreichtum und -diversität zu identifizieren und eine Clusteranalyse, um homogene Gruppen von HG zu extrahieren. Anschließend wurden durch eine Diskriminanzanalyse jene Pflanzenarten ermitteln, welche wesentlich zur Clusterbildung beitrugen.

Zwischen den Dörfern wurde ein vergleichsweise hoher Pflanzenreichtum und hohe Diversiätsparameter als auch stark variierende sozioökonomische und bodenchemische Charakteristika gefunden. Das entlegendste Dorf und das Dorf mit dem stärksten Marktzugang zeigten einen ähnlich hohen Pflanzenreichntum und Diversität (ohne Zierpflanzen). Zierpflanzenarten auf der anderen Seite wurde durch Dörfer dominiert, die den besten Marktzugang besaßen. Die Schlüsselfaktoren, welche Pflanzereichtum und –vielfalt beeinflussten waren Grad der Kommerzialisierung, der Standort, ein interner Haushaltsarmutsindex sowie Bodenfaktoren wie der pH-Wert. Abhängig von der Pflanzenzusammensetzung konnten vier homogene Gruppen von HG extrahiert und entsprechend ihrer sozio-ökonomischen Eigenheiten und pflanzlichen Hauptnutzungsgruppen klassifiziert werden: 1. 'traditionell-Grundnahrungspflanzen'-, 2. 'Gemischt-Grundnahrungspflanzen'-, 3. ‚Hobby-gemischt'- und 4. 'Kommerziell-Gemüse'-HG. Die 15 Pflanzenarten, die wesentlich zur Clusterbildung beitrugen waren: *Sorghum bicolor*, *Zea mays*, *Abelmoschus esculentus*, *Arachis hypogeae*, *Balanites ageyptiaca*, *Solanum melongena*, *Solanum lycopersicum*, *Sesamum indicum*, *Cucumis melo*, *Vigna unguiculata*, *Terminalia laxiflora*, *Acacia nubica*, *Physalis angulata* und *Cajanus cajan*.

In der zweiten Untersuchung wurden 250 *Z. spina-christi* Bäume von fünf räumlich getrennten Standorten geographisch erfasst, dendrometrische und fruchtmorphometrische Parameter ermittelt und Blattmaterial gesammelt. Von jedem Standort wurden insgesamt 125 Bäume in HG und 125 Bäume in Wäldern erfasst. Die Daten wurden allgemeinen lineare Modellen (GLM) und Varianzanalysen (ANOVAs) unterzogen, um die Ausprägungen zwischen Standorten zu vergleichen. Amplizierter Fragmentlängenpolymorphismus (AFLP) wurde angewendet, um die genetische Vielfalt, Variation, Differenzierung und Struktur zwischen den untersuchten Populationen zu studieren.

Die Vielfalt an dendro- und fruchtmorphometrischen als auch genetischen Parametern war deutlich standortabhängig. In Wildpopulationen waren dünnere Stammdurchmesser zu beobachten als in HG-Populationen. Obwohl statistisch nicht signifikant, waren die mittleren Fruchtmorphologien in HG jeweils größer als in den benachbarten Waldpopulationen. Umweltvariablen schienen einen gewissen Einfluss auf die Fruchtmorhologie zu haben. Die angewendeten multiplen Regressionsmodelle waren jedoch eher von geringer Aussagekraft, während eine starke negative Korrelation der

Fruchtmerkmale entlang eines zunehmenden Höhengradienten gezeigt werden konnte. Die genetische Diversität war etwas höher in HG Populationen, statistisch jedoch nicht signifikant. Die genetische Differenzierung zeigte vergleichsweise hohen Fixierungsindices, was auf einen behinderten Genfluss zwischen Population hindeutet und wahrscheinlich zur Separierung der zwei gefundenen Genpoole führte.

Größere dendro- und fruchtmorphometrische Merkmale dürften durch bessere Anbaubedingungen in HG und/oder durch anthropogene Selektion von Pflanzenmaterial herrühren. Dies steht im Einklang mit der höheren genetischen Vielfalt in HG, die wahrscheinlich als Folge der Beimischung von Pflanzenmaterial aus unterschiedlicher Herkunft stammte und eines der ersten Schritte zur Domestizierung dieser Art erklären würde. Obwohl ein geringer Domestikationsfortschritt bei *Z. spina-christi* gefunden wurde, kann ein hohes Potential für zukünftige Schutz- und Züchtungsmaßnahmen in HG für diese Art festgestellt werden.

In der dritten Studie wurden insgesamt 306 *A. digitata* Bäume von sieben Standorten in den Nuba Bergen gesammelt und in ähnlicher Weise wie bei *Z. spina-christi* in HG- und Waldpopulationen unterteilt. Die Verfügbarkeit bereits entwickelter Mikrosatelliten (SSR) für *A. digitata* ermöglichte die Anwendung dieser zur Studie der genetischen Diversität und genetischen Struktur. Aufgrund der tetraploiden Konstitution von *A. digitata* wurden zwei Datenmatrizen zugrunde gelegt: einer direkt abgeleiteten Allelefrequenzmatrix und eine transformierten binären Phänotypenmatrix. Ein Bayes'scher Clusteransatz zeigte, dass zwei Genpoole in der gesammelten Stichprobe vorhanden waren. Die genetische Vielfalt war ausgewogen und unterschied sich weder zwischen den Standorten, zwischen HG- und Wildpopulationen noch zwischen den Clustern ($P>0,05$). Eine leicht erhöhte genetische Diversität wurde in den Wildpopulation festgestellt. Ebenfalls ähnlich zu *Z. spina-christi*, wurden dendrometische und fruchtmorphometrische Merkmale gemessen, um die morphologische Variabilität zu studieren. Die zwischenstandortliche Variabilität der dendrometrischen Parameter war hoch ($P<0,05$), jedoch gering bezüglich der Fruchtmorphometrie ($P>0,05$). HG- und Wildpopulationen unterschieden sich ebenfalls nicht hinsichtlich der Parameter, obwohl leicht größere Früchte in HG-Populationen gemessenen wurden.

Die genetische und morphologische Variabilität verdeutlicht das Potenzial dieser Baumart für die zukünftige Untersuchungen und Zucht. Die genetische Struktur legt die Einführungen von Pflanzenmaterial in der jüngere Geschichte nahe und wahrscheinlich durch menschliche Translokationen verursacht wurde. Unsere Studie zeigt die dringende Notwendigkeit bei dieser Art nachhaltige Managementstrategien in beiden genetisch unterschiedlichen Clustern zu implementieren.

Unter Berücksichtigung der biologischen Vielfalt als integraler Bestandteil nachhaltiger Agroforstsysteme wurde deutlich, dass das *jubraka* HG-System in den Nuba-Bergen ein überraschend breites Spektrum an Pflanzenarten und –diversität aufwies. Der Grad der Kommerzialisierung allein hatte offenbar nicht den wesentlichen Einfluss auf die Pflanzendiversität, da nur geringe Unterschiede zwischen beiden Managmenttypen festgestellte wurden. Allerdings markieren die großen Unterschiede zwischen den Dörfern, den gefundenen Clustern als auch die eher schwachen Modelle die Komplexität der Faktoren im *jubraka* HG-System. Indigene Obstbaumarten spielen dabei nach wie vor eine wichtige Rolle und besitzen morphologisch und genetisch viel Potential. Weitere Forschung auf diesem Gebiet und Implementierungsmaßnahmen könnte die inter-spezifische Diversität der HG und intra-spezifische Obstbaumdiversität erhalten oder erhöhen und damit die Nahrungssicherheit für zukünftige Generationen sicherstellen.

Chapter 1 – Introduction

1.1 Thesis outline

The work is sub-divided into five chapters, containing three peer reviewed papers (Figure 1.1). The first chapter introduces the assumed effects of recent transformation processes on plant diversity in HG systems worldwide as well as in Sudan and gives insights into the topic of domestication and genetic diversity of indigenous fruit tree species. Chapter 2 describes the inter-specific plant richness and diversity of the *jubraka* HG system in four different locations. Here, underlying bio-physical and socio-economic factors that are assumed to affect plant species richness and diversity are taken into consideration. Intra-specific diversity of the two important indigenous fruit trees *Ziziphus spina-christi* (L.) Willd. and *Adansonia digitata* L. are described in chapters 3 and 4, respectively. For each species, morphological and genetic parameters are compared and considered with respect to recorded environmental variables. Based on the results, a general overview, critical data evaluation, final conclusions and recommendations are given in chapter 5.
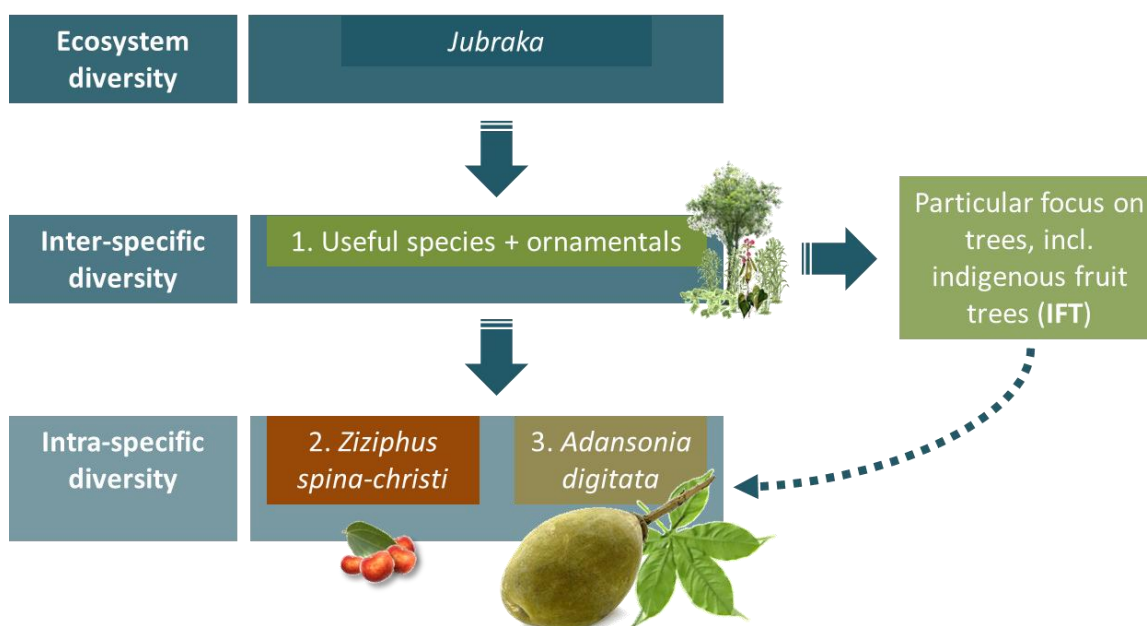
Figure 1.1 Schematic overview of the content and topics of the present work. Picture sources: Moringa tree: freegreatpicture.com (accessed March 2013), Adansonia digitata fruit: chocholistic.com (accessed May 2013), Baobab leaf: Jens Gebauer, Ziziphus spina-christi fruits: Jens Gebauer.

1.2 Agricultural transformation processes and constraints of homegardens in the Nuba Mountains

Impacts of agricultural innovations in the Nuba Mountains, South Kordofan Province, Sudan, date back to the beginning of last century with a strong shift towards large-scale agriculture mainly to produce cotton (Colvin 1939; Abdelgabar 1997). Huge expansion of mechanized farming, application of chemical fertilizers and pesticides, introduction of modern

varieties and exotic species induced fast and significant changes to the bio-physical and socio-economic assemblages (Abdelgabar 1997; Abdallah 2007). Traditional crops such as sorghum (*Sorghum bicolor* Moench)*,* pearl millet (*Pennisetum glaucum* (L.) R.Br.), and sesame (*Sesamum indicum* L.), subsequently lost importance as intensified cultivation spread over the decades (Abdallah 2007). Yet, an estimated 60% of South Kordofan's arable land is not cultivated at present (Klugman and Wee 2008), which has several reasons: since the Nuba Mountains received international attention for the production of cash crops, they were concomitantly pushed into international structures with highly fluctuating market prices (Suliman 2007). This in turn forced the farmers of Kordofan to strongly depend on global economic feedback mechanisms. The independence of Sudan in 1956 with subsequent long lasting civil wars up to 2005 lead to unstable political and economic conditions and famine periods due to droughts of the 1970s and 1980s that affected most of the population in South Kordofan (WorldBank 1990). These circumstances led for instance to constant declines of grain yields (Ayoub 1999). It is thought that these factors hampered the improvement of crop production in Kordofan, which is said to potentially be the "bread basket of East Africa" (Suliman 2007). Predictions of future climatic conditions also paint a bleak picture with regard to the already difficult basis of crop production in the area (UNEP 2008). However, the very one-sided focus on large-scale agriculture and the partially negligence of research hampered the monitoring of recent agricultural changes, which particularly holds true for the existing small-scale homegarden (HG) system, locally called '*jubraka*'. Very little is known about this type of agroforestry system for which historical backgrounds, constitution, structure, function and biodiversity, and information are merely available in descriptive manners (Tothill 1948; Obeidalla and Riley 1983; Makki and Gebreel 2009). This is remarkable, because jubrakas are seen as 'the fruit of labor of generations' (Tothill 1948) and are an important resource of primarily food for the local population in the dry and starting rainy season, the "hungry periods" (Obeidalla and Riley 1983). The *jubraka* represents the most common type of small-scale farming system in the semi-arid zone of Sudan and is distributed from Darfur up to the Kordofan province, southern Sudan (Harragin 2003; Elsiddig 2007). Typically, the *jubraka* (pl. *jabreek*; an alternative term exists in the eastern Nuba Mountains: *najad*) is a rain-fed cropping system of about 0.5 ha that surrounds homesteads and has the capability to supply food throughout the year (Babiker et al. 1985; Elsiddig 2007). A traditional year around production and food provision of these HGs is thereby only accomplished by the presence of fruit trees, whose edible fruits reach maturity foremost during the dry seasons. Most common indigenous fruit tree species (IFTs) in HGs of the Nuba Mountains are: Doum palm (*Hyphaene thebaica* (L.) Mart.), Christ's thorn Jujube (*Ziziphus spina-christi* (L.) Willd.), African baobab (*Adansonia digitata* L.) and Desert date (*Balanites aegytiaca* (L.) Delile) (Goenster et al. 2011). The same authors found that the role of IFTs as a source of fruit is

likely a minor one in the Nuba Mountains, because cash crop tree species of exotic origin seem to be more appreciated by the local people. Exotic tree species, mainly introduced into the area during the times of Turco-Egyptian conquest and Anglo-Egyptian condominium (UNEP 2009) are for instance: Custard apple (*Annona squamosa* L.), Lime (*Citrus × aurantiifolia* (Christm.) Swingle) and Mango (*Mangifera indica* L.) (Abdallah 2007). The introduction of exotic herb species into Kordofan's HGs such as radish (*Raphanus sativus* L.), rocket (*Eruca sativa* Mill.) or dill (*Anethum graveolens* L.) can be vaguely traced back to the beginning of the last century (Bedri 1984), while the earlier arrival of crops such as tomato (present with a variety of small fruits and long lasting greenery) and maize into Sudan from South America is to our knowledge not documented. Reoccurring introductions were particularly due to improved infrastructure, opening of markets, increased mobility of people, land use policies, introduction of non-native germplasm material and external inputs such as fertilizers and pesticides during the Anglo-Egyptian condominium (Obeidalla and Riley 1983) and likely after revising ceasefire agreements. In addition to introductions and potential manifestations of new practices in the area of the Nuba Mountains, national and international land grabbing also contributes to the loss of traditional indigenous knowledge and HG structures by undermining the position of native people (Large and El Basha 2010). There is also evidence that the Nubian population has moved extensively over short distances the past 200 years (Pantuliano 2005). Such repeated movements towards the hills and mountains are known to have been driven by the slave raids of the conquerors (Turco, Anglo, Egyptian) in the beginning of the 19th century (Pantuliano 2005) as well as recent displacements due to internal post-independent conflicts (Hassan 2005), which has resulted in the establishment of so called hill-farms or the total reliance on home gardens. Hill-farms or their visible remainders can be still found in remote areas, and are today revived by poor peri-urban people who live near such hills (personal observation). Moreover, the proportion of internally displaced people in Sudan is the highest in the world likely leading to significant translocations of preferred germplasm and cultural practices when (re-)settling new areas (Suliman 2007).

In contrast to large-scale agriculture, investments and support by governmental agencies to promote these *jubraka*s in Sudan are factually not present, as large financial benefits are not expected. However, strengthening of research and extension programs for Kordofan's *jubraka*s were highly recommended by (Obeidalla and Riley 1983) and resulted in at least a decentralized distribution of cash crop germplasm material, fertilizers and pesticides for far fields and homegardening activities, even at village level (personal communication, Omar Balandia deputy of Agricultural division). Recently, non-governmental organizations such as the Sudanese Red Crescent and the German Red Cross are promoting commercialized cash cropping in urban and per-urban areas to empower women

and improve households' cash income (personal observations). This is important, because it is mainly women who manage the *jubraka* and their contribution to household income is often underestimated in development strategies (Makki and Gebreel 2009).

Taking into account all the described factors that have influenced and shaped the *jubraka* HG system, it is assumed that many transitional stages of this type of agroforestry system exist in the Nuba Mountains.

1.3 Why homegardening? Definitions, benefits and threats

The apparently insurmountable world food crisis has affected economies, nations, societies and local populations over decades (WHO 2008). An urgent need to find and develop strategies to overcome the current constrains at global levels refers directly to the importance of locally adapted agricultural production systems. It has been recognized that traditional small-scale agriculture and regional marketing are fundamental and disproportionately important tools to tackle world's food security in future (Weltagrarbericht 2009). The United Nations Millennium Development Goals (MDG) to be complied by 2015 include the objectives of ensuring 'empowerment of women', 'environmental sustainability' and 'reverse loss of environmental resources'; all of which can be achieved by homegardening.

HGs 'represent intimate, multistory combinations of various trees and crops, sometimes in association with domestic animals, around the home stead' (Kumar and Nair 2004). They are considered as the oldest and most diverse agro-ecosystem on our planet (Nair 2001). Their worldwide distribution suggests the strong cultural linkage to humankind and the fundamental improvement of rural livelihoods (Fernandes et al. 1984; Soemarwoto 1987). HGs can serve as corridors for flora and fauna (Kabir and Webb 2008), build buffer zones at peripheries of conservation forests (Michon et al. 1986) and deal as sanctuaries of rare genetic resources as well as hotspots for fast evolutionary processes through selection and domestication (Esquivel and Hammer 1992). Thus, HGs contribute to *in situ* conservation of biodiversity (Esquivel and Hammer 1992), *ex situ* conservation of rare species (Kabir and Webb 2008) and even more applied to *circa situm* conservation-through-use (Hughes 1998). By integrating and maintaining wild species (Abraham et al. 2008), indigenous crops (Dash and Misra 2001), and traditional varieties (FAO 2001), HGs become living gene banks of inter- and intra-specific diversity and therefore contribute to diversified and region-specific HG systems. Moreover, they are regarded as sustainable systems given their efficient nutrient cycles and low external inputs (Torquebiau 1992; Jensen 1993). The capability of HGs to combine ecosystem services, food security and biodiversity conservation boosts even recent developments and understandings for rearranging and reviving urban and per-urban areas even in industrialized countries (ETC 2006; Galluzzi et al. 2010).

In case of HG ecosystems, however, structure, function and even existence are threatened by 'transformation' processes (term used in the present study) that alter the prevalent assemblages in fast and sometimes unpredictable manners and are described in literature as: simplification (Garcia-Fernandez and Casado 2005), homogenization (Peyre et al. 2006) and commercialization of production (Gebauer 2005; Abdoellah et al. 2006). According to (Kehlenbeck et al. 2007) effects of these processes are highly diverse and affected by region-specific and time-related characteristics of the respective HG systems. The main driver of recent transformation processes is suggested to emerge from intensified cash-crop production in HGs due to improved income opportunities (Major et al. 2005; Abdoellah et al. 2006; Peyre et al. 2006) particularly thanks to simplified market access (Abdoellah et al. 2006; Hashemi et al. 2013). Hence, traditional HGs with subsistence purpose segue into modernized ones with a strong market orientation. Beyond edible cash crop production, more recent developments revealed that ornamental species are also being produced for cash or simply for joy and aesthetic reasons in HGs of better-off families, whereby the role of HGs is fundamentally changed and subsistence food crop production is no longer of major importance (Christanty et al. 1986; Soemarwoto and Conway 1992; Tscharnke et al. 2007). These on-going processes may result in altered garden structures, practices and the neglect or promotion of certain plant genetic resources and are thus suggested to substantially affect the socio-economics, nutrient fluxes, food security and biodiversity. In contrast to humid-tropical regions, comparatively little is known about HG systems in the semi-arid tropics (Wezel and Bender 2003; Azurdia and Leiva 2004; Bernholt et al. 2009), indicating the need for more research, monitoring and development in these regions.

A substantial loss of useful crops species and varieties is a very obvious parameter when looking into HG systems. This holds particularly true for tropical agroforestry systems where a global decline of diversity is observed (Kumar and Nair 2006). Sunwar et al. (2006) for instance reported a loss of 20 species within 10-15 years from HGs in Nepal. However, on-farm germplasm material is additionally highly vulnerable to become rare or extinct by the loss of inter-specific diversity, which may occur through on-going human selection, domestication and transformation processes. These processes are known to accelerate the loss of genetic diversity through the extinction of wild progenitors and traditional varieties or through narrowing of their genetic base.

1.4 The importance of high inter- and intra-specific plant diversity in homegardens

'Agro-biodiversity is the result of natural selection processes and the careful selection and inventive developments of farmers […] over millennia. Agro-biodiversity is a sub-set of

biodiversity' (FAO 2004). It comprises three levels of diversity: agro-ecosystem diversity, species diversity [inter-specific diversity] and diversity of genetic resources [intra-specific diversity] (FAO 2004); all levels are found in agroforestry systems and strongly associated to human activities (Altukhov 2006; Galluzzi et al. 2010).

The coexistence of a diverse set of species in a given ecosystem becomes feasible by niche differentiation. Agro-ecosystems are suggested to match tight nutrient cycling, complex structure and biodiversity if they mimic the functioning of the surrounding ecosystems (Alteri 2002). This is also evident for the agroforestry HG system that is seen as the closest mimic of natural forest patches (Scales and Marsden 2008). Combined advantages of forest ecosystems such as stable microclimates, increased biodiversity, promotion of humus production and mineralization, hampered soil erosion through reduced effects of rain, enhanced water recycling capabilities and the production of agricultural commodities can be achieved in these HG systems. Tilman et al. (1997) showed that productivity and nutrient retention in a given ecosystem increases with biodiversity, since inter-specific differences have different resource requirements. By integrating plant species of different life cycles and multilayer constitutions, the provision of a diverse range of agricultural produce and ecological services over time and space is ensured (Kumar and Nair 2004; Galluzzi et al. 2010). Inter-specific diversity in HGs can therefore be a stimulus for improved food security (Atta-Krah et al. 2004; Kumar and Nair 2004) and can serve as stabilizing and beneficial elements for households and rural populations. The frequently found limitation or reduction of species richness due to economic or horticultural necessity in commercialized gardens may increase the risk of pest and disease outbreaks (Abdoellah et al. 2006) as well as decrease the use efficiency of limited resources such as light, water and nutrients through multistory constitution (Nair 2001). Thus, the reliance on a few, but valuable cash crop species eventually triggers ecological instability of agro-ecosystems and increases the risk of severe impacts in case of crop failures. Furthermore, it is still unclear if the commercialization of HGs automatically improves the situation of households in terms of nutritional health and additional income (Braun and Kennedy 1986; Abdoellah et al. 2006).

Apart from inter-specific diversity as a substantial parameter of vital agro-ecosystems, the importance of intra-specific diversity has received increasing attention over the last decades (IPIGRI 1993). Intra-specific diversity maintained by variation of genes is known to be the raw material of evolutionary change and is crucial for dynamic species performance, including breeding purposes. This is important for adaptability, speciation and, therefore, survival of species under altering environmental conditions (Templeton et al. 2001) as well as matching the demands of humans. The collection and translocation of wild plants by humans as well as subsequent cultivation and selection of preferred germplasm material in human-managed systems is an on-going and fast evolutionary process, termed as domestication.

This human-mediated crop evolution dates back 10,000 years (Doebley et al. 2006; Thomas and Van Damme 2010). Domestication fundamentally alters the morphology and genetic constitution of species compared to their progenitors by filtering out those progenies which best fit the demands and needs of humans (Doebley et al. 2006; Zeder et al. 2006). In contrast to natural selection with non-directed and random shifts of traits, human intervention can be seen as non-random, leading to unidirectional shifts of traits. On the one hand, effects on plant morphology such as larger fruits, extended time of fruit attachment to the plant, determinate growth or more synchronized fruit maturity are described as the "domestication syndrome" (Hammer 1984; Zohary and Hopf 2000). Traits that have been developed under these circumstances are well recognized by breeders and indigenous people and important for easier harvesting and higher yields. On the other hand, genetic erosion - a change in the frequency or even total loss of adaptive alleles - is most evident for many domesticated cash crops such as tomato (Bai and Lindhout 2007) or maize (Hufford et al. 2012), resulting in genetic drift through bottleneck effects (Figure 1.2). These shifts may implicate higher levels of homozygosity known to expose deleterious recessive alleles that finally reduce fitness (Lowe et al. 2005). An additional reduction of census numbers which appears with selective collection/logging or habitat fragmentation of stands might accelerate inbreeding depression, observable for instance in reduced seed sets or infertility (Keller and Waller 2002; Lowe et al. 2005). According to Brodie et al. (1997) this risk is even increased for fruit trees, because reproductive material on-farm or from markets is repeatedly selected and translocated. The process of domestication should therefore be considered as a potential threat to intra-specific diversity, but also as chance to promote a diverse set of locally adapted varieties on-farm and thus a greater stability and biodiversity of HG systems.

1.5 The role of indigenous fruit trees in agroforestry systems and their state of domestication in Africa and the Nuba Mountains

The lack of genetically superior germplasm is considered to be a hidden wealth of wild fruit trees (Akinnifesi et al. 2004). Africa has been suggested to have one of the greatest potentials for tree domestication (Simons and Leakey 2004), and is seen as a cornucopia of wild fruit resources that have not yet been discovered or are underutilized/neglected (NRC 2008). The terms underutilization and neglect of wild genetic resources, implies that there are potential threats of losing these resources of value to human well-being. Several reasons of the low reputation of IFT species can be stated: IFTs are often recognized as being "famine foods" or "food of the poor"; there exists a preference for exotic tree species over IFTs since the latter are felt to be slow growing (Jama et al. 2008) resulting in replacements with exotic species in HGs of Africa; planting of IFTs is discouraged because of their free availability in the wild (Kindt et al. 2006); as reported by Muneer (2008) from Kordofan,

Sudan, family size and respective demands for food production also seems to limit the planting of trees as people tend to devote more space to growing staple foods such as sorghum or millet; furthermore, literate households seems to harbor more edible fruit trees on farms in Ethiopia (Fentahun and Hager 2009). Nevertheless, since most of these species are also valuable wood resources (furniture, fuel, fencing), selective logging and fragmentation of natural habitats is threatening their existence (Hassan and Hertzler 1988). This is likewise suggested for a set of different tree species experiencing that are over-exploited in the wild in Sudan (Gebauer et al. 2002; Robinson 2005; Robinson 2006; El Tahir et al. 2010), in Uganda (Agea et al. 2007) and in Kenya (Farwig et al. 2008). To confront the problem of neglect, underutilization or even over-exploitation, appropriate processes such as scientifically-based selection and domestication might be suitable to promote the presence and performance of IFTs in the respective area of origin (Simons and Leakey 2004). Tree nurseries are thus seen as important strategies in providing trees with beneficial characteristics to rural communities in Africa (Lengkeek et al. 2006); however, the same authors highlighted the simultaneous risk of genetic bottlenecks that may emerge by selecting single individuals and propagating them on-farm. Thus, there are both threats and high potentials for IFT species in Africa (Muok et al. 2000; Gebauer et al. 2002) in terms of breeding, germplasm conservation and production as well as awareness rising.

The importance of both multiple tree species diversity (Atta-Krah et al. 2004) and high levels of genetic diversity, i.e. high levels of heterozygosity (Reed and Frankham 2003), seems to ultimately improve the function and sustainability in such systems. The concept of tree crop domestication is thereby seen as strategy to improve human nutrition and income, and has been promoted over the past 15 to 20 years by the World Agroforestry Center (formerly ICRAF). By focusing on the West African region as well as Central and South Africa, important priority species were chosen, for instance *Uapaca kirkiana* Müll. Arg., *Strychnos cocculoides* L., *Sclerocarya birrea* A. Rich., *Ziziphus mauritiana* Lam., *Irvingia gabonensis* (Aubry-Lecomte ex O'Rorke) Baill., *Dacryodes edulis* H. J. Lam., *Ricinodendron heudelotii* (Baill.) Heckel, *Adansonia digitata* L. and *Tamarindus indica* L., cf. Akinnifesi et al. (2007) and Asaah et al. (2011)). We could identify no priority species or programs for Sudan, although wild fruit harvesting is important for livelihoods and the national economy as indicated by Adam and Pretzsch (2010) and Gebauer et al. (2002). Based on the available literature, however, little research has gone into describing and evaluating the importance and impact of wild harvesting, the diversity of IFT species and their contribution to the nutrition of local communities in the country.

In particular, the loss of IFT genetic resources through human intervention such as long-term domestication in agroforestry systems and recent habitat fragmentation in Africa has not been adequately studied (Hollingsworth et al. 2005; Miller and Schaal 2006; Ekué et

al. 2011). Results from preliminary studies revealed, very mild shifts of genetic losses, mainly due to the nature of perennial species, such as long lifespans, usually high levels of heterozygosity, stable outcrossing sexual systems and long distance dispersal of pollen and sometimes seeds (Parker et al. 2010). In conclusion, the few tropical IFT species studied at genetic levels are if at all semi-domesticated species which is evident for instance for *Adansonia digitata* (Assogbadjo et al. 2006) or *Vitellaria paradoxa* C. F. Gaertn. (Bouvet et al. 2004). Semi-domestication is often alternatively named as incipient domestication (Clement 1999a).
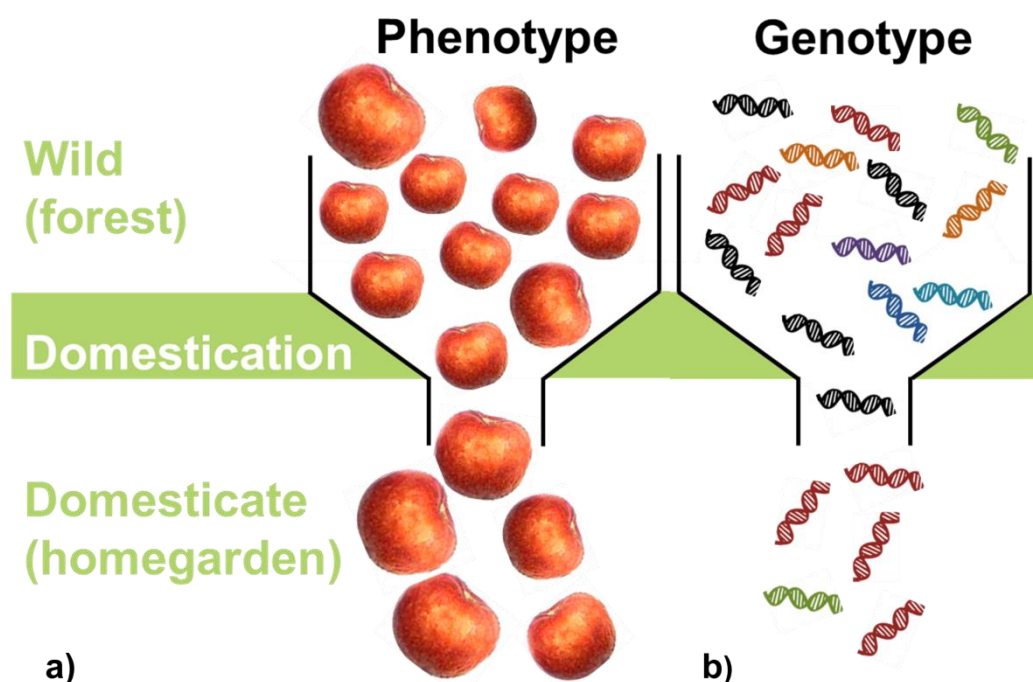
Figure 1.2 Assumed effect of domestication on morphometric [one-sided selection (towards larger fruits)] and genetic traits (loss of genetic diversity due to uni-directed selection) in Ziziphus spina-christi. Modified after Doebley et al. (2006).

1.6 Study area

1.6.1 Climate

The Nuba Mountains region that belongs to the Kordofan Province of Sudan (Figure 1.3) occupies an area about 42.000 km² extending from 10°30'N to 12°30'N latitude and from 29°00'E to 30°30' E longitude (Bedigian and Harlan 1983). The prevailing semi-arid tropical climate of the Sudano-Sahelian zone is characterized by three climatic periods: the cold-dry season from November to February (no precipitation), hot-dry conditions from March to April (no precipitation), and the uni-modally distributed rainy season from May to October. In that latter period, 400-800 mm of rainfall are measured with an increasing north-south gradient and pronounced inter-annual variations (Suliman 2007). The mean annual

temperature is 30 °C, varying from 31 °C in April to 24 °C in January (Ismail and Elsheikh 2007), (Figure 1.3).

1.6.2 Geomorphology and soil

The Nuba Mountains area has an altitudinal gradient of 300 up to 1460 m and consists of three main geomorphological units: (1) hilly or mountainous areas, (2) rocky outcrops of inselbergs and (3) clay plains (Babiker et al. 1985). One of the world's main distributions of Vertisols ('cracking soils' or 'black cotton soils') is present in stretches of plains and valleys between hills and the intrusive inselbergs. Along the foot hills, Ustalfs (United States Soil Taxonomy, locally called '*gardud*') are predominantly present consisting of heavy clays with sand of Aeolian origins, thus sometimes named transitional soils (Ismail and Elsheikh 2007). Weathered granitic or syenitic-derived rocky soils build the higher elevated hills and mountain ranges, sometimes present as monolithic inselbergs. The presence of a diverse and pronounced topography in the Nuba Mountains therefore directly affects the patterns of vegetation including crop species and agricultural practices.

1.6.3 Vegetation

Based on Barthlott's global plant species richness distribution map, Kordofan harbors between 500 and 1,500 plant species per 10,000 m², indicating a medium rich vegetation (Barthlott et al. 1999). The predominant climate determines the vegetation of the Nuba Mountains which is typically classified as a woodland savanna with scattered tree density of about 500 trees ha^{-2} (Babiker et al. 1985). The approach by Kindt (2011) classified the Nuba Mountains into two main vegetation types: 1) transition from Ethiopian undifferentiated woodland to *Acacia* deciduous bushland and wooded grassland surrounded by 2) a mosaic of edaphic grassland and *Acacia* wooded grassland. The lowlands consist of a mosaic of grassland (e.g. *Antropogon* sp., *Brachiaria* sp., *Beckeropsis* sp.) and sparse forest. The most common trees are *Acacia senegal* (L.) Willd., *A. seyal* Del., *A. nilotica* (L.) Willd. ex Delilie, *A. millifera* (Vahl) Benth., *Faidherbia albida* (Delile) A. Chev. and *Balanites aegyptiaca* (L.) Del. The highlands likely harbor a more diverse set of species, including tree species (El Tahir et al. 2010); however, no recent comprehensive data are available. Shifting cultivation is practiced in the plains, resulting in patchy patterns of forests, cultivated land and fallow areas. Burning of tall grasses in the plains and mountain areas during with the beginning of the dry season is a common practice to get rid of weeds and pests as well as to redirect pastoralists that destroy food crops on agricultural land with their livestock (personal communication).
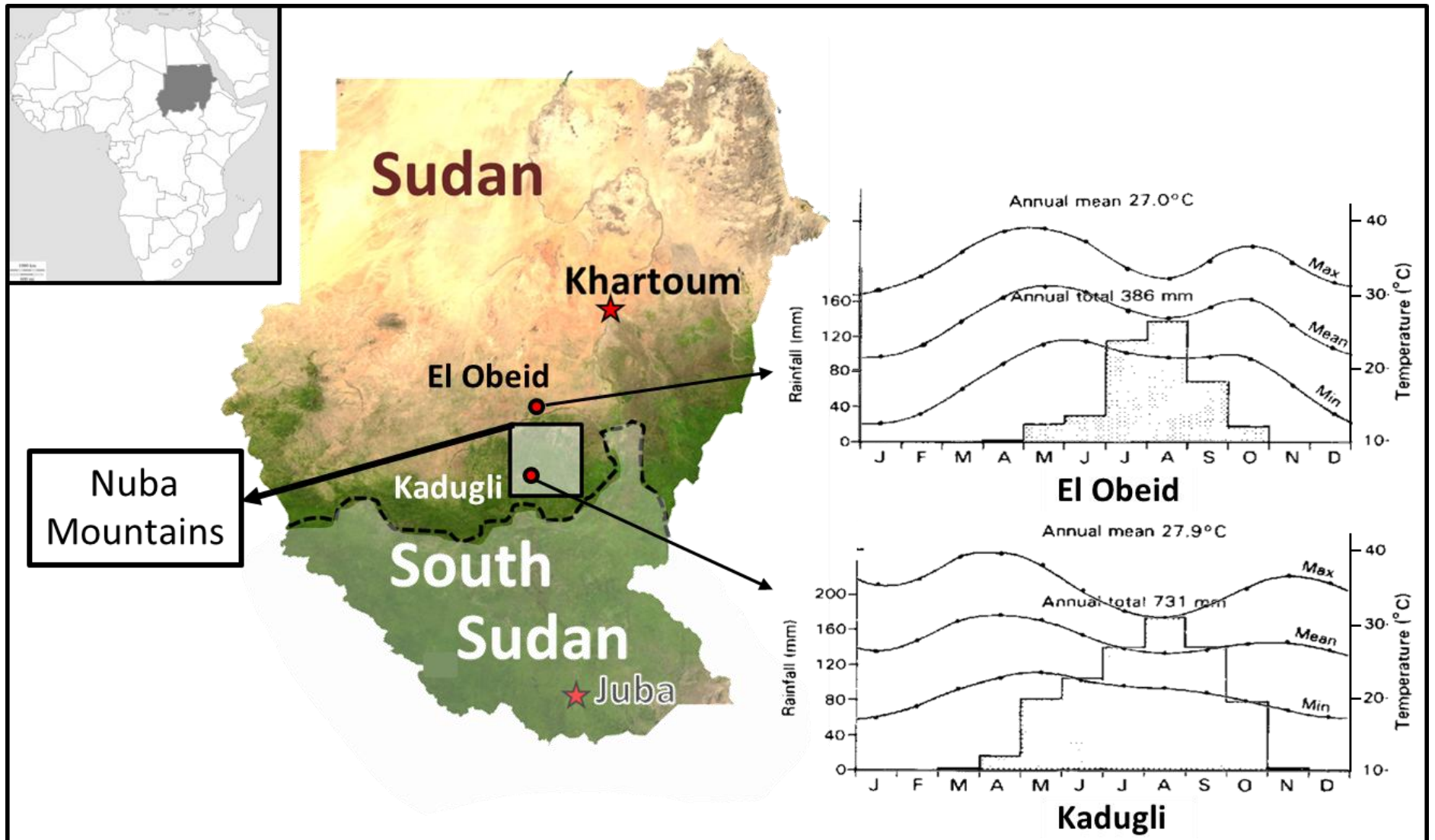
Figure 1.3 Vegetation cover map of Sudan and South Sudan, including the location of two climate stations and respective climate diagrams (Babiker et al. 1985). Source of maps: d-maps.com, nasa.com (both accessed 12 May 2013).

1.7 Investigated indigenous fruit tree species

1.7.1 Christ thorn Jujube (Ziziphus spina-christi (L.) Willd.)

Ziziphus spina-christi belongs to the buckthorn family (Rhamnaceae). The pantropical distribution (Figure 1.4) of this genus comprises about 100 species with some economically important ones such as *Z. mauritania* or *Z. jujube*. *Z. spina-christi* is native to semi-arid tropical regions of sub-Saharan Africa and the sub-tropical areas of the Near and Middle East (Anonymous 1989; Dafni et al. 2005; Orwa et al. 2009). Sudan can be considered as the focal point of the species' distribution emphasizing the country's responsibility for conservation. The deciduous tree strongly resists hot and dry conditions due to deep taproot development enabling a continuous water uptake (Saied et al. 2008). Thus, the tree can be found in a relatively wide range of biomes covering precipitation regimes of 50 mm along streams (von Maydell 1986) up to high rainfall of 1000 mm (Adam and Pretzsch 2010). Tree growth is limited to soils of alluvial plains, but survives partial waterlogged and saline conditions (Orwa et al. 2009). *Z. spina-christi* is a middle large tree reaching up to 10 m, with a brownish-greyish bark and is densely branched with spines.

The edible fruit is exploited commercially and is one of the most important socio-economic plant genetic resource in Sudan (Ezeldeen and Osman 1997; Gorashi 2001). The root and bark are used for medicinal purposes, wood is logged for cabinetry, and leaves are utilized as forage for livestock and for embalming for decedents. The spiny fresh or dry branches are ideal for fences to prevent animals from entering gardens. However, the viability of the species in its natural distribution is threatened by logging, pruning and browsing (HCENR 2000; Robinson 2006; Saied et al. 2008; El Tahir et al. 2010) yet quantitative and qualitative data for Sudan are missing.
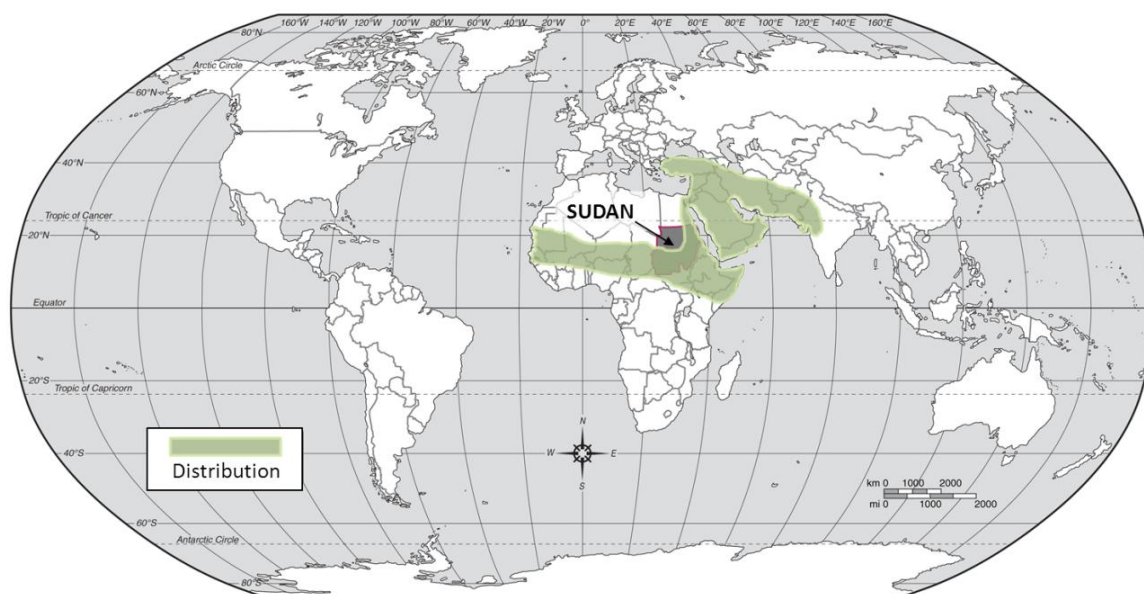
Figure 1.4 Natural distribution of Z. spina-christi (green area) according to various sources (NAC 1980; Alniami et al. 1992; El-Siddig 2003; Arbonnier 2004; Orwa et al. 2009). Map source: printable-maps.blogspot.com, accessed 27 July 2012).

1.7.2 African baobab (Adansonia digitata L.)

The African baobab, *Adansonia digitata* belongs to the mallow family (Malvaceae). The genus of *Adansonia* comprises eight species and *A. digitata* is the most economically important and widely distributed species (Figure 1.5). The species reaches a size of 30 m and is reported to develop one of the world's largest stem diameters within tree species. The wood consists of a spongy structure enabling the tree to store extraordinary amounts of water, likewise referring to stem-succulent characteristics that are needed to maintain tree's stability (Chapotin et al. 2006). Photosynthesis is even possible when leaves are shed due to its chlorophyll rich parenchymatic bark. Digitate leaves comprise five to seven leaflets with a large variability in size and shape (Gebauer and Luedeling 2013). The large white flowers that are pollinated by bats and likely other mammal and insect species produce a vast diversity of fruit shapes and sizes (Sidibe and Williams 2002; Gebauer et al. 2002a). Baobab's fruit pulp provides local nutrition and supports national economies and even export markets. Leaves are eaten, bark is used as fibre, and seeds are utilized to produce edible oil. Due to its multipurpose uses and a generally strong association to human settlements (Wickens 1982; Sidibe and Williams 2002; Duvall 2007), unique evolutionary effects on species distribution, morphology and genetic diversity as well as structure are assumed. Despite its importance, information of the tree's ecology, distribution, morphology and genetic diversity is lacking, particularly for the East African range. Within that region, Sudan harbours the northernmost populations with potential adaptations to dry conditions (Figure 1.5). However, the diversity and viability of Sudan's baobab might be negatively affected by factors such as climate change (Cuni Sanchez et al. 2011a) and fragmentation of

habitats by humans (Lowe et al. 2005; Robinson 2006). Die-back and logging are thus likely to prevent efficient gene flows, resulting in lower genetic diversity of stands in future. The lower germination rate of baobab seeds in the Sudanian zone (Assogbadjo et al. 2011; Korbo et al. 2012) might additionally result in stagnating or decreasing establishment and rejuvenation of existing stands. Considering both threats of decreasing stands and the economic potentials, *A. digitata* was identified as one of the priority IFT species for domestication in the Sahel region of Sub-Saharan Africa (Simbo et al. 2012).
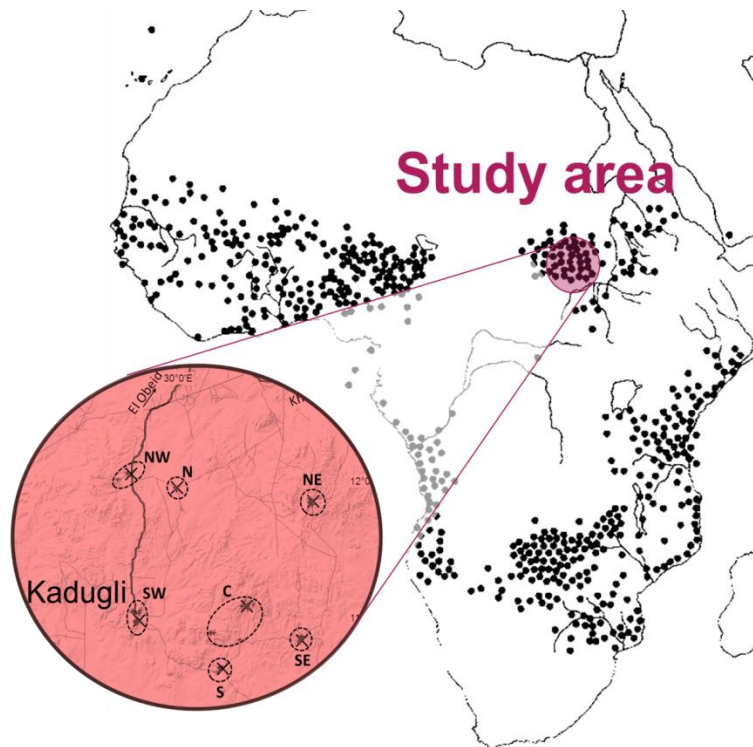
Figure 1.5 Natural distribution of the African Baobab and sampling region (small reddish circle) in the Nuba Mountains, Sudan (2010-2011). Magnified circle displays sampling locations (given as abbreviations of cardinal points) of the present study. Modified after (Wickens 1979).

1.8 Study objectives and hypotheses

Against the background of increasing concerns about the fate of plant genetic resources in agro-ecosystems, such as HGs, the present study was conducted to assess the effect of recent transformation processes on intra-specific plant diversity and to identify long-term domestication processes in IFT species. Understanding the complex forces that drive gardeners' decisions of selecting or rejecting crop species, varieties and wild species is important to understand the human-biodiversity linkage and to potentially improve livelihoods by maintaining biodiversity through region-specific and suitable recommendations and future management strategies.

Hypotheses:

1. Species richness and diversity, share of perennials and vegetation stratification in *jubraka*s decrease with increasing market access and commercialization.

2. Human-induced domestication processes in the two indigenous fruit tree species *Z. spina-christi* and *A. digitata* lead to larger fruit traits and a reduction of genetic diversity.

Objectives:

To assess species richness and diversity in the *jubraka* HG system and extract socio-economic and bio-physical factors affecting these parameters.

To determine the morphological and genetic variability of *Z. spina-christi* regarding tree dendrometric and fruit morphometric traits as well as genetic parameters in relation to environmental variables.

To determine the morphological and genetic variability of *A. digitata* by using similar approaches as for *Z. spina-christi.*

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Chapter 2 - Inter-specific diversity of the jubraka HG system

Effects of transformation processes on plant species richness and diversity in homegardens of the Nuba Mountains, Sudan

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2.1 Abstract

Traditional homegardens (HGs) are considered to harbor high levels of plant diversity and have been therefore characterized as sustainable agro-ecosystems suitable for on-farm (incl. *circa situm*) conservation of plant genetic resources. While the functional structure of traditional HGs is poorly understood specifically for semi-arid and arid regions, their plant species richness and diversity is increasingly threatened by recent and fast evolving agricultural transformation processes. This has been particularly claimed for traditional *jubraka* HG systems of Sudan.

Therefore, sixty-one HGs in four villages of the Nuba Mountains, South-Kordofan Province, Sudan, were randomly selected, geographically recorded and plant richness and abundance determined and plant diversity parameters calculated. In addition, socio-economic household data were assessed by interviews and soil samples taken to allow a comprehensive analysis of putative factors affecting HG plant diversity across different villages, levels of commercialization and plant species composition based clusters.

A total of 110 species from 35 plant families were grown in the HGs along with 71 ornamentals. Perennial species accounted for 57% including 12 indigenous fruit tree (IFT) species and six exotic fruit tree species. Mean species richness of useful plant species (excluding ornamentals) per HG was 23 (range 6-46). On average, 41% of the 23 species per HG were of exotic origin, however, with a large range (21-83%) among locations. Mean diversity and evenness indices were 1.46 (range 0.49-2.42) and 0.48 (0.15-0.87), respectively. The level of commercialization of HGs only marginally affected species diversity

measures although the species richness was significantly higher for commercial than subsistence HGs. Species richness was higher on lower (6.6-7.2) pH soils. IFT richness was highly variable, but non-significantly different across the four locations. Plant species richness and diversity was high in comparison with other HG systems in semi-arid regions. Cluster analysis was found to be a valuable tool to classify HGs and to extract homogeneous HG types with low, intermediate and high richness and diversity. In addition, the share of exotic and ornamental species in HGs indicated a trend towards the loss of traditional farming practices, particularly in areas with good market access.

The data did not indicate the hypothesized loss of inter-specific diversity due to commercialization and species richness was numerically even higher for market-oriented HGs compared to subsistence ones.

Keywords Agroforestry; *Circa situm* conservation; Commercialization; *Jubraka*; Shannon index; Subsistence gardening

2.2 Introduction

Traditional homegardens (HG) are known to harbor high levels of plant diversity and have therefore been claimed to play a pivotal role in *circa situm* (i.e. on-farm) conservation of plant genetic resources (Hughes 1998; Atta-Krah et al. 2004; Galluzzi et al. 2010; Bardhan et al. 2012). Structurally complex and species diverse agro-ecosystems are reported to reduce the risk of total crop failure, increase the utilization of limited resources and provide several ecological service functions (Eyzaguirre and Linares 2004; Abdoellah et al. 2006; Vlkova et al. 2011). Multi-strata vegetation structures in HGs are particularly important in hot, semi-arid regions where they provide shade for understory plants (Blanckaert et al. 2004) and may protect soils from degradation, leaching, and erosion during the rainy season (Soemarwoto et al. 1985). Particularly in rural settings diverse HGs can enhance a family's nutritional status and food security by producing a range of fruits, vegetables, spices, medicine, forage and fuel (Sunwar et al. 2006; Kabir and Webb 2009; Maroyi 2009). In addition, surplus produce may be sold to contribute to the family's cash income (Mendez et al. 2001; Abdoellah et al. 2006; Maroyi 2009). Despite their importance throughout the tropics and subtropics (Fernandes and Nair 1986; Soemarwoto 1987), the functional structure of traditional HGs is poorly understood (Pandey et al. 2006) specifically for semi-arid and arid regions (Bernholt et al. 2009).

This holds also true for the traditional *jubraka* agroforestry systems in the Nuba Mountains of Sudan that are an important source of food and partly income for local communities throughout the year, but particularly at the end of the dry and onset of the rainy season, the so called 'hungry periods' (Obeidalla and Riley 1984). *Jubraka* represent the

most common type of homegardens within the small-scale farming systems in the semi-arid zone of Sudan and they are distributed from Darfur in the western part of the country to the South Kordofan province in the south (Harragin 2003; Elsiddig 2007). These agroforestry HGs are also seen as controlled/protected habitats for first domestication efforts of wild species, including indigenous fruit trees such as *Ziziphus spina-christi* and *Adansonia digitata* (Wiehle et al., in press and submitted, respectively).

After decades of civil war which hindered economic and agricultural development, rapid transformation processes arose with the Comprehensive Peace Agreement between the warring parties in 2005. This has allowed the opening of regional markets, the development of infrastructure, an influx of external inputs for agriculture including plant genetic resources and easy access to comparatively cheap imported food (USAID 2011). The introduction of exotic species (including ornamentals) and improved varieties e.g. of vegetable species into this region started in the late 19th century (Bedri 1984; Mahmoud et al. 1996) and is still on-going. However, reliable data and historical documentation is lacking and remain particularly vague for the province of South Kordofan (Abdalla 2007). These changes may affect richness and diversity of useful plants cultivated in agro-ecosystems including HGs to different extents and complexity as described by Shackleton et al. (2008), Scales and Marsden (2008), and Kabir and Webb (2009) for similar systems in Africa and Asia. The frequently reported reduced agrobiodiversity of commercialized gardens may increase the risk of pest and disease outbreaks (Abdoellah et al. 2006), may negatively impact year-round availability of food products for subsistence farming and imply a reduced resilience to match the challenges of changing human demands (Atta-Krah et al. 2004) and climate change (Albrecht and Kandji 2003).

Transformation processes in HGs are often highly time- and region-specific (Kehlenbeck et al. 2007) and have been described as reflecting intensification (Scales and Marsden 2008), homogenization (Peyre et al. 2006), commercialization of production (El Tahir and Gebauer 2004; Abdoellah et al. 2006), and urbanization (Kehlenbeck et al. 2007). Proximity to markets for instance can strongly affect species richness in HGs (Christanty et al. 1986), whereby richness and abundance of useful plants can be both enhanced and hampered for different crop groups (Mendez et al. 2001; Wezel and Ohl 2005; Kehlenbeck et al. 2007). The wealth status of gardeners' families and duration of HGs being used for cultivation were important determinants for diversity patterns in Ethiopian HGs (Coomes and Ban 2004; Tolera et al. 2008).

Using the Nuba Mountains as a model zone for transformation processes in HGs of East Africa the aim of the present study was (i) to analyze plant species richness and diversity in HGs, focusing particularly on exotic and indigenous fruit trees and their role for food and nutrition security of the gardeners' families. Further objectives were (ii) to determine

socio-economic and bio-physical factors affecting plant species richness and diversity and (iii) to evaluate the suitability of HGs for *circa situm* conservation purposes of plant genetic resources, particularly of indigenous fruit tree species.

2.3 Materials and methods

2.3.1 Natural environment and socio-economic characteristics of the research area

The study was conducted between June and October 2010 in the Nuba Mountains, South-Kordofan Province, Sudan, ranging from 11°57'N, 29°43'E to 10°50'N, 30°59'E (Figure 2.1). The region belongs to the semi-arid Sudano-Sahelian climate zone and receives a mean annual precipitation of 500 to 800 mm decreasing from the south to the north (Bedigian and Harlan 1983). Rainfall is distributed uni-modally from May to October with a pronounced inter-annual variation. Three climatic periods exist within one year: the cold dry season from November to February (no precipitation), hot and dry conditions from March to April (no precipitation), and the cooler rainy season from May to October. The mean annual temperature is 30 °C ranging from 31 °C in April to 24 °C in January (Ismail and Elsheikh 2007).

Between the mountain ranges, large plains, which are characterized by deep vertisols (the so called 'black cotton soils'). Settlements are scattered along the drained piedmonts, locally called '*gardud*', on shallow, sandy, weathered granitic soils classified as Ustalf (United States Soil Taxonomy). These are also used to establish HGs where staples (S*orghum bicolor* (L.), *Pennisetum glaucum* (L.) R. Br., *Sesamum indicum* L.), vegetables and fruits for daily consumption and/or to gain cash income. The natural vegetation consists of a woodland savannah dominated by tall grasses (*Antropogon* spp.), Acacias (*Acacia* spp.) and *Balanites aegyptiaca* trees.
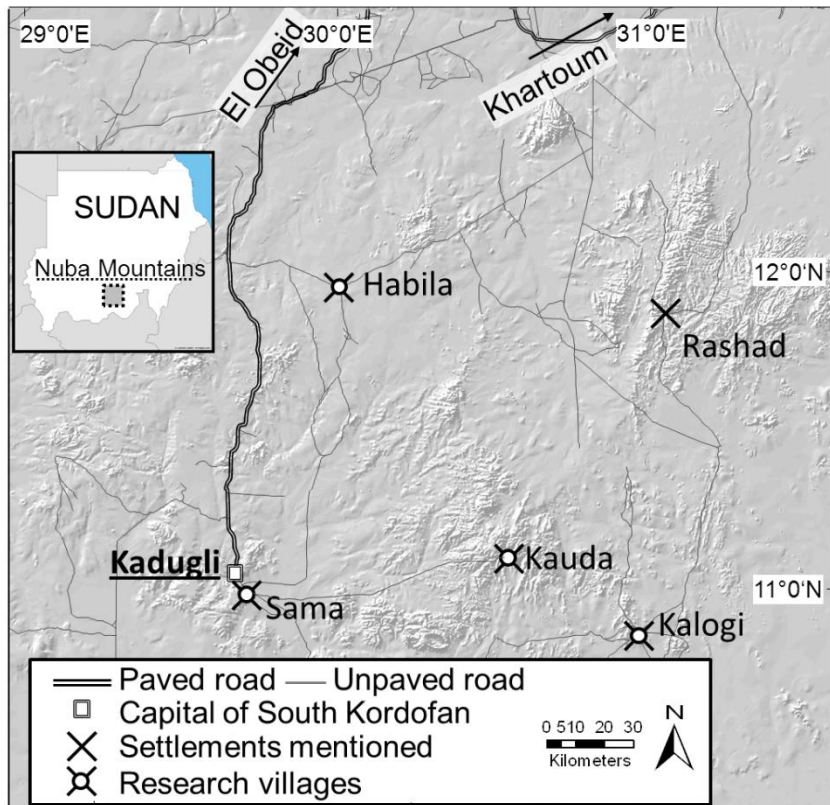
Figure 2.1 Hill shaded map of the research area in the Nuba Mountains, Sudan (2010) with the locations of the four surveyed villages as well as mentioned settlements in text. Sources: modified after CDE (Centre for Development and Environment), University of Bern, Switzerland (2005); country map: dmaps.com.

Ethnically the Nuba Mountains are characterized by diverse tribal communities with vague early history (Bedigian and Harlan 1983), which can be classified into three main groups: the Nuba (likely prehistoric inhabitants, small groups of diverse origins), the Arabs (originated from North Africa, settled and partly mixed with Nuba tribes), and other African tribes (mainly pastoralists) migrated to the area from Central and West Africa.

2.3.2 Data collection

Four villages – Kauda, Kalogi, Habila and Sama – were chosen along gradients of rainfall, altitudes, ethnicity and accesses to main markets (Table 2.1, Figure 2.1). Sixty-one households with a HG (15 per village, except of Sama (n=16)) were selected within an area previously circulated and mapped with a handheld GPS device (Vista HCx eTrex, accuracy ± 2 m, GARMIN® Ltd., Ireland). To select a HG, a previously GIS-generated random point was visited and the nearest HG within a 30 m radius from that random point was identified. The household head managing the identified HG was visited and asked for permission to conduct the survey. In case these conditions were not met, the next random point was taken and the occurrence of a HG within the given radius evaluated.

Table 2.1 Geographical and general socio-economic characteristics of the four surveyed villages in the Nuba Mountains, Sudan (2010).

	Coordinates N	Coordinates E	Elevation (m)	Precipitation rank (600-800 mm)	Distance to next city (km)	Main ethnic group	No. of inhabitants (estimated)	Socio-economic characteristics
Sama	10°58'34"	29°44'20"	514	medium	5	Shawabna (Arab)	13,000	Old settling area, close to main market and administrative unit Kadugli
Habila	11°57'09"	30°01'07"	662	low	40	Tama (other African)	12,000	Youngest village of surveyed locations, large agricultural schemes, village on a vertisol soil
Kauda	11°05'57"	30°33'13"	743	high	80	Otoro (Nuba)	6,000	Most remote village and very old settling area, in 2010 a runway to Kadugli has been opened
Kalogi	10°51'22"	30°58'54"	511	medium	50	Hawasma (Arab)	14,000	Second most remote village, established relatively recently by settled nomadic tribes

Geographic location, altitude, HG size and size of cultivable area of each HG were determined by GPS and measuring tapes. Basic socio-economic farm and household data such as total farm size, household possessions, including livestock (calculated as tropical livestock unit (TLU)), number of household members and their ages, education level, ethnic affiliation and main occupation of the gardener as well as information about the age and management of the HG and the proportion of sold produce from HGs was gathered through individual interviews with the household head and the household member mainly responsible for gardening using a semi-structured standardized questionnaire modified from Kehlenbeck et al. (2007). All questions and replies were translated from English into Arabic or local languages and *vice versa* by a native bi-lingual assistant. HGs of those households selling any HG produce were considered as 'market-oriented', and as 'subsistence-oriented' if no produce was sold.

Soil characteristics were determined in all HGs after collecting topsoil samples (0-20 cm) from the vegetable and cereal plots of each HG. In each separate plot, three sub-samples of 100 cm³ each were taken from randomly chosen points with a 5 cm inner diameter steel tube, bulked, and about 150 g air-dried for analysis after sieving to <2 mm. Effective cation-exchange-capacity (CEC_{eff}) and exchangeable aluminium (Al^{3+}), calcium (Ca^{2+}), potassium (K^+), sodium (Na^+), magnesium (Mg^{2+}) as well as available P (Bray-P1), organic carbon (C_{org}) and total nitrogen (N_{total}) were determined by standard methods (van Reeuwijk 1993; Houba et al. 1995) at the Charles Renard Analytical Laboratory, ICRISAT, Niamey, Niger. Extractable Al was below detection limits and thus not further considered in analyses. Soil pH (1:2.5, 0.01 *M* KCl) was determined by a pH-meter (WTW GmbH, Weinheim, Germany). Except for Na^+, the measurement of all parameters revealed non-significant differences between the two plot types (vegetable and cereal plots). Thus, results of the two plots were averaged to obtain one value per HG for each of the soil parameters.

Table 2.2 Mean soil quality parameters in 61 homegardens (HGs) surveyed in four villages, in the Nuba Mountains, Sudan (2010) arranged by village, economic orientation of HG production and cluster affiliation.

	n	pH	Na^+	K^+	Ca^{2+}	Mg^{2+}	CEC_{eff}	Bray-P $(mg\ kg^{-1})$	C_{org} (%)	N_{total} (%)	C/N
Kauda	15	6.6 [b]	0.2	0.8 [b]	5.4 [b]	2.2 [a]	8.7 [b]	34 [ab]	1.0	0.11 [a]	9.9 [a]
Kalogi	15	7.2 [a]	0.2	1.2 [ab]	5.7 [ab]	1.4 [b]	8.5 [b]	60 [a]	0.9	0.07 [b]	12.2 [b]
Habila	15	6.7 [b]	0.3	1.0 [ab]	6.2 [a]	2.3 [a]	9.8 [a]	23 [b]	1.1	0.09 [ab]	12.3 [b]
Sama	16	6.9 [ab]	0.2	1.4 [a]	5.4 [b]	1.3 [b]	8.4 [b]	69 [a]	0.9	0.08 [b]	11.4 [b]
P		**<0.001**	0.122	**0.021**	**0.013**	**<0.001**	**<0.001**	**0.002**	0.187	**0.009**	**<0.001**
Market-oriented	19	7.0	0.2	1.2	5.8	1.6	8.9	40	0.9	0.07	11.9
Subsistence	42	6.7	0.2	1.0	5.6	1.9	8.8	51	1.0	0.09	11.3
P		**0.009**	0.202	0.151	0.266	0.092	0.808	0.263	0.089	**0.032**	0.243
Cluster 1	15	6.6	0.2	0.8	5.4	2.2 [a]	8.7 [ab]	34	1.0	0.11 [a]	9.9 [b]
Cluster 2	22	6.9	0.2	1.1	5.7	1.7 [b]	8.7 [ab]	44	0.9	0.07 [b]	11.9 [a]
Cluster 3	11	7.0	0.2	1.1	5.6	1.5 [b]	8.4 [b]	77	1.1	0.09 [ab]	11.9 [a]
Cluster 4	13	6.9	0.3	1.4	5.9	1.8 [ab]	9.5 [a]	42	1.0	0.08 [ab]	12.3 [a]
P		0.192	0.377	0.067	0.313	**0.007**	**0.036**	0.183	0.243	**0.010**	**<0.001**
Total	**61**	**6.8**	**0.2**	**1.1**	**5.7**	**1.8**	**8.8**	**47**	**1.0**	**0.1**	**11.5**

Different letters behind means in a column and bold P-values indicate significant differences at *P*<0.05 (Mann-Whitney or Kruskal-Wallis tests, depending on the data structure).

Most soil quality parameters differed significantly among villages (Table 2.2), but not between the type of plots (except Na which showed higher contents on vegetable plots). Mean soil pH per village varied from 6.6 to 7.3 (Table 2.2). Bray-P levels were three times lower in Habila than in Sama. Concentrations of Ca, Mg and CEC_{eff} were highest in Habila, while K was highest in Sama. N_{total} was highest in Kauda, while C_{org} contents did not differ among villages. When comparing soil quality parameters of subsistence and market-oriented HGs, N was higher and pH lower in soils of subsistence HGs (Table 2.2).

In each HG a botanical inventory was conducted. Scientific names of the species, their potential uses, particularly as food and geographical origins (indigenous to the study area or exotic) were determined using various field guides (Andrews 1948; El Amin 1990; Bebawi and Neugebohrn 1991; Braun et al. 1991). The occurrence, local name, abundance and use of each individual plant species were recorded, excluding species regarded as 'not useful' or 'weeds' by the respective gardener. We are well aware that terms such as 'useful' and 'useless' are location-specific and subjective terms and interviewees may have mixed up theoretical knowledge about a species and its practical current use by the interviewee. Ornamental plants were also recorded, but skipped for some subsequent analyses because they do not contribute to food and nutrition security (Sunwar et al. 2006). According to Bernholt et al. (2009) each species was grouped into one of the following nine categories, based on its main use according to the gardener: fruit, vegetable, stimulant, condiment, medicine, staple, wood/multipurpose use (MPU), ornamental and 'other uses'. The group of 'other uses' included cosmetics, living fence, fiber, fodder, biofuel, household articles and insect repellents. For many species, respondents mentioned several uses, but for easier analyses, we focused on the 'main use' only. Since many tree species, however, compile

several use categories, we asked also for the secondary uses. Regarding fruit tree species, we also included those species as 'fruits', which were not mentioned with that specific use by the respondents, but are assigned as having edible fruits in the available literature (see above) to assess and analyze their potential for family nutrition. Height strata of the vegetation (0-0.99, 1-1.99, 2-4.99, 5-10 and >10 m) were only determined for tree species.

2.3.3 Data analysis

To test if minimum size of sampled areas was covered, species area curves were generated by using the Mao Tao estimator calculated with EstimateS (Colwell 2011). Such curves are especially useful when comparing species richness at a fixed number for subsets of different sample sizes (Kindt and Coe 2005). An asymptotic stagnation at a certain ordinate value would be equal to the maximal possible species richness at one area and shows that enough sites were sampled.

Species abundance was transformed to individual density per 1,000 m² HG area to balance out effects of different HG sizes and used for all subsequent analyses. For the same reason and also based on 1,000 m², a modified Arrhenius equation was used to determine species density (Evans et al. 1955). Species richness and abundance data were used to calculate Shannon-Weaver diversity index (*H'*) and Shannon evenness index (*J'*) separately for total plant species excluding ornamentals and for exotic and indigenous fruit tree (EFT and IFT, respectively) species using the MS$^{®}$ Excel based Diversity Add-In Calculator (SSC, Reading, UK). To compare the importance of species in different use categories for the surveyed villages the summed dominance ratio (SDR) was calculated by using relative density and frequency of the species per village and then summing up the values within the respective use category (McCune and Grace 2002).

All data were subjected to statistical analysis using SPSS® 19.0 for Windows$^{®}$ (SPSS Inc., Chicago, Illinois, USA), whereby the significance level was set to *P*<0.05. As the data were not normally distributed, non-parametric Mann-Whitney or Kruskal-Wallis-tests were used to compare parameters between two or more groups, respectively. Wilcoxon signed-rank tests were performed for same parameters assessed for different plant categories such as indigenous and exotic species richness or soil fertility parameters in vegetable and staple plots of the same HG. Chi-square (χ^2) tests were applied to test nominal and categorical variables.

Three multivariate techniques were applied to analyze factors affecting species richness, density, diversity and composition: stepwise multiple regression analyses, cluster analysis, and stepwise discriminant analysis. Stepwise multiple regression analyses was employed to analyze the influence of the socio-economic and bio-physical independent variables HG size and age, elevation, locations (as dummy variables), level of subsistence-

oriented production, household poverty index (HPI; see below) and the soil parameters pH and CEC_{eff} on the dependent variables richness, species and individual densities, share of exotic individuals, as well as diversity and *J'* indices for total plant species excluding ornamentals. The influence on IFT species richness was further evaluated based on the mentioned parameters. To evaluate the relative wealth of each household, a poverty index (HPI) was obtained by the method following Henry et al. (2003) based on principal component analysis scores. The following socio-economic parameters, determined during the household interviews, were included: family size, number of meals in past two days, weeks of stock for food staple, number of rooms per household member, quality of dwelling floors and walls, value of owned livestock species, and total value of assets per household member. The lower the HPI value, the more severe is the relative poverty of the respective household in comparison with the entire interviewed households.

To characterize HGs based on their species composition and to determine relationships among them, minimum variance (Ward's method) cluster analysis with squared Euclidian distance as a measure of dissimilarity of ln-transformed plant individual density data was performed with the software MVSP (Kovach 2001). A preliminary nearest-neighbor procedure was conducted to test for outliers; the most likely number of clusters was assessed by means of the 'elbow-criterion' (Leyer and Wesche 2007). To identify the plant species that were most responsible for the cluster formation and to assess the strength of the classification model, stepwise DA was performed by SPSS, which also determined the derived Wilks' lambda values. High power of discrimination between groups is denoted by Wilks' lambda values near zero.

2.4 Results

2.4.1 Socio-economic characteristics of the surveyed households

Most of the interviewed gardeners belonged to the ethnicity of Arabs (44%) or Nuba (41%) and only 15% to other African tribes. About 26% of the respondents migrated to their current village from other regions of the Nuba Mountains or even further parts of Sudan. Gardeners' average age was 39 years (range 13-81 years); 13% of the respondents were Christians, whereas the remaining were Muslims. While 92% of the surveyed households were male-headed, 90% of HGs were managed by women. Family size was on average nine persons (range 2-19), the ratio of children to adults was 0.9 and illiteracy of family members >14 years was 52% with significant differences between villages (Table 2.3). Sixty-two percent of the 61 interviewed gardeners had no formal school education and were illiterate with lowest numbers of years in school in Kauda (Table 2.3). The mean size of the total landholding (HG and additional fields) was 7.2 ha however with large differences among villages (smallest in Kauda and largest in Habila). Eighty-seven percent of the respondents owned livestock with significantly higher numbers of TLUs in Kauda (P=0.024; Table 2.3). In all cases, livestock was kept outside the HG or in small corals within. Cattle were mainly led by herdsman to the surrounding forests and grasslands, while goats, sheep and chickens were freely roaming or chained up around and within the villages. Pigs, only present in Kauda, were kept in small shelters inside HGs during the crop cultivation period, but were roaming around during the remaining time. Household poverty index (HPI) was lowest for Kauda and Habila (Table 2.3) and positively correlated with gross cash income from HGs (r=0.353, P=0.006).

When comparing the economic orientation of HG production, 69% of the surveyed HGs were subsistence-oriented, and 31% market-oriented, with no differences among villages. Although not statistically significant, market-oriented gardens were comparatively more likely managed by men than women (P=0.069). When comparing subsistence- and market-oriented HGs, gardener's age (data not shown), literacy rate of family members >14 years, HPI and income generated from the HG were significantly higher and gross income lower in market-oriented HGs (Table 2.3), while total farm and HG sizes as well as education level of the gardener did not differ.

Table 2.3 Mean socio-economic parameters in 61 homegardens (HGs) surveyed in four villages, in the Nuba Mountains, Sudan (2010) arranged by village, economic orientation of HG production and cluster affiliation. One of the 15 households in Kauda could not be interviewed resulting in missing information on socio-economic characteristics.

		HG characteristics				Social household characteristics			Economic household characteristics			
		HG size	Slope	Duration of being used as HG		No. of family members	Level of formal education in school	Literacy of the household (members >14 years)	Total land holding	Tropical livestock units (TLU) per family member	House-hold poverty index (HPI)	Gross cash income from HG
	n	(m²)	(%)	(years)	n		(years)	(%)	(ha)			SDP
Kauda	15	4644 a	7.3 a	67 a	14	8.5	0.9 b	22 b	0.7	0.4 a	-1.0 b	13
Kalogi	15	1109 b	0.1 b	13 b	15	9.3	3.7 a	62 a	2.1	0.4 a	0.4 a	140
Habila	15	1084 b	0.0 b	14 b	15	8.7	1.9 a	50 ab	21.7	0.2 ab	-0.6 b	33
Sama	16	1168 b	4.1 b	21 b	16	7.3	3.9 a	70 a	4.1	0.1 b	1.0 a	178
P		**<0.001**	**<0.001**	**0.001**		0.800	**0.033**	**0.001**	0.057	**0.024**	**<0.001**	0.234
Market-oriented	19	1899	1.7	45	19	9.2	2.7	69	5.2	0.1	0.5	296
Subsistence	42	1904	3.5	37	41	8.3	2.6	44	8.1	0.4	-0.2	0
P		0.510	0.225	0.629		0.278	0.799	**0.005**	0.110	0.053	**0.011**	**<0.001**
Cluster 1	15	4644 a	7.3 a	67 a	14	8.5	0.9	22 b	0.7	0.4 a	-1.0 b	13 b
Cluster 2	22	1331 b	2.3 b	16 b	22	8.7	2.6	54 ab	6.5	0.2 b	0.1 a	36 ab
Cluster 3	11	808 b	1.1 b	18 b	11	7.5	4.4	64 a	5.3	0.5 ab	0.9 a	3 b
Cluster 4	13	1032 b	0.4 b	14 b	13	8.7	3.2	70 a	17.0	0.2 ab	0.2 a	356 a
P		**<0.001**	**<0.001**	**0.002**		0.887	0.058	**<0.001**	0.053	**0.021**	**<0.001**	**0.003**
Total	**61**	**1988**	**2.9**	**40**	**60**	**8.6**	**2.7**	**52**	**7.2**	**0.3**	**0.0**	**94**

Different letters behind means in a column and bold P-values indicate significant differences at $P<0.05$ (Mann-Whitney or Kruskal-Wallis tests, depending on the data structure). SDP: Sudanese pound; 1 SDP equal to 0.324 € (based on the mean exchange rate during the study period between 01 June and 01 October 2010, www.oanda.com, accessed June 2013).

2.4.2 Garden characteristics and management

The total area surveyed in the 61 HGs (cultivatable area) covered 12.1 ha. Mean total HG size was 1,988 m², ranging from 168 to 7,934 m². Kauda had by far the oldest HGs ($P<0.001$), the largest cultivable HG areas ($P<0.001$) and most hilly conditions ($P<0.001$) with a mean slope inclination of about seven degree (Table 2.3). Terraces for erosion control were found in all of Kauda's HGs, while only two times in the remaining HGs. Fences surrounded most of the surveyed HGs, except for Kauda where fences were absent. All 61 HGs were owned by the gardeners. According to the respondents, the main function of HGs was growing crops for self-consumption (88%). Only 12% of the respondents mentioned market production as main function. However, market production was the most important secondary function, mentioned by 57% of the respondents, followed by self-consumption (30%) and pastime/recovering (13%). In seven percent of all HGs, laborers were hired for certain tasks, e.g. to establish fences or to weed the garden. The use of mineral fertilizers accounted for three percent of the respondents, while organic fertilizers were used by 41% of the respondents. Pesticides (as ash or chemicals) were applied in 48% of the HGs. The most important needs mentioned to improve HG production were fencing (15%), extending the cultivation area and soil enrichment by manure (each 10%), crop rotation and use of improved seeds/varieties (each 7%). About 93% of the interviewed 61 HG owners claimed to have fertile soils. When asked about changes over time, 38% of the gardeners reported

degradation, while 10% observed improvements in soil fertility. Twenty percent of all respondents attributed changes in soil fertility to changes in rainfall, but no one mentioned that use of fertilizers may be influential. None of the respondents ever had contact with governmental or non-governmental agricultural extension services. Planting material was mostly obtained through using own seeds from the previous harvest or by exchange with neighbors. Only in Kauda gardeners had access to a nursery (managed by a NGO) where they had purchased planting material, foremost ornamental trees.

2.4.3 Total plant species richness, diversity, and use

A total of 110 useful plant species from 33 plant families were grown in the HGs plus 71 ornamental species. Out of the overall 181 species, 105 (58%) were of exotic origin. Sixty-three species (89%) of the ornamental species were exotics, markedly higher than the 42 exotics (38%) of the useful plant species. Fifty-seven percent of the 181 species were perennial species including 12 IFT and six EFT species. Many other tree species also had edible fruits, although not of primarily importance, resulting in a total of 23 IFT and nine EFT species if the secondary use as fruit was included (Table 2.4). Most of the 110 useful species were used as source of wood/MPU (25%), vegetable (20%), fruit (17%), 'other uses' (15%), and staple and medicinal (each 8%). Species with their main uses as stimulants and condiments (each 3%) were negligible. The five most frequent species were *Abelmoschus esculentus* (occurring in 95% of the surveyed HGs), *Zea mays* and *Solanum lycopersicum* (each 90%), *Sorghum bicolor* (89%) and *Cucumis melo ssp.* (84%). The five most abundant species were *Sorghum bicolor* (48% of all useful plant individuals without ornamentals)*, Sesamum indicum* (22%), *Arachis hypogaea* (8%), *Zea mays* (4%), and *Corchorus fascicularis* (3%). Species accumulation curves for exotic and indigenous species based on sampled HGs showed that the minimum sample size was partly not covered (Figure 2.2). For example, overall indigenous species numbers would increase slightly if more HGs were sampled (Figure 2.2a). When comparing fruit tree species accumulation curves total saturation was reached for EFTs, but not at all for IFTs (Figure 2.2b).

All five vegetation strata of woody species were recorded in the surveyed HGs, showing a continuous increase of tree abundance from the highest (1.7%, >10 m) to the lowest strata (64.8%; 0-0.99 m). Regarding fruit trees, the most frequent IFT species (1st use category, Table 2.4) were *Ziziphus spina-christi* (found in 61% of the surveyed HGs), *Adansonia digitata* (46%), *Balanites aegyptiaca* (43%, not present in Kauda), and *Sclerocarya birrea* (26%) and the most frequent EFT species were *Phoenix dactylifera* (23%), *Annona squamosa* (18%) and *Mangifera indica* (16%). Within the fruit use group, *Ziziphus spina-christi* was the most abundant (201 out of a total of 553 fruit tree individuals), followed by *Balanites aegyptiaca* (107) and *Adansonia digitata* (74).

2.4.4 Plant species richness, density, diversity, and use among villages

Mean species richness of all observed plant species was 30 species per HG, with lowest richness in Kauda (28) and highest one in Sama (33, P=0.001). By excluding ornamentals, 23 species per HG were found, (range 6-46), of which 41% were of exotic origin (range 21-83%, Table 2.5). The richness was lowest in Kalogi but highest in Kauda, while share of exotic species was highest in Kalogi, but lowest in Kauda and Sama (Table 2.5). Species density was lowest in Kalogi and similar for the other three villages (Table 2.5). A mean of 12,097 individuals of useful plants were documented per HG (Table 2.5) in addition to a median of 100 ornamental plant individuals. Kauda showed highest abundance of useful species, where also HG sizes were largest (Table 2.3). The mean individual density was 4,137 plants per 1,000 m^2, of which 46% were exotics (Table 2.5). Individual density was highest in Kauda and lowest in Kalogi, while the share of exotic individuals was lowest in Kauda and highest in Kalogi (Table 2.5). Kalogi was highest in mean number of ornamental species per HG (13), with the largest difference to Kauda (one species, data not shown).

Mean *H'* and *J'* in the surveyed 61 HGs were 1.46 (range 0.49-2.42) and 0.48 (0.15-0.87), respectively (Table 2.5). Both *H'* and *J'* were significantly lower in Kauda than in Kalogi, Habila and Sama (*P*<0.001). Per HG, a mean of four staple, three fruit, eight vegetable, two wood/MPU, one condiment, medicinal and stimulant species each as well as three species with other uses were cultivated. Mean number of vegetable (6, P=0.018), fruit (4, P=0.134) and medicinal species (2, *P*<0.001) were highest in Sama. Habila exhibited highest numbers of staple (5, P=0.001) and condiment species (1, P=0.014), while Kauda harbored most of wood/MPU (5, P=0.001), stimulant (1, *P*<0.001) and 'other use' species (4, P=0.001). Calculations of the summed dominance ratio (SDR) per plant use category showed some similarities among villages (only Kauda had a higher dominance of staple crops and wood/MPU species than the other villages, data not shown).

Table 2.4 Fruit tree species found in 61 homegardens (HGs) surveyed in four villages in the Nuba Mountains, Sudan (2010). Note: Not only species mentioned as fruits by the respondents (either as primary (1st use) or secondary (2nd) use), but also those with edible fruits according to the literature are listed below.

	Scientific name	Author	Family	Vernacular name		Use		Abundance	Frequency
				English	Arabic	1st	2nd	(individuals)	(% of HGs)
Indigenous fruit trees (IFT)	*Adansonia digitata*	L.	Malvaceae	Baobab tree	Tabaldi/humeir	fr	v	74	45.9
	Balanites aegyptiaca	(L.) Del.	Zygophyllaceae	Desert date	Heglig/lalub	fr	w	107	42.6
	Borassus aethiopum	Mart.	Arecaceae	African fan palm	Deleb	fr	w	6	1.6
	Capparis decidua	(Forssk.) Edgew.	Capparaceae	-	Doumduneidii	w	fr	2	1.6
	Commiphora africana	(A. Rich.) Engl.	Burseraceae	African myrrh	-	w	-	2	1.6
	Commiphora pedunculata	(Kotschy & Peyr.) Engl.	Burseraceae	-	Gureng	w	-	1	1.6
	Cordia africana	Lam.	Boraginaceae	Large-leaved cordia	San	w	o	14	16.4
	Ficus sp.	L.	Moraceae	-	-	w	fr	1	1.6
	Ficus sycomorus	L.	Moraceae	Sycomore fig	Gumeiz	fr	m	3	3.3
	Gardenia ternifolia	Schumach. & Thonn.	Rubiaceae	-	-	w	o	3	3.3
	Grewia bicolor	Juss.	Malvaceae	Bastard brandy bush	Basham	fr	-	2	3.3
	Grewia tenax	(Forsk.) Fiori	Malvaceae	White cross-berry	Geduem	fr	-	8	4.9
	Grewia villosa	Willd.	Malvaceae	Mallow raisin	-	fr	-	6	6.6
	Hyphaene thebaica	L.	Arecaceae	Gingerbread tree	Doum	other	fr	136	41.0
	Lannea acida	A.Rich.	Anacardiaceae	-	Duoam	v	fr	64	14.8
	Lannea microcarpa	Engl. & K.Krause	Anacardiaceae	-	-	w	fr	2	1.6
	Nauclea latifolia	S. M.	Rubiaceae	African peach	Karmadoda	fr	w	2	3.3
	Piliostigma thonningii	(Schum.) Milne-Redh.	Fabaceae	Camel's foot	Kharub	w	fr	58	16.4
	Salvadora persica	Wall.	Salvadoraceae	Toothbrush tree	Arak	m	fr	7	9.8
	Sclerocarya birrea	A.Rich.	Anacardiaceae	Marula	Homeid	fr	-	28	26.2
	Tamarindus indica	L.	Fabaceae	Tamarind tree	Ardeb	fr	w	11	11.5
	Vangueria venosa	(Hochst.) Sond.	Rubiaceae	-	Kirkir	fr	-	2	1.6
	Ziziphus spina-christi	(L.) Desf.	Rhamnaceae	Christ's thorn jujube	Sidr/nabak	fr	other	201	60.7
Exotic fruit trees (EFT)	*Annona squamosa*	L.	Annonaceae	Sugar-apple	Gishta	fr	-	23	18.0
	Azadirachta indica	A. Juss.	Meliaceae	Neem tree	Neem	w	m	125	49.2
	Carica papaya	L.	Caricaceae	Papaya	Pawpaw	fr	-	7	8.2
	Citrus × aurantiifolia	(Christm.) Swingle	Rubiaceae	Lemon	Lemon	fr	-	8	9.8
	Mangifera indica	L.	Anacardiaceae	Mango	Manga	fr	-	13	16.4
	Melia azedarach	L.	Meliaceae	White cedar	-	w	o	10	6.6
	Parkinsonia aculeata	L.	Fabaceae	Jerusalem thorn	Seisaban	w	o	38	8.2
	Phoenix dactylifera	L.	Arecaceae	Date palm	Ballah	fr	-	47	23.0
	Psidium guajava	L.	Myrtaceae	Common guava	Guava	fr	-	5	6.6

o=ornamental, other=other uses (fiber and fencing material), v=vegetable, w=wood/multipurpose use

Table 2.5 Mean richness, density, abundance and diversity for useful plant species (without ornamentals) and for ornamental species in 61 homegardens (HGs) surveyed in four villages, in the Nuba Mountains, Sudan (2010) arranged by village, economic orientation of HG production and cluster affiliation.

	n	Richness	Share of exotic	Arrhenius species density per	Abundance	Individual density per 1000	Share of exotic individual	Shannon	Evenness
				Plant species without ornamentals					
Kauda	15	27.5 [a]	33.5 [b]	23.0 [a]	39363 [a]	8552 [a]	11.4 [b]	0.94 [b]	0.28 [b]
Kalogi	15	16.5 [b]	50.0 [a]	16.7 [b]	1822 [b]	1851 [b]	64.0 [a]	1.45 [a]	0.53 [a]
Habila	15	23.1 [ab]	43.8 [ab]	24.0 [a]	4560 [b]	3732 [b]	55.7 [a]	1.69 [a]	0.54 [a]
Sama	16	23.6 [a]	36.8 [b]	23.9 [a]	3236 [b]	2521 [b]	51.6 [a]	1.74 [a]	0.58 [a]
P		**0.001**	**<0.001**	**0.006**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Market-oriented	19	25.9	45.1	24.8	8570	3757	52.6	1.56	0.49
Subsistence	42	21.0	39.2	20.6	13179	4294	42.2	1.43	0.49
P		**0.032**	0.107	0.058	0.313	0.617	0.174	0.305	0.830
Cluster 1	15	27.5 [a]	33.5 [c]	23.0 [ab]	39363 [a]	8552 [a]	11.4 [b]	0.94 [b]	0.28 [b]
Cluster 2	22	20.7 [b]	38.3 [bc]	20.7 [bc]	4562 [b]	3353 [b]	51.0 [a]	1.58 [a]	0.53 [a]
Cluster 3	11	13.3 [b]	47.6 [ab]	14.5 [c]	197 [c]	321 [c]	71.4 [a]	1.44 [a]	0.57 [a]
Cluster 4	13	28.5 [a]	48.5 [a]	29.2 [a]	3459 [b]	3598 [b]	54.9 [a]	1.89 [a]	0.57 [a]
P		**0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Total	**61**	**22.7**	**41.1**	**21.9**	**12097**	**4137**	**45.8**	**1.46**	**0.48**

Different letters behind means in a column and bold P-values indicate significant differences at $P<0.05$ (Mann-Whitney or Kruskal-Wallis tests, depending on the data structure).

Regarding fruit tree species richness, significant differences among villages were only found for IFT richness, which was lowest in Kalogi (mean=1) and highest in Sama (3, Table 2.6). Several IFT species were exclusively found in Kauda such as *Nauclea latifolia*, *Grewia villosa*, *G. bicolor*, *Lannea acida* or *Commiphora africana*, the two latter only secondarily regarded as fruit trees (Table 2.4). Highest abundance and individual density of IFTs was found in Sama (Table 2.6). Mean IFT *H'* and *J'* were 0.56 and 0.65, but non-significantly different among villages (Table 2.6). EFT abundance was significantly highest in Sama, while differences among villages for the other assessed EFT parameters were non-significant (Table 2.6). Mean richness, abundance, species density, individual density, *H'* and *J'* were significantly lower for EFT than for IFT species (each $P<0.001$, two latter: P=0.001 and 0.002, respectively, Wilcoxon signed-rank test). However, the fruit tree species accumulation curves at village level (Figures 2c and d) indicated that not enough HGs were inventoried to cover the total species richness, both for IFTs and EFTs. Regarding IFTs, Habila showed still increasing levels of species, while Kalogi reached saturation after about six sampled HGs (Figure 2.2c). Less pronounced differences among villages were found for EFT species, though more species can be expected in all villages, except for Kalogi (Figure 2.2d).

Table 2.6 Mean richness, density, abundance and diversity for indigenous and exotic fruit tree species in 61 homegardens (HGs) surveyed in four villages in the Nuba Mountains, Sudan (2010) arranged by village, economic orientation of HG production and cluster affiliation.

	n	Indigenous fruit trees (IFT)						Exotic fruit tree species (EFT)					
		Richness	Arrhenius species density per 1000 m²	Abundance	Individual density per 1000 m²	Shannon	Evenness	Richness	Arrhenius species density per 1000 m²	Abundance	Individual density per 1000 m²	Shannon	Evenness
Kauda	15	2.4 ab	2.1 ab	6 b	1 b	0.68	0.66	0.8	0.7	1.3 b	0.5	0.17	0.18
Kalogi	15	1.3 b	1.6 b	3 b	5 ab	0.29	0.38	0.9	0.9	1.5 ab	1.9	0.41	0.48
Habila	15	1.9 ab	2.2 ab	5 b	8 ab	0.52	0.55	0.7	0.5	1.6 ab	2.1	0.22	0.20
Sama	16	2.8 a	3.0 a	15 a	19 a	0.70	0.62	1.4	1.1	3.8 a	4.6	0.26	0.34
P		**0.030**	**0.031**	**0.020**	**0.001**	0.055	0.491	0.131	0.188	**0.014**	0.136	0.537	0.474
Market-oriented	19	2.5	2.6	10	8	0.70	0.63	1.1	0.9	2.8	2.6	0.23	0.25
Subsistence	42	1.9	2.1	6	9	0.49	0.52	0.8	0.7	1.6	2.2	0.25	0.31
P		0.249	0.178	0.182	0.295	0.119	0.481	0.293	0.569	0.131	0.513	0.803	0.687
Cluster 1	15	2.4	2.1	6	1 b	0.68	0.66	0.8	0.7	1.3	0.5 c	0.17	0.18
Cluster 2	22	1.9	2.1	7	9 ab	0.46	0.49	0.8	0.5	2.1	2.2 bc	0.35	0.44
Cluster 3	11	1.6	2.0	5	12 ab	0.40	0.48	1.1	1.1	1.6	3.4 ab	0.26	0.38
Cluster 4	13	2.5	2.8	12	13 a	0.69	0.61	1.3	1.2	3.1	3.5 a	0.31	0.28
P		0.354	0.474	0.097	**0.001**	0.242	0.594	0.505	0.109	0.343	**0.047**	0.700	0.653
Total	**61**	**2.1**	**2.2**	**7**	**9**	**0.56**	**0.65**	**1.0**	**0.8**	**2.0**	**2.3**	**0.27**	**0.31**

Different letters behind means in a column and bold P-values indicate significant differences at $P<0.05$ (Mann-Whitney or Kruskal-Wallis tests, depending on the data structure).
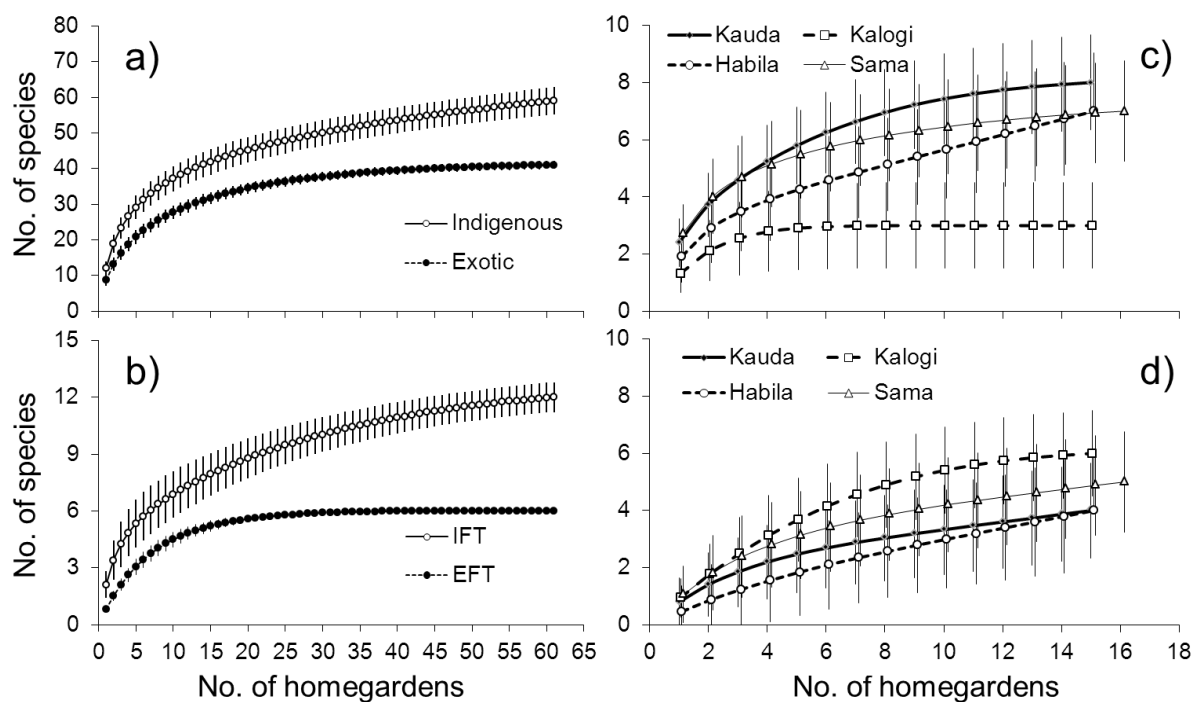
Figure 2.2a-d Species accumulation curves using observed richness (Mao Tao estimator ± standard deviation (SD) for 61 surveyed homegardens (HGs) in four villages of the Nuba Mountains, Sudan (2010). For all gardens: a) exotic *vs.* indigenous useful plant species; b) exotic fruit tree (EFT) species *vs.* indigenous fruit tree (IFT) species. Per village: c) IFT species; d) EFT species. Graphs per village are slightly displaced to avoid SD-bar overlaps.

2.4.5 Plant species richness, diversity and use between market-oriented and subsistence HGs

Market-oriented HGs showed a statistically significantly higher mean of useful species than subsistence gardens (Table 2.5). Further richness and diversity parameters (incl. those assessed for IFT and EFT species) showed no significant differences, though market-orientated HGs exhibited slightly higher values for some of the parameters (Tables 2.5 and 2.6). Subsistence and market-oriented HGs differed, however, in the dominance of plant use categories. Subsistence HGs showed a higher dominance of staple crops, while vegetable species dominated market-oriented HGs (Figure 2.4a). Although generally lower in proportion, also medicinal and fruit species had a higher SDR in market-oriented HGs. Market- and subsistence-oriented HGs also slightly differed in their species composition. Of the 110 plant species found, 79 were present in both subsistence- and market-oriented HGs, while 21 and 11 species were exclusively found in subsistence and market-oriented gardens, respectively. Species uniquely found in subsistence gardens were for instance *Sorghum ×* *drumondii* and *Citrus × aurantiifolia*, whereas *Acacia nubica* and *Physalis angulata* were only found in market oriented gardens.

2.4.6 Determinants of richness, density and diversity of useful plant species

Gardens of the indigenous Nuba people contained higher richness of useful plant species (excluding ornamentals) than those of non-Nuba households (21 *versus* 25; P=0.029). However, *H'* and *J'* indices were lower in gardens of Nuba households (1.26 *versus* 1.60, P=0.007, and 0.41 *versus* 0.54, P=0.003, respectively). The gender of the person mainly managing the garden did not affect species richness and diversity.

Table 2.7 Results of stepwise multiple regression analyses of selected socio-economic and bio-physical factors affecting species richness and diversity parameters in 61 homegardens (HGs) surveyed in four villages in the Nuba Mountains, Sudan (2010).

	Useful plant species richness (excluding ornamentals)					Indigenous fruit trees (IFT)
	Richness	Indiviudal density per 1000 m²	Share of exotic individuals	Shannon diversity	Shannon evenness	Richness
Adjusted R²	0.417**	0.573***	0.467**	0.506***	0.568***	0.278**
Location Kauda (0=no; 1=yes)	0.335*	0.813***	-0.693***	-0.768***	-0.760***	
Location Habila (0=no; 1=yes)		0.282*				
Location Kalogi (0=no; 1=yes)				-0.267*		
Level of subsistence (0=selling produce, 1=subsistence)	-0.586***					
pH	-0.463**					-0.581***
CEC$_{eff}$						
Household poverty index (HPI)						0.443**
Cultivated HG area (m²)						
HG age (years)						
Elevation (m)						

For each explanatory variable, the standardized regression coefficient (β) and its significance levels are given (*, **, ***: P≤0.05, ≤0.01, <0.001, respectively); ns=not significant.

Multiple regression analyses confirmed some of the effects of the above mentioned factors on species richness and diversity, although the strength of the obtained models was rather moderate or weak, explaining less than 60% of the variation (Table 2.7). The models fit best for individual density, *H'*, and *J'* index (more than 50% of variation explained; Table 2.7). Species richness was positively influenced by the location Kauda, but negatively influenced by subsistence-oriented production and increasing soil pH levels. Individual density was positively influenced by the locations Kauda and Habila. Share of exotic individuals was solely negatively influenced by the location Kauda. A strong negative influence on *H'* as well as *J'* was caused by the location Kauda, slightly also by Kalogi on *H'*. Furthermore, IFT richness was negatively affected by pH, but positively by HPI. Putatively affecting variables such as CEC$_{eff}$, cultivated HG area, age of the HG as well as elevation did not contribute to the models.

2.4.7 Classification of gardens according to species composition

Nearest neighbor cluster procedure did not identify any outlier and allowed to include all surveyed HGs in the subsequent minimum variance cluster analysis. Based on the 'elbow-

criterion' four different clusters of HGs were found (Figure 2.3). HGs of Kauda clearly separated from all others and clustered as a whole together (cluster 1), whereas HGs of the other three villages were assigned to different clusters each. Stepwise discriminant analysis confirmed that the four clusters were correctly classified (98.4% of cases in the right cluster) and the two first ordination functions together explained already 96.3% of variation. The low and significant Wilks' λ value of 0.1% unexplained variation out of 100% reflected the goodness of clustering and the independence between each of the clusters ($P<0.001$). Discriminant analysis extracted 15 plant species with a major predictive power to separate HGs into the four clusters (in decreasing order): *Sorghum bicolor*, *Zea mays*, *Abelmoschus esculentus*, *Arachis hypogaea*, *Balanites aegyptiaca*, *Solanum melongena*, *Solanum lycopersicum*, *Sesamum indicum*, *Cucumis melo*, *Vigna unguiculata*, *Terminalia laxiflora*, *Acacia nubica*, *Physalis angulata*, and *Cajanus cajan*. While the first four species were frequently found in all villages even though differencing individual densities, the remaining 11 species were rather present in unbalanced densities or were limited to certain villages. In addition to the above mentioned differences in species composition, the four clusters also differed in various variables including species richness and diversity parameters (Tables 2.5 and 6) as well as socio-economic and bio-physical variables (Tables 2.2 and 2.3).

HGs of cluster 1 most clearly separated from all other HGs as revealed by the deepest dendrogram node position (Figure 2.3). These HGs were all located in Kauda and managed by young female Nuba (Otoro tribe), native to the location. HGs of this cluster were old and had the largest sizes, managed by rather poor households with very little additional land holdings and of low literacy rate (Table 2.3). Commercialization of production was low. In HGs of cluster 1, highest total soil N and Mg values were recorded (P≤0.01), while overall mineral content, P and C/N was lowest (Table 2.2). Plant species richness was high, however, diversity and *J'* indices as well as share of exotic species and individuals were lowest (Table 2.5). In contrast, IFT richness and diversity were highest ($P<0.05$, Table 2.6). Regarding SDR values, staple crops dominated this cluster while the importance of vegetable and condiments species was lowest (Figure 2.4). Fiber plants were largely cultivated in HGs of cluster 1. The five most important and dominant species were *Sorghum bicolor*, *Sesamum indicum*, *Arachis hypogaea*, *Corchorus fascicularis* and *Vigna unguiculata*. Only in this cluster, the two latter species were among the five most dominant species. According to the above mentioned characteristics, HGs of cluster 1 were named as 'traditional-staple' HGs.

HGs of cluster 2 were of rather young mean age and small size (Table 2.3). These HGs were mostly for subsistence purpose (73%, Figure 6); about 50% of the gardeners were illiterate and non-native to the particular village. TLUs per household member were lowest,

but the rate of commercialization of HG production was the second highest of our study. Regarding soil quality, N was low in HGs of cluster 2, while soil mineral values were rather moderate (Table 2.2). Richness and diversity measures of both total useful plant species and IFTs were intermediate or low (Tables 2.5 and 2.6). The most balanced mixture of plant use categories was found in this cluster that was relatively similar to cluster 1, but with a higher importance of vegetables at the expense of staples (Figure 2.4). HGs of cluster 2 had the highest number of medicinal plants (data not shown). Only in this cluster the staple *Pennisetum glaucum* was among the five most dominant crop species, the other four were *Sorghum bicolor*, *Zea mays*, *Arachis hypogaea* and *Sesamum indicum*. Since household as well as plant diversity characteristics were both at intermediate stages and the importance of plant use categories relatively balanced, HGs in this cluster were named as 'transitional-staple' HGs.

Cluster 3 comprised rather young and small HGs (Table 2.3). The share of female gardeners was low and literacy rate high (Table 2.3). Households managing HGs of cluster 3 were wealthy as expressed by the high HPI and TLUs per household member (Table 2.3). As much as 91% of HGs in this cluster were subsistence-oriented. Income gained from the HG produce was by far the lowest recorded, while employment rate was highest (both P<0.05; Table 2.3). Soils in these HGs had lowest CEC_{eff} and intermediate N concentrations (Table 2.2). Species richness was low, but share of exotic species high (Table 2.5). J' was highest, similar to cluster 4. IFT richness and diversity were relatively low, whereas the corresponding EFT parameters were intermediate (Table 2.6). HGs of cluster 3 were dominated by vegetables, but the categories fruits and 'other uses' were also important. The five most dominant species were *Abelmoschus esculentus*, *Zea mays*, *Solanum lycopersicum*, *Corchurus fascicularis* and *Ocimum gratissimum*. The latter species - used as repellent against insects, but with a 'weedy' behavior - was exclusively found in HGs of cluster 3. We observed a low dependence of households on HG produce and lower maintenance levels in these HGs, which were consequently described as 'pastime-mixed' HGs.

'Commercial-vegetable'
31% subsistence, 54% in Habila
High diversity

'Pastime-mixed'
91% subsistence, 64% in Kalogi
Medium to low diversity

'Transitional-staple'
73% subsistence, 46% in Sama
Medium to low diversity

'Traditional-staple'
80% subsistence, 100% in Kauda
High diversity

Market-oriented
Subsistence

Cluster 4
n=13

Cluster 3
n=11

Cluster 2
n=22

Cluster 1
n=15

Squared Euclidean - log(e)

Figure 2.3 Dendrogram resulting from minimum variance (squared Euclidean distances) cluster analysis based on ln-transformed density data (individuals per 1,000 m² HG area) of 110 useful plant species (without ornamentals), in 61 homegardens (HGs) of the Nuba Mountains, Sudan (2010). The dashed line indicates the separation into four clusters according to the 'elbow criterion'. Brief cluster description (left side) gives parameters in the order: assigned HG type, percentage of market-orientation and share of the main village present as well as a rough diversity assignment.

Cluster 4 comprised small and young HGs managed by households with relatively large landholdings and high illiteracy rates (Table 2.3). Almost 39% of these HGs were managed by male gardeners. Fifty-five percent of the gardeners were of Arabic affiliation. In line with the high proportion of market-oriented HGs in cluster 4 (69%), gross income derived from HG produce was highest (Table 2.3). Soils of HGs in this cluster showed high mineral levels resulting in the highest CEC_{eff}, while total N was moderate (Table 2.2). Useful plant species richness and diversity were comparatively high (Table 2.5). Also richness and diversity of IFT and EFT species generally ranged highest among all clusters (Table 2.6). The importance of staple crops was lowest while that of vegetables highest (Figure 2.4). Only in this cluster, a 'living fence' made of *Jatropha curcas* and *Xanthium brasilicum*, an invasive weed from South America, was found, the latter was used as a fuel. The two vegetables, *Eruca sativa* and *Corchorus olitorius* grown as cash crops were among the five most dominant species. The three others were *Abelmoschus esculentus*, *Zea mays* and *Solanum lycopersicum*. Based on the HG features extracted we named this type as 'commercial-vegetable' HG type.
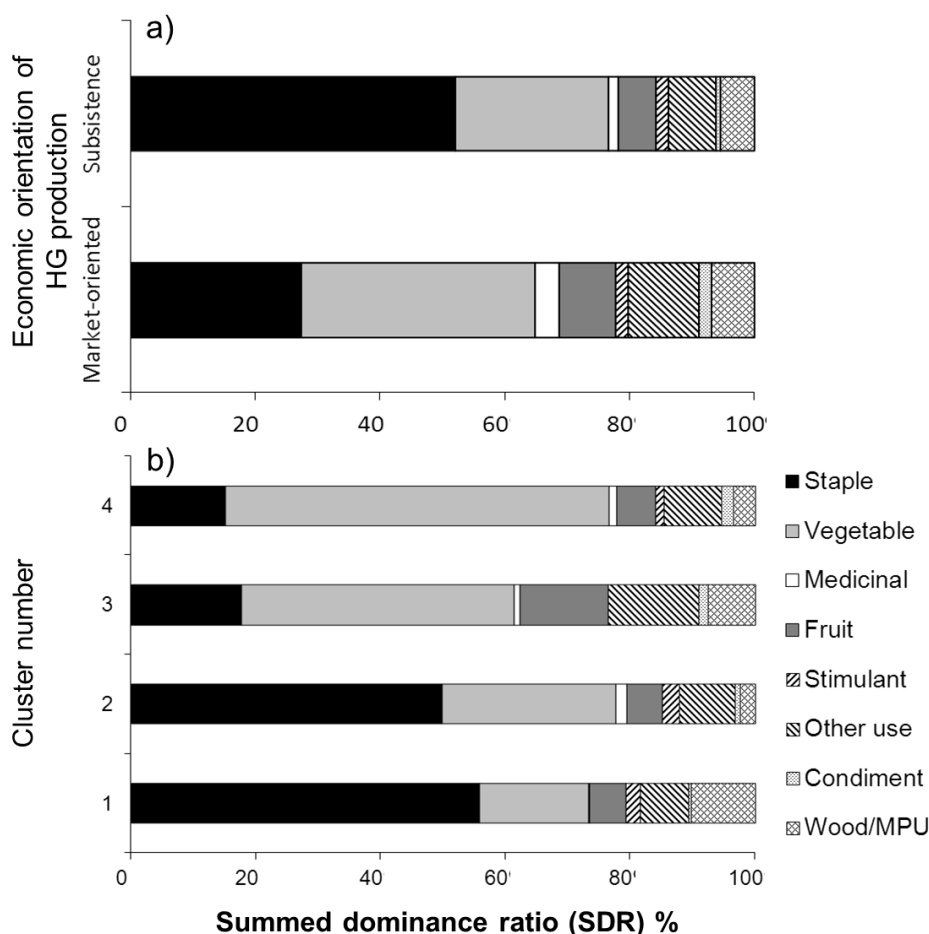
Figure 2.4 Summed dominance ratios for eight plant use groups (without ornamentals), separately for a) the two types of economic orientation of HG production and b) four clusters of 61 homegardens surveyed in four villages of the Nuba Mountains, Sudan (2010). MPU: multipurpose use.

2.5 Discussion

The present HG study revealed highly variable levels of plant diversity and socio-economic household characteristics of this agroforestry system (Tables 2.2, 2.5 and 2.6) as well as clear signs of transitional processes.

The mean HG size with 1,900 m² was in range with other studies from semi-arid regions (Okafor and Fernandes 1987; Albuquerque et al. 2005; Bernholt et al. 2009). HGs of Kauda, however, were four times larger compared with the other three villages (Table 2.3), laying within the range of 0.4 to 3.0 ha known for homegardens of East and Central African highlands (Abebe et al. 2006). The dominance of staple crops in HGs of Kauda (see cluster 1 in Figure 2.4) reflects their importance for subsistence farming as similarly shown for HGs in Nepal (Gautam et al. 2008).

2.5.1 Plant species richness and diversity

The total of 110 useful plant species (without ornamentals) and the mean of 23 species per HG (Table 2.5) was comparatively high (and would have even been higher for

total numbers according to the species accumulation curves, Figure 2.2a and b) regarding the region of Kordofan where Gebauer (2005) documented a total of only 32 species and a mean of three per HG, however, in an urban setting. Studies from Niger (Bernholt et al. 2009) and Yemen (Ceccolini 2002) also reported lower mean richness ranging from four to 14 species per garden. Although not a main focus of our analyses, a closer look on ornamental species contributed to the observed differences and further understanding. The mean ornamental species richness with nine species per HG and a range of 1-13 per village was comparatively higher to gardens of semi-arid tropical Niger (Bernholt et al. 2009), where on average only two ornamental species were cultivated. As ornamentals mainly have aesthetic function instead of subsistence food production and a gradual substitution of crops by ornamental plants is known to occur in HGs of wealthier families (Christanty et al. 1986), the richness of ornamental species can serve as an indicator for transformation processes. This was evident for HGs of clusters 3 and 4 that grouped gardens managed by better-off families or market-oriented HGs, which at the same time had highest richness of ornamentals (mean=12 species, data not shown) and high dominance of vegetables (Figure 2.4). The opportunity to gain off-farm incomes (cluster 3) or cash income from HG produce (cluster 4) may thus have contributed to shifting HG production away from growing basic staple crops for self-consumption. In our study, the mean *H'* of 1.46 (Table 2.5) can be considered as moderate according to Barbour et al. (1987), who rated *H'* values of >2 as high. Diversity was still higher than for urban gardens of Sudan's capital Khartoum (*H'*=1.20, Thompson et al. 2010), gardens of a rural urban gradient in Zambia (*H'*=0.81-1.35, Drescher 1998) as well as for mostly commercial gardens in Niamey, Niger (*H'*=0.77-0.93, Bernholt et al. 2009). A study from Ethiopia showed a similar range of diversity with a mean of 1.45 (Abebe et al. 2009). Although species richness was highest for Kauda, diversity was lowest (Table 2.5) while at the same time garden sizes were largest in Kauda. However, HGs in Kauda were largely dominated by few species, such as *Sorghum bicolor* and *Vigna unguiculata*. It was already shown in other studies that *H'* is influenced by single dominant species (Bernholt et al. 2009) as well as rare species (McCune and Grace 2002; Fentahun and Hager 2009b) such as *Commiphora africana* (Table 2.4) in our study, which only occurred in HGs of Kauda. Gardeners of Kauda rely on cultivating a broad diversity of traditional and non-exotic species for food and nutrition security of their families. The very traditional gardening practices in Kauda may also be a result of the limited migration history of the respondents at this particular location. This fact, together with the remoteness and rather homogenous ethnicity of inhabitants in Kauda may have led to limited exchange of planting materials with other communities and a certain dependence on internal seed/seedling exchange networks though a high useful plant species richness could be maintained. Such dynamics are known from Peru (Wezel and Ohl 2005), Iran (Hashemi et al.

2013) and Zambia (Drescher 1998) where poor market proximity resulted in lower richness through hampered introduction of new species (including ornamentals). Coomes and Ban (2004) showed that exchange of plant material contributed to an increased plant species diversity in homegardens of Amazonian Peru. Better access to markets and enhanced exchange of plant material through mobility of people could, have resulted in the high species richness and diversity (particularly of ornamentals) in the other villages (Table 2.5) such as Sama (close to Kadugli, the capital of South Kordofan, Figure 2.1) even though a functional loss of some HG types as a staple food production system may have occurred (Figure 2.3).

2.5.2 Indigenous fruit tree (IFT) diversity

Total IFT richness of our study (12) was similar to HGs in Kordofan, Sudan (10 species, Gebauer 2005) as well as Niamey, Niger (14, Bernholt et al. 2009), but higher to urban gardens of Khartoum, Sudan (2, Thompson et al. 2010). However, the species accumulation curves showed a still increasing IFT richness if more HGs had been inventoried, particularly in Habila (Figure 2.2c). The mean *H'* for IFTs (0.56, Table 2.6) in our study was low compared with farmland of Uganda (Agea et al. 2007), Ethiopia (Fentahun and Hager 2009a) and Tanzania (Munishi et al. 2008), where fruit tree *H'* of 2.2, 1.9 and 2.7, respectively, were documented, the latter calculated for all tree species. Higher richness, but lower diversity reflects an imbalance of tree species abundances (dominated by *Ziziphus spina-christi*, *Balanites aegyptiaca* and *Adansonia digitata*) in our study. J' however, showed a higher value (0.65) in our study, as compared for instance with Ethiopian farmland (Fentahun and Hager 2009a), where an J' of only 0.4 was found. In our study, mean IFT richness and abundance was highest in Sama (Table 2.6) indicating the function of wild food resources in these villages where trees were left for special purposes when clearing natural vegetation for establishing HGs. On the other hand, the remote village Kauda also had a high IFT species richness and some IFT species such as *Grewia villosa*, *Grewia bicolor* and *Nauclea latifolia* were exclusively found in Kauda, which possibly reflects also inter-site differences of the current natural tree species distribution due to climatic differences (Table 2.1) and human influence, such as logging and over-exploitation of forests and woodlands in Kordofan (El Tahir et al. 2010). However, also the higher age of the HGs in Kauda (Table 2.3) might have had a positive influence on IFT richness, as similarly stated for HGs in Peru (Coomes and Ban 2004).

Market-oriented HGs harbored similar mean numbers of fruit tree individuals and species (Table 2.6), but showed a slightly higher dominance of the use group fruits (and wood/MPU tree species) than subsistence gardens (Figure 2.4) which was in contrast to results of Muneer (2008) in Sudan, who found commercial HGs with a reduced set of woody

species, including fruit trees. Mendez et al. (2001) on the other hand, showed that HGs in Nicaragua devoted to fruit tree cultivation were not particularly for generating cash income, but rather for self-consumption of fruits. Regarding the present study, this was in line to HGs of cluster 1, but in contrast to HGs of cluster 4: although both HG types harbored rather high IFT richness (Table 2.6), density of IFTs was relatively high in the latter with the largest share of market-oriented HGs. However, cash income generation from these on-farm fruit tree resources seemed to play only a minor role in the Nuba Mountains particularly of IFTs in the area of Sama (Goenster et al. 2011). Instead, branches of on-farm IFTs were for example used for fencing the garden like those from thorny *Ziziphus spina-christi* and *Balanites aegyptiaca*. In addition, wild fruits were mainly collected in the nearby forests, however, not for sale but rather for home consumption, similar to results from Tanzania

(Munishi et al. 2008). Other studies, reported higher contributions of non-timber forest products to household cash income generation in Kordofan (El Tahir and Gebauer 2004; Adam et al. 2013).

2.5.3 Determinants of species richness and diversity

The medium to low correlations of determinants revealed by multiple linear regressions (Table 2.7) reflected the difficulty to find single or combined key parameters influencing species richness and diversity. The location as such had some informative power, where type of ethnicity, remoteness, level of market access and mobility of people are likely to boost or hamper exchange of plant material or level of staple crop production, among others. The strong influence of the location Kauda is likely related to the traditional function of these HGs for subsistence production as compared to the marked differences in all the remaining villages (Figure 2.3). Latter are obviously more affected by recent transformation processes, including the decreasing HG sizes that has happened for the last 20 years according to key informants (Amir Mahmoud el-Murad, chief of the Shawabna ethnicity in Sama, personal communication) - a process that will most probably continue in future. At the same time, the importance of HGs for subsistence may further decrease because: (i) additional activities in tertiary sectors limit the time to work the garden and increase incomes to purchase food from local markets; (ii) informal land use regulations prevent families to own at maximum 400 m² of land around their houses including restrictions to grow crops on unused areas such as in the front of homesteads; (iii) decreasing knowledge of traditional gardening practices and motivation to grow crops, and (iv) changed patterns of husbandry and increased livestock numbers in settlements resulting from demographic growth. As a consequence, gardeners need to establish fences typically made of branches of local tree species that are cut in the forests and installed around the HGs. Collection, transport and installation of fencing material is labor and thus cost intensive. The factors listed above and

recent changes through external influences may also threaten the suitability of the surveyed HGs for *circa situm* conservation of plant genetic resources (see below).

Little differences in overall as well as IFT species richness and diversity parameters were detected between subsistence and market-oriented *jubraka*s. Instead, market-oriented gardens harbored higher total species richness (Table 2.5). While Bernholt et al. (2009) documented a similar trend, other studies reported a loss of vegetation strata, richness and diversity due to commercialization (Abdoellah et al. 2006; Peyre et al. 2006). Particularly, a trend of losing traditional vegetables, often with a high nutritional value, may occur in commercial HGs as mentioned by Abdoellah et al. (2006). This was observed in our study for indigenous vegetable species such as *Amaranthus viridis* or *Lactuca taraxacifolia* that were more frequently cultivated and used by subsistence gardeners, *Lactuca taraxacifolia* even as malaria preventive.

2.5.4 Classification of HGs

Using cluster analysis to classify the surveyed HGs was practical and efficient as it allows identifying HG types which differ not only in species richness and diversity parameters (Tables 2.5 and 2.6), but also in socio-economy and soil quality characteristics (Tables 2.2 and 2.3, Figure 2.3). This approach should be applied more frequently to classify agro-ecosystems as it may help to design more comprehensive recommendations regarding plant species conservation and management (Peyre et al. 2006; Kehlenbeck et al. 2007). In the present study, cluster analysis identified a gradient along an evolutionary time-scale of HG development. The most traditional HGs were grouped in cluster 1 (Figure 2.3), located in the most remote village, managed exclusively by women, characterized by a high species richness, dominance of staples for subsistence, low portions of exotic (Table 2.5) and few ornamentals. When taking these characteristics as the traditional *jubraka* features, changes in the other clusters are substantial, particularly in cluster 4 with its commercial vegetable gardens rich in exotic and ornamental species (Table 2.5), and often managed by male gardeners. HGs of clusters 2 or 3 were on an intermediate state or used as pastime gardens, respectively (Figure 2.3). They are characterized by a mixed species composition mainly grown for home consumption and low levels of commercialization, but including already numerous ornamental and exotic species (Table 2.5) as similarly found in non-commercial HGs of Indonesia (Abdoellah et al. 2006). The large dominance of staples in HGs of cluster 1 may also be explained by less additional landholdings of the same households (Table 2.3). Lack of sufficiently large fields for staple crop production forces households to grow the needed staples in their HGs, which was also observed in HGs of migrant families with little additional farm land in Sulawesi, Indonesia (Kehlenbeck et al. 2007).

The varying species composition also reflected the ethnical differences of the surveyed villages (Table 2.1). Several plant species were limited to certain villages and linked to the cultural traditions of the gardener's ethnic affiliation. *Pennisetum glaucum* for instance, the most expensive local grain (2 € per kg^{-1} grain) in the study region was absent in Kauda, but cultivated in Kalogi and Habila where pastoral ethnicities originally from Northern and Western Africa are predominantly present and traditionally cultivate drought-tolerant millets instead of sorghum. On the other hand, traditional vegetable species such as *Corchorus fascilaris* and *Stylochaeton hypogeum* occurring in 60 and 18% of the surveyed HGs, respectively, were preferably used by the gardeners grouped in cluster 1 (Kauda), but, although known, less by the gardeners in the other villages. Similar influences of ethnicities were reported from urban gardens in Niamey, Niger (Bernholt et al. 2009), and HGs in ethnically diverse villages of Peru (Wezel and Ohl 2005).

The high levels of plant species richness and relatively homogeneous species composition in cluster 1 (Tables 2.5 and 2.6) may be further explained by the limited access of the rather poor farmers of Kauda (low HPI, Table 2.3) to external agricultural inputs and labor force, which is said to conserve plant species, even those of no or limited utility value (Kaihura et al. 2001). In a summary, our cluster analysis confirmed the results of the regression analysis that the factors 'location' and 'commercialization level' had an important influence on species richness and diversity parameters, but cluster analysis also revealed additional influencing factors and differences of species composition among garden types.

2.5.5 Suitability of HGs for on-farm conservation of indigenous plant species

Farmers have to define their cultivation goals according to the subsistence needs of their families and recent demands of the market, which may sometimes not favor indigenous plant species. While the first is likely to be matched with indigenous and old neophytic crop species that have been used for centuries, are adapted to local climatic conditions, and are often strongly linked with traditional knowledge and cultural values (Kumar and Nair 2004), the latter will be more related to newly introduced cash crops (Abdoellah et al. 2006; Peyre et al. 2006) or improved varieties of traditional crops. Cash cropping and using improved materials can be seen as beneficiary for farmers, for example if low yielding traditional landraces are replaced by better varieties as reported for instance for the Indian Himalaya (Bisht et al. 2006). However, often exotic species and improved varieties may develop high productivity only under intensive systems using high levels of external inputs, which might not be accessible by resource-poor subsistence farmers. In our study, more than 40% of the useful species were of exotic origin, although large spatial differences were observed. Particularly for the food use classes fruits, vegetables, staples and spices, 47, 55, 56 and 67% of the species were exotics, respectively, while for wood and MPU species only 18%.

Many of the indigenous species were found only in low frequencies (44% of the 68 indigenous useful species were detected in less than five HGs, 15 species even in only one single HG) and/or low abundances (almost 50% of the 68 indigenous species were present with less than 20 individuals, most of them perennial species). Even the 12 IFT species, although relative frequent (five species occurred in more than 10% of the surveyed HGs), were present with only few individuals (seven species with less than 10 individuals each). Many further IFT species such as *Azanza garckeana*, *Boscia angustifolia*, *Celtis integrifolia*, *Diosporus mespiliformis* or *Ximenia americana* were found in the natural vegetation surrounding the surveyed villages in the Nuba Mountains (personal observation), but not in the surveyed HG. Thus, the value of the surveyed HGs for on-farm conservation of indigenous and traditional plant genetic resources is questionable, particularly when considering the current transformation processes. Many of the indigenous plant species recorded in the HGs were either common and very frequently cultivated food crops (e.g. *Sorghum bicolor*, *Cucumis melo* and *Sesamum indicum*), weed-like vegetables and fodder species (e.g. *Cleome gynandra*, *Corchorus tridens* and *Commelina* sp.) or common fuel wood and timber species, quite abundant in the surrounding woodlands (e.g. *Albizia amara*, *Acacia nilotica* and *Faidherbia albida*). Only a few indigenous species found in the surveyed HGs could be regarded as 'rare' in the surrounding natural vegetation, for instance the IFT *Grewia tenax*. A similar rather low value of HGs for the conservation of indigenous plant species was also reported from Indonesia (Kehlenbeck et al. 2007), while Bennett-Lartey et al. (2001) stated that HGs in Ghana are largely suitable for crop species conservation. However, as the pressure on the remaining woodlands is still increasing in the Nuba Mountains and abundance of many indigenous species is said to decrease (El Tahir et al. 2010), the importance of the existing HGs for *circa situm* conservation of plant genetic resources might increase in the future. Out of the surveyed HGs, the ones grouped into cluster 1 with their high species richness (including IFTs) and low portion of exotics seem to be most promising for species conservation. This fact is furthermore supported by the low shares of ornamentals that has been likely prevented a replacement of indigenous species and use groups to some extent at this cluster. On the other hand IFT and EFT species were more abundant in cluster 4 (commercial vegetable HGs), maybe because the wealthier families managing these HGs (Table 2.3) needed less space for own staple food production in their gardens than the poorer families in remote Kauda, where in addition efficient weeding of tree seedlings was observed. Promotion of agroforestry systems may contribute to enhancing the value of HGs in the Nuba Mountains for *circa situm* conservation of tree species including IFTs, e.g. by increasing household incomes from sale of tree products. IFT species are often neglected by research and development, but may fetch high market prices. For instance fruits of *Grewia tenax* were sold in Sudan for about 2.5 € kg^{-1} in 2004 at El

Obeid market (Gebauer et al. 2007) and 5 € kg^{-1} in 2010 at the Umdurman market near Khartoum (personal observation). The high potential of IFTs for income generation, but also for family nutrition (particularly of children, who were observed to extensively collecting and consuming IFT fruits from woodlands in the study area) could be further increased through participatory tree domestication of the most preferred and valuable IFT species, which should be performed in a participatory approach as suggested by Leakey and Simons (1997) and partly achieved in Southern and Western Africa (Akinnifesi et al. 2007). However, both on-farm species conservation approaches as well as IFT domestication programs are still to be developed in Sudan, and *jubraka* HG systems could offer a suitable environment for initiating and testing the mentioned programs and approaches.

2.6 Conclusions

The *jubraka* HG systems of the Nuba Mountains harbored a surprisingly high plant species richness and diversity. However, various constraints of gardening such as lack of fencing material, small garden sizes as well as poor access of gardeners to germplasm – both for traditional species, but also for improved varieties – seem to affect the motivation of households to cultivate their HGs. Since these HG most probably will be more and more subjected to the introduction of exotic species as well as to transformations as a result of socio-economic changes such as commercialization, their plant species composition is likely to change in the near future which may possibly lead to losses of traditional species. In addition, the current and future importance of the surveyed HGs for *circa situm* conservation of indigenous and traditional species might be questionable. It remains unclear if the HGs in the Nuba Mountains can still fulfill their current function in contributing to food and nutrition security of the families managing them in the future. In contrast to popular beliefs, however, a modest commercialization of HG production may contribute to maintaining and even enhancing species richness and diversity in these systems. However, looking at the many factors affecting and possibly threatening species richness and diversity in HGs, there is the need to (i) raise awareness of local communities on the nutritional and ecological advantages of growing traditional plant species and varieties, (ii) improve access of gardeners to decentralized distribution systems of germplasm, and (iii) promote subsistence and semi-commercial cultivation of diverse plant species (including IFTs) and varieties for home consumption and income generation. Species diverse agricultural production systems are of particular importance for smallholder farmers to ensure resilience and sustainability of food production in a region which is subject to climate change, severe health and food security problems and unstable political conditions.

2.7 Appendix

Table. Plant species cultivated in 61 homegardens surveyed in four villages in the Nuba Mountains, Sudan (2010), sorted by their main use categories.

No.	Scientific name	Author	Family	English	Vernacular name	Origin
Condiments						
1	Anethum graveolens	Mill.	Apiaceae	Dill	Shamar	ex
2	Capsicum frutescens	L.	Solanaceae	Hot chili	Shatta	ex
3	Unknown species 1		Cucurbitaceae	-	Jedual kaui	in
Fruits						
4	Adansonia digitata	L.	Malvaceae	Baobab tree	Tabaldi	in
5	Annona squamosa	L.	Annonaceae	Sugar-apple	Gishta	ex
6	Balanites aegyptiaca	(L.) Del.	Zygophyllaceae	Desert date	Lalub	in
7	Borassus aethiopum	Mart.	Arecaceae	African fan palm	Deleb	in
8	Carica papaya	L.	Caricaceae	Papaya	Pawpaw	ex
9	Citrus × aurantiifolia	(Christm.) Swingle	Rubiaceae	Lemon	Lemon	ex
10	Ficus sycomorus	L.	Moraceae	Sycomore fig	Gumeiz	in
11	Grewia bicolor	Juss.	Malvaceae	Bastard brandy bush	Gedem	in
12	Grewia tenax	(Forsk.) Fiori	Malvaceae	White cross-berry	Gedem	in
13	Grewia villosa	Willd.	Malvaceae	Mallow raisin	Gedem	in
14	Mangifera indica	L.	Anacardiaceae	Mango	Manga	ex
15	Nauclea latifolia	S. M.	Rubiaceae	African peach	Karmadoda	in
16	Phoenix dactylifera	L.	Arecaceae	Date palm	Ballah	ex
17	Physalis angulata	L.	Solanaceae	Chinese lantern	Tebek	ex
18	Psidium guajava	L.	Myrtaceae	Common guava	Guava	ex
19	Sclerocarya birrea	A.Rich.	Anacardiaceae	Marula	Hameid	in
20	Tamarindus indica	L.	Fabaceae	Tamarind tree	Ardeb	in
21	Vangueria venosa	(Hochst.) Sond.	Rubiaceae	-	Kirkir	in
22	Ziziphus spina-christi	(L.) Desf.	Rhamnaceae	Christ's thorn jujube	Nabak	in
Medicinals						
23	Aristolochia bracteata	Lam.	Aristolochiaceae	Worm killer	Um galagil	in
24	Aristolochia macrophylla	Lam.	Aristolochiaceae	Pipevines	-	ex
25	Calotropis procera	(Ait.) R.Br.	Apocynaceae	Apple of sodom	Usher	in
No.	Scientific name	Author	Family	English	Vernacular name	Origin

26	Datura innoxia	Mill.	Solanaceae	Thorn-apple	Sekeran	ex
27	Ricinus communis	L.	Euphorbiaceae	Castor oil plant	-	ex
28	Rogeria adenophylla	J. Gay ex Delile	Pedaliaceae	-	Dabib	in
29	Salvadora persica	Wall.	Salvadoraceae	Toothbrush tree	Arak	in
30	Tribulus terrestris	L.	Zygophyllaceae	Yellow vine	Deressa	ex
31	Unknown species 2		Boraginaceae	-	-	in
Ornamentals						
32	Acalypha wilkesiana		Euphorbiaceae	Copper leaf	-	ex
33	Agave americana	L.	Asparagaceae	Century plant	-	ex
34	Agave desmetiana	Baker	Asparagaceae	-	-	ex
35	Alocasia sp.	(Schott) G.Don	Araceae	-	-	ex
36	Aloe vera	(L.) Burm.f.	Xanthorrhoeaceae	Aloe	-	ex
37	Alternanthera ficoidea	(L.) P. Beauv.	Amaranthaceae	Sanguinaria	Teshtesha	ex
38	Amaranthus cruentus	L.	Amaranthaceae	-	-	ex
39	Basella rubra	L.	Basellaceae	-	Grunfulia malauana	ex
40	Bougainvillea spectabilis	Willd.	Nyctaginaceae	Bougainvillea	-	ex
41	Caladium bicolor	Vent.	Araceae	Angel wings	-	ex
42	Canna indica	L.	Zingiberaceae	Indian shot	-	ex
43	Catharanthus roseus	(L.) G.Don	Apocynaceae	Madagascar periwinkle	Winka	ex
44	Celosia argentea	L.	Amaranthaceae	Plumed cockscomb	Shahid	in
45	Clitoria ternatea	L.	Fabaceae	Butterfly pea	Lablab	ex
46	Conocarpus lancifolius	Engl.	Combretaceae	Common tig tree	Damas	ex
47	Cosmos sulphureus	Cav.	Asteraceae	Yellow cosmos	-	ex
48	Cryptostegia grandiflora	R.Br.	Apocynaceae	Rubber vine	Nadiana	ex
49	Delonix regia	(Bojer ex Hooker) Rafin.	Fabaceae	Flamboyant	-	ex
50	Dodonea viscosa	Jaqu.	Sapindaceae	Hobush	Akawit	in
51	Eichornia azurea	(Swartz) Kunth	Pontederiaceae	Water hyazinth	-	ex
52	Euphorbia heterophylla	L.	Euphorbiaceae	-	Lisanusfur	ex
53	Euphorbia milii	Desmoul.	Euphorbiaceae	Christ plant	Shurkia	ex
54	Euphorbia tithymaloides	L.	Euphorbiaceae	Devil's Backbone	Tabkha sudani	ex
55	Euphorbia trigonia	L.	Euphorbiaceae	-	Malik	ex
56	Ficus nitida	(Th.) Miq.	Moraceae	IndianlLaurel fig	-	ex
57	Gomphrena globosa	L.	Amaranthaceae	Globe amaranth	Gudni	ex

No.	Scientific name	Author	Family	English	Vernacular name	Origin
58	Gossypium barbadense	L.	Malvaceae	-	Gutton	in
59	Graptophyllum pictum	(L.) Griff.	Acanthaceae	Caricature plant	Sahaba rakhla	ex
60	Helianthus annuus	L.	Asteraceae	sunflower	-	ex
61	Helianthus sp.	L.	Asteraceae	-	-	ex
62	Impatiens balsamina	L.	Balsaminaceae	Garden balsam	Aurag al kalifa	ex
63	Ipomoea batatas	(L.) Lam.	Convolvulaceae	Sweet potato	Bambei	ex
64	Ipomoea carnea	Jaqu.	Convolvulaceae	Pink Morning Glory	Awir	ex
65	Ipomoea quamolit	L.	Convolvulaceae	Cardinal vine	-	ex
66	Ipomoea sp.	L.	Convolvulaceae	-	-	ex
67	Jatropha gossypifolia	L.	Euphorbiaceae	Belly-ache bush	Sim	ex
68	Kalanchoe daigremontiana	Raym.-Hamet & H.Perrier	Crassulaceae	-	Woada	ex
69	Kalanchoe delagoensis		Crassulaceae	-	Woada	ex
70	Kalanchoe pinnata	(Lam.) Pers.	Crassulaceae	Goethe glant	Tabkha al msr	ex
71	Lantana camara	L.	Anacardiaceae	Spanish flag	Dud	ex
72	Mammilaria sp.	Haw.	Cactaceae	Nipple cactus	-	ex
73	Merremia dissecta	(Jacq.) Hall.f.	Convolvulaceae	-	-	ex
74	Mirabilis galapa	L.	Nyctaginaceae	Four o'clock flower	Sar arbara	ex
75	Moringa oleifera	Lam.	Moringaceae	-	-	ex
76	Nerium oleander	L.	Apocynaceae	Oleander	Amira	ex
77	Opuntia sp.	Mill.	Cactaceae	Paddle cactus	Sabar	ex
78	Pancratium trianthum	Herb.	Amaryllidaceae	-	Nargis	in
79	Pandanus veitchii	Veitch ex Mast. & T.Moore	Pandanaceae	Veitch's screwpine	-	ex
80	Plectranthus sp.	L'Hér.	Lamiaceae	Spurflowers	Grunfulia	ex
81	Plumeria rubra	L.	Apocynaceae	Frangipani	Yasmin	ex
82	Portulaca grandiflora	Hook.	Portulacaceae	Moss-rose	Sabakh al khair	ex
83	Portulaca oleracea	L.	Portulacaceae	Common purselane	Rigla	ex
84	Pseuderanthemum reticulatum	(W.Bull) Radlk.	Acanthaceae	-	-	ex
85	Sanchezia sp.	Ruiz & Pav.	Acanthaceae	-	-	ex
86	Sansevieria	Thunb.	Asparagaceae	Mother-in-law's tongue	Santri	in
87	Scadoxus multiflorus	(Martyn) Rafin.	Amaryllidaceae	Blood flower	Ain al agil	in
88	Senna alata	(L.) Roxb.	Fabaceae	Candle bush	-	ex
89	Senna italica	Mill.	Fabaceae	-	Senna	in
90	Senna siamea	(Lam.) Irwin et Barneby	Fabaceae	-	-	ex

No.	Scientific name	Author	Family	English	Vernacular name	Origin
91	Solenostemon scutellarioides	(L.) Codd	Lamiaceae	Common coleus	-	ex
92	Stapeliinae	L.	Asclepiadoideae	-	Malik	ex
93	Synadenium grantii	Hook.	Euphorbiaceae	African milk bush	Fulia	in
94	Syngonium podophyllum	Schott	Arecaceae	American evergreen	Chalip achdar	ex
95	Tagetes erecta	L.	Asteraceae	Marigold	Tagetes	ex
96	Talinum fruticosum	(Jaqu.) Willd.	Portulacaceae	Sweetheart	Camara	ex
97	Thevetia peruviana	(Pers.) K. Schum.	Apocynaceae	Lucky nut	Balsam	ex
98	Tithonia rotundifolia	(Mill.) S.F.Blake	Asteraceae	Red sunflower	-	ex
99	Tradescantia pallida	(Rose) D.R.Hunt	Commelinaceae	Purple queen	-	ex
100	Zinnia elegans	L.	Asteraceae	Zinnia	Aurag al kharif	ex
101	Unknown species 3		Cactaceae	-	-	ex
102	Unknown species 4	Grisebach	Zingiberaceae	-	-	ex
Other uses						
103	Abutilon theophrasti	Medik.	Malvaceae	Velvetleaf	Niada	ex
104	Anthropogon sp.	L.	Poaceae	-	Merera	in
105	Commelina erecta	L.	Commelinaceae	-	Dahanei	in
106	Commelina sp.	L.	Commelinaceae	Day flower	Bayat	in
107	Gossypium hirsutum	L.	Malvaceae	-	Gutton	ex
108	Hibiscus cannabinus	L.	Malvaceae	-	Liha	in
109	Hyphaene thebaica	L.	Arecaceae	Gingerbread tree	Dum	in
110	Jatropha curcas	L.	Euphorbiaceae	Purging nut	-	ex
111	Lagenaria siceraria	(Molina) Standl.	Cucurbitaceae	Calabash	Kalabas	ex
112	Luffa aegyptiaca	Mill.	Cucurbitaceae	Sponge gourd	Lifa	ex
113	Ocimum basilicum	L.	Lamiaceae	Basil	Abu rehan	in
114	Ocimum gratissimum	L.	Lamiaceae	-	Abu rehan	in
115	Ocimum sp.	L.	Lamiaceae	-	Abu rehan	in
116	Sida sp.	(G.Forst.) Schltdl.	Malvaceae	-	Um shideida	in
117	Sonchus sp.	L.	Asteraceae	-	Abu marua	in
118	Sorghum × drummondii	(Steud.) Millsp. & Chase	Poaceae	Sudan gras	Adar	in
119	Xanthium brasilicum	Vell.	Asteraceae	Cockleburs	Jabara khamisa	ex
Staples						
120	Arachis hypogaea	L.	Fabaceae	Ground nut	Ful sudani	ex
121	Cajanus cajan	(L.) Millsp.	Fabaceae	Pigon pea	Lubia adas	ex

No.	Scientific name	Author	Family	English	Vernacular name	Origin
122	Pennisetum glaucum	(L.)R.Br.	Poaceae	Pearl millet	Duchun	in
123	Phaseolus vulgaris	L.	Fabaceae	Common bean	Fasulia	ex
124	Sesamum indicum	L.	Pedaliaceae	Sesame	Simsim	in
125	Sorghum bicolor	(L.) Moench	Poaceae	Sorghum	Dura	in
126	Vigna subterranea	(L.) Verdc.	Fabaceae	Bambara groundnut	Abu gauwi	ex
127	Vigna unguiculata	(L.) Walp.	Fabaceae	Black-eyed bean	Lubia	in
128	Zea mays	L.	Poaceae	Corn	Ashrif	ex
Stimulants						
129	Hibiscus sabdariffa	L.	Malvaceae	Roselle	Karkade	in
130	Nicotiana rustica	L.	Solanaceae	-	Tumbak	ex
131	Senna occidentalis	(L.) H.S. Irwin & R.C. Barneby	Fabaceae	Coffee senna	Soarib	in
Vegetables						
132	Abelmoschus esculentus	(L.) Moench	Malvaceae	Lady's finger	Bamir	ex
133	Acalypha indica	L	Euphorbiaceae	Indian nettle	Hejak kuru	ex
134	Allium cepa	L.	Liliaceae	Onion	Bassil	ex
135	Amaranthus viridis	L.	Amaranthaceae	Wild amaranth	Hejak kuru	in
136	Citrullus lanatus	(Thunb.) Matsum. & Nakai	Cucurbitaceae	Watermelon	Ptikh	in
137	Cleome gynandra	L.	Cleomaceae	Wild spider flower	Tamaleika	in
138	Corchorus fascicularis	Lam.	Malvaceae	Jew's mallow	Khudra	in
139	Corchorus olitorius	L.	Malvaceae	Jew's mallow	Khudra	in
140	Corchorus tridens	L.	Malvaceae	Jew's mallow	Khudra	in
141	Cucumis melo spp. agrestis	(Naud.) Greb.	Cucurbitaceae	Cucumber	Tbish	in
142	Cucurbita maxima	Duchesne	Cucurbitaceae	Pumpkin	Gara	ex
143	Eruca vesicaria spp. sativa	(Mill.) Thellung	Brassicaceae	rocket	Girgir	ex
144	Hibiscus sp.	L.	Malvaceae	-	Kabru	in
145	Lactuca taraxacifolia	(Willd.) Schum.	Asteraceae	African lettuce	Moleta	ex
146	Lannea acida	A.Rich.	Anacardiaceae	-	Duoam	in
147	Momordica balsamina	L.	Cucurbitaceae	Balsam apple	Yero	ex
148	Portulaca oleracea	L.	Portulacaceae	Common purselane	Rigla	ex
149	Raphanus sativus	L.	Brassicaceae	Radish	Figl	ex
150	Senna obtusifolia	(L.) H.S.Irwin & Barneby	Fabaceae	Sicklepod	Kaual	ex
151	Solanum lycopersicum	L.	Solanaceae	Tomato	Tomatim	ex
152	Solanum melongena	L.	Solanaceae	Eggplant	Asuat	ex

No.	Scientific name	Author	Family	English	Vernacular name	Origin
153	Stylochaeton hypogeum	Lepr.	Araceae	Ground arum	Mururo	in
Timbers						
154	Acacia millifera	(Vahl) Benth.	Fabaceae	Blackthorn	Kitr	in
155	Acacia nilotica	(L.) Willd. ex Delile	Fabaceae	Gum arabic tree	Garad	in
156	Acacia nubica	Benth.	Fabaceae	-	Leot	in
157	Acacia polyacantha	Willd.	Fabaceae	White thorn	Humsineina	in
158	Acacia senegalensis	(Houtt.) Roberty	Fabaceae	-	Hashab	in
159	Acacia seyal	Del.	Fabaceae	Red acacia	Taleh	in
160	Acacia sieberiana	DC.	Fabaceae	Paperbark thorn	Kuk	in
161	Albizia amara	Boivin	Fabaceae	Bitter albizia	Arad	in
162	Albizia lebbek	(L.) Benth.	Fabaceae	Lebbeck tree	Dign al basha	ex
163	Anogeissus leiocarpa	(DC.) Guill. & Perr.	Combretaceae	African birch	Sahab	in
164	Azadirachta indica	A. Juss.	Meliaceae	Neem	Neem	ex
165	Boswellia papyrifera	(Delile ex Caill.) Hochst.	Burseraceae	-	Sammok	in
166	Capparis decidua	(Forssk.) Edgew.	Capparaceae	-	Dumduneidii	in
167	Combretum sp.	Loefl.	Combretaceae	-	Habil	in
168	Commiphora africana	(A. Rich.) Engl.	Burseraceae	African myrrh	-	in
169	Commiphora pedunculata	(Kotschy & Peyr.) Engl.	Burseraceae	-	Gureng	in
170	Cordia africana	Lam.	Boraginaceae	Large-leaved cordia	San	in
171	Dichrostachys cinerea	(L.) Wight & Arn.	Fabaceae	Sicklebush	Kadad	in
172	Faidherbia albida	(Delile) A.Chev.	Fabaceae	Apple-ring acacia	Haraz	in
173	Ficus sp.		Moraceae	-	-	in
174	Gardenia ternifolia	Schumach. & Thonn.	Rubiaceae	-	-	in
175	Lannea microcarpa	Engl. & K.Krause	Anacardiaceae	-	-	in
176	Melia azedarach	L.	Meliaceae	White Cedar	Neem	ex
177	Parkinsonia aculeata	L.	Fabaceae	Jerusalem thorn	Seisaban	ex
178	Piliostigma thonningii	(Schum.) Milne-Redh.	Fabaceae	Camel's foot	Kharub	in
179	Pithecellobium dulce	(Roxb.) Benth.	Fabaceae	-	Tamar hindi	ex
180	Terminalia laxiflora	Engl. & Diels	Combretaceae	-	Durut	in
181	Xeromphis nilotica	(Stapf) Keay	Rubiaceae	-	Gabu	in

ex=exotic, in=indigenous

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Chapter 3 - Intra-specific diversity of *Ziziphus spina-christi*

The role of homegardens and forest ecosystems for domestication and conservation of *Ziziphus spina-christi* (L.) Willd. in the Nuba Mountains, Sudan

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3.1 Abstract

Ongoing and iterative domestication processes by humans such as selection, translocation and cultivation are known to influence the morphological and genetic diversity of tree species. Since many of these species occur also in human-created homegardens (HG) this type of agroecosystem therefore represents a set which is ideal to study domestication processes. The threatened indigenous fruit tree *Ziziphus spina-christi* occurs in HGs and forests of the Nuba Mountains, Sudan, and was therefore selected and studied.

Five locations were sampled and the geographical position of 250 trees determined. Each location was subdivided into HG and forest sites. The diversities of morphological traits and amplified fragment length polymorphisms (AFLPs) were assessed to study variation within and among locations and sites.

A high diversity of dendrometric parameters and fruit morphometries was found that differed significantly among locations. Environmental parameters affected dendrometry and fruit size, but applied regression models were rather of low explanatory power. Although statistically not significant mean fruit measures were continuously larger in HGs compared to forests. Higher genetic diversity was observed in HG samples.

Larger dendrometric and fruit morphometric traits are likely to result from better growing conditions in HGs and/or human selection of germplasm. This is in line with the

higher genetic diversity in HGs, which is explained as a consequence of the admixture of germplasm from different origins planted in HGs.

Z. spina-christi underwent incipient steps of domestication. High genetic diversity in HGs suggests those as valuable spots of improved germplasm and for on-farm conservation purposes.

Keywords AFLP; Agroforestry; Deme; Indigenous fruit tree; *Jubraka*; Molecular marker; Morphological characterization; On-farm conservation

3.2 Introduction

Domesticated plant and animal species are seen as a cumulative result of human-driven interventions, of matching intraspecific diversity to the needs of subsistence farmers, product markets, and of agricultural environments (Simons and Leakey 2004). Recent publications show the high potential of wild genetic resources for domestication purposes including indigenous fruit tree (IFT) species (Brodie et al. 1997; Anegbeh et al. 2005; Weinberger and Lumpkin 2005; Abasse et al. 2011). In fruit trees, domestication is often accompanied by morphometric shifts and results mainly in improved fruit traits. However, fruit tree domestication can also have negative effects on the genetic structure of a species. A unidirectional selection by humans, who may have used a limited number of maternal parents, is therefore likely leading to bottleneck effects narrowing the genetic base of populations (Brodie et al. 1997; Miller and Schaal 2006; Dawson et al. 2008; Ayelea et al. 2011; Ekué et al. 2011). With regard to fruit trees, on-going domestication processes were recently reported for, e.g., *Dacryodes edulis*, *Irvingia gabonensis*, *Blighia sapida* and *Adansonia digitata* (Leakey et al. 2004; Tchoundjeu et al. 2006; Duvall 2007; Ekué et al. 2011). However, little information is available about the domestication status of many IFT species in Eastern Africa, particularly in Sudan.

The diploid Christ's thorn jujube (*Ziziphus spina-christi* (L.) Willd., Rhamnaceae) is native to semi-arid tropical regions of sub-Saharan Africa and the sub-tropical areas of the Near and Middle East (Anonymous 1989; Orwa et al. 2009). As a priority and economically important IFT species in Sudan regarding quantity of collected fruits (Ezeldeen and Osman 1997), *Z. spina-christi* provides nutritious fruits, which are used for home consumption and sale. The species is documented to occur in forests (Robinson 2006; El Tahir et al. 2010) and homegarden (HG) agroforestry systems (Gebauer 2005), particularly in those of the Nuba Mountain area (Goenster et al. 2011) locally named as '*jubraka*'. The abundance of *Z. spina-christi* has been reported to decrease due to deforestation, overgrazing, expansion of agricultural land and unsustainable over-exploitation of the tree, such as for making furniture (HCENR 2000; Robinson 2006; Akinnifesi et al. 2007; Muneer 2008; Orwa et al.

2009). Small-scale agroforestry systems such as HGs with their generally high species richness may offer a refuge for the conservation of threatened plant species and their genetic diversity, including IFTs that are of importance for local communities (Eyzaguirre 2001; Trinh et al. 2003; Hollingsworth et al. 2005; Doebley et al. 2006). Recruitment of *Z. spina-christi* in both HGs and natural forests takes place through volunteer or rarely planted seedlings. In *Z. spina-christi* fruit setting starts after three to five years and the seeds are mainly dispersed by humans, other mammals, birds and lizards (Miehe 1986; Zhang and Wang 1995; Grice 1996; Varela and Bucher 2002; Varela and Bucher 2006). The exclusive outcrossing nature of the species and long-distance dispersal of its pollen and seeds result in a wide morphometric and genetic heterogeneity within this species (Sudhersan and Hussain 2003).

As far as we know, *Z. spina-christi* has not been explicitly domesticated in its natural distribution range and no varieties or landraces are documented yet. However, the large variability of fruit size, skin color and taste indicates the existence of local types in Sudan (Saied et al. 2008). Analyzing and understanding the phenotypic and genetic variation of this species provides an opportunity to identify and document diversity hotspots, and to develop domestication and conservation approaches, including selection and breeding strategies for further genetic improvement (Saied et al. 2008). The use of DNA-based methods from vegetative plant tissues enables the analysis of diversity and domestication effects independently from environmental influences on morphotypes. Thus, molecular marker analyses can additionally contribute to the selection process, e.g., identification of gene pools with a high genetic diversity (Jama et al. 2008). For example, the fingerprinting technique Amplified Fragment Length Polymorphisms (AFLPs, Vos et al. 1995)) allows to characterize genetic diversity by generating a large number of markers spanning the whole genome without prior knowledge about its genomic structure or specific sequence information (Mwase et al. 2010). Regarding *Z. spina-christi*, however, data on systematic characterization of tree individuals or the use of molecular markers are largely lacking.

This study aimed to characterize sub-populations of *Z. spina-christi* based on morphological tree and fruit traits as well as their genetic diversity. We tested the hypothesis that first steps of *Z. spina-christi* domestication have been occurred in agroforestry systems of the Nuba Mountains. The study's specific objectives were (i) to compare dendrometry, fruit traits and genetic diversity patterns of trees in HGs and adjacent forests; (ii) to identify factors influencing individual phenotypic and genotypic characteristics; and (iii) to assess a possible loss of intra-specific diversity after domestication by comparing the genetic diversity of sub-populations.

Results of this study might be used to develop strategies for improving tree genetic resources in domestication programs and for enhancing the suitability of agroforestry

systems for *circa situm* (Hughes 1998) conservation of this IFT resource, being most valuable for rural people in the Nuba Mountains and Sudan's economy.

3.3 Materials and Methods

3.3.1 Study area

The field study was conducted from October 2010 to January 2011 in the Nuba Mountains, South Kordofan, Sudan (Figure 3.1). The research area is located along an altitudinal gradient ranging from 481 to 895 m a.s.l (Table 3.1). The Nuba Mountains cover an area extending from 10°30'N to 12°30'N latitude and 29°00'E to 30°30'E longitude and are situated within the low rainfall woodland savanna of the Sudano-Sahelian region with a hot semi-arid climate. The unimodal average annual rainfall of 600-800 mm decreases slightly from high to low elevations and from south to north (Ferguson 1954). The annual temperature is almost 30 °C with a mean of 31 °C in April and 24 °C in January (Ismail and Elsheikh 2007). The soils of HGs along the piedmonts are weathered granite-derived Ustalfs, while those of forests are predominantly vertisols (USDA 2012). On the latter mainly staples are grown, such as sorghum (*Sorghum bicolor* Moench.) or pearl millet (*Pennisetum glaucum* (L.) R.Br.), whereas on Ustalfs traditional mixed agriculture predominates with a wide range of plants including maize (*Zea mays* L.) tomato (*Solanum lycopersicum* L.) and okra (*Abelmoschus esculentus* (L.) Moench).

3.3.2 Site and tree selection

Five locations were chosen across the Nuba Mountains (Figure 3.1), to cover maximum ranges of environmental factors (i.e. rainfall, elevation, soil nutrient contents) found in the region (Figure 3.1 and Table 3.1). Pairwise minimum and maximum linear distances between the study locations ranged from 55 to 163 km, respectively. A distance limit of at least seven km (range 7-25 km) was used to differentiate between the two sampled habitats HGs and forests and to limit possible effects of human interventions such as seed dispersal activities in the forest habitat. Within each village or forest, 25 trees were randomly selected, with a minimum distance of 100 m between sampled trees to reduce the risk of sampling of related plants (Dawson and Jamnadass 2008).
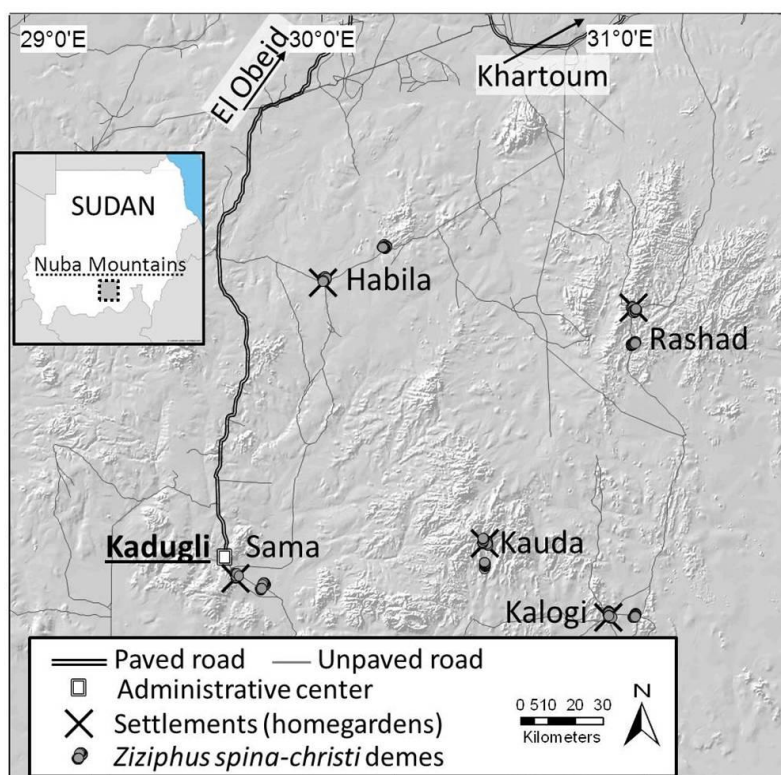
Figure 3.1 Hill shade map of the study area displaying the five selected village and forest demes of the sampled Ziziphus spina-christi trees in the Nuba Mountains, South Kordofan, Sudan, 2010. Demes are considered as a local population that can be clearly differentiated by distance or the assemblage it is embedded. Source: modified after CDE (Centre for Development and Environment), University of Bern, Switzerland, 2005.

Table 3.1 Physical parameters of the five surveyed study locations and their corresponding sites in the Nuba Mountains, Sudan (2010). Latitude and longitude values of each location are the focal points between the two sites (HG and forest).

	Location					Site		Total
	Habila	Kauda	Kalogi	Sama	Rashad	HG	Forest	
Latitude (N)	11°59'	11°02'	10°51'	10°57'	11°47'	11°20'	11°19'	11°19'
Longitude (E)	30°06'	30°33'	31°01'	29°46'	31°02'	30°27'	30°32'	30°29'
Rainfall (mm)	566	714	701	698	711	-	-	678
Elevation (m)	643	687	495	495	810	660	592	625

3.3.3 Tree characterization

The geographic position (WGS 84) and elevation of each of the 250 sampled tree individuals was determined using a hand-held GPS unit (GARMIN® Vista HCx eTrex, Ireland ltd., accuracy ± 2 m). Tree height was measured by intercept theorems (Kramer and Akca 2002), and diameter at breast height (dbh) was arithmetically determined from circumference at breast height taken with a measurement tape. Further individual tree characteristics were recorded such as number of main branches, and canopy diameter in N-S and W-E direction to calculate canopy area afterwards. In addition, the age of each HG tree was estimated by interviewing its owner.

3.3.4 Fruit and leaf sampling and measurement

From the 219 trees with fruits, 24 or sometimes less mature fruits (mean 18 fruits per tree) were randomly collected, and their height and width (both in cm) were measured with a vernier caliper at a resolution of 0.1 mm. Furthermore, after air drying the fruit weight (g) was determined using an electronic scale (Tomopol p250) to the nearest 0.05 g. Fruit volume was calculated assuming a spherical shape of the fruit and the shape ratio was calculated dividing fruit width by height. Means and coefficient of variation (CV%) were calculated for all five morphometric variables. Ten to 15 apparently uninjured, fresh leaves per tree were collected from all 250 sampled trees, air dried and subsequently stored in plastic bags with silica gel to avoid fungal infections and degradation of DNA.

3.3.5 Soil sampling

Six samples were taken from the topsoil (0-20 cm) around each tree at a distance of 1 m from the stem (modified after Asfaw and Agren 2007), mixed and a sub-sample of 200 g was air-dried before sieving to <2 mm. Exchangeable protons (H), aluminum (Al), calcium (Ca), potassium (K), sodium (Na), magnesium (Mg), Bray-P, organic carbon (C_{org}) and total nitrogen (N_{total}) were determined by standard methods at the Charles Renard Analytical Laboratory of ICRISAT Sahelian Centre, Niamey, Niger. Effective cation-exchange-capacity (CEC_{eff}) was calculated by summing up all analyzed ions. pH (1:2.5, 0.01 M KCl) was determined with an electronic pH-meter (WTW GmbH, Weinheim, Germany).

3.3.6 DNA isolation and AFLP analysis

Total genomic DNA was extracted from 1 cm² leaf material from each of the 250 samples with the DNeasy® Plant Mini Kit according to the protocol of Qiagen (Hilden, Germany).

Amplified fragment length polymorphisms (AFLP) were applied to assess the proportion of genetic variation captured in wild and HG stands of *Z. spina-christi*. The AFLP procedure used followed the protocol of Vos et al. (1995) with the following minor modifications: Purified genomic DNA (4 µl) was digested simultaneously with the two restriction enzymes *EcoRI* and *MseI*. Ligation of double-stranded *Mse*I and *Eco*RI adaptors to the ends of the restriction fragments were performed overnight to generate template DNA for polymerase chain reaction (PCR) amplification. The pre-selective primer pairs E01/M03 (Keygene N.V.® nomenclature, *Eco*RI-A/*Mse*I-G) were used with diluted DNA from the ligation reaction for the pre-amplification reactions. A thermal cycler (Peltier, PTC-200 ver. 4.0, MJ Research) was programmed to start at 72 °C for 2 min, 20 cycles each consisting of 94 °C for 10 s, 56 °C for 30 s, 72 °C for 2 min and finally 60 °C for 30 min. Selective amplifications were carried out using diluted pre-amplified DNA and the two primer

combinations E33/M50 and E32/M62 (Keygene N.V.® nomenclature; *EcoRI*-AAG/*MseI*-CAT and *EcoRI*-AAC/*MseI*-CTT, respectively). Primers *MseI*-CAT and -CTT were labeled with the fluorescent dye FAM^{TM}. The selective amplification reaction was set to start at 94 °C for 2 min, eightcycles, each consisting of 10 s at 94 °C, 30 s at 65 °C and 2 min at 72 °C. The 65 °C annealing temperature of the first cycle was successively reduced by 1 °C for the following eightcycles and continued at 56 °C for 30 s for the remaining 23 cycles. The final extension step lasted for 30 min at 60 °C. The two primer combinations were chosen from a pilot test of 12 primer combinations used by Singh et al. (2006) in 15 samples of *Z. spina-christi* and selected based on a clear and undoubtedly production of scorable fragments. The final amplified PCR products were diluted in Hi-Di^{TM} formamide including the internal size standard GeneScan^{TM} 500 ROX^{TM} and electrophoretically separated on an ABI Genetic Analyzer 3100 (Applied Biosystems Inc.). The size of the AFLP fragments was displayed and evaluated with the software package Genotyper 3.7 (Applied Biosystems Inc., Foster City, California, USA).

Reproducibility for the two primer pairs was checked with two samples of the pilot test, repeatedly present in all reactions and electrophoreses as well as two negative controls. Only reproducible and polymorphic loci of the AFLPs were scored and compiled as a binary matrix (1/0 for present/absent).

3.3.7 Data analysis

All obtained dendrometric and morphometric as well as soil data were analyzed by SPSS® 19.0 for Windows® (SPSS Inc., Chicago, Illinois, USA). Data were checked for normal distribution of residuals and homogeneity of variances followed by t-tests or analyses of variance (ANOVA) combined with post-hoc tests (Hochberg's GT2 or Tamhane's 2 for data with homogeneous or non-homogeneous variances, respectively). Since the geographical design of this study did not allow the collection of truly independent sites, comparisons between HGs and forests were done using General Linear Models (GLMs). Factors influencing dendrometric and morphometric traits were extracted by applying stepwise multiple linear regression analyses. Multi-colinearity was checked by the condition index CI whereby an index lower than 15 was considered as indicating non-colinearity of the data, although certain risks of misinterpretation remain attached (O'Brien 2007).

AFLPs were analyzed using the software package AFLPdiv 1.0 (Petit 2007) to compute percentages of polymorphic loci at the 5% level (*PPL5%*) and band richness (*Br*, rarefaction samples size n=24). Nei's (1973) gene diversity (*H$_j$*) was calculated by AFLPsurv 1.0 (Vekemans 2002). The number of private and rare alleles (number of alleles at frequency <5%) was counted by GenAlEx 6.41 (Peakall and Smouse 2006) and used to evaluate the efficiency of gene flow between demes (i.e. local populations of intercrossing

organisms of one species; Gilmour and Gregor 1939). Analyses of molecular variance (AMOVA) were applied to detect group differentiations based on Φ_{ST} by ARLEQUIN 3.1 (Excoffier and Schneider 2005). Here, two nested approaches were applied: First, a comparison among and within groups (two hierarchical level), and second, comparisons among and within groups and subgroups (three hierarchical level; based on two-way statistics). Mantel tests (Mantel 1967) were conducted based on Nei's genetic distances and spatial distances to investigate the interrelation of genetic differentiation by geographic distance, implemented in the software package GenAlEx 6.41 (with 999 permutations). A Bayesian model-based analysis was performed with STRUCTURE 2.3.1 (Pritchard et al. 2000) to check for individual's group membership based on their multilocus AFLP types. The selected admixture model was carried out with 10,000 Markov Chain Monte Carlo replications, 50,000 burn-in periods and K was set from 1 to 10. The most reasonable number of groups (K) was obtained by the open-access software STRUCTURE-HARVESTER (Earl and von Holdt 2012) according to the procedure with log likelihood (ΔK) between consecutive K values (Evanno et al. 2005). For all calculations, Hardy-Weinberg equilibrium was assumed and groups of demes were defined by splitting them into sub-groups: overall demes (all sampling areas separately, n=10), locations (village + adjacent forest together, n=5) and sites (HG and forest, n=2).

3.4 Results

3.4.1 Dendrometric characteristics and fruit traits

All measured dendrometric characteristics differed among the five villages, apart from the number of trunks (Table 3.2). Means were highest in Kalogi, followed by Rashad, Sama, Kauda and Habila. Similarly, age of the trees in HGs was lowest in Habila (eight years vs. 12-16 yrs, p > 0.001). Differences between HGs and adjacent forests were detected, although dbh, tree height and number of main branches tended to be slightly higher in HG demes (Table 3.2).

Considerable variation among the five villages was observed for all measured fruit traits apart from fruit shape ratio (Table 3.2). Means of the significantly different variables were highest at Kalogi and Sama, intermediate at Habila and Kauda, and lowest at Rashad (Table 3.2). The heaviest fruit weighed 1.95 g and maximum mean fruit weight per tree was 1.34 g. Coefficient of variation was highest for size and weight (41 and 37%, respectively), followed by width, height and shape ratio (15, 13 and 8%, respectively, data not shown).

Differences between HGs and adjacent forests were significant for fruit height and fruit shape ratio, whereby fruits were significantly smaller in forest demes (Table 3.2). Fruit

width, size and weight were slightly larger for fruits from HGs than from forests, but these differences were not significant.

3.4.2 Soil chemical properties

Soil properties differed among the five villages for all parameters analyzed (Table 3.3). Habila had the highest C_{org} and N_{total} status, followed by Sama and Kalogi and Kauda and Rashad. Variability was particularly high for Bray-P, ranging from 6.6 mg kg^{-1} in Kauda to 34.5 mg kg^{-1} in Kalogi (Table 3.3). When comparing the two sites, the C_{org} and N_{total} and particularly Bray-P status was significantly higher in HGs than in adjacent forests.

Table 3.3 Selected soil chemical properties of the five surveyed study locations and their corresponding sites in the Nuba Mountains, Sudan (2010).

Parameter	Unit	Location					ANOVA P value	Site		GLM P value	Total
		Habila	Kauda	Kalogi	Sama	Rashad		HG	Forest		
pH (KCl)		6.51 [a]	5.96 [b]	6.33 [ab]	5.86 [b]	6.18 [ab]	**<0.001**	6.57	5.76	**<0.001**	**6.17**
CEC_{eff}	(cmol$_c$ kg^{-1})	10.31 [a]	9.00 [b]	11.41 [a]	10.27 [a]	7.34 [c]	**<0.001**	9.97	9.37	**<0.001**	**9.67**
Bray-P1		24.74 [ab]	6.57 [b]	34.53 [ab]	25.71 [a]	20.08 [a]	**<0.001**	39.20	5.46	**<0.001**	**22.33**
C_{org}	(mg kg^{-1})	1.38 [a]	1.15 [a]	0.90 [b]	0.95 [b]	0.92 [b]	**<0.001**	1.13	1.00	**0.001**	**1.06**
N_{total}		0.16 [a]	0.13 [ab]	0.11 [b]	0.11 [bc]	0.09 [c]	**<0.001**	0.13	0.11	**<0.001**	**0.12**

Small letters indicate significant differences between locations at $p < 0.05$. GLM procedure includes the fixed factors location and site.

Table 3.2 Dendrometric and fruit morphometric data for the five surveyed study locations and their corresponding sites in the Nuba Mountains, Sudan (2010).

	Location					ANOVA	Site		GLM	
	Habila	Kauda	Kalogi	Sama	Rashad	P Value	HG	Forest	P value	Total
Dendrometric data										
Diameter at breast height (cm)	11.89 [b]	14.34 [ab]	16.62 [a]	15.33 [ab]	14.24 [ab]	**0.020**	16.32	12.62	0.594	**14.48**
Age (yrs)	7.76 [a]	12.29 [ab]	16.19 [b]	16.50 [b]	15.69 [b]	<0.001	14	-		**14**
Tree height (m)	4.24 [b]	4.95 [ab]	5.71 [a]	4.92 [ab]	4.99 [ab]	**<0.001**	5.07	4.86	0.290	**4.97**
No. of trunks	1.78	1.92	1.48	1.58	1.40	0.159	1.43	1.83	0.342	**1.63**
No. of main branches	12.63 [b]	16.18 [ab]	18.36 [a]	16.40 [ab]	19.70 [a]	**<0.001**	17.14	16.24	0.093	**16.69**
Canopy area (m²)	127.94 [b]	163.05 [ab]	243.23 [a]	182.41 [a]	185.19 [a]	**<0.001**	181.52	179.35	0.240	**180.43**
Fruit data										
Fruit height (cm)	1.16 [b]	1.11 [bc]	1.26 [a]	1.28 [a]	1.07 [c]	**<0.001**	1.18	1.17	**0.040**	**1.18**
Fruit width (cm)	1.25 [b]	1.22 [b]	1.37 [a]	1.40 [a]	1.15 [b]	**<0.001**	1.32	1.24	0.434	**1.28**
Fruit size (cm³)	1.01 [b]	0.91 [b]	1.33 [a]	1.40 [a]	0.78 [b]	**<0.001**	1.16	1.03	0.187	**1.10**
Fruit dry weight (g)	0.62 [b]	0.52 [bc]	0.77 [a]	0.83 [a]	0.47 [c]	**<0.001**	0.67	0.62	0.846	**0.65**
Fruit width:height ratio	1.08	1.11	1.09	1.09	1.08	0.453	1.12	1.06	**0.012**	**1.09**

Small letters indicate significant differences between locations at p < 0.05. Exact significances and overall means are given in bold values.

3.4.3 Factors affecting dendrometric and fruit morphometric traits

Stepwise multiple linear regression analyses revealed significant effects of bio-physical variables on the fruit traits height, width and dry weight, but the resulting models were low in explanatory power (Table 3.4). Elevation and the site 'forest' seemed to have negative effects, but Bray-P a positive one (model adjusted R^2=0.279, 0.282 and 0.313, respectively). At Kauda, fruit weight was particularly low. Among the independent variables, elevation had the strongest effect on fruit dimensions (Table 3.4).

Dendrometric characteristics were much weaker explained (9.7-11.7%) by bio-physical parameters (Table 3.4). Positive effects of 'forest' or Bray-P were noted for dbh, tree height, number of main branches, number of trunks and canopy area. Neither location, nor the measured soil chemical properties had clear effects. Only soil Bray-P appeared to influence fruit traits, because in the village with the highest Bray-P status, Kalogi, the assessed tree and fruit traits were highest, and in the two villages with the lowest Bray-P values Rashad and Kauda, fruit traits were lowest (Tables 3.2 and 3.3).

Table 3.4 Stepwise multiple regression analyses for selected soil and physical variables on overall morphometric fruit and dendrometric data in the Nuba Mountains, Sudan (2010).

	Dendrometric data					Morphometric fruit data			
	Diameter at breast height	Height	No. of trunks	No. of main branches	Canopy area	Height	Width	Dry weight	Shape ratio
Physical variables	(cm)	(m)			(m²)	(cm)	(cm)	(g)	
Adjusted R^2	0.117***	0.100***	0.022*	0.097***	0.104***	0.279***	0.282***	0.313***	0.113***
Elevation (m)	-	-	-	-	-	-0.492***	-0.471***	-0.533***	-
Site (0=HG/1=Forest)	-	-	0.161**	-	-	-	-0.256***	-0.260***	-0.342***
Bray-P (mg kg^{-1})	0.303**	0.193**	-	0.206**	0.148*	0.198**	0.162*	-	-
Kauda	-	-	-	-	-	-	-	-0.127*	-
Habila	-0.193**	-0.186**	-	0.200**	-0.177**	-	-	-	-
Kalogi	-	0.138*	-	-	0.189**	-	-	-	-
Rashad	-	-	-	0.129*	-	-	-	-	-

The standardized regression coefficient (β) is given including its significance level *, ** and *** ($p \leq 0.05$, ≤ 0.01 and ≤ 0.001), (-) not significant.

3.4.4 Genetic diversity

A total of 371 scorable AFLP fragments were scored in 249 individual trees (125 from HGs and 124 from forests, one sample had to be excluded due to non-amplification by the second primer combination) ranging from 75 to 500 bp of which 303 (81.7%) were polymorphic. The mean number of polymorphic fragments for each primer combination ranged from 152 (85.6%, E-AAC/M-CTT) to 138 (77.5%, E-AAG/M-CAT). Among the ten surveyed demes, HGs of Kalogi and Sama showed highest values for *PPL5%* and *Br[24]*, and forests of Sama and Habila showed lowest values (Table 3.5). Nei's gene diversity (H_j) was highest for the HG and forest of Rashad, and lowest for Sama forest.

Across locations, *PPL5%* and *Br*$_{[24]}$ was highest at Sama and Kalogi and lowest at Kauda (p > 0.05) (Table 3.5). Overall *H*$_j$ was highest for Rashad and lowest at Kauda and Habila. All genetic diversity measures were consistently lower in forest demes than in HGs, but these differences were significant only for *PPL5%* and *Br*$_{[24]}$ (Table 3.5). The number of rare alleles was higher across forests (60) than across HGs (50), while only two private alleles were found in HGs (Table 3.5). The mean number of private alleles in HG demes was slightly higher than in forest demes (mean 3 and 2; range 1-5 and 1-4, respectively, Table 3.5).

Table 3.5 Diversity parameters assessed for all surveyed demes, study locations and their corresponding sites in the Nuba Mountains, Sudan (2010) using 371 AFLP markers. Given is also the overall calculated diversity of each artificial grouping.

	Grouping	Diversity measures			No. of alleles	
		Br$_{[24]}$	*PPL5%*	*H*$_j$	Private	Rare
Deme	Habila HG	1.815	82.2	0.203	5	59
	Kauda HG	1.815	82.2	0.202	1	57
	Kalogi HG	1.854	86.0	0.226	2	40
	Sama HG	1.849	85.4	0.228	3	45
	Rashad HG	1.820	82.5	0.239	2	36
	Mean HG	*1.831*	*83.7*	*0.220*	3	47
	Habila forest	1.787	79.2	0.200	2	49
	Kauda forest	1.809	80.9	0.207	1	58
	Kalogi forest	1.815	82.2	0.226	3	47
	Sama forest	1.751	75.7	0.186	4	47
	Rashad forest	1.801	80.6	0.232	2	40
	Mean forest	*1.793*	*79.7*	*0.210*	2	48
	Mean deme	***1.812***	***81.7***	***0.215***	**3**	**48**
	Site (t-test p value)	0.029	0.022	0.426	0.820	0.886
	Location (ANOVA p value)	0.080	0.080	0.767	0.928	0.150
Location	Habila	1.919	92.2	0.201	2	66
	Kauda	1.898	89.8	0.201	0	60
	Kalogi	1.931	93.3	0.228	0	54
	Sama	1.947	94.9	0.219	0	50
	Rashad	1.904	90.6	0.234	0	39
	Mean location	**1.920**	**92.2**	**0.217**	**0**	**54**
Site	HG	2.000	70.4	0.230	2	50
	Forest	1.995	67.4	0.223	0	60
	Mean site	**1.998**	**68.9**	**0.227**	**1**	**55**

Br: band richness (1 ≤ *Br* ≤2; based on a rarefaction sample size of 24 individuals per deme)
PPL5%: percentage of polymorphic loci at a 5% level
Hj: Nei's genetic diversity (0 < *Hj* <1)

3.4.5 Genetic differentiation

Pairwise genetic Φ_{ST} values were very variable and ranged between 0.008 and 0.294 (Table 3.6). Within a location the genetic distances between HG and forest were generally lower than 0.099, except for Rashad (0.227). However, the lowest genetic distance of 0.008 was found between Rashad HG and Kauda forest (geographic distance 97 km) and the second lowest (0.012) between Sama forest and Kauda forest (geographic distance 82 km; Table 3.6). The highest genetic distances, on the other hand, partly correlated with geographic distance. For example, genetic distance was highest (0.294) between Rashad forest and Sama HG, which were 165 km apart. The second highest genetic distance (0.290) existed between Kalogi HG and Sama HG (geographical distance 139 km). In general, however, Φ_{ST} values were not necessarily lower between nearby demes and higher between distant ones. Apart from demes and locations, two and three hierarchical AMOVAs showed the lowest differentiation between sites (Φ_{ST}=0.002, p < 0.01 and -0.032, p > 0.05, Table 3.7). Overall, HG demes exhibited slightly lower genetic differentiation (Φ_{ST}=0.166) than forest demes (Φ_{ST}=0.178). The multi-locus fixation value Φ_{ST} resulting from AMOVA on two-hierarchical levels indicated significant variations among demes and locations (p < 0.001, Table 3.7). At three hierarchical levels, variation among the locations was low (Table 3.7).

Table 3.6 Pairwise genetic ΦST values (number of permutations=1000, below diagonal) and mean distance in km (above diagonal) for all surveyed demes in the Nuba Mountains, Sudan (2010).

	Habila HG	Habila forest	Kauda HG	Kauda forest	Kalogi HG	Kalogi forest	Sama HG	Sama forest	Rashad HG	Rashad forest
Habila HG	.	25	102	108	149	157	99	100	115	117
Habila forest	0.070	.	100	107	142	149	117	116	94	97
Kauda HG	0.065	0.128	.	**7**	51	60	93	84	91	83
Kauda forest	0.213	0.250	0.099	.	49	59	92	82	97	89
Kalogi HG	0.054	0.102	0.101	0.236	.	**10**	139	129	96	85
Kalogi forest	0.036	0.095	0.030	0.185	0.037	.	149	139	96	85
Sama HG	0.256	0.235	0.173	0.078	**0.290**	0.239	.	10	**169**	**165**
Sama forest	0.241	0.260	0.138	**0.012**	0.265	0.217	0.053	.	162	157
Rashad HG	0.213	0.243	0.106	**0.008**	0.238	0.187	0.079	0.020	.	11
Rashad forest	0.060	0.118	0.105	0.227	0.030	0.056	**0.294**	0.266	0.227	.

Bold marked values indicate the two lowest and highest values each.

The STRUCTURE analysis estimated the individual's group membership coefficients displayed by differently colored partitions resulted in admixed genotypes originating from different ancestors (Figure 3.2). The total sample showed a sub-structure of two segments peaking at *K*=2 with highest *ΔK* (550.3) and lowest standard deviation values. A second peak occurred at *K*=4 with second largest likelihood *ΔK* (47.8) and increasing standard deviation. As the latter did not add information about the structure of demes the most plausible grouping of all investigated genotypes was two.

Table 3.7 Analysis of Molecular Variance (AMOVA) for two and three hierarchical groups of demes, locations and sites in the Nuba Mountains, Sudan (2010) using 306 AFLP markers and 1000 permutations.

	Source of variation	Hierarchy level	df	Sum of squares	Variation components	Variation (%)	Fixation value (Φ_{ST})
Total	Among demes	2	9	2177.32	7.99	15.71	0.157 ***
	Within demes		239	10249.15	42.88	84.29	
	Among locations	2	4	1357.93	5.91	11.52	0.115 ***
	Within locations		244	11068.55	45.36	88.48	
	Among sites (HG, Forest)	2	1	61.94	0.10	0.19	0.002 **
	Within sites		247	12364.53	50.06	99.81	
	Among locations		4	1357.93	3.53	6.88	0.069 ***
	Among demes within locations	3	5	819.40	4.86	9.48	0.102
	Within demes		239	10249.15	42.88	83.64	0.164
	Among sites (HG, Forest)		1	61.94	-1.63	-3.24	-0.032 ns
	Among demes within sites	3	8	2115.38	8.90	17.74	0.172
	Within demes		239	10249.15	42.88	85.50	0.145
HG	Among demes	2	4	1043.78	8.69	16.56	0.166 ***
	Within demes		120	5251.44	43.76	83.44	
Forest	Among demes	2	4	1071.60	9.11	17.82	0.178 ***
	Within demes		119	4997.71	42.00	82.18	

df=degree of freedom, ** and *** ($p \leq 0.01$ and ≤ 0.001), ns=not significant.

Thereby, HGs and forests of Habila and Kauda, and HGs of Kalogi as well as forests of Sama shared one cluster, while forests of Kalogi, HGs of Sama and HGs and forests of Rashad shared a second one (Figures 3.2 and 3.3). At Kalogi and Sama, the two adjacent sites belonged to different clusters. The dominant sub-structure of the Rashad demes was found again at the remote location of Sama, whereas the demes of the nearby Habila belonged to a different sub-structure.
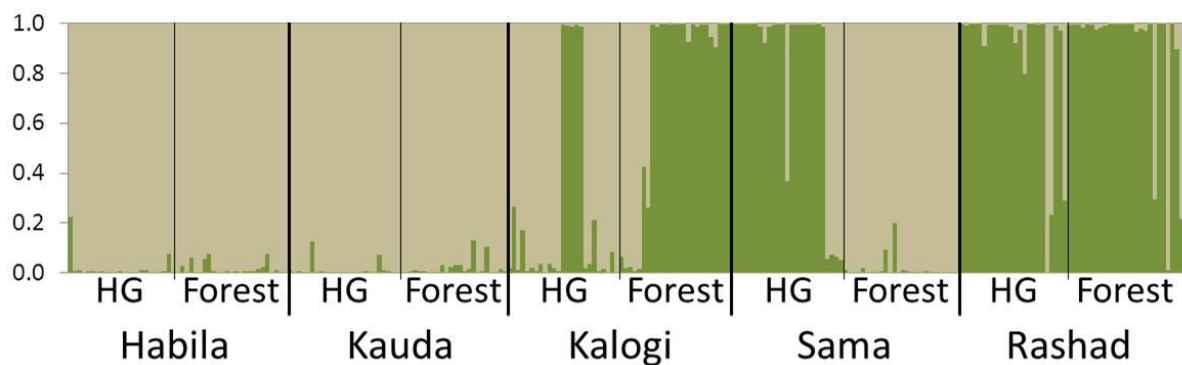
Figure 3.2 Inferred population structure based on Bayesian approach for a) K=2 and b) K=4 showing Q profiles. Each vertical bar represents one individual, with K colored segments. Each color estimates the individual's group membership fractions and thus showing admixed genotypes originated from different ancestors. All individuals are in sample order and grouped into ten demes separated by black lines; locations emphasized by long and sites by shorter black lines.

The correlation between genetic and geographic distances (Mantel test) was weak and non-significant for all locations and sites (data not shown). While overall demes showed

no trend (r=0.183, p=0.150, n=10), the two sites separately showed weak correlations. Genetic differentiation of HG demes were slightly negatively correlated with their respective geographical distances (r=-0.330, p=0.140, n=5), while those of forests exhibited a positive trend close to significance (r=0.461, p=0.080, n=5). However, correlations of sample numbers between n=5 and n=10 need to be generally treated with caution.

3.5 Discussion

The slightly larger dendrometric traits in the studied *Z. spina-christi* trees with regard to declining latitude and increasing longitude may reflect the slightly lower annual rainfall in the north-west areas resulting in slower growth rates of seedlings and trees as reported for *Prosopis africana* in the West African Sahel (Burkina Faso and Niger (Sotello Montes and Weber 2009). In Habila, however, the low values of dendrometric variables are also caused by the different population structure (that is younger trees in HGs at this location). When comparing HG and forests, only a trend towards slightly larger tree dimensions in HGs was found. This might be explained by a higher pressure on wild growing individuals, such as browsing by animals, cutting for fencing material or fire disturbance (Sawadogo et al. 2005; Holdo 2006). In addition, the growth of wild individuals may be reduced due to less favorable soil conditions (lower pH and Bray-P, Tables 3.2 and 3.3), as well as higher level of inter- and intra-specific competition in forests (El Tahir et al. 2010; Parker et al. 2010). On the other hand, the increased disturbance of forest trees resulted most likely in re-sprouting and thus in more numerous trunks with lower diameters. But, as found by Anegbeh et al. (2005) for *Dacryodes edulis* in Nigeria, dendrometric values (e.g., dbh) can also be lower in cultivated and fallow areas (HGs and crop fields) than in forests, indicating regional, management-dependent and inter-specific differences.

Despite the relatively small sampling area, differences for some of the assessed fruit traits were significant (Table 3.2). The high variation found for fruit dry weight and size (highest CV%) indicates the suitability of these two traits for differentiating trees and populations. Increased morphometric fruit traits can be indicators of domestication (Doebley et al. 2006), although interacting environmental factors may interfere with human effects. The larger fruit traits in the surveyed HGs compared to forests (Table 3.2) may support our hypothesis of human-mediated, unidirectional selection of fruits from 'superior' trees in the wild (e.g., trees producing fruits with more pulp) and the subsequent introduction of this germplasm into HGs as first steps of domestication. Significantly larger fruit traits of trees on managed as compared to unmanaged land were likewise found for *Chrysophyllum cainito* (Parker et al. 2010), *Irvingia gabonensis* (Atangana et al. 2002; Leakey et al. 2004), *Sclerocarya birrea* subsp. *birrea* (Leakey 2005) and *Dacryodes edulis* (Leakey et al. 2004). However, increased fruit traits in HGs may also reflect higher soil fertility (particularly in plant

available P) in the gardens as compared to forests (Table 3.3). Thus, we cannot unambiguously differentiate selection from favorable environmental conditions in HGs as causes for the observed differences in fruit traits between forests and HGs.

Multiple regression analyses confirmed most of the results discussed above. Physical characteristics such as elevation, soil chemical concentration and the location affected dendrometric data (Table 3.4). Fruit traits were affected by elevation and the site effect 'HG'. However, soil fertility parameters did not seem to have major impacts on fruit traits, possibly because the model already accounted for the influence of the site 'HG', which was characterized by higher soil fertility (Table 3.3). The weakness of the models (adj. $R^2 < 0.35$) made it challenging to determine factors of major impact on phenotypic trait differences. A similar problem of weak explanatory models was also described for *Adansonia digitata* in Mali (De Smedt et al. 2011) and *Balanites aegyptiaca* in Niger (Abasse et al. 2011). However, in our study associated factors such as a soil's water holding capacities (likely lower in Ustalf HG soils) and amount of rainfall may also have affected fruit traits. For example, the data show that fruits were heaviest and largest in the southernmost demes with their slightly higher annual precipitation and lower elevation (Figure 3.1 and Table 3.2). For *Vitellaria paradoxa* a similar trend of significantly larger fruits in wetter regions of Mali and Burkina Faso was reported by Maranz and Wiesmann (2003). Nevertheless, Abasse et al. (2011) documented reverse results for fruit and seed sizes of *Balanites aegyptiaca* in Niger, suggesting that seedlings in drier environments need to develop faster, thus, higher energy reserves of the embryo from larger seeds are advantageous.

The absence of significant differences of fruit traits between the two sites compared to those among locations indicated that regional characteristics affect fruit traits more than site-specific ones. Thus, our data do not allow to differentiate the relative role of environmental factors and human impact on fruit traits (see below). Therefore, the potential to select superior trees from HGs for future domestication programs based on morphometric data alone remains vague, but genetic characteristics can be used to enhance decisions of purpose (see below).

Percentages of polymorphic loci were lower (68%) in the studied *Z. spina-christi* accessions than for *Z. mauritania* (72%) and *Z. nummularia* (87%) accessions reported by Singh et al. (2006). In our study, trees from forest demes had lower levels of genetic diversity than those from HGs (Table 3.5). This is in contrast to the described losses of genetic diversity in other cultivated tree species, which often have a higher diversity in their natural habitats (Hollingsworth et al. 2005; Miller and Schaal 2006; Singh et al. 2006; Ekué et al. 2011). In the case of *Z. spina-christi*, fruits are traded extensively in the research region and beyond, and they are sold at many village markets in the Nuba Mountains. Some of the collected or purchased seeds and fruits, being brought to homesteads may have been

inadvertently thrown away, germinated and were thus introduced into HGs. The increased caption of genetic diversity in some HGs may reflect two scenarios. First, the natural stands adjacent to HGs where fruits are collected harbor already a high diversity. Second, the mixture of fruits brought from distant origins and/or diverse locations contributes to the admixture of diversity. Additional caption of genetic diversity through a collection of seeds from various natural stands was also reported by Stefenon et al. (2008) for *Araucaria angustifolia* plantations in Brazil. In our study, trees throve from seeds, and the rather randomly collected fruits from the wild likely contributed to the admixture effect observed in HGs. The lower number of rare alleles in accessions from HGs as compared to forests (Table 3.5) might provide evidence of short-term bottleneck effects, known to reduce susceptible rare alleles more than effecting diversity (Allendorf and Luikart 2007; Cornelius et al. 2010). Rare alleles are particularly important for conservation and adaption studies as they may represent the populations' potential to adapt under changing environmental conditions (Bashalkhanov et al. 2009). In our study, the probably lower exchange of seed material within forests might be a further reason for higher numbers of rare alleles as compared to the admixtured origin of trees in HGs. Likewise, low numbers of private alleles result from effective gene flow among populations (Allendorf and Luikart 2007). Those alleles arise through, e.g., mutation and will accumulate in populations where migration of plant material is low. Since our study showed few private alleles (Table 3.5), sufficient gene flow can be assumed proving the rather panmictic character of the *Z. spina-christi* distribution in the Nuba Mountains. Additionally, unknown modes of asexual propagation of *Z. spina-christi* by local people and the still abundant presence of trees in the wild for collecting fruits seems to prevent clear signs of shifts in the genetic due to domestication processes. Consequently, we rejected our hypothesis that *Z. spina-christi* experienced losses of genetic diversity during first steps of domestication.

The lower differentiation by distance correlations in HGs compared to the forest demes as indicated by Mantel tests are indications of a faster exchange of plant material (i.e., seeds) in the gardens due to human transfer of reproductive material. Similar trends have been shown for wild and cultivated varieties of species such as *Sorghum bicolor* (Mutegi et al. 2012) and *Ficus carica* (Aradhya et al. 2010). Non-significant differentiation-by-distance patterns for all demes such as in our study were also reported by Abdelkheir et al. (2011) for *Sclerocarya birrea* subsp. *birrea* using samples from larger distances among five demes in South Sudan. In this study, even stronger gene flow events were found compared to the studied *Z. spina-christi* accessions. Strong correlation-wise variations may be caused by natural selection, differentially structured gene flows and random genetic drift as suggested by (Farwig et al. 2008) particularly when landscapes become fragmented.

Pairwise genetic Φ_{ST} values and overall genetic structure as shown by AMOVA confirmed moderate to strong genetic differentiation according to Wright (1978) between locations, HGs and forest demes (range 11.5-17.8%, respectively, Tables 3.6 and 3.7). Our values revealed much stronger differentiation patterns as compared to results from *Blighia sapida* in Benin (0.3-6.2%, Ekué et al. 2011), but were comparable to populations of *Adansonia digitata* in Benin (5.0-17.6%, Assogbadjo et al. 2006). Such relatively high differentiation among populations is rarely found in woody species (Hamrick et al. 1992), because of their long lifespans, predominantly outcrossing mating systems and long distance dispersal of pollen and, in some cases, seeds (Parker et al. 2010). The comparatively high genetic differentiation among the studied populations is likely to be related to restricted gene flow among populations without human intervention in the investigated region.

Genetic differentiation among the investigated sites (HG and forest) based on two and three hierarchical levels was almost absent (Table 3.7). The low differentiation may reflect the rather short domestication time for *Z. spina-christi* and is in strong contrast to crop species domesticated for millennia such as soybean or wheat, whose cultivated relatives lost considerable amounts of genetic diversity (34 and 70-90%, respectively) compared to their wild ancestors (Hyten et al. 2006; Haudry et al. 2007). The moderate differences of genetic structure within HG and forest demes (16.6 and 17.8, respectively, Table 3.7) are in contrast to findings of Hamrick and Godt (1997), who showed higher mean Φ_{ST} values for species under cultivation. The slightly lower genetic differentiation (16.6%) in HGs might be a further hint of an improved admixture in HG demes, boosted by easy access of gardeners to fruits from markets and mobility of villagers as mentioned above. Usually, the selective human collection and translocation of planting material from markets and/or farms is known to increase the risk of genetic bottlenecks that may occur during the process of domestication, particularly of fruit trees (Brodie et al. 1997). Contrarily, in our study genetic erosion in *Z. spina-christi* may rather occur in natural environments. This is of special importance with regard to the conservation of this species' genetic resources since logging and fragmentation of forests takes already place in the study area. However, genetic diversity of *Z. spina-christi* can also be threatened in HGs due to unawareness of farmers, insignificant planting activities, weeding of *Z. spina-christi* seedlings and the species' substitution by exotic species (Jama et al. 2008; El Tahir et al. 2010).

The Bayesian clustering approach confirmed the variation among the demes (Figure 3.2). The identified number of clusters (*K*=2) revealed two distinct gene pools, one located in the central areas of the Nuba Mountains, the other flanking their periphery (Figure 3.3).
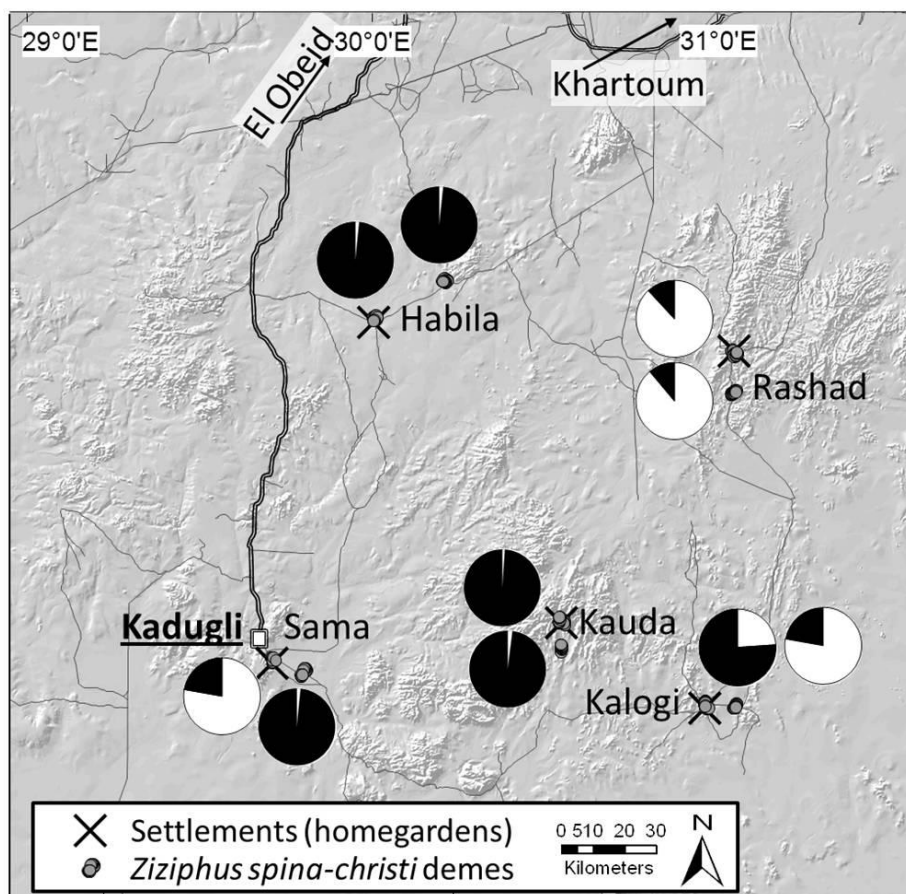
Figure 3.3 Hill shade map of the Nuba Mountain area, displaying surveyed villages, tracks and pie charts based on the proportion of membership of each pre-defined deme in each of the two inferred clusters. Map source: modified after CDE (Centre for Development and Environment), University of Bern, Switzerland (2005).

Since relationships cannot be detected with the used STRUCTURE software the migration of introduced plant material remains unclear and shows moreover that geographic distance did not always affected cluster grouping of the ten demes. According to Kumar (2008) firm generalizations of ancestry or geographical origin are difficult to make given the likely complex patterns of germplasm exchange of many indigenous cultures and multiple origins of cultivated plant populations. However, large-scale collection of *Z. spina-christi* fruits is known to occur north of Kadugli and in the surroundings of Rashad rather from the wild populations than from single trees in HGs (Adam and Pretzsch (2010), personal observation Wiehle). Furthermore, local retailers often purchase additional fruits from nearby markets instead of collecting fruits from the trees in their HGs (personal observation). The distinction between the two clusters, therefore, is most likely due to genetic drift, whereby a strong interaction and admixture of far distant material occurred. The locations Sama and Kalogi showed highly different gene pools between their sites HG and forest, indicating introduced plant material from distant areas into the HGs. Most likely the introduced material may have originated from the north-east regions of the Nuba Mountains, such as Rashad that showed

similar inferred cluster patterns. Even more distant areas may be sources for new material, since one family in Habila reported the planting of a seed from Darfur, West Sudan.

3.6 Conclusions and practical implications for Z. spina-christi conservation in the Nuba Mountains

The larger fruit traits and genetic measures of *Z. spina-christi* found in HGs of the study area as compared to forests areas are explainable with human intervention in shifting morphometric fruit traits and the genetic base. A serious loss of genetic diversity reflecting major efforts of domestication was not observed, suggesting an on-going gene flow among demes. Since future breeding and conservation efforts should focus on viable demes, where inbreeding and subsequent loss of alleles are minimal and individual's recruitment as well as growth conditions are most favorable, HG demes with highest genetic diversity and fruit trait measures may provide superior mother trees needed for future cultivar development. In a summary, HGs are valuable spots for identifying and maintaining superior mother trees, which are a prerequisite for developing further conservation-through-use approaches and breeding strategies for this important fruit tree species.

3.7 References

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Chapter 4 - Intra-specific diversity of *Adansonia digitata*

The African Baobab (*Adansonia digitata* L.) – Adequate genetic resources in neglected populations in the Nuba Mountains, Sudan

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4.1 Abstract

Adansonia digitata L., the famous 'baobab' tree, is one of the most important indigenous fruit trees of mainland Africa. Despite its significance for subsistence and income generation of local communities, little information is available about the morphological and genetic variability of East African populations of *A. digitata*, including those of Sudan. The aim of the present study therefore was to analyze variation patterns of different baobab populations in Kordofan, Sudan and to estimate the effect of human intervention on genetic differentiation and diversity.

A total of 306 trees were randomly sampled from seven spatially separated locations in the Nuba Mountains, Sudan, which where sub-structured into 'homesteads' and 'wild' stands to cover a wide range of differing environmental gradients and management regimes. Genetic analyses were conducted using nine microsatellite markers. Due to the tetraploid nature of *A. digitata*, different approaches were applied to estimate patterns of genetic diversity. Investigations were completed by measurements of dendrometric and fruit morphological characters.

Genetic diversity was balanced and did not differ between locations or management regimes (*P*>0.05) although tendencies of higher diversity in 'homesteads' were observed. A Bayesian cluster approach detected two distinct gene pools in the sample set mainly caused by one highly diverse population close to a main road. The variability of tree characters and fruit morphometries was high, and significant differences between locations were observed (*P*≤0.05).

Adequate genetic resources were investigated at a local scale, and results indicate a rather positive effect of human intervention. The observed populations provide a promising gene pool and likely inhabit ecotypes well-adapted to environmental conditions in the northern range of the species which should be considered in conservation and management projects.

Keywords Admixture; Distribution; Diversity; Fruit trait; Microsatellite; Molecular marker; South Kordofan; Phenotype; Tetraploidy

4.2 Introduction

Adansonia digitata L. (Malvaceae, subfamily Bombacoideae), the baobab, is one of the most important indigenous fruit trees of mainland Africa aligned to the so-called "Big Five" species which contribute significantly to food and nutritional security (Figure 4.1a) of rural communities (Sidibé and Williams 2002). Moreover, many products of the species provide income as they are traded at local and national markets, and baobab products become more and more interesting for international markets due to their wide spectrum of purposes as novel food (e.g., fruit pulp, Figure 4.1b) and ingredients of pharmaceutical and cosmetic products (von Maydell 1986; Osman 2004; Bennett 2006; Gebauer et al. 2014). Therefore, the baobab is one of the main target species for future domestication programs of 'wild' fruit species in Africa (Kalinganire et al. 2008).

Despite its importance and impressive character (Figure 4.1c), relatively little scientific information exist about phenotypic and genetic variation in baobab (Pock Tsy et al. 2009; Jensen et al. 2011). The majority of these baobab studies have concentrated on Western and Southern Africa with a strong focus on morphology (Cuni Sanchez 2011; Cuni Sanchez et al. 2011; Mpofu et al. 2012), while genetic studies are rare (Sidibé and Williams 2002; Kalinganire et al. 2008). Few studies used amplified fragment length polymorphisms (AFLPs) to investigate effects of human intervention on genetic diversity and structure of baobab in Benin, Burkina Faso, Ghana and Senegal (Assogbadjo et al. 2006; Assogbadjo et al. 2008b; Kyndt et al. 2009). Despite *A. digitata*'s autotetraploid nature (2n=160) and thus challenging data analyses as well as interpretation of results, microsatellite (SSR) markers developed by Larsen et al. (2009) and were successfully used to differentiate populations and individuals

(Munthali et al. 2012). These markers allow for the analysis of the genetic diversity of the species, seed- and pollen-mediated gene flow and inbreeding, and may even help to predict consequences of climatic fluctuations on genetic structures (Larsen et al. 2009). The approach is particularly effective in evaluating genetic bottlenecks associated with anthropogenic interventions (Hollingsworth et al. 2005; Larsen et al. 2009; Ekué et al. 2011).
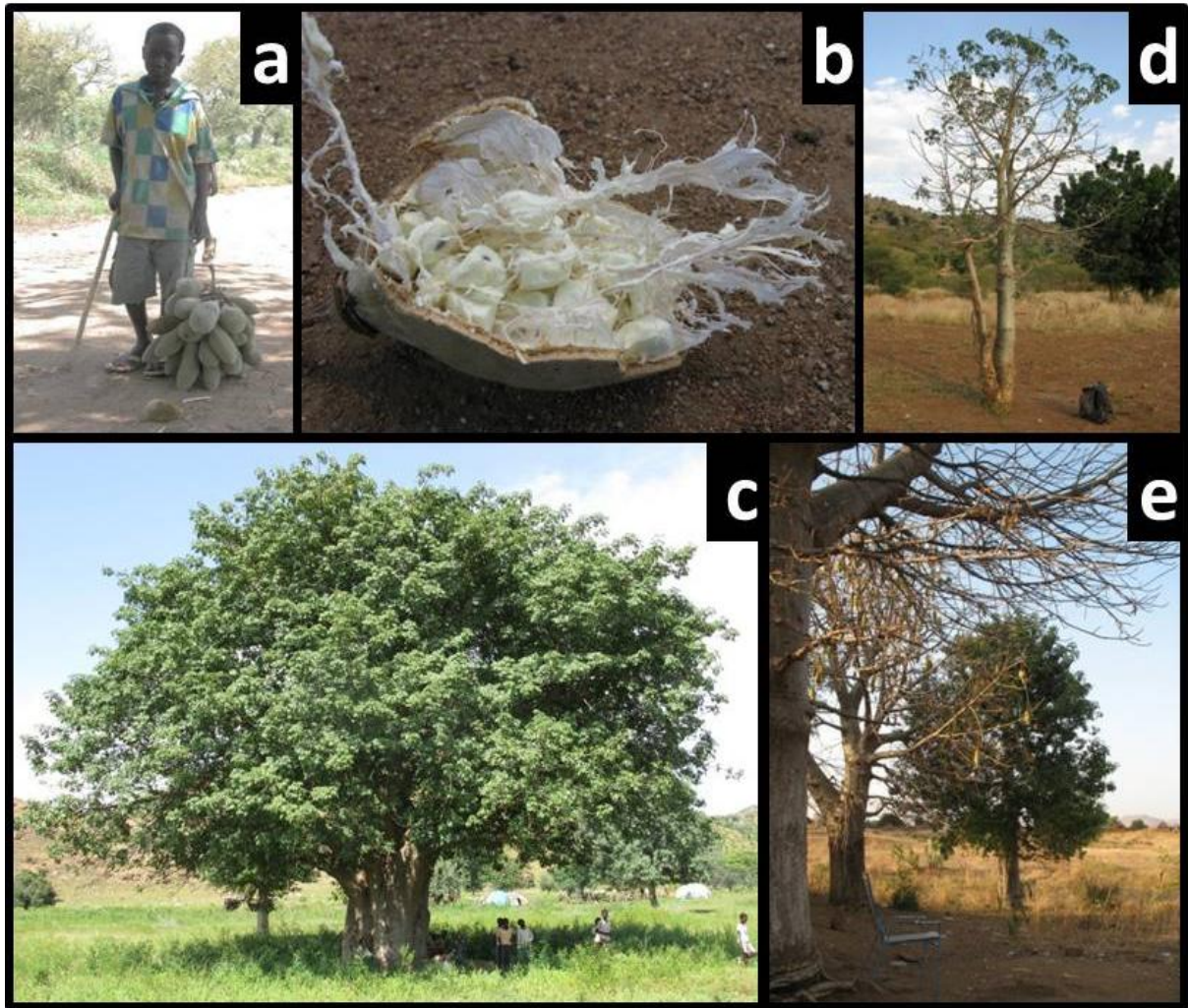
Figure 4.1a-e a) Baobab fruit bundle bend just with their peduncles by a child; used for home consumption, b) opened baobab fruit capsule with seeds embedded in whitish fruit pulp , c) vital baobab tree in Kadugli district, d) young tree in the central Nuba Mountains , e) Different appearances of three baobab trees at one time in Kadugli district: in front left, tree without fruits, leaves shed; in between left, fruit producing tree, leaves shed; in the back middle (slightly lower elevated tree), tree without fruits, in the leafy stage.

Agroforestry systems (e.g., homegardens) located in human settlements are ideal to study anthropogenic interventions on genetic and morphological variation in tree species. These systems are known to harbour a variety of plant genetic resources and can serve as sanctuaries for relict crops or varieties, thereby maintaining high levels of genetic diversity (Rocha et al. 2008; Galluzzi et al. 2010). It is well known that human intervention through selection may reduce the genetic diversity of cultivated species including indigenous fruit

trees such as *Vitex fisheri* or *Blighia sapida* (Lengkeek et al. 2006; Ekué et al. 2011). However, increased diversity in planted populations may also occur caused by non-random admixture of certain genotypes (Stefenon et al. 2008). Both possibilities have been suggested for baobab because of its often close association to past and present human settlements (1982; Sidibé and Williams 2002; Duvall 2007) and common transplanting of seedlings from the 'wild' into villages in West African regions (Dhillion and Gustad 2004) . Thus, humans may have influenced the genetic structure of baobab by on-going and iterative non-random selection and migration processes since centuries or even millennia leading to incipient domestication (Lovett and Haq 2000; Sidibé and Williams 2002; Pock Tsy et al. 2009; Munthali et al. 2012).

In Sudan, baobab is of particular importance for local communities indicated by separate terms that exist for the fruit ('Gonguleize' or 'Humeir') and for the tree ('Tabaldi'). Here, baobab trees are regarded as personal property (Wickens 1982; El Tahir et al. 2010). In the Nuba Mountains, Sudan, baobab is one of the most important fruit trees in agroforestry systems being the third most abundant (16%) indigenous fruit tree species in 61 surveyed homegardens (Wiehle et al., unpublished data). These populations are located at the northern edge of the distribution area in Eastern Africa characterized by low rainfall. Thus, special adaptation to arid conditions can be assumed which is especially important for future management of baobab resources regarding climate change (Cuni Sanchez et al. 2011). Beside natural fragmentation of stands in Sub-Saharan regions, overexploitation strongly threatens the species' gene pool. In consequence, conservation is urgently needed (Wickens 1982; Assogbadjo et al. 2008b; Cuni Sanchez et al. 2011). The development of management and conservation strategies requires a detailed investigation of genetic resources in the neglected populations in the Nuba Mountains, Sudan. We thus aimed to analyze genetic diversity and variation of baobab in the Nuba Mountains among locations as well as between stands and genetic clusters, combined with phenotypic observations. We further investigated the effects of human intervention on genetic resources.

4.3 Materials and Methods

4.3.1 Study sites and sampling conditions

The field study was carried out between December 2010 and January 2011 in the Nuba Mountains, South Kordofan, Sudan (Table 4.1, Figure 4.2), covering an altitudinal range from 613 to 1013 m asl. The Nuba Mountains (latitude 10°30'N to 12°30'N, longitude 29°00'E to 30°30'E) belong to the Sudano-Sahelian zone with a semi-arid climate. The average annual rainfall increases from north (500 mm) to south (800 mm), while the overall mean annual temperature is 29.9 °C with a variation from 31.0 °C in April to 24.2 °C in

January (Ismail and Elsheikh 2007). Vertisols ('cracking clay soils') are present in stretches of plains and valleys between hills and intrusive inselbergs. Along the foot hills Ustalfs are regularly found (United States Soil Taxonomy, locally called '*gardud*') predominantly consisting of heavy clays with aeolian sand. Weathered granitic-derived rocky soils dominate the higher elevated mountain ranges.

Table 4.1 Physical parameters at seven study locations of 306 baobab individuals in the Nuba Mountains, Sudan (2010). Values are the means of each location. Rainfall based on www.levoyageur.net (accessed 02 January 2013). (n) number of samples.

	n	Longitude E	Latitude N	Elevation (m)	Slope (%)	Rainfall (mm)
North	22	30° 00' 44"	11° 56' 01"	690	10	566
Northeast	26	31° 03' 03"	11° 50' 03"	875	7	711
Northwest	5	29° 35' 37"	12° 01' 12"	718	0	557
Central	70	30° 28' 25"	11° 00' 29"	783	10	714
South	30	30° 21' 31"	10° 37' 19"	500	7	752
Southeast	41	30° 58' 23"	10° 51' 09"	513	2	701
Southwest	112	29° 43' 25"	10° 59' 20"	562	10	698
Total	306	30° 15' 22"	11° 05' 44"	638	7	711

In total, 306 trees were randomly sampled from seven spatially separated locations to cover a wide range of gradients of rainfall and elevation (Table 4.1, Figure 4.2). The trees were further classified according to the distance to human settlements: 'homesteads' (less than 100 m distance from the house compounds/gardens) and 'wild' (more than 100 m distance from last compounds/gardens). We used this classification to differentiate the intensity of human intervention on baobab stands assuming strong direct impact within rather than outside the settlements. The distance was chosen based on the assumption that village sizes in this area rather decrease than increase. Although trees are sometimes growing in groups with short distances between each other, a minimum distance of 100 m between trees was generally kept for sampling following the commonly used strategy to reduce the risk of sampling closely related individuals (Gillies et al. 1999). However, close nearby trees were also sampled if tree-to-tree variation of fruit morphometry was obvious.
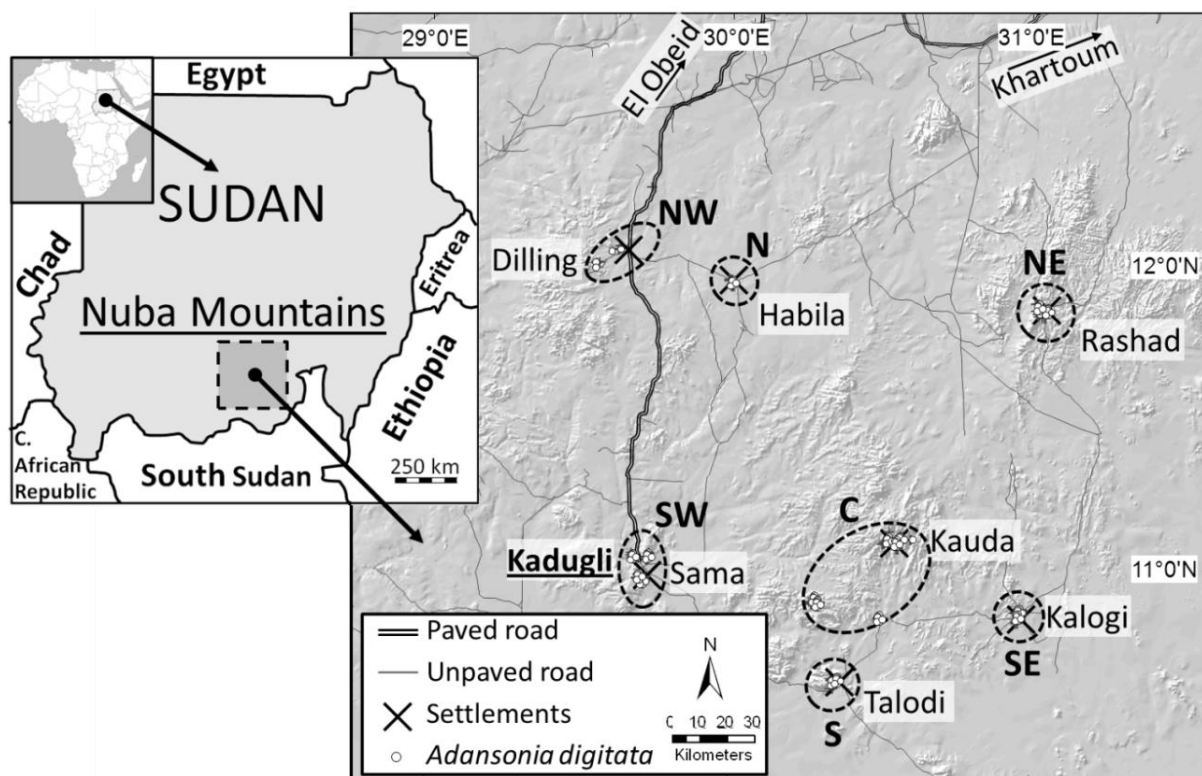
Figure 4.2 Hill-shade map displaying locations of surveyed populations of *Adansonia digitata* in the Nuba Mountains, South Kordofan, Sudan, 2010 and 2011. Kadugli city (underlined) is the administrative unit of South Kordofan province. Sources: modified after CDE (Centre for Development and Environment), University of Bern, Switzerland (2005), UTM zone 36, WGS 84; continent and country map: dmap.com.

For each tree five young and healthy leaflets were collected, air-dried in the shade and subsequently stored in plastic bags with silica gel to avoid DNA deterioration. For reference purposes and to test the extent of genetic differentiation, dried leaf material previously sampled from 26 randomly selected trees of three West African countries (Burkina Faso (n=14), Mali (n=5), Nigeria (n=7)) was included in the genetic analyses.

Geographic position (WGS 84) and elevation was determined for each individual tree using a hand-held GPS unit (eTrex Vista HCx, Garmin Ltd., Southampton UK; accuracy ± 2 m). Tree height was measured by intercept theorems (Kramer and Akca 2002). The girth at breast height (1.3 m above ground) was determined twice with a measuring tape (Wickens and Lowe 2008), and the geometric mean was arithmetically transformed to diameter at breast height (DBH). Since reliable age estimations are known to be impossible for the baobab (Johansson 1999), six successive size classes for the overall samples were created assuming lower DBH for younger trees and higher DBH for older trees (Table 4.2). This size class structure may allow to evaluate different recruitment patterns of locations and stands (Gebauer and Luedeling 2013). In addition to DBH, the number of main branches and canopy diameters were recorded. Canopy area was calculated based on the ellipse equation ($A = \pi ab$) by measuring the canopy diameter twice in north-south (a) and west-east (b)

direction. The occurrence of bark harvest was also recorded as binary code (1='harvested'/0='never harvested') to test if debarking can serve as a proxy for human impact on stands.

Table 4.2 Percentages of individuals in different DBH size classes at different sampling locations, within 'homesteads' and 'wild' stands and between genetically derived clusters of 302 baobab trees in the Nuba Mountains, Sudan (2010). The number of missing values per category is given in brackets after number of samples (n).

			DBH size classes (%)						
			1	2	3	4	5	6	
			>0-0.99 m	1.00-1.99 m	2.00-2.99 m	3.00-3.99 m	4.00-4.99 m	>4.99 m	
		n	66	82	76	51	20	7	Chi²
North	(N)	22	14	4	4	6	20	0	
Northeast	(NE)	25 (1)	11	5	11	10	5	0	
Northwest	(NW)	5	5	0	0	2	5	0	
Central	(C)	70	29	26	30	12	5	0	<0.001
South	(S)	30	3	17	11	8	5	14	
Southeast	(SE)	41	9	12	9	18	25	57	
Southwest	(SW)	109 (3)	30	37	36	45	35	29	
'Wild'		237	64	80	86	80	80	100	0.033
'Homestead'		65 (4)	36	20	14	20	20	0	
Cluster 1		185 (3)	67	57	64	53	60	86	0.448
Cluster 2		117 (1)	33	43	36	47	40	14	

One to 16 fruits (mean=5) per mature tree were directly harvested from trees or picked from the ground underneath the canopy during fruiting season. Length and girth (at the widest point of the fruit) were determined with a measurement tape, and girth was arithmetically transformed to diameter. The fruit shape ratio was calculated by dividing fruit length by diameter. Fruit production was only observed in 145 trees, and thus, fruit availability was set to 0 (not present on tree) or 1 (present on tree).

4.3.2 DNA extraction and genetic analyses

Total DNA was extracted from leaves using the DNeasy™ 96 Plant Kit (Qiagen GmbH, Hilden, Germany). Nine highly polymorphic microsatellite markers were applied originally developed for this species by Larsen et al. (2009). PCR reactions were set up in a final volume of 15 µl containing 2 ng of genomic DNA (about 10 ng), 1x reaction buffer (0.8 M Tris-HCl pH 9.0, 0.2 M $(NH_4)_2SO_4$, 0.2% w/v Tween-20; Solis BioDyne, Tartu Estonia), 2.5 mM $MgCl_2$, 0.2 mM of each dNTP, 1 unit of Taq DNA polymerase (HOT FIREPol® DNA Polymerase, Solis BioDyne), 0.3 µM of each forward and reverse primer. The forward primers of all loci were labeled with different fluorescent dyes (FAM, HEX). The PCR was performed under the following conditions: initial denaturation at 95 °C for 15 min followed by 30 cycles of 94 °C for 1 min, 58 °C for 1 min and 72 °C for 1 min and a final elongation at

72 °C for 20 min. Only the loci Ad01 and Ad14 were multiplexed in one PCR reaction, but all loci were combined in three electrophoresis sets (set 1: Ad01/14/04/08, set 2: Ad02/09/17, set 3: Ad10/12/18). Separation of microsatellite fragments was carried out in an ABI PRISM® 3100 Genetic Analyzer (Applied Biosystems, Foster City, CA, USA). Fragment sizes were determined by GeneScan™ 3.7 using the internal size standard GS 500 ROX™. Analysis and scoring of the fragments were carried out using Peak Scanner™ Software v0.1 (Applied Biosystems, Foster City, CA, USA). In addition, one polymorphic chloroplast microsatellite primer (ccmp3) was applied under similar conditions using an annealing temperature of 50 °C to test for the haplotype distribution between the samples.

4.3.3 Data analyses

The genetic and morphological variation within several groups was analyzed per region (West Africa, Nuba Mountains), per location (seven cardinal points: north (N), northeast (NE), northwest (NW), central (C), south (S), southeast (SE), and southwest (SW), per stand ('homestead'/'wild'), and corresponding to two genetic clusters found in the structure analysis (clusters 1 and 2; see below).

Two approaches were used to analyze the genetic diversity patterns in baobab due to its tetraploid nature and therefore unknown allele dosage of partial heterozygotes. The program TETRASAT (Markwith et al. 2006) was used to compute all possible allele combinations for partial heterozygotes. These combinations were used to estimate a multi-locus mean value for Hardy-Weinberg expected heterozygosity (H_E), Shannon-Weaver Diversity Indices (*H'*; Shannon and Weaver, 1949) and Nei's measure of population differentiation (G_{ST}; Nei, 1986). All calculations were based on a 100 value subset of all possible multi-locus values for each group. As a consequence of computational limits of the program, only ten randomly chosen individuals per group were included in the analysis. Thus, all analyses were repeated three to five times to enlarge the sample number per group, and mean values were calculated. In addition, co-dominant allele patterns were converted into 'allele phenotypes' and analyzed in the manner of binary markers (Becher et al. 2000; Bockelmann et al. 2003; Rodzen et al. 2004; Markwith and Parker 2007). Presence or absence of alleles was entered as (1) or (0) using the program AllelEncoder01 v1.0 (Bonow, 2009). A significant correlation of r=0.300 (*P*=0.01, Mantel-test; Mantel 1967) for both co-dominant and binary matrices was assessed with GenAlEx v6.41 (Peakall and Smouse 2006) indicating the simultaneous applicability of both approaches. The same software package was used to calculate percentages of polymorphic loci (alleles) at the 5% level ($PPL_{5\%}$), Nei's gene diversity (H_j; Nei, 1973) and number of rare and private alleles. Band richness ($Br_{[n]}$) was computed with AFLPdiv (Vekemans 2002) to estimate a standardized measure of diversity independent from sample size. Isolation-by-distance

correlations (Mantel tests) were conducted with GenAlEx v6.41 (Peakall and Smouse 2006). Analyses of molecular variance (AMOVA) were computed by ARLEQUIN v3.0 (Excoffier and Schneider 2005) to show genetic variation (F_{ST}) among groups based on 1000 permutations. A Bayesian clustering analysis was conducted with STRUCTURE v2.3.1 software (Pritchard et al. 2000) to identify genetic sub-structures within regions and locations. The algorithm was originally developed for co-dominant data. Thus, we defined the binary data as haploid data with second alleles entered as missing values (Munthali et al. 2012). We chose the admixture model with correlated allele frequencies among populations. The setting consisted of 10 replicated analyses for testing each K=1 to K=10 with a burn-in period of 10,000, followed by 50,000 Markov chain Monte Carlo iterations. The most likely number of groups was identified by STRUCTURE Harvester vA.1 (Earl and von Holdt 2012) including the *ad hoc* statistic ΔK and the corresponding mean rate of change of the ln-likelihood (ln'K) suggested by Evanno et al. (2005). The procedure was performed for both the entire data set including West Africa and the Nuba Mountains only.

SPSS® 19.0 for Windows® (SPSS Inc., Chicago, IL, USA) was used to detect dendrometric and fruit morphometric differences among groups performing non-parametric tests including Kruskal-Wallis (all variables failed the Shapiro-Wilkinson normality test) and Mann-Whitney-U tests. In case of nominal or ordinal data, Fisher's exact χ² tests were applied. Statistical results were evaluated based on a two-tailed significance level at P>0.05. Coefficients of variation (CV%) were computed for fruit length, fruit diameter and fruit shape ratio for the overall data set.

4.4 Results

4.4.1 Genetic variation among Sudan and West Africa

Bayesian cluster plots resulted from STRUCTURE analyses for both regions revealed highest ln'K and lowest standard deviation values for the most likely number of clusters at K=2 (Figure 4.3a) clearly separating all individuals in West Africa from those in the Nuba Mountains. Two distinct chloroplast haplotypes inferred from ccmp3 markers correspondingly differentiated Sudanese and West African samples, whereas no chloroplast variation was observed in each region. Genetic diversity (H_j, Br, H_E, H') was significantly higher for populations of West Africa compared to the Nuba Mountains except for the percentage of polymorphic loci (Table 4.3). Significant differences between the regions Sudan (Nuba Mountains) and West Africa were found for rare alleles with highest ones in the Nuba Mountains, while private alleles were equal zero (Table 4.3). Molecular variance obtained by AMOVA indicated 41.4% of variation between and 58.6% of variation within the two regions (P<0.001, Table 4.4).

4.4.2 Genetic diversity patterns in the Nuba Mountains

Genetic structure analyses for the seven surveyed locations based on the Bayesian approach revealed highest likelihood for two clusters (*K*=2, Figure 4.3b) differentiating the gene pool of 90% of all individuals from SW (cluster 2) and the gene pool containing 91% of individuals from the remaining six locations (cluster 1).

The location-wise *H'* ranged from 1.737 (Northwest, NW) to 2.052 (Southwest, SW) and H_E correspondingly varied between 0.586 (NW) and 0.680 (SW). H_j was also highest for SW (0.147) and lowest for NW (0.114). The correlation of H_E (tetraploid approach) and H_j (binary conversion) was significant (r=0.856, *P*<0.05) and proved the application of both analysis methods to study the population genetics of baobab. Band richness ($Br_{[5]}$) was highest in NW (1.366) and lowest in southeast (SE; 1.410). Mean $PPL_{5\%}$ was 66% (range: 41-78%) with the lowest value in NW and the highest in SW (Table 4.3). The lowest percentage of rare alleles was found in NW (0%) and the highest in the central location (C; 24%), and lowest percentages of private alleles were observed in the south location (S; 0%) and the highest ones in SW (50%, Table 4.3).
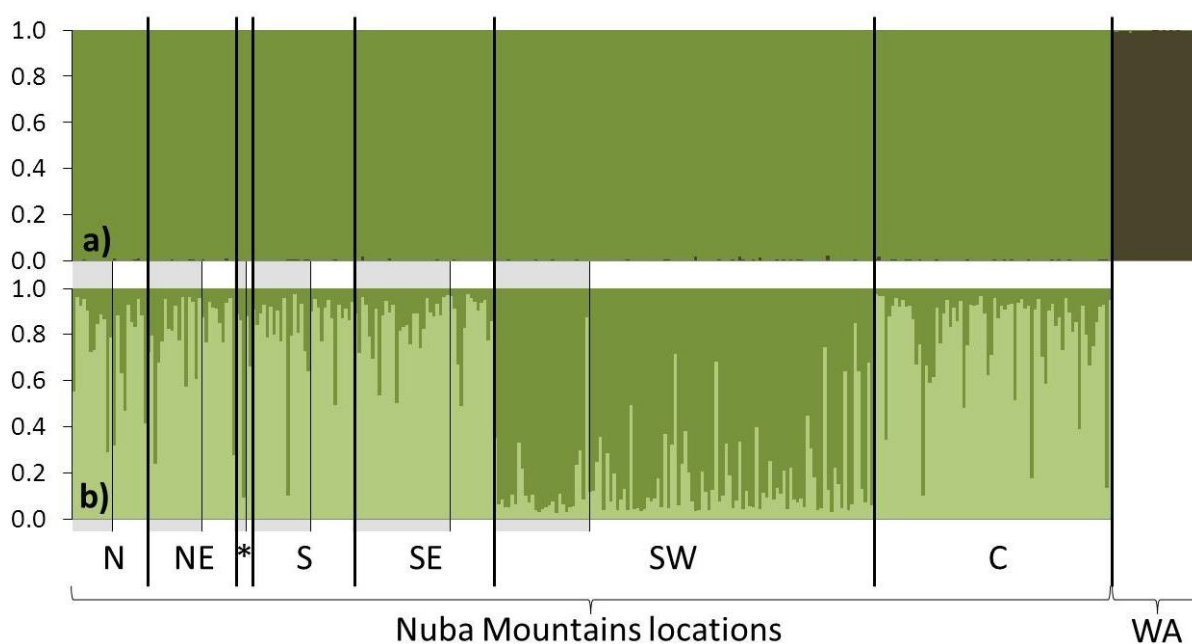
Figure 4.3a and b Bayesian cluster plots obtained with the STRUCTURE software package 2.3.1 (Pritchard et al. 2000) for a) Nuba Mountains locations and the West African region (n=332), b) only Nuba Mountains locations (n=306). Per figure the most plausible grouping of all investigated genotypes are given (both at *K*=2). Each vertical bar partitioned into two colored segments corresponding to *K*=2 refers to a particular tree and illustrates the assignment likelihood of the respective genotype to one of the two clusters. Light grey colored background blocks separated by a thin black line ion are individuals of the 'homestead' trees. Legend: N (north), NE (northeast), *NW (northwest), S (south), SE (southeast), SW (southwest), C (central), WA (West Africa).

Low differences in genetic diversity were found between 'homestead' and 'wild' stands (Table 4.3), but $PPL_{5\%}$ for rare and private alleles were slightly higher in the 'wild'

stands (*P*>0.05). Differences were found between clusters 1 and 2 with a trend towards slightly higher genetic diversity in cluster 1, but only significant for *PPL$_{5\%}$* (Table 4.3).

Location-wise analyses (AMOVA) revealed low variation among locations (7.1%), but high within-location variation (92.9%, *P*<0.001, Table 4.4). 'Homestead' and 'wild' individuals were the most similar with less than 1% between-group variation (*P*<0.001). Individuals of clusters 1 and 2 showed 7.0% between- and 93.0% within-group variation (*P*<0.001), similarly found among and within locations (Table 4.4). To test whether SW was mainly responsible for the differentiation we excluded one location each from the AMOVA analysis by performing six separate analyses. As expected, the exclusion of SW resulted in lower between-location variation (5.5%, *P*<0.001). The mean *G$_{ST}$* difference between the stands 'homestead' and 'wild' was 2.9% (Table 4.4). Although numerically different, the level of pairwise differentiation (*G$_{ST}$*) based on directly derived allele frequencies confirmed the results of the corresponding *F$_{ST}$* value for all groups (Table 4.4).

Mean *G$_{ST}$* within locations ranged from 0.025 to 0.048 (mean: 0.035, Table 4.5). The lowest value was detected between the north location (N) and C and the highest between NW and SW. *G$_{ST}$* values were correlated to geographical distances (Mantel test: r=0.443, *P*=0.01, data not shown). Mantel tests for 'homestead' and 'wild' trees separately revealed marginally higher isolation-by-distance correlations among individuals from 'homesteads' compared with 'wild' ones (r=0.405, *P*=0.04 and r=0.371, *P*=0.02, respectively).

Table 4.4 Molecular variance analyses (AMOVAs) for baobab trees grouped into different locations, stands and genetically derived clusters of Sudan, West Africa and Nuba Mountains locations.

	Source of variation	df	Sum of squares	Variance components	*F$_{ST}$* Variation (%)	*G$_{ST}$* Variation (%)
Total	Between West Africa and Sudan	1	349.29	7.08	41.4	13.5
	Within West Africa and Sudan		3309.36	10.03	58.6	86.5
Nuba Mountains	Among locations	6	222.14	0.70	7.1	3.7
	Within locations		2766.99	9.25	92.9	96.3
	Between homesteads and 'wild'	1	13.58	0.04	0.4	2.9
	Within homesteads and 'wild'		2975.55	9.79	99.6	97.1
	Between Bayesian clusters 1 and 2	1	112.63	0.71	7.0	3.2
	Within Bayesian clusters 1 and 2		2876.50	9.46	93.0	96.8

df=degree of freedom
F$_{ST}$ values were assessed with ARLEQUIN 3.0
G$_{ST}$ values were assessed with TETRASAT
Both measures were significantly different at *P*>0.001 each

Table 4.3 Genetic diversity measures for baobab stands grouped into different locations, stands and genetically derived clusters in the Nuba Mountains of Sudan and in West Africa.

	Grouping	No. of samples	Polymorphic loci at 5%-level ($PPL_{5\%}$)	Rare alleles	Private alleles	Nei's gene diversity	Band richness	Expected heterozygosity	Shannon diversity
		n	(%)			H_j	$Br_{[n]}$	H_E	H'
Total	West Africa	26	61	0	0	0.161	1.504 [26]	0.706	2.216
	Nuba Mountains	306	66	10	0	0.140	1.385 [26]	0.651	1.942
	P-value		*0.833*	*0.033*	*1.000*	*0.017*	*0.017*	*0.017*	*0.017*
Nuba Mountains	North	22	66	13	14	0.139	1.393 [5]	0.656	1.985
	Northeast	26	68	13	7	0.137	1.380 [5]	0.651	1.984
	Northwest	5	41	0	7	0.114	1.410 [5]	0.586	1.737
	Central	70	74	24	7	0.144	1.376 [5]	0.670	2.027
	South	30	62	13	0	0.145	1.376 [5]	0.668	1.952
	Southeast	41	70	14	14	0.144	1.366 [5]	0.639	1.880
	Southwest	112	78	22	50	0.147	1.392 [5]	0.680	2.052
	'Wild'	237	95	57	76	0.150	1.843 [69]	0.649	2.013
	'Homestead'	69	85	43	24	0.147	1.860 [69]	0.685	2.125
	P-value		*0.073*	*0.366*	*0.534*	*0.234*	*0.534*	*0.945*	*0.445*
	Cluster1	186	89	60	67	0.146	1.869 [120]	0.664	2.018
	Cluster2	120	79	40	33	0.148	1.790 [120]	0.653	1.998
	P-value		*0.038*	*0.318*	*0.805*	*0.073*	*0.097*	*0.836*	*0.628*

H_j (Nei's genetic diversity, $0<H_j<1$)
H_E (expected heterozygosity, $0<H_e<1$)
H' (Shannon-Wiener index $0 \leq H' \leq \ln(n)$)
$Br_{[n]}$ (band richness, $1 \leq Br \leq 2$, based on a rarefaction sample size of [n])

Table 4.5 Genetic differentiation given as pairwise G_{ST} values between locations based on 158 loci (above diagonal: pairwise geographical distances in km). The lowest and highest G_{ST} value and geographical distances within Nuba Mountains samples are marked in bold.

	Northwest	Northeast	Northwest	Central	South	Southeast	Southwest
Northwest		116	47	103	132	149	97
Northeast	0.028		163	102	139	94	168
Northwest	0.036	0.042		138	159	**190**	101
Central	**0.025**	0.035	0.041		**39**	58	83
South	0.029	0.036	0.046	0.032		72	79
Southeast	0.033	0.037	0.045	0.032	0.033		140
Southwest	0.029	0.035	**0.048**	0.033	0.034	0.037	

4.4.3 Phenotypic variation in the Nuba Mountains

Significant differences were found for tree dimensions among seven sampling areas (Table 4.6, Figure 4.1c and d). Mean DBH, tree height and canopy area was highest in SE and lowest in C (P<0.001). Number of main branches was highest in NE and lowest in C (P=0.002). In 'homesteads', DBH and proportions of larger size classes were significantly lower than in the 'wild' stands (P=0.011 and 0.033, Tables 4.2 and 4.6), and the largest size class was even absent in 'homesteads' (Figure 4.4). The population structure differed also in shape, with a 'inverse J - shaped' distribution of size classes for 'homestead', that is the highest proportion of trees found in the smallest size class, and a right skewed distribution for 'wild' trees (Figure 4.4). Tree heights and canopy areas were slightly higher in 'wild' stands than in 'homestead' stands, though none was significantly different (Table 4.6). Debarking activities did not differ between the 'homestead' and 'wild' stands (83 and 79%, respectively, P>0.05). The genetically derived clusters showed no significant differences in dendrometric traits (Table 4.6).

In total, fruits were collected from 47% of the sampled trees due to the total lack (4%) or immature status of fruits. Fruit size and shape ratio did not differ significantly between locations, stands or genetically derived clusters, but fruit shape ratio tended to be lower at the southern locations compared to the northern ones (Table 4.6). The CV for fruit length was 35.3%, for diameter 26.3% and for fruit shape ratio 33.5%. The longest individual fruit measured 37.5 cm, the widest had a diameter of 16.2 cm and a maximum fruit shape ratio of 4.9 (all measured in the SW, data not shown). The values for the trees with the highest fruit trait means for the respective variables each were 29.0 cm (SW), 12.3 cm (C) and 3.7 (S). Although differences of fruit traits between stands were low, a trend towards a higher frequency of longer fruits in 'homesteads' was observed (data not shown).
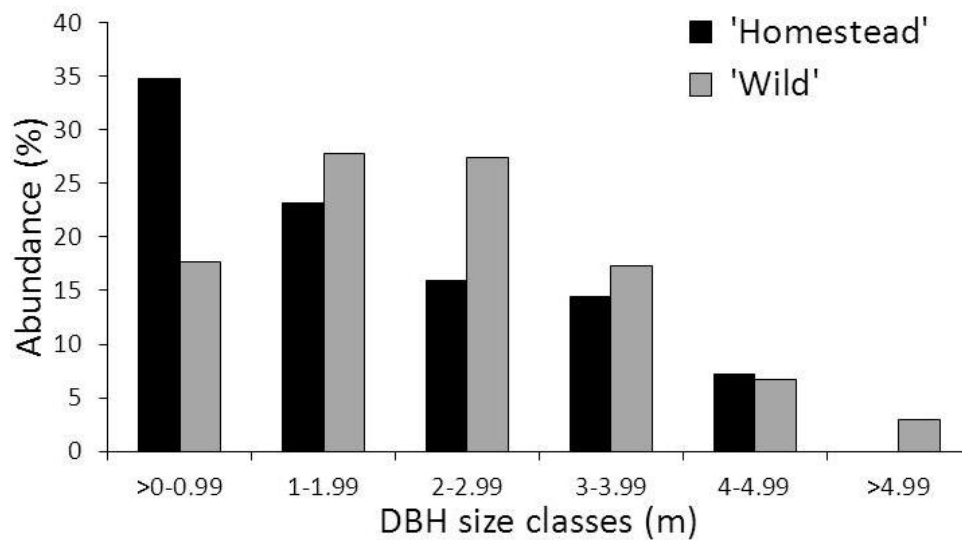
Figure 4.4 Percentage of baobab trees in the significantly different DBH size classes of 'homesteads' (n=237) and 'wild' (n=65, three missing values) stands in the Nuba Mountains, Sudan (2010).

Table 4.6 Dendrometric tree and morphometric fruit traits (mean ± standard deviation) of baobab stands in relation to sampling location, stand and genetically derived clusters in the Nuba Mountains, Sudan (2010 and 2011). The numbers of missing values are given in brackets after number of samples (n).

Groupings	n	Dendrometric characters DBH (m)	Tree height (m)	No. of main branches	Canopy area (m²)	n	Fruit morphometric characters Fruit length (cm)	Fruit diameter (cm)	Fruit shape ratio
North	22	2.07 ± 1.63 ab	10.86 ± 4.83 ab	14.18 ± 6.81 ab	203.23 ± 208.40 ab	9 (13)	16.53 ± 2.98	7.54 ± 2.39	2.38 ± 0.65
Northeast	25 (1)	1.98 ± 1.10 ab	11.32 ± 3.42 ab	16.88 ± 8.09 a	187.33 ± 131.25 ab	9 (17)	14.29 ± 4.02	6.85 ± 1.99	2.16 ± 0.57
Northwest	5	1.95 ± 1.75 ab	12.40 ± 4.04 ab	11.60 ± 5.81 ab	174.41 ± 171.95 ab	1 (4)	15.60 ± .	8.59 ± .	1.82 ± .
Central	70	1.73 ± 0.98 b	11.68 ± 3.65 b	10.69 ± 4.37 b	154.50 ± 110.84 b	28 (42)	15.21 ± 3.98	8.40 ± 1.73	1.84 ± 0.42
South	30	2.15 ± 1.05 ab	14.00 ± 3.29 ab	12.90 ± 4.71 ab	208.23 ± 120.46 ab	17 (13)	15.65 ± 4.93	8.46 ± 1.60	1.91 ± 0.76
Southeast	41	2.75 ± 1.61 ab	14.20 ± 3.95 a	14.56 ± 6.76 ab	335.00 ± 203.62 a	18 (23)	13.87 ± 3.99	7.50 ± 1.98	1.91 ± 0.53
Southwest	110 (2)	2.27 ± 1.21 a	13.10 ± 3.66 ab	11.97 ± 5.29 ab	209.76 ± 133.53 ab	63 (47)	16.11 ± 5.61	8.02 ± 1.60	2.02 ± 0.58
P-value		*0.029*	*0.002*	*0.004*	*<0.001*		*0.667*	*0.330*	*0.239*
'Wild'	237	2.25 ± 1.28	12.86 ± 3.77	12.44 ± 5.77	217.82 ± 156.03	118 (119)	15.23 ± 4.50	7.97 ± 1.84	1.96 ± 0.55
'Homestead'	66 (3)	1.81 ± 1.17	12.08 ± 4.17	13.60 ± 6.30	181.50 ± 143.49	27 (42)	16.78 ± 5.92	8.01 ± 1.45	2.11 ± 0.68
P-value		*0.011*	*0.146*	*0.233*	*0.092*		*0.361*	*0.770*	*0.361*
Cluster 1	185 (1)	2.13 ± 1.33	12.63 ± 3.94	13.20 ± 6.18	215.59 ± 163.28	80 (106)	15.16 ± 4.22	7.96 ± 1.79	1.97 ± 0.58
Cluster 2	118 (2)	2.19 ± 1.18	12.79 ± 3.76	11.88 ± 5.34	202.37 ± 138.60	65 (55)	15.95 ± 5.46	8.02 ± 1.76	2.02 ± 0.58
P-value		*0.433*	*0.803*	*0.091*	*0.806*		*0.604*	*0.872*	*0.460*
Total	**303 (3)**	**2.15 ± 1.27**	**12.69 ± 3.86**	**12.68 ± 5.89**	**210.44 ± 154.02**	**145 (161)**	**15.52 ± 4.81**	**7.98 ± 1.77**	**1.99 ± 0.58**

Small letters within columns indicate significant differences between variables. Significance level is given at *P*<0.05.

4.5 Discussion

4.5.1 Genetic variation and diversity

Genetic variation is considered as requirement of adaptation and evolution and is thus significant for the survival of plant populations (May 1994; Mace et al. 2003; Jump et al. 2009). Despite its local limitation, our study revealed a substantial amount of genetic variation in the surveyed Sudanese populations of *Adansonia digitata*. Some genetic diversity measures were reduced in the Nuba Mountains compared to the West African samples, but this finding can be explained by the geographical sampling range (Bashalkhanov et al. 2009) which was regionally limited in Sudan, but large in the three West African countries. However, higher numbers of rare alleles in the Nuba Mountains might be indications for hidden genetic resources. Unfortunately, our microsatellite results cannot be directly compared to other genetic studies of *A. digitata* mostly using an AFLP approach, and additionally a comparison to other microsatellite studies of indigenous fruit tree species may also be limited. Although successfully established markers exist (Larsen et al. 2009), data analysis of microsatellite results are challenging in *A. digitata* as a consequence of its tetraploid nature. We therefore applied two different approaches based on an artificial estimation of allele frequencies on the one hand, and a converted binary presence/absence matrix on the other hand. This combination allows for an adequate investigation of population genetics in tetraploid plant species (Markwith and Parker 2007; Sampson and Byrne 2012; Prinz et al. 2013). So far, one investigation based on microsatellite markers exists for baobab populations in Malawi (Munthali et al. 2012). Nei's genetic diversity was slightly higher in Malawian populations (0.12 to 0.18) as compared to the Sudanese locations (0.11 to 0.15), but more individuals per population were analysed in Malawi. Despite methodological limitations, a comparison of genetic variation may be complicated among populations from both the West and East African distribution ranges of *A. digitation* for several reasons. First, former populations especially in Benin are well-investigated in contrast to the neglected populations in Eastern Africa. Second, a deep differentiation was observed among the distribution ranges. Thus, almost 60% of the total variation was observed among the West African and Sudanese samples (Table 4.4; a result supported by the results of the Bayesian cluster analysis (Figure 4.3a) and the distribution of different haplotypes accordant to the distribution ranges. These findings reflect the idea of a Mega-Chad Lake existing millennia ago that may have suppressed effective long-distance gene flow between these two regions (Wickens and Lowe 2008) also indicated by the distribution of chloroplast haplotypes in a large-scale analysis (Pock Tsy et al. 2009).

Within the Nuba Mountains, genetic diversity differed among locations, especially the numbers of rare and private alleles (Table 4.3). Such alleles are considered useful for adaptation under changing environmental conditions (Allendorf and Luikart 2007), and they are thus needed to maintain the species's diversity. Shared rare alleles among locations (Table 4.3) and low genetic differentiation (G_{ST}, Tables 4.4 and 4.5) indicate efficient gene flow among the seven surveyed locations, e.g., through pollen dispersal by fruit bats, seed dispersal by monkeys and humans (Wickens and Lowe 2008). The result somehow contradicted the detected spatial genetic structure of 11 West African populations, where pollination and dispersal vectors were efficient at local scales (Kyndt et al. 2009). Efficient pollen and seed dispersal promote the adaptive potential of populations by increasing genetic diversity (Lowe et al. 2005), whereas hampered gene migration has been shown to negatively affect the fitness of a species with regard to productivity or responses to disturbances in environmental contexts (Hughes et al. 2008). In the Nuba Mountains, NW showed lowest diversity most probably due to the very low sample size. In contrast, highest values were found in SW represented by the highest number of samples. This location also captured one of the highest number of rare and the highest number private alleles (Table 4.3). Consequently, two gene pools were determined by the Bayesian analysis grouping almost all individuals from SW, and forming a second group with individuals from remaining populations (Figure 4.3b). This separation and thus the distribution of genetic variation may be explained in different ways.

Restricted gene flow among subpopulations is known to increase the genetic differentiation (Hartl and Clark 1997). In the Nuba Mountains, the often rough and impassable outcrops and hill ranges in the Nuba Mountains may form barriers for seed dispersal. However, these efficient gene flow and seed dispersal can be expected as monkeys or baboons are present in the research area, which are known to disperse baobab seeds (Wickens 1982). Apart from wild animals, humans are apparently more important vectors of baobab seed dispersal. Particularly long-distance dispersal through improved mobility and increased trade of fruits by humans will promote seed-mediated gene flow. In the Nuba Mountains, distinct gene pools may have been caused by repetitive waves of human immigration over the millennia following changes in agro-ecological conditions (Bedigian and Harlan 1983). In addition, more recent human-mediated transfer of reproductive material may have influenced the genetic diversity of baobab populations in the different locations in the Nuba Mountains. The most diverse 'southwest' area is located at the end of a paved road reaching the city of Kadugli, the administrative unit and main market – also for edible wild fruits – of South Kordofan. This road may have facilitated the exchange of plant material for marketing not only within the region, but also from far away. Nevertheless, the introduction of germplasm by the road may, if ever, hold only true for the young and mid-

aged (approximately 10-100 years) trees and remains vague for older trees. Thus, unequal extents of past admixture and introduction of seeds from areas not surveyed in this study may have led to the present appearance of two distinct gene pools in the Nuba Mountains.

In general, a weak impact of humans on genetic structure within the research area was observed as 'homestead' and 'wild' stands were only weakly differentiated. Non-significant isolation-by-distance patterns for 'homestead' and 'wild' stands of baobab also contradicted the idea of human intervention as shown for on-farm *Vitex fisheri* in Kenya (Lengkeek et al. 2006) or *Blighia sapida* in Benin (Ekué et al. 2011). However, the long life cycle of baobab trees as well as the unknown settlement history and mobility of humans in the surveyed area may have prevented for detailed interpretation. Moreover, the risk of losing genetic diversity by human intervention is considered as low since polyploidy enhances genetic diversity (Gulsen et al. 2009; Pock Tsy et al. 2009) and outcrossing is common in baobab due to pollination by fruit bats (Sidibé and Williams 2002; Kyndt et al. 2009).

4.5.2 Morphological diversity

The partly substantial differences of morphological parameters (Table 4.6) could be explained by a rainfall gradient within the research area as well as by human impact. Moreover, morphological characters, i.e., canopy area and number of main branches are often considered as indicators for the tree's vitality as well as a predictor for its wildlife habitat value(Wickens and Lowe 2008).The slightly larger dendrometric values in the southern areas of the Nuba Mountains may be due to the rainfall gradient between north and south, because growth rates of tropical trees are known to be positively influenced by higher seasonal water availability (Worbes 1999). However, we are aware that inter-site differences largely depend on plant species demography and microclimatic conditions, which should particularly be considered in the case of *A. digitata* (Assogbadjo 2008b). The differences in size class distribution with lower mean diameters in 'homesteads' (Table 4.2) can possibly be explained by the relative young age of 'homesteads' (determined by around 40 years, Wiehle et al., unpublished). Therefore, relative recent baobab tree establishment at villages is indicated by largest proportions of the smallest DBH class as well as the missing size class category >4.99 m in the 'homesteads' compared with the 'wild' stands. Our results confirm the importance of protected areas (e.g., homegardens and parklands) as survival strategy for future baobab populations (Venter and Witkowski 2013)

The mean fruit lengths recorded in the present study (13.9-16.5 cm, Table 4.6) were in the range of those found by Cuni Sanchez et al. (2011) in Mali and Malawi (15.7-22.2 and 12.9-17.6 cm, respectively) as well as reported by Munthali et al. (2012) in Malawi (11.9 to

16.5 cm). In the present study, CVs were highest for fruit shape ratio and fruit length, and thus, these traits were most informative in explaining tree-to-tree fruit variation. Our study did not indicate strong human impact as larger fruit dimensions – which are considered as first signs of pre-selection in indigenous fruit tree species (Atangana et al. 2002; Leakey et al. 2004; Parker et al. 2010); Wiehle et al., unpublished), though a numerically higher frequency of longer fruits was present in 'homesteads' as hypothesized by Leakey et al. (2004) for domesticated species.

The total absence of fruits in some trees (4.1%) may be caused by early harvest of the fruit prior to our sampling. However, it is also possible that these trees did not fruit during the surveyed season as similarly observed of very closely spaced trees in our study (Figure 4.1e) suggesting genetic aspects that may have affected fruit production. Ecotypes of baobab, locally known as 'female' (fruit production) or 'male' (absence of fruit production) are distinguished due to their different fruiting behaviour as for instance recognized by local communities in South Africa (Venter 2012). According to Assogbadjo et al. (2008b) the absence of fruit production in the 'male' ecotypes might be explained by incompatibility at the tree level. Another explanation might be alternate fruiting that is known to occur in many perennial species (Newbery et al. 2006), and which is claimed to be caused by temporal patterns and environmental gradients (Okullo et al. 2004). The same authors also observed differences in fruiting and shedding of leaves of *Vitellaria paradoxa* trees and related them to the effects of variable rainfall patterns.

We used CV values to evaluate the impact of genetic or environmental factors on morphometric fruit traits. Kimmins (1987) allocated values between 14 and 19% to genetic control and 40 to 45% to environmental control. Since CV values in our study ranged from 26-36%, both genetic and environmental determinants may have affected fruit morphometry in the studied baobabs. This results is supported by Assogbadjo et al. (2005) and Cuni Sanchez et al. (2011), though Assogbadjo et al. (2011) suggested a strong maternal heritability of baobab fruit characteristics in Benin. However, our approach to extract genetic or environmental factors has also certain limitations. First, fruits were sometimes collected from the ground below the canopy area for measurement with the risk that these fruits may have been moved from other trees by humans or animals. Second, the often low number of fruits collected per tree may have affected tree-to-tree variation. Additional sampling and monitoring of baobab populations in the Nuba Mountains involving more locations and individuals would broaden our understanding of the mechanisms that effect morphological and genetic diversity in baobab as well as to find potentially more gene pools with certain adaptive alleles.

4.6 Conclusions

Our study revealed a promising pool of genetic resources of *Adansonia digitata* at a local scale in the northernmost distribution range of the species in East Africa. Although geographically limited, observed genetic and morphological variation indicated a vital network of populations. Since the Nuba Mountains area is highly influenced by humans who have been settled there since hundreds of years and baobab is generally considered to be supported rather than restricted by human intervention, a further source of variation in the selected study sites was assumed. Unfortunately, only few genetic studies still exist for baobab and morphological investigation is restricted preventing us from detailed comparison of different scales of human intervention. As a consequence of its impressive character and multipurpose function*, A. digitata* is regarded as a valuable key species for '*circa situm* reservoirs of biodiversity' particularly in the diverse and sustainable agroforestry systems such as homegardens and parklands. The development of region-specific, sustainable tree management strategies as part of *circa situm* conservation approaches for baobab would contribute to maintaining the genetic resources of this important species in the Nuba Mountains.

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Chapter 5 – General discussion

5.1 Contribution of the present work

Work on plant diversity of small-scale agro-ecosystems and subsistence farming in Sudan is negligible. The keywords 'diversity', 'garden', 'plant' and 'Sudan' searched in the ISI Web of Science database (accessed 22 May 2013) revealed a total of three publications dealing with this topic: Gebauer (2005), Goenster et al. (2011) and Thompson et al. (2010). It can be argued that a lack of research on biodiversity and productivity of traditional small-scale agro-ecosystems indicates Sudan's focus on rather large-scale mono-culture food production. With respect to an increasing population that still depends on subsistence farming on the one hand, the country's cash earnings by large-scale monoculturally produced agricultural products on the other hand (Mahmoud et al. 1996) as well as economic and political instability, Sudanese agriculture is based on steady ground. Research in semi-arid regions in general seems to be omitted since most research has been conducted in plant and animal diverse humid-tropical regions, e.g., Dash and Misra (2001), Puri and Nair (2004); Kehlenbeck et al. (2007), Thomas and Van Damme (2010). This study hence fills knowledge gaps that prevailed for HG systems in semi-arid regions and provides useful information about the status quo and possible drivers of inter- and intra-specific plant diversity in case of Sudanese *jubraka* HG systems. These data could be used to develop suitable and regionally adjusted strategies to maintain food security in the unique *jubraka* HG systems of the Nuba Mountains, Kordofan, Sudan as well as in similarly constituted HGs of semi-arid regions.

5.2 Evaluation of hypothesis 1

Species richness and diversity, share of perennials and vegetation stratification in jubrakas decrease with increasing market access and commercialization.

Time-demanding counting of plant individuals and determination of species in HG systems is a very cost-effective tool to get an in-depth insight into inter-specific diversity as done by e.g. Abdoellah et al. (2006), Kehlenbeck et al. (2007) and Bernholt et al. (2009) or partially by focusing on perennial tree species (Agea et al. 2007; Fentahun and Hager 2009). In some cases of the present study, the numbers of recorded individuals may have been slightly over- as well as underestimated. This could be true for large-scale *jubraka*s (particularly in Kauda) and vegetable beds (mostly commercial HGs), since orientation and counting within dense and/or high (> 1.5 m) crop vegetation became occasionally difficult. Over- or under-estimation logically results in higher or lower abundances, which might in turn affect species diversity and similarity distance measures as the applied squared Euclidean distance and thus the outcome of assigned cluster groups.

Another important factor of diversity estimation and the possibility to compare the data with other studies is the census number of sample units (Gotelli and Colwell 2001). To avoid biased species estimations due to different census numbers, species accumulation curves (based on rarefaction procedures) were calculated to assess the potential species richness in a certain area (Colwell 2011). In the present study, most species accumulation curves approximated or reached saturation as indicated by a slight increase or stagnation of slopes. Taking into account the short time between growth and harvest of crops (May/June-September/October), where determination of plants in their vegetative states was possible or the former presence of already harvested crops was still traceable (e.g., sorghum stubbles or ladyfinger trunks), the census number of 61 HGs in four villages appeared to be appropriate to obtain first insights into the *jubraka*'s plant diversity. The groups of ornamental and IFT species, however, indicated insufficient sampling sizes due to still rising species accumulation curves. Group-specific reactions of internally assigned plant categories that are based on biological characteristics or use groups (such as: annuals/perennials, IFTs, ornamentals, etc.) should therefore be considered in all plant richness based studies separately.

In contrast to studies that indicated a reduction of species richness and diversity in commercialized agroforestry systems, the present study indicated a slightly higher diversity in market-oriented *jubraka*s (chapter 2). However, the separation into two types of HG managements (HGs selling produce at the farm gate and HGs without outside sales) needs to be critically examined. In Indonesia for instance (Abdoellah et al. 2006), HG were assigned as commercial when more than 50% of the produce was sold at farm gate, which gives likely a better approximation and resolution of plant compositional differences. In our study, however, the proportion of sales was a quiet obscure criterion, since the share of sold products could often not be estimated by the respondents.

To examine the unique and complex nature of human-environmental linkages in given agro-ecosystems, richness and diversity measures were combined with socio-economic and bio-physical data. Cluster analyses for instance seem to be much more informative to extract hidden constitutions of homogeneous garden and household features in comparison to multivariate techniques such as multiple regression analyses (Petraitis et al. 1996). While frequently applied for socio-economic data e.g., Mendez et al. (2001), Dossa et al. (2011) and Riedel et al. (2012) or in molecular genetic contexts e.g., Aradhya et al. (2010), Arango-Ulloa (2009) and Mwase (2010), cluster analyses based on on-farm plant species abundance are rarely used to extract underlying socio-economic and bio-physical characteristics of respective households and HGs (Peyre et al. 2006; Kehlenbeck 2007; Chandrashekara 2009). In the present study, key factors that were reported to affect plant species richness and diversity were location, level of commercialization, household poverty

indices as well as the soil parameter pH. Increased market-access and concomitant shifts towards a commercialization of production in peri-urban and rural areas has been generally indexed as one of the main factors changing plant species richness and diversity even within short times (Abdoellah et al. 2006; Kehlenbeck et al. 2007; Mercerat et al. 2012). However, not only richness and diversity, but also productivity and hence capability to sell produce at farm gate seems to largely fluctuate within years. This was confirmed in the project area of Sama between two consecutive years were farmers practiced non-commercial subsistence farming in 2009 but were selling produce at the farm gate in the following year (unpublished data). Thus, future evolution of plant species composition can hardly be predicted from this short-term study. Bearing in mind that present factors might be artifacts and rather represent indirect effects of other more powerful factors that have not been recorded in the field or considered during analysis, a final and conclusive statement remains difficult. Although not considered in the present study, strong seasonal rainfall fluctuations between the two surveyed years (2009 and 2010) could lead to higher plant species richness and production as similarly suggested for HGs in Costa Rica (Zaldivar et al. 2002). In the Nuba Mountains, the total rainfall amounted to 535 mm in 2009, while in 2010 a precipitation of 768 mm (31% increase) was recorded (Goenster 2013, unpublished). Ayoub (1999) reported significant positive relationships between rainfall and crop production in Kordofan strengthening the assumption of high seasonality of HG production resulting in different surpluses. Thus, market-orientation (i.e. cash crop cultivation of for instance *Ercua sativa* and *Raphanus sativus*) is likely governed by short-term decisions of farmers as well as water availability, including the proximity to water pumps. These factors might have influenced the number of farmers involved in commercialization which was found to be generally low. To counteract crop failures due to high rainfall fluctuations and increase productivity, Terry and Ryder (2007) recommended additional irrigation on tenure land in semi-arid regions of Swaziland with similar climatic conditions as found in Sudan. However, such practices require water harvesting techniques, which are rarely present in the study area.

With regard to the many advantages of homegardens such as soil protection, improved nutrient availability, stabilized micro-climates, food security provided by agroforestry farming systems and the large structural and functional differences, there is still potential towards improvement and diversification of this *jubraka* HG system in the Nuba Mountains. Various authors stated management approaches that can positively improve HG performance and food security for instance by vegetable production (Obeidalla and Riley 1983) and IFT promotion (Gebauer et al. 2002; Muneer 2008) in Sudan. These approaches comprise improved cultivars, appropriate cultural practices, necessary agricultural inputs, credit, more efficient irrigation methods and access to tree seedling nurseries, as well as monitoring, selection, breeding and conservation of germplasm of priority species and the

level of formal gardener's education, contact of households with extension agents, the level of environmental awareness, farmers's cosmopoliteness, the total area of owned land and the extent of social participation such as market access and exchange of plant material within and among communities. Gardeners should therefore take advantage of mentioned management approaches. A careful planning and actively managed HGs are needed to accommodate the complex nature of this agroecosystem and its traditional practices. This will support on-farm conservation strategies and to maintain and improve diverse HG characteristics.

5.3 Evaluation of hypothesis 2

Human-induced domestication processes in the two indigenous fruit tree species *Z. spina-christi* and *A. digitata* lead to larger fruit traits and a reduction of genetic diversity.

To our knowledge, no single IFT species of Sudan was investigated in depth with combined morphological and genetic approaches. The present study provided first comprehensive information of morphometric fruit traits and genetic measures in *Ziziphus spina-christi* and *Adansonia digitata* in the Nuba Mountains and might therefore give initial attempts to the field of hard data IFT monitoring and research.

Morphological and genetic diversity measures for the selected key species *Z. spina-christi* and *A. digitata* were highly variable indicating high potentials for future domestication. However, the reasons for this high variability among individuals and locations of morphometric fruit traits and genetic diversity could not be finally explained.

Fruits sampled from HG trees tended to be slightly larger supporting the idea of human-mediated selection of fruits as similarly revealed for African IFT species such as *Blighia sapida* (Ekué et al. 2011), *Dacryodis edulis* and *Irvingia abonensis* (Leakey et al. 2004). In contrast to *Z. spina-christi*, differences in fruit dimension of *A. digitata* between sites (HG and wild) were less different and even negligibly small. Effects of semi-domestication through human intervention on fruit morphology of baobabs as assumed by Sidibe and Williams (2002) and Pock Tsy et al. (2009) could therefore not be confirmed. For *Z. spina-christi*, differences were more pronounced, but also not significant. To identify factors having an impact on species performance and appearance in order to obtain comprehensive information about phenotypic processes is known to be general difficult for species grown naturally (Mwase et al. 2010; Parker et al. 2010). The kind of sampling strategy such as sample size and coverage of the area are furthermore important to represent the status of entire population (Gotelli and Colwell 2001). In addition, the long lifespan of trees with extended times of growth and maturity is contributing to a delayed response to human activity (Parker et al. 2010). Thus, unknown historical germplasm pathways, diverse responses on natural factors such as soil chemical parameters or insect infestations,

people's preferences and farmers' decisions to cultivate and use plants in agro-ecosystems lead to high morphometric fruit plasticity (Sultan 2000; Asaah et al. 2011).

Such uncertainties can be reduced by applying genetic markers on extracted DNA from vegetative plant tissues to allow for an analysis of genetic diversity and domestication effects by human intervention (Finkeldey and Hattemer 2007). The so gained information is relatively unbiased and independent from environmental influences. The choice of the most suitable marker techniques in the present study was based on the availability of markers for each species. While both, AFLP and SSR markers were already used for *A. digitata* (Assogbadjo et al. 2006; Larsen et al. 2009; Munthali et al. 2012), only related species of the *Ziziphus* genus were investigated with both marker systems (Singh et al. 2009; Gitzendanner et al. 2012). A pre-test with SSR markers originally developed for *Ziziphus celata* (Gitzendanner et al. 2012) resulted in low levels of polymorphism. This fact simplified the decision in favor of AFLPs for *Z. spina-christi*, a molecular marker technique where no prior knowledge of the plant's genome is needed.

The genetic diversity measures applied in this study were in the range of other African IFTs such as *Sclerocarya birrea* in South Africa (Moganedi et al. 2011), *Blighia sapida* in Benin (Ekué et al. 2011) and *Vitex fischeri* in Kenya (Lengkeek et al. 2006). The assumed process of domestication on genetic diversity revealed opposite results in the two species. *Z. spina-christi* exhibited slightly higher diversity on-farm, while *A. digitata* showed slightly higher diversity in the forest populations. The latter case is consistent with the observed, but small losses of diversity under human influence as frequently found in tropical tree species such as *Blighia sapida* (Ekué et al. 2011), *Spondias purpurea* (Miller and Schaal 2006), *Ziziphus* accessions of *Z. mauritania* and *Z. nummularia* (Singh et al. 2009) and *Vitellaria paradoxa* (Kelly et al. 2004). Increased diversity in on-farm stands found for *Z. spina-christi* has however rarely been reported. To our knowledge it was once reported on *Araucaria angustifolia* plantations in Brazil (Stefenon et al. 2008) and explained with the transplantation of wild *A. angustifolia* individuals from different regions into plantations, which may have resulted in higher diversity on-farm compared with single wild stands.

Based on the results of the investigated IFT species, two aspects need to be considered to explain the found differences:

The type of germplasm mediation in nature and cultivation practice by humans

The type of sampling strategy used in the present study

With respect to point 1, differences in genetic constitution are likely to appear through different seed and pollen mediating vectors as suggested for *Prunus africana* in western Kenya (Berens et al. 2013). The extent and impact of different species on seed dispersal efficiency thereby depends on the mediating species itself as found for seed dispersal of the fig tree species *Ficus cyrtophylla* in China (Zhou and Chen 2010). Pollen dispersal in both

cross-pollinated species is likely to be of similar long-distance nature since *Z. spina-christi* is insect pollinated and *A. digitata* predominantly fruit bat pollinated (Sidibe and Williams 2002). On the other hand, short-distance dispersal of seeds in the *Ziziphus* genus is reported to occur through lizards, birds and livestock species such as cows and goats (Miehe 1986; Varela and Bucher 2002; Varela and Bucher 2006). A similarly number of taxa is known or suggested to disperse seeds of baobab, cf. Wickens (1982) and Sidibe and Williams (2002). Although no information is available for the Nuba Mountains, primate species likely play a role for long distance dispersal in both *Z. spina-christi* (Zhang and Wang 1995) and *A. digitata* (Wickens 1982; Sidibe and Williams 2002). The direction and intensity of human-mediated transports of reproductive plant material on the other is likely higher due to improved infrastructure and increased people's mobility (Assogbadjo et al. 2008a; Parker et al. 2010).

With respect to point 2, we could not apply the same sampling design with balanced numbers of trees and almost same distances between locations and sites for *A. digitata* as done for *Z. spina-christi* because:

In the Nuba Mountains, baobabs were not spatially and attitudinally as equally distributed as *Z. spina-christi*. The lowlands that were partially covered by scattered forests (regarded as 'wild') with flood resistant tree species such as *Acacia* spp., *Balanites aegyptiaca* and *Z. spina-christi*) did normally not harbor baobab individuals, since this tree species generally prefers well drained soils (Wickens 1982; Wilson 1988). Instead, baobab was largely found on rocky terrains.

A. digitata was less frequently found in HGs of the Nuba Mountains than *Z. spina-christi* (Wiehle et al., in press)

Distances within groups of *A. digitata* trees were often smaller than 100 m, which is considered as the minimum distance in sampling trees for genetic analyses (Dawson and Jamnadass 2008).

It is often difficult to assign a tree as 'wild', since many baobabs show signs of past human settlement in their vicinity. This fact has already been raised by (Wickens 1982) questioning whether humans follow baobabs or *vice versa*.

Aside of a sophisticated sampling design, addressed hypotheses and used laboratory techniques, also the census number ('effective population size') and the pairwise spatial distance influence genetic diversity estimations in tree species (Dawson and Jamnadass 2008; Farwig et al. 2008). Thus, more samples per location and extended sampling within the Nuba Mountains and beyond could further enlighten the genetic diversity and structure in both surveyed species, particularly for *A. digitata* since some locations were sampled insufficiently. This may help to extract the drivers of morphological variation and factors responsible for separation into genetically different pools as found for both species.

For both investigated IFT species, however, only mild genetic differences, but continuously lower diversity in the wild (*Z. spina-christi*) or on-farm (*A. digitata*) were observed. Since local agro-pastroalists have been probably collecting and selecting both fruits for millennia, both species are likely subjected to initial steps of domestication. However, low selection pressure due to the still large abundance of trees in the wild as well as absence of vegetative propagation techniques for both IFT species may have prevented genetic narrowing and constitutional shifts. Participatory approaches and scientific guidance would be beneficial to gain further knowledge about the ecology, physiology and ethnobotany of both species as suggested by (Simons and Leakey 2004). Such approaches have been intended for instance by (Akinnifesi et al. 2004; Schreckenberg et al. 2006; Akinnifesi et al. 2007) to guarantee high quality germplasm materials and to prevent over-exploitation in the wild. However, results from these research projects are still lacking indicating the difficulties and long-term efforts of wild fruit tree research.

5.4 Concluding recommendations

- Extended surveys in other villages of the Nuba Mountains would improve the understanding of factors affecting plant richness and diversity.

- Careful selection, promotion, supply and awareness rising of indigenous crop and tree species which are well adapted to the environmental conditions may be beneficial to strengthen livelihood strategies of local communities.

- Decentralized extension services are needed to implement improved management strategies and germplasm material particularly for families with recent migration histories and small *jubraka* gardens.

- Comparatively high intra-specific plant and intra-specific diversity and strong spatial genetic differentiation of *Z. spina-christi* and *A. digitata* indicated promising grounds for future on-farm or *in situ* conservation, breeding, and domestication strategies.

- Low genetic differentiation between human managed and natural ecosystems in *Z. spina-christi* and *A. digitata* indicated on-going gene flows among populations without losing genetic diversity in one or another habitat

- *Z. spina-christi* and *A. digitata* were among the three most abundant IFTs found in the *jubraka*s as well as in the wild of the Nuba Mountains. Nevertheless, over-exploitation of fruits may bear the risk of reduced natural regeneration if market demand increases for the products.

- Since the heritability and environmental effects on fruit traits in both species is unknown, trials under standardized conditions are recommended to study progeny performance from different locations and management sites.

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Conferrence contributions

Talk

2012	**Wiehle, M.**, Prinz, K., Kehlenbeck, K., Goenster, S., Mohamed, S. A., Finkeldey, R., Buerkert, A., Gebauer, J.	Homegardens in Sudan – domestication spots for wild fruit trees: The case of *Ziziphus spina-christi* (L.) Willd.
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Poster

2014	**Wiehle, M.**, Goenster, S., Gebauer, J., Mohamed, S. A., Buerkert, A., Kehlenbeck, K.	Woody-plant species richness and diversity in homegardens of the Nuba Mountains, Sudan
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2013	**Wiehle, M.**, Prinz, K., Kehlenbeck, K., Goenster, S., Mohamed, S. A., Finkeldey, R., Buerkert, A., Gebauer, J.	Baobab (*Adansonia digitata* L.) - Morphological and genetic diversity of a neglected population in the Nuba Mountains, Sudan
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2011	**Wiehle, M.**, Goenster, S., Kehlenbeck, K., Gebauer, J., Mohamed, S. A., Buerkert, A.	Socio-economic factors and garden size affect plant species richness and diversity of homegardens of the Nuba Mountains, Sudan
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2010	**Wiehle, M.**, Goenster, S., Kehlenbeck, K., Gebauer, J., Buerkert, A.	Diversity determinants of indigenous fruit trees in homegardens of the Nuba Mountains, Central Sudan
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