Production, local trade and diversity of avocado (*Persea americana* Mill.) in the southern highlands of Tanzania

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Cover: Variation in fruit shape in Tanzanian avocado which is one of the morphological traits used to study the diversity of the germplasm.
(Photo: Ibrahim Juma)

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Abstract

Avocado (*Persea americana* Mill) has a long cultivation history in Tanzania and adds to the country's revenue through trading within (local and commercial avocado cultivars) and outside (commercial cultivars) the country. Research has been, however, scanty to characterize the country's avocado production, local trading and diversity. In order to contribute to this research area, the present study was conducted in eight districts of Tanzania's southern highlands. For the purpose of describing aspects of avocado production and trading throughout the value chain, 275 avocado growers, 231 traders and 16 key informers were interviewed. As for the diversity study, 226 seed-originated avocado trees were sampled in the eight districts and 14 morphological and 10 simple sequence repeat (SSR) loci genetic characters were evaluated. The analyses of the data generated through the interviews showed that the average avocado yield per district varied from 52 to 156 kg/plant. Approximately, 28 and 79% of the growers and the traders were content with the earnings from the avocado trading. The majority of the growers and traders mentioned some challenges affecting the value chain including limited extension services, drought, pathogens and pests, poor marketing environment, and the short shelf life of the fruits. Resolving these issues is the key towards the improvement of the earnings and living standards of avocado farmers and traders, which is also applicable to many other crops sharing similar challenges. The sampled trees showed great variation in the investigated morphological features. These included 11, 21 and 17 different shapes of the leaf, mature fruit and seed, respectively. As for the genetic characteristics, an average of 16.7 ± 1.3 alleles per locus, 0.65 ± 0.04 and 0.84 ± 0.02 observed and expected heterozygosity, respectively, and a Shannon's information index of 2.17 ± 0.10 were obtained. These results imply a high genetic diversity of the trees investigated. Most of the observed morphological and genetic characters were not unique for a particular area as revealed by the district/region-free clustering of the trees in the principal coordinates and components analyses or by dendrograms. Introduction of highly similar (overlapping) germplasm to more than one districts and cross-transfer of seeds (propagules) among the districts/regions could be the reason for this distribution.

Keywords: crop improvement, crop yield, dendrogram, morphological traits, principal components analysis, principal coordinates analysis, SSR loci, value chain

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Produktion, lokal handel och diversitet för avokado (*Persea americana* Mill.) från Tanzanias södra högländer

Sammanfattning

Avokado (*Persea americana* Mill) har en lång odlingshistoria i Tanzania och bidrar till landets intäkter genom handel inom (lokala och kommersiella sorter) och utanför (kommersiella sorter) landet. Få studier har dock genomförts vad gäller landets avokadoproduktion, den lokala handeln och diversiteten inom växtmaterialet. För att bidra med kunskap inom forskningsområdet genomfördes denna studie i åtta distrikt i Tanzanias södra högländer. I syfte att beskriva olika aspekter av avokadoproduktion och handel genom värdekedjan, intervjuades 275 avokadoodlare, 231 handlare och 16 viktiga nyckelpersoner. Vad beträffar diversitetsstudien analyserades 226 fröförökade avokadoträd i de åtta distrikten och 14 morfologiska egenskaper och 10 SSR-lokus utvärderades. Analyser av de svar som inhämtades visade att odlarna i genomsnitt producerade 52 till 156 kg per träd, vilket dock varierade mellan distrikten. Cirka 28 och 79% av odlarna respektive handlarna var nöjda med inkomsterna från avokadohandeln. En majoritet av odlarna och handlarna nämnde utmaningar som på olika sätt påverkar värdekedjan. Dessa utmaningar inkluderade begränsad rådgivningsservice, torka, sjukdomar/skadedjur, dålig marknadsföring och fruktens korta hållbarhet. Att lösa dessa utmaningar är nyckeln till ökade intäkter och förbättrade levnadsförhållande för jordbrukare och handlare av avokado men är viktigt också när det gäller andra grödor med liknande utmaningar. De analyserade träden visade stor morfologisk variation i 11, 21 och 17 olika former av blad, mogen frukt respektive frö. När det gäller den genetiska variationen erhölls ett genomsnitt på 16,7 ± 1,3 alleler per lokus, 0,65 ± 0,04 och 0,84 ± 0,02 vad gäller observerad respektive förväntad heterozygositet, samt ett Shannons informationsindex på 2,17 ± 0,10. Dessa resultat pekar på en stor variation inom det analyserade växtmaterialet. De flesta av de studerade morfologiska och genetiska egenskaperna var inte unika för ett specifikt område, vilket tydligt framgick av principal coordinates och components analyser och i dendrogram. Detta kan förklaras av en introduktion av mycket likartat (över-lappande) genmaterial till mer än ett distrikt och vid utbyte av frön mellan distrikt/regioner.

Dedication

To Hudhayfah, Hunayfah and Hunaydah, my lovely kids.

"Disability need not be an obstacle to success"

Stephen Hawking

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Juma I*, Fors H, Hovmalm HP, Nyomora A, Fatih M, Geleta M, Carlsson AS, Ortiz R (2019). Avocado production and local trade in the southern highlands of Tanzania: A case of an emerging trade commodity from horticulture. *Agronomy*, 9, 749. Doi: 10.3390/agronomy9110749.

II Juma I*, Nyomora A, Hovmalm HP, Fatih M, Geleta M, Carlsson AS, Ortiz R (2020). Characterization of Tanzanian avocado using morphological traits. *Diversity*, 12, 64. Doi: 10.3390/d12020064.

III Juma I, Geleta M, Nyomora A, Saripella GV, Hovmalm HP, Carlsson AS, Fatih M, Ortiz R. Genetic diversity of avocado from the southern highlands of Tanzania as revealed by microsatellite markers. Manuscript

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The contribution of Ibrahim Juma to the papers included in this thesis was as follows:

I. Planned the study with co-authors. Collected data together with the fourth co-author. Evaluated the data under the guidance of the sixth and eighth co-author. Produced the first draft and wrote the manuscript with co-authors.

II. Planned the study with co-authors. Collected data together with third co-author. Evaluated the data under the guidance of the fifth and seventh co-author. Produced the first draft and wrote the manuscript with co-authors.

III. Planned the study with co-authors. Designed the experiment together with the second co-author. Collected data. Evaluated the data under the guidance of the second and fourth co-author. Produced the first draft and wrote the manuscript with co-authors.

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Abbreviations

AFLP	Amplified Fragment Length Polymorphism
AMOVA	Analysis of Molecular Variance
ANOVA	Analysis of Variance
DNA	Deoxyribonucleic Acid
GPS	Geographic Positioning System
masl	Metre above sea level
PCA	Principal Components Analysis
PCoA	Principal Coordinates Analysis
PCR	Polymerase Chain Reaction
RAPD	Random Amplified Polymorphic DNA
SNP	Single-Nucleotide Polymorphism
SSR	Simple Sequence Repeat
Taq	*Thermus aquaticus*
UPGMA	Unweighted Pair Group Method with Arithmetic Mean
US$	United States Dollar

1 Introduction

1.1 Taxonomy, origin and domestication of avocado

Avocado (*Persea americana* Mill) is an evergreen tree species in the Lauraceae family that produces highly nutritious and commercially valuable fruits (Morton, 1987; Radha and Mathew, 2007; Paz-Vega, 2015). Based on the Integrated Taxonomic Information System (2020), the avocado is hierarchically classified as:

Kingdom: Plantae
Super division: Embryophyta
Division: Tracheophyta
Subdivision: Spermatophytina
Class: Magnoliopsida
Superorder: Magnolianae
Order: Laurales
Family: Lauraceae
Genus: *Persea* Mill
Species: *Persea americana* Mill

Based on the evidences collected from analyses of isozymes, leaf terpenes, morphology, physiology and field observations, the genus *Persea* probably originated in the western African Gondwanaland flora (Scora and Bergh, 1990; 1992). The ancestral species of this genus then migrated to Asia, North America through Europe, and South America through Africa, probably during Paleocene time. When the North and South America linked in the late Neogene, the genus *Persea* united again. Mountain building in Central America formed new habitats where speciation might have occurred. In these habitats *Persea americana* evolved from its progenitors (Scora and Bergh, 1992). Among the recognized species in this genus are *P. americana, P. guatemalensis, P. drymifolia, P.*

nubigena, P. steyermarkii and *P. floccosa* (Scora and Bergh, 1992). In Asia, about 80 species of *Persea* exist today (Scora and Bergh, 1992). The genus died out in Africa, except for *P. indica* which survives on the Canary Islands, due to an increasingly dry climate starting with the development of the Benguela Current and the glaciation on Antarctica in the early Miocene (Scora and Bergh, 1992; Valley et al., 1999).

P. americana has three botanical varieties, namely, the Mexican, Guatemalan, and West Indian. The three taxa are also referred to as horticultural races. Avocado was domesticated in Mesoamerica where archaeological records in the Tehuacán region (Puebla State, Mexico) showed that man consumed avocado about 10,000 years ago (Smith, 1966). This fruit tree was cultivated and domesticated by the *Mokayas*, the first Mesoamerican culture, who passed the knowledge to the next cultures including the *Mayas* and *Olmecs* (Galindo-Tovar et al., 2007). The larger seeds in the latest archaeological strata at the Tehuacán (Puebla State, Mexico) and Oaxaca Valley (Oaxaca State, Mexico) sites propose that avocado selection may have started about 4,800 to 6,000 years ago (Smith, 1966, 1969). The avocado name appears in the proto-Maya languages about 4,000 years ago as 'on' (Fox and Justeson, 1980). The tree was named differently in different Mayan languages. These include 'uj' (the Huasteco language), 'on' (the Maya Maya or Peten, Tzental, Tzontzil and Chanabal languages) and 'un' (the Chontal and Tzontzil languages). Others are 'um' (Choi), 'o' (Quekchi) and 'oj' (Pokomchi, Pokoman, Cakchiquel, Quiche, Uspanteca and Aguacatecaon) (Stoll, 1884; Berlin et al., 1973). This suggests that these indigenous people consumed avocado for a substantial length of time (Gama-Campillo and Gomez-Pompa, 1992).

The cultivated avocado's wild ancestor was a polymorphic tree species that grew in Mexico's eastern and central highlands, Guatemala and the Central America's Pacific coast (Smith, 1966). Neolithic people selected primitive domesticated progenies from these populations, gradually replacing the wild *P. americana* ancestor by the three well-distinguished avocado ecotypes recognised by their presumed centres of origin, namely, the Guatemalan, Mexican and West Indian horticultural races (Bergh and Ellstrand, 1986). These three races were previously identified as *Persea americana* var. *guatemalensis* Williams (the Guatemalan), *P. americana* var. *drymifolia* Blake (the Mexican) and *P. americana* var. *americana* Mill (the West Indian) (Bergh and Ellstrand, 1986). As recent evidence shows that the West Indian race evolved on the west coast of Central America (Coastal Guatemala), it has been called the lowland variety, to reflect both the western and eastern sides of the mountain range (Scora and Bergh, 1992; Scora et al., 2002). Ethnobotanical data

(Williams, 1976, Storey et al., 1986) and different DNA marker analyses, such as restriction fragment length polymorphism (RFLP) of avocado chloroplast genome, nuclear ribosomal DNA and the cellulose-coding genes (Furnier et al., 1990) and microsatellites (Ashworth and Clegg, 2003), suggest that the three avocado races evolved through separate domestication processes. They came into contact after the European invasion in the 16th century.

1.2 Avocado genetics and reproduction/breeding

Avocado is a diploid species with 12 chromosomes in each of the two sets and a 1,766 Mbp full genome (Arumuganathan and Earle, 1991). It reproduces sexually mainly through cross-pollination. Its flowering system is diurnally synchronous protogyny, which potentially reduces the inbreeding rate. Based on the flowering system, avocado cultivars are grouped into type A and type B cultivars. The flowers of type A cultivars operate as females in the morning of the first day up to early afternoon when they close. In the afternoon of the next day, these flowers operate as males. Cultivars in this group include 'Pinkerton', 'Hass', and 'Reed'. The flowers of type B cultivars operate as females in the afternoon of the first day and as males in the morning of the second day. Examples of type B cultivars are 'Ettinger', 'Sharwil', 'Fuerte' and 'Zutano'. The diurnally synchronous protogyny and the long juvenile period of the avocado plant contribute to the difficulties encountered in crop breeding programmes. However, the outcrossing property of this crop has been harnessed in the development of cultivars by intentional or chance crossing of two different seedling plants. Other cultivars have been developed by introducing mutations in the pre-existing cultivars. Clonal propagation of cultivars is then carried out through grafting (University of California, 2007; Crane et al., 2007).

Some cultivars exhibit alternate (biennial) bearing in which the tree yields heavily one season and little or none in the next. Possible causes for this are genetic factors, limited root and leaf replacement in the previous ‘heavy crop’ season, limited food reserves to support flower and fruit setting and development in the coming season. Other causes are seed and fruit gibberellins that inhibit floral induction (for the next season) in the previous ‘heavy crop’ season, orchard management practices and environmental stresses like hail, cold weather, drought and heavy wind. Diseases like *Phytophthora* root rot and pests can worsen the alternate bearing (Garner and Lovatt, 2008; Wolstenholme, 2010). Under normal circumstances, although avocado fruit formation (flowering, fruit setting and development) requires high levels of energy (carbohydrates), the plant normally utilizes resources in a balanced manner thus expending the energy in the whole plant body (Wolstenholme, 1987; Whiley et al., 1996). Such energy balance ensures that current preparations for the incoming fruiting season such as renewal of roots, growth of flushes and new fruiting sites are unaffected. When the plant cannot maintain the energy balance and devotes most of its energy in the current fruit setting and development, preparations for the next fruiting season are jeopardized resulting in low yield (Scholefield et al., 1985; Whiley et al., 1996; Wolstenholme, 2010). Alternate bearing can be intervened by management practices like reducing the crop load during the 'on' season, pruning, girdling and application of growth retardants such as uniconazole (Wolstenholme, 2010).

1.3 Economic importance of avocado crop

Avocado fruits are used worldwide as food, being consumed as plain fruit, in salads or as juice. Due to its high nutritional contents and health benefits, avocado fruit is an important commodity traded globally. In Mexico, avocado seeds are used in making bioplastics that are processed into biodegradable straws and cutlery. In 2018, the Biofase Company in Mexico used 15,000 kg of avocado seeds per day in making bioplastics that were exported to Peru, Colombia, Canada, United States and Costa Rica (Barrett, 2018; Hares, 2018). In Tanzania, the local population uses avocado branches and old stems in making wood for cooking and timbers that are processed into furniture. Dried avocado leaves are used for making tea, which is thought to have several health benefits including removing free radicals in the body, breaking kidney stones, lowering blood pressure and glucose level and reducing convulsions caused by seizures (Ritz, 2019).

1.4 Health benefits of avocado fruits

Avocado fruits are rich in vitamins. According to the USDA (2019), 100 g of raw avocado fruit may contain 21µg of vitamin K, 81 µg of folate, 10 µg of vitamin C, 21 µg of potassium, 1.4 mg of vitamin B5, 0.3 mg of vitamin B6 and 2.1 mg of vitamin E. This may change with cultivar and growing environment. Avocado may also harbour small quantities of vitamins A, B1 (thiamine), B2 (riboflavin) and B3 (niacin). Likewise, some minerals like magnesium, phosphorous, manganese, iron, copper and zinc may be found in small amounts.

A 100 g fruit may contain 2 g of protein, 15 g of healthy fats and 160 calories. It is rich in fibres (7g/100g fruit) but rather poor in carbohydrates (2g/100g fruit) making it a low-carb food (USDA, 2019). Fibres may help lowering the risk of developing type 2 diabetes, obesity, hypertension, stroke and coronary heart disease (Ware, 2017). They are also important for a healthy digestion and constipation prevention (Ware, 2017). Dietary fibre consumption has been reported to assist in improving the insulin sensitivity and helping obese people to rapidly lose weight (Ware, 2017).

Avocado contains higher levels of potassium (339mg/100g) than most other fruits. Potassium is important in regulating muscle activity and safeguarding our bodies from cardiovascular diseases (Canciam et al., 2008). The fruit also contains antioxidant compounds like glutathione which neutralizes potentially carcinogenic compounds (Wang et al., 2012).

Avocado contains 88.3 mg/100g of β-sitosterol, a natural plant sterol that appears to be associated with maintenance of healthy cholesterol levels (Ware, 2017). β-sitosterol assists the body in fighting against the human-immunodeficiency virus (HIV) and other infections through enhancing production and activity of lymphocytes which are important components of body defence against pathogens (Bouic et al., 1996; Bouic, 2002).

Avocado contains two phytochemicals (zeaxanthin and lutein), which protect our eyes from being damaged by ultraviolet light. Avocado consumption helps in improving the absorption of fat-soluble antioxidants, such as beta-carotene. These antioxidants decrease the risk of developing macular degeneration, an age-related condition that impair human vision through affecting the retina (Ware, 2017).

Avocado is essential for bone health and prevents osteoporosis. A 100 g of avocado may offer 21 μg of phylloquinone, a vitamin K1, which corresponds to 21% of the daily recommended intake for adults. Phylloquinone is important for healthy bones as it increases absorption of calcium while reducing its excretion through urine (Ware, 2017).

Avocado contains folate (81.0 μg/100g), an antioxidant that is believed to play a role in protecting our bodies from stomach, pancreatic, colon, and cervical cancers. Moreover, the avocado phytochemicals have been shown to selectively impede the growth of precancerous/cancerous cells, killing cancer cells, and promoting lymphocyte proliferation (Ware, 2017). Folate has also been reported as important during pregnancy as it helps lowering occurrences of birth defects such as neural tube defects and miscarriage (Ware, 2017). Avocado harbours substances with antimicrobial properties against bacteria like *Escherichia coli,* which is the main causative agent of food poisoning (Ware, 2017).

1.5 Avocado consumption

Due to its beneficial heath properties, avocado has gained popularity in recent years and its consumption is increasing globally. The United States leads the avocado consumption. The consumption was 883.8×10^6 kg (1948.5×10^6 pound) in 2014. In 2019, the consumption had increased to 1200.5×10^6 kg (2646.6×10^6 pounds) (Shahbandeh, 2020a). The per capita consumption was 1.8 kg in 2010 and 3.6 in 2018 (Shahbandeh, 2019).

On the main European markets (Germany, Scandinavia, France, United Kingdom and the European Union new member states), the May–October avocado consumption was 225.2×10^6 kg in 2018, which is a 165% increase compared to 2011 (8489.7×10^4 kg) and a 25% increase compared to 2017 (1802.3×10^5 kg). France is the leading consumer followed by the United Kingdom, with an avocado consumption of 7297.8×10^4 and 6229.3×10^4 kg, respectively, during May-October 2018. The countries with the highest per capita consumption in 2018 were Denmark (2710 g), Norway (2510 g), Sweden (2170 g) and France (2060 g) (FruTrop, 2019).

In China, which is a rapidly growing avocado market, the consumption was 3100×10^1 kg in 2011, and then it drastically increased to 4800×10^4 kg in 2018. The increase in China's avocado consumption suggests that the country may become the leading global avocado market in the near future (Freshfruitportal, 2019).

1.6 Global avocado production and trade

The worldwide avocado production was 2.71×10^6 metric tonnes in 2001 and it increased by 42.8% to about 3.87×10^6 metric tonnes in 2010. The production then rose steadily reaching 6.41×10^6 metric tonnes in 2018 (Shahbandeh, 2020b). Mexico has been the leading avocado producer over the past two decades. The country produced 34% (2.18×10^6 metric tonnes) of the global avocados in 2018/2019 (Alves, 2020a), followed by Indonesia (410.09×10^3 metric tonnes; Hirschmann, 2019), Colombia (403.18×10^3 metric tonnes; Alves, 2020b) and Peru (338×10^3 metric tonnes; Freshfruitportal, 2019). Tanzania's total avocado production is difficult to estimate due to a lack of comprehensive data from Tanzania's responsible ministry or institutions (Mwakalinga 2014). The country produced about 20,000 metric tonnes of avocado in 2010/2011. Mwakalinga (2014) predicted that the total production would reach about 106,000 metric tonnes in 2019/2020. Yet, the Tanzania's National Bureau of Statistics (NBS) indicated that the production was 19,449 metric tonnes in 2016/2017; i.e., lower than that of 2010 (NBS, 2017). According to the FruiTrop (2019), commercial avocado was produced on 1,200 to 1,400 ha of land in Tanzania in 2018 and was estimated to have a yearly growth rate of 300 to 400 ha reaching an estimated export potential of 15,000 to 20,000 metric tonnes in 2023.

World avocado imports are rapidly growing. In 2018, the total imports were 2.5×10^6 metric tonnes (worth US$ 6.1 billion), which was 12% more than the import value for 2017. In 2018, the leading avocado importers were the United States, the Netherlands, and France, which together imported 1.5×10^6 metric tonnes (about 60% of all avocado imports) worth US$ 3.5 billion (Opportimes, 2019).

In 2018, the top five leading avocado exporters were Mexico (43% of the total avocado exports, worth US$ 2.4 billion), the Netherlands (13.2%, US$ 733.8 million), Peru (13%, US$ 722.3 million), Spain (6.2%, US$ 346.9 million) and Chile (5.8%, US$ 323.2 million). These were followed by United States (3.2%, US$ 179.6 million), Kenya (2.1%, US$ 118.3 million) and South Africa (2.1%, US$ 116.7 million) (Workman, 2019). As for Tanzania, its export in 2018 was 7,551 metric tonnes (worth US$ 8.5 million), of which 89.6 and 8.8% were shipped to the European Union and Kenya, respectively (FruiTrop 2019). Previous reports show that in 2011, Tanzania's avocado export was 86 metric tonnes (worth US$ 22,000) (Mwakalinga, 2014). The 2017 export increased to 8380.87 metric tonnes (worth US$ 10.47 million) (Apeda, 2019). While Kenya imported 57.3% of Tanzania's export in 2017, the Netherlands, United Kingdom and France imported a total of 36.4% (Apeda, 2019).

1.7 Avocado value chains

In Tanzania, a couple of investigations evaluated the avocado value chain, particularly for the commercial cultivars. In his study, Mwakalinga (2014) investigated avocado value chains in the Siha and Njombe districts and observed that the majority of Tanzania's avocado produce was sold on the domestic market. For instance, in 2013 only about 3% of the total production was exported. Among the challenges identified along the supply chain were bad agricultural practices which included mishandling of pesticides, poor harvesting methods like tree shaking, and harvesting immature fruits that never ripen. Others were absence of proper methods for sorting/grading of fruits, poor postharvest fruit handling/packaging like the use of polythene bags in long distance fruit transportation, higher operating costs for cold storage facilities as well as lack of volume/weight measuring standards in the wholesale transactions. Also, transport related problems that included loading of fruits beneath other cargo and delayed delivery to the markets due to poor roads, police road check-ups and sometimes truck mechanical failure were mentioned. Diseases and pests that affected the quantity and quality of avocado produce were *Phytopthora* root rot, sun blotch, dieback, anthracnose, red spider mite, false codling moth and fruit fly. These factors reduced the quality of the commodity and resulted in about 40% of the losses in traders' purchases. Lack of funding to support horticultural research, minimum support from the government and lack of enough skilled human resources to develop the industry could also be seen as contributing factors. To add value to the fresh avocados, the study recommended deployment of proper methods for sorting, grading and packaging as well as branding the product. Constraints that limited avocado export were delays on the road, superfluous certificates, bureaucracy in the registration system, crop seasonality, limited water supply and quantity/quality assurance of the fruit from the smallholders. Some of these challenges were later on noted by REPOA (2019) in the policy briefing aimed at improving the country's avocado value chain and exports. Among the challenges were underprivileged transportation and logistics facilities, unstable electricity supply, quality control and safety assurances, limited capital, insufficient market support, lack of production/market information and limited land availability. Others were limited storage facilities (cold rooms) to handle fruits at the seaports, shipping cancellations or delays due to fewer shipping lines and high insurance costs due to related risks. Also mentioned were superfluous, unfriendly agribusiness regulation that focused on agrochemicals, food safety, immigration and labour regulations, land policy and management, repeated testing, multiple certifications, infinite fees or taxes, licences and registrations.

1.8 Avocado morphological characterization

Morphological characteristics have been used in the description of avocado and for assessment of its diversity. In the United States, UCAVO (Undated) described leaf, fruit and seed characteristics of about 1000 avocado cultivars. A cultivar database was developed from this information and it is now used as reference material in morphological identification of different avocado cultivars. The Florida Department of Agriculture and Consumer Services (Undated) also described tree, fruit and seed characteristics as well as fruiting season of about 40 Florida avocado cultivars.

Nkansah et al. (2013) used agro-morphological characteristics to study the diversity among the local and commercial avocado cultivars in two different areas in Ghana. They noticed a substantial diversity among the sampled trees in tree, leaf, fruit and yield characteristics. Moderate to strong positive correlations were noticed among tree height, canopy, stem circumference and branch numbers. Also, Abraham et al. (2018) observed considerable variation in the examined tree, leaf, fruit and seed characteristics when studying diversity in local avocados grown in the Central and Ashanti regions of Ghana. They suggested that the analysed trees were most likely of Guatemalan and West Indian origin. Comparative analyses of the characteristics observed in avocado trees sampled in different areas revealed pronounced similarities, possibly due to propagules shared by people in the investigated areas.

Gutiérrez-Díez et al. (2015) used 10 quantitative morphological characteristics of fruit and seed to study diversity and relationships among 42 avocado trees (9 wild creoles, 7 creoles and 26 trees of 11 improved creoles) in Nuevo Leon, Mexico. A considerable variation was detected among the trees in the characteristics investigated with 39.42% (seed weight) being the highest coefficient of variation detected. Principal components analysis and UPGMA (unweighted pair group method with arithmetic mean)-based cluster analysis did not, generally, group different forms of the same cultivar and thus classification was not in line with cultivar names.

Isimadi and Hafifa (2017) employed morphological characteristics to study the diversity of avocado in the Central Aceh region of Indonesia. They found substantial variation among the sampled trees in tree, branch and leaf characteristics. However, no uniqueness of the characteristics was observed among the trees sampled in different geographical areas.

In Tanzania, morphology has not been exploited in the description and diversity analysis of avocado genetic resources in the country.

1.9 Avocado genetic characterization

Genetic markers have widely been employed in characterizing avocado germplasm. In Florida, Ellstrand et al. (1986) used isozymes to establish the parentage of 'G755' hybrid avocado rootstock selections whose intermediate morphological characteristics suggested that they originated from a hybridization between coyou (*P. schiedeana* Nees) and avocado (*P. americana* Mill.). Evaluation of the genetic diversity at the five loci confirmed the findings based on morphological characterization and further indicated that the avocado parent was most probably from Guatemala.

Fiedler et al. (1998) used randomly amplified polymorphic DNA (RAPD) markers to study the genetic relationships among the Israeli and Mexican avocado germplasm from all three races. Their results showed that the similarity between accessions varied from 46 to 85%, with a within race average similarity being 71, 73 and 75% for the West Indian, Guatemalan and Mexican races, respectively.

Cuiris-Pérez et al. (2009) utilized inter-simple sequence repeat (ISSR) to study diversity among 77 avocado accessions sampled from seven states of Mexico. They detected an average of 22 allele per locus with a polymorphism information content (PIC) ranging from 0.82 to 0.95. A sequential agglomerative hierarchical non-overlapping (SAHN) cluster analysis grouped the 77 avocado accessions in two major groups which were not in line with geographic origin.

Schnell et al. (2003) utilised SSR to study the genetic diversity among 224 avocado accessions sampled in Florida, and 34 clones sampled in California. The study detected a diversity value of 0.83 and an average of 18.8 alleles per locus. Based on principal coordinate analysis, the Mexican and Guatemalan avocados clustered into two distinct groups, whereas the West Indian avocados formed a separate group with some outliers.

Alcaraz and Hormaza (2007) employed SSR to characterize 75 avocado accessions in Spain from local and imported germplasm. They detected an average of 9.75 alleles per locus with an average expected heterozygosity of 0.76. An unweighted pair group method with arithmetic mean (UPGMA) based cluster analysis grouped the sampled trees into three major clusters that mainly corresponded to racial origin.

Acheampong et al. (2008) utilised SSR to study the origin, horticultural race and genetic relationships among 172 avocado trees sampled in six regions of Ghana. They detected an average of 4.42 alleles per locus with an average observed and expected heterozygosity of 0.36 and 0.51, respectively. A low genetic distance from 0.00 to 0.07 was detected between populations from different regions. The neighbor-joining based cluster analysis also revealed high similarities among the studied trees and only 8.7% of the samples clustered separately. Comparative evaluation of the sampled trees and representatives of the three avocado races showed that the sampled trees were more closely related to the West Indian race. Abraham and Takrama (2014) also employed SSR to study the diversity among 71 avocado trees sampled in the Central and Ashanti regions of Ghana. They detected an average of 11.5 alleles per locus, with an average observed heterozygosity and gene diversity of 0.48 and 0.75, respectively. The UPGMA based cluster analysis revealed clustering of the sampled trees into two groups.

Borrone et al. (2008) employed SSR to study the outcrossing rate among 'Tonnage' and 'Simmonds' avocado offspring raised from seeds in Florida. The results showed that 96 and 74% of the 'Tonnage' and 'Simmonds' offspring, respectively, were the product of cross-pollination. The overall outcrossing rate varied from 63 to 85%. Furthermore, Borrone et al. (2009) made use of SSR to assemble the genetic linkage map from the 'Tonnage' × 'Simmonds' avocado reciprocal cross. A total of 163 important loci were amplified using a total of 135 primer pairs. 'Simmonds' and Tonnage' were heterozygous for 39 and 93% of the loci, respectively. The composite linkage map comprised 12 linkage groups (LGs) whose size varied from 2.4 cM (LG12) to 157.3 cM (LG2). The study was followed by phenotyping of the population to identify quantitative trait loci (QTL) for marker-assisted selection.

Guzman et al. (2017) used SSR to study the genetic diversity and population structure of 318 avocado accessions representing the three races sampled in Mexico. They detected an average expected and observed heterozygosity of 0.75 and 0.59, respectively. The population structure analysis assigned the studied samples to two admixed major groups, and thus no clear distinction was noticed among the three avocado races.

Ge et al. (2019a) employed single-molecule long-read sequencing approach to generate 15 polymorphic SSR markers which were utilized in investigating genetic diversity among 46 avocado trees collected in three provinces of China. They detected an average of 4.73 alleles per locus with an average observed and expected heterozygosity of 0.49 and 0.50, respectively. The average polymorphism information content of the markers was 0.45. The neighbor-joining based cluster analysis and the principal coordinate analysis grouped the trees in line with their geographic origin.

Other genetic works include Ge et al. (2019b) and Rubinstein et al. (2019), both of whom employed single nucleotide polymorphisms (SNPs) to study genetic diversity and population structure among 21 and 100 avocado accessions in China and Israel, respectively. Likewise, Magallanes et al. (2017) utilized both microsatellites and SNPs to study genetic relationships among five avocado accessions in Mexico.

Although, as noted above, genetic markers have been used to characterize avocado in several countries, such markers have not been exploited for characterizing Tanzania's avocado genetic resource.

2 Objectives

2.1 Statement of research problem

Tanzania’s economy heavily relies on agriculture, which has given employment to approximately 65% of the labour force. The majority is engaged in small-scale agriculture. Avocado, as being a cash crop, has gained much interest in recent years, and has grown in importance. Most of the avocados in Tanzania are sold on the local unstable market whereas only small quantities are traded on the export market, thus limiting the country’s possibility to earn foreign currency. Despite the crop’s long cultivation history and its significance in providing employment to the farmers and traders, most of the latter being women, and securing the government’s revenue, scanty research has been executed in Tanzania to strengthen the production and trade. Hence, the current study aimed at assessing the avocado’s diversity, production and marketing in the country, particularly in the southern highlands area.

2.2 Objectives of the study

The overall research objective was to assess the production, marketing and diversity of avocado from Tanzania’s southern highlands. The specific objectives were:

- To study the production and marketing of avocado as well as to identify setbacks of this industry in Tanzania’s southern highlands.
- To characterize seed propagated avocado trees in Tanzania’s southern highlands using morphological traits.
- To investigate genetic diversity among the seed propagated avocado trees in Tanzania’s southern highlands.

2.3 Significance of the study

The findings from the study on avocado production and local trade, and the identification of setbacks in the avocado industry in Tanzania will help shedding light on the industry and possibly awaken Tanzania's government to act accordingly. Morphological characteristics for identifying plant material of potential economic interests will be used in the future avocado breeding programmes of Tanzania. Determining the level of genetic diversity in this crop will set the basis for future research on how to improve the crop to meet the market needs. Evaluation of crop genetic diversity will help the responsible government authority to plan for genetic resource utilization, management and conservation.

2.4 Research questions

I. What are the characteristics of the small-scale avocado production and marketing and what are the setbacks in the avocado industry in Tanzania's southern highlands?

II. How do the extent and distribution of variation in morphological traits of seed-originated avocado trees in the southern highlands of Tanzania look like?

III. What is the extent of genetic diversity of seed-originated avocado trees grown in different districts and regions of Tanzania's southern highlands? How is the genetic variation partitioned within and among districts/regions?

3 Materials and Methods

The study sites were eight districts of the Mbeya, Songwe and Njombe regions in Tanzania's southern highlands (Figure 1). Fieldwork was performed between February and July 2017.

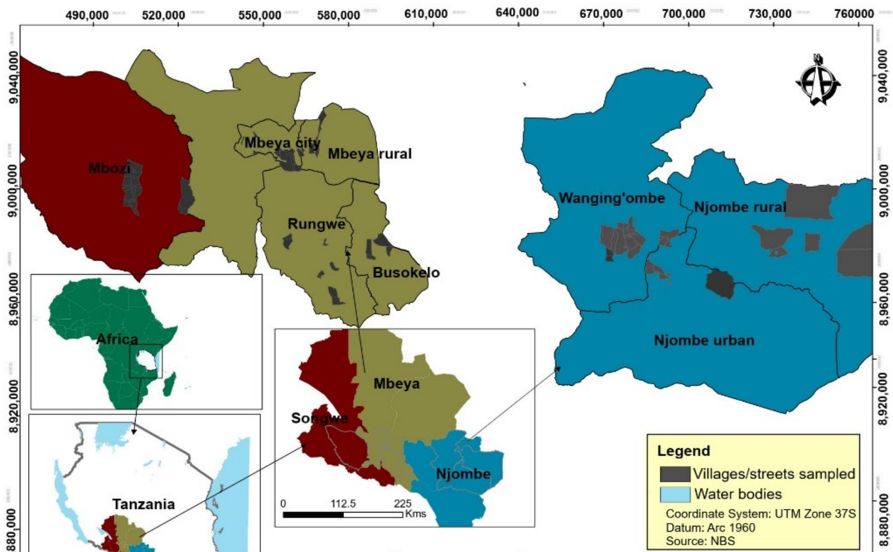

Figure 1. Location map showing the study sites; bottom left is a map of Tanzania showing the location of the three regions included in the study; atop the location of Tanzania within Africa is shown; the upper section displays the targeted eight districts; within the districts, streets/villages with sampled trees are marked in greyish.

3.1 Avocado production and local trade

Data on the production and marketing of avocado were collected from 275 small-scale growers, 231 traders and 16 key informers (Table 1). The key informers were either leaders of avocado farmers' network or agricultural officers at the local authorities. Data gathering was done mostly through face-to-face interviews employing three distinct semi-structured questionnaires for farmers, traders and key informants, respectively. In addition, focus group discussions and a survey were exploited in collecting information from the avocado farmers' networks and their leaders (Paper I).

Table 1. *Number of respondents involved in the study*

Region	District	Number of growers			Number of traders			Number of key informers
		Female	Male	Sub Total	Female	Male	Sub total	
Mbeya	Mbeya city	14	22	36	28	4	32	1
	Mbeya rural	7	24	31	12	0	12	1
	Rungwe	10	30	40	9	23	32	1
	Busokelo	10	31	41	17	12	29	0
Njombe	Njombe urban	2	24	26	28	3	31	8
	Njombe rural	9	20	29	20	10	30	0
	Wanging'ombe	9	31	40	20	11	31	4
Songwe	Mbozi	10	22	32	34	0	34	1
Total		71	204	275	168	63	231	16

3.2 Morphological characterization of avocado

Morphological characteristics were evaluated for 226 seed propagated adult trees, and the number of trees per district ranged from 7 to 43 (Table 2). The avocado field guide used for characterization was the list of descriptors for avocado species from the International Plant Genetic Resources Institute

(IPGRI, 1995). By using it, 14 of the most important plant descriptors were recorded in the 226 trees (Paper II). The overall tree descriptors were trunk surface, surface and colour of the young twig, leaf shape, pubescence of underside of the leaf, number of primary veins and divergence of primary leaf vein. As for the fruits, the descriptors evaluated were fruit and pedicel shape, colour of ripe fruit peel, fruit peel thickness and flesh texture. The seed descriptors recorded were the seed shape and cotyledon surface. Study site information like latitude, longitude and elevation were also documented (Paper II).

Table 2. *Number of avocado trees sampled in each district*

Region	District	Number of trees sampled
Mbeya	Mbeya city	43
	Mbeya rural	43
	Rungwe	34
	Busokelo	18
Njombe	Njombe rural	32
	Njombe urban	7*
	Wanging'ombe	24
Songwe	Mbozi	25
Total sampled trees		226

* Small sample size was due to paucity of seed-originated avocado trees in this district (Njombe urban). Formally, the district was rich in seed-originated avocados, but most of them were replaced with commercial cultivars.

3.3 Genetic characterization of avocado

Young leaves were collected from the 226 avocado trees in 2017 and then dried in silica gel. By employing the Thermo Scientific Genomic DNA Purification Kit, DNA was extracted from the dry leaf tissues (Paper III).

Sixteen polymorphic SSR markers were used to amplify microsatellite regions of the 226 avocado trees, but only the amplification of 10 of the markers were consistent and used in the present study (Paper III).

4 Results and Discussion

4.1 Avocado production and local trade (Paper I)

The male avocado growers outnumbered the females with a proportion ranging from 61 to 92% over the districts. This finding concurred with Musimu (2019), who observed that 70% of the Mbeya bean growers were males. On the other hand, the females outnumbered the males in the avocado trade, amounting to 72% of all the interviewed traders. However, the majority of them were retailers whereas the male traders mostly worked as suppliers. Oduol and Mithöfer (2019) reported a similar case among avocado traders in Kenya. Also, Fischer et al. (2017) observed that the majority of the vegetable retailers in Tanzania were females.

More than 75% of the growers had intercropped avocado orchards while other growers either had mono-cropped or both intercropped and mono-cropped orchards. About 24 and 4% of the growers reported having less than 2 and 2–5 acres, respectively. Few farmers, about 5%, owned more than 5 acres. About 65% of the growers did not measure their orchard in acres but reported an average of 41 trees/grower. The size of the orchards varied significantly across the districts (χ^2 (df = 28, N = 273) = 175.35, P = 0.001). Around 29% of the growers cultivated both commercial and local avocado cultivars whereas approximately 27 and 44% of the growers cultivated only commercial or local avocado cultivars, respectively. There was a statistically supported association between the avocado types grown and the districts (χ^2 (df = 14, N = 273) = 199.89, P = 0.001). The majority of the commercial avocados were 'Hass' and 'Fuerte'. However, 'Simmonds', 'Zutano', 'Ettinger', Booth 7' and 'Nabal' were cultivated by a limited number of growers. Although the fruits of local avocado cultivars have a shorter lifespan than the commercial cultivars, there is a higher demand for these local cultivars in the domestic markets owing to their outstanding taste. The average crop yield across districts spanned from 52 (Wanging'ombe) to 156 (Busokelo) kg per tree. This was in accordance with the crop yield range reported by Thomas (1997) (17–327 kg tree^{-1}) and Lovatt et al. (2015) (28–190 kg tree^{-1}) for the 'Hass' avocado in Australia and United States, respectively.

The average income for the growers ranged from US$ 0.18 per kg in Busokelo to US$ 0.52 per kg in Wanging'ombe. The Busokelo and Rungwe growers generally sold their produce at lower prices, probably due to the fact that they were remotely situated from the town/city but had the highest avocado supply. They mostly traded with the wholesalers and middlemen from other districts. The growers of commercial cultivars generally received a higher price, US$ 0.45 per kg, compared to the growers of local cultivars (US$ 0.30 per kg). The growers' average earnings, in US$ per tree, varied from 24.38 in Busokelo to 74.88 in Mbeya city. The growers that only grew commercial avocado cultivars earned less (US$ 25.63 per tree) than the ones who grew only the local cultivars (US$ 46.47 per tree). This was attributed to the fact that local avocado trees grow more massive and as a result produce a larger number of fruits that also are bigger than the commercial fruits. However, around 72% of all the growers were not satisfied with their earnings due to the low fruit prices that did not reflect the high production costs. Low fruit prices, US$ 0.05–0.57 per kg, have been reported to discourage avocado growers in Ethiopia (Shumeta, 2010), Kenya (Omolo et al., 2011) and Colombia (DANE, 2014).

The procuring capacity of the traders during one week varied from 14 (Mbeya rural) to 349 (Busokelo) kg, with the traders working in rural areas showing lower capacity. Also, female traders, due to their limited capital, showed lower capacity (64 kg/about a week) than the males (212 kg/about a week). This corresponds to results from Kenya, where Oduol and Mithöfer (2014) observed that the male avocado traders had higher purchasing capacity and were mostly involved in whole sales.

The avocado fruit quality was affected by a series of factors from improper orchard management and harvesting, through poor transportation to improper fruit storage. The traders reported losses ranging from 9 (Njombe rural) to 33% (Busokelo), with those having lower capacity displaying lower losses. It was easier for traders with lower capacity to store fruits compared to traders with higher capacity, given the fact that the majority of the fruits of the latter was local avocados with a limited shelf life. Around 80% of the traders were happy with the avocado trade earnings. Poor harvesting and improper post-harvest handling are reported as affecting the quality also in other avocado producing areas. About 18 and 19% avocado losses were reported among avocado traders in Kenya (World Economic Forum, 2014) and Ethiopia (Bantayehu et al., 2017), respectively.

About 98% of the growers interviewed reported challenges constraining the avocado production. These challenges included limited extension services, drought, pests and diseases, poor marketing conditions, limited access to agricultural inputs as well as vandalism, theft and yield decline. Drought causes heavy flower and immature fruit drop, whereas *Phytophthora* root rot, bacterial blast, anthracnose, leaf rust, mealybugs and insect borers reduce crop harvest and quality. Unreliable markets, unfavourable trader-dictated wholesaling price, and the use of unstandardized volume measuring tools like buckets and bags instead of weight were reported to affect the sale. Limited availability/high price of the quality planting materials, fertilizers and pesticides affected the production. Also, traders stated some challenges constraining their business, e.g. limited fruit shelf life, unfavourable marketing environments, poor transportation and seasonal fruit availability/quality related problems. These challenges have earlier been reported to limit the avocado industry in other countries. For instance, limited extension services were reported in Ethiopia (Shumeta, 2010), Kenya (Gorge et al., 2018) and the Philippines (Sotto, 2000), whereas pests and diseases were observed in Kenya (Aloo, 2005), Australia (Muirhead et al., 1982), the Philippines (Sotto, 2000) and Latin America (Ploetz et al., 2002).

4.2 Morphological characterization of avocado (Paper II)

The trunk surface characters recorded across all the trees were either rough (36.9%), very rough (38.7%) or smooth (24.4%) and were significantly associated with both district and elevation range. Ismadi and Hafifah (2017) observed only very rough and rough trunk surface across some Indonesian avocados. Bergh (1992), attributed both rough and very rough trunk surface to the West Indian race, and smooth surface to the Mexican and Guatemalan races.

Eleven leaf shapes were documented (Paper II, Figure 5) with the commonest and rarest shape being lanceolate (31.1%) and ovate (0.9%). Approximately, 4% of the trees displayed leaf shapes not listed in the field guide. Ismadi and Hafifah (2017) described only two leaf shapes (oblong lanceolate and lanceolate) across some Indonesian avocado trees. Nkansah et al. (2013) and Abraham et al. (2018) reported a total of seven leaf shapes across 154 Ghanaian avocado trees sampled from different ecological zones of the country. The higher number of leaf shapes encountered in the present study points to the higher diversity among trees from the southern highlands of Tanzania.

As for the pubescence on the abaxial leaf surface, the trees either lacked pubescence (23.1) or had sparse (25.3%), dense (45.5%) or intermediate (6.1%) pubescence. While 60 and 100% of the trees investigated in Mbozi and Njombe urban, respectively, presented absence and sparse pubescence, trees from other districts showed a higher proportion of dense pubescence. The leaf pubescence was significantly associated with the region. Pubescence on the leaf surface has been reported to affect the light absorption by the plant, and in turn lowering the rate of photosynthesis (Ehleringer et al., 1976).

The average number of primary leaf veins across the eight districts spanned from 17.857 ± 1.773 (Njombe urban) to 20.14 ± 3.623 (Mbeya rural). Across the elevation ranges, the average number of primary leaf veins spanned from 17.65 ± 2.346 (719–1200 masl) to 19.875 ± 2.773 (1601–1800 masl). While 71.7% of the investigated trees presented 16–20 primary veins, Abraham et al. (2018) observed that 72% of avocado trees sampled in Ghana displayed 14–16 primary veins. A higher number of primary veins on the leaf improves not only the transfer of mineral salts and water along xylem vessels to the photosynthetic tissues, but also the transfer of nutrients along the phloem vessels to all parts of the plant (Answers, 2013).

Unripe mature fruits showed 21 different shapes of which rhomboidal was the commonest (Paper II, Figure 7). Twelve of the shapes were not described in the field guide. This high number of different shapes can be compared to the studies by Nkansah et al. (2013) and Abraham et al. (2018), which reported a total of nine fruit shapes across 154 avocado trees investigated in Ghana. Fourteen fruit shapes observed in our study were earlier described for avocado cultivars belonging to the three races (Paper II, Table 4).

Various colours were displayed by the fruit peel (Paper II, Figure 10a) with the most frequent individual colour being black 203A. However, the speckled colour was most abundant as it accounted for around 45% of the trees. Barrett et al. (2010) reported that the fruit colour is an important morphological characteristic that makes the fruits appealing to the customers, hence motivating their procurements.

The flesh texture was either buttery, watery, granular or pastose. Granular was rarest (1.4%) and buttery most frequent (58.3%). Popenoe (1974) attributed buttery texture to Guatemalan and Mexican races while Morton (1987) found the character among Mexican × Guatemalan hybrids. This suggests that among the trees investigated in the present study, there are Guatemalan and Mexican avocados.

The analysed seeds presented 17 shapes (Paper II, Figure 11). Eight of these shapes, i.e. base flattened-apex rounded, base flattened-apex conical, broadly ovate, cordiform, ovate, spheroid, oblate and ellipsoid, were common and listed in the field guide. The combined occurrences of the other, uncommon seed shapes was 3.2%. Popenoe (1974) recorded broadly ovate, spheroid and base flattened-apex conical seed shapes among some West Indian, Guatemalan and Mexican avocados, respectively. Observing these shapes among our investigated trees, suggests that Tanzania is endowed with all the three races.

The investigated trees displayed diversified characteristics, of which some pose varying levels of attraction to the consumers. These include the shape of mature fruits, and the ripe fruit's peel colour and flesh texture. These characteristics have potential for being exploited in breeding to satisfy consumers' demands. The high morphological variability observed among these trees is an indication of the crop's adaptation to diverse geographical habitats of Tanzania.

The principal coordinate analysis and dendrogram grouped the trees with common features irrespective of the district/region of collection (Paper II, Figures 13 and 14). This suggests an exchange of avocado seeds among farmers across the surveyed areas.

4.3 Genetic characterization of avocado (Paper III)

The 10 microsatellite loci used in this study were polymorphic with a total of 167 distinct alleles across all the trees. The allele number per locus spanned from 10 (LMAV35) to 23 (AVAG22) with an average of 16.70 ± 1.30 (Paper III, Table 2). This is higher than the average values, 11.5 and 11.4, reported by Abraham and Takrama (2014) and Gross-German and Viruel (2013), respectively. The average number of alleles per locus is however lower than the ones recorded by Guzmán et al. (2017) and Schnell et al. (2003), i.e.19.5 and 18.8, respectively. These differences possibly arose from variation in the polymorphism of the employed microsatellite markers, number of sampled trees, the diversity of the analysed samples and the equipment or programmes used in resolving the PCR amplicons (Lacape et al., 2007). Other contributing factors might be poor optimization of PCR protocols and DNA quality which both may lead to a high proportion of missing data. Also, differences in data (allele) scoring accuracy may contribute to differences in number of alleles reported. The average effective number of alleles was 6.81 ± 0.66.

The average observed heterozygosity was 0.65 ± 0.04, ranging from 0.46 (LMAV14) to 0.82 (LMAV31). Comparable average values, 0.61 and 0.64, were earlier reported by Guzmán et al. (2017) and Schnell et al. (2003), respectively, suggesting a comparable diversity for the groups of trees investigated in these three studies. However, Abraham and Takrama (2014) recorded a lower value, 0.48, and so did the Boza et al. (2018), i.e. 0.56. This suggests that the germplasm analysed in the present study is more diverse than the germplasm investigated in the latter two studies. The high genetic variability detected in the present study is an indication of the crop's adaptation to diverse geographical habitats of Tanzania. The average Shannon's information index (I) was 2.17 ± 0.10, ranging from 1.69 (LMAV35) to 2.59 (AVAG22). The polymorphism information content recorded was lowest and highest for AVAG05 (0.70) and AVAG22 (0.89), respectively. Eight of the ten loci displayed statistically supported deviation from the Hardy-Weinberg equilibrium.

At the district level, the mean observed number of alleles was highest for Mbeya rural (10.70 ± 2.26; Paper III, Table 3) and Njombe rural (10.70 ± 0.70), and lowest for Njombe urban (4.20 ± 0.36). The average effective allele number was highest for Mbozi (5.93 ± 0.57) and lowest for Njombe urban (2.96 ± 0.29). As for the average observed heterozygosity, the maximum and minimum values were recorded in Mbozi (0.71 ± 0.10) and Wanging'ombe (0.51 ± 0.06), respectively. The maximum average expected heterozygosity was noticed for Mbozi (0.83 ± 0.03) and Njombe rural (0.83 ± 0.03), while the minimum average expected heterozygosity was noticed for Njombe urban (0.71 ± 0.04). The average gene diversity was higher in Mbeya rural (0.65±0.11) and lower in Njombe urban (0.47 ± 0.09). The six diversity measures hint at a higher diversity for the Njombe rural, Mbozi or Mbeya rural trees. On the other hand, lower values for almost all the diversity measures detected in Njombe urban point to a lower diversity in this area. The paucity of seed-originated avocado trees and the limited level of genetic variation observed in Njombe urban suggests an impending genetic erosion in this district, thus advocating the deployment of conservation strategies.

Analysis of molecular variance (AMOVA) revealed that the highest molecular variance was within individuals (76.87%), whereas the remaining variance was subdivided among the districts (6.08%) and among individuals within districts (17.04%; Paper III, Table 4). The low molecular variance among the districts (presumed populations) was possibly due to introduction of highly similar (overlapping) germplasm to more than one districts, gene flow between the districts and a hidden partitioning of the eight presumed populations. Gross-German and Viruel (2013) and Boza et al. (2018) detected a higher molecular variance of 25.07 and 19.30%, respectively, among the investigated avocado populations. The inclusion of at least two more species in addition to *Persea americana* and a wider geographic area covered could be the reason for the higher population differentiation in their studies. On the other hand, Cañas-

Gutiérrez et al. (2019) recorded a molecular variance of 6.80% among avocado populations, indicating a similar genetic differentiation among populations as in our study.

The PCA (Paper III, Figure 2) and dendrogram (Paper III, Figure 3) generated based on the SSR data grouped the trees irrespective of the district/region of collection, suggesting genetic admixture in the study area. This is in line with the AMOVA findings that recorded a low genetic differentiation among the districts investigated. All the MedMeaK, MedMedK, MaxMeaK, MaxMed approaches of the Puechmaille (2016) method for estimating the K-values showed that the 226 trees could be grouped into four clusters (hidden partitioning of the presumed eight geographic/district populations) based on their genetic characteristics (Paper III, Figure 5). The Njombe urban and Busokelo populations had a similar population structure, and so had the Njombe rural and Wangingo'mbe populations. The high similarity (low genetic differentiation) observed among some populations is in accordance with the findings from the AMOVA, the PCA and the dendrogram which all showed low differentiation among the eight district populations.

5 Conclusions

A number of challenges were found hampering the development of the avocado industry in Tanzania. Addressing these challenges is important for improving the livelihood of the farmers and increasing the production. A pronounced variation in morphological traits and microsatellite markers suggests high diversity within the analysed plant material that may help in planning germplasm management and conservation, as well as breeding strategies in the future. The main conclusions and findings are:

- Both commercial and local avocado cultivars were cultivated by many growers in Tanzania. However, few growers cultivated only commercial avocados.
- The proportion of women was lower among growers but higher among traders; as traders they were often involved in retailing.
- Tanzania's avocado value chain is challenged by several factors.
  - ✓ The challenges at all levels, i.e. villages, districts, regions and nation, must be solved in order to improve this industry and consequently the lives of farmers and traders.
  - ✓ As many women participate in avocado vending, resolving the raised challenges will positively contribute to improving women's income and consequently reducing their dependency on their male partner.
- The investigated trees displayed diversified morphological traits of which some, such as the shape of mature fruit, the ripe fruit's peel colour and flesh texture, are characteristics that make the fruits appealing to the consumers, and hence potentially can be exploited in breeding for consumers' demands.
- Comparative analysis of the observed morphological characteristics suggests that Tanzania's avocados comprise elements from all the three races; the West Indian, Guatemalan and Mexican.

- The high morphological and genetic variability observed among the evaluated trees is an indication of the crop's adaptation to diverse geographical habitats of Tanzania.
- The rapid decline in seed-originated avocado trees in Njombe urban and the observed limited level of genetic variation, suggests the crop's genetic erosion in this district, thus advocating the deployment of conservation strategies.
- The morphology-based and genetic clustering of the trees sampled in different districts/regions, in the principal coordinate and component analyses, and dendrograms, indicates similarities of the trees sampled in different places. This points to the introductions of highly similar germplasm to more than one districts and seed cross-transfer between districts and regions.

6 Future perspectives

The study was conducted in a small part of the country; i.e., the southern highlands, with only three regions investigated of which one region, Songwe, was not thoroughly sampled. Since avocado cultivation is also undertaken in the eastern, north-eastern and north-western Tanzania, further research should include also these areas for completing the study throughout the country.

The present work did not detail earnings by growers or traders at each marketing channel. For instance, we did not resolve how much the farmer could earn by selling the crop to middlemen, to wholesalers, to retailers or directly to consumers. Future socioeconomic research may be able to provide such details.

The crop yields were just estimates offered by growers for one of their many trees. For the purpose of identifying the most accurate crop yield, future research should aim on collecting data directly from thousands of trees for 3 to 5 years. Such a study can provide more reliable data on variation in fruit yield among different avocado cultivars.

There seemed to be a shortage of propagules to the extent that some of the farmers decided to produce propagules themselves for their own use or selling to other growers. This approach not only takes longer time but also poses risks for spreading diseases as phytosanitary procedures are not followed. Additionally, there was no proper rootstock used by commercial avocado growers for grafting, which in turn could affect the plant responses to pathogens/pests and also crop yield. We call for not only research towards exploring rootstock material suitable for Tanzanian environments but also exploiting the bioreactor technique for rapid, highly efficient and cost effective production of thousands of clonal, disease-free planting materials.

We noticed some undesirable traits like susceptibility to root rot disease and shorter shelf life of the local avocado fruits, both of which affect crop yield and quality and consequently its price. Several factors contribute to this including the genetic make-up. Future research should investigate these undesirable traits and exploit new breeding techniques like gene editing to "correct" candidate genes.

We used not many morphological characteristics and less advanced techniques in characterizing morphology of the sampled trees. We recommend that future research includes more morphological characteristics such as, *inter alia*, tree height, girth and canopy, fruit size and weight as well as seed size. They should also exploit modern phenotyping techniques that collect a vast amount of useful data in a relatively short period, which in turn will give more insight into Tanzanian avocado germplasm.

Although we have studied avocado fruit quality (results not included in this thesis) in terms of antioxidant potential of seeds, pulp and peels, we only sampled 30 trees and analysed few parameters; DPPH (2,2-diphenyl-1-picrylhydrazyl) scavenging activities, total phenolic and flavonoid contents. Indeed, further research should be conducted on fruit quality of Tanzanian avocados.

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Popular science summary

Avocado fruits are used worldwide as food, being consumed as plain fruit, in salads or as juice. Due to it high nutritional content and health benefits, the avocado fruit is now an important trade commodity globally. In Mexico, avocado seeds are used in making organic plastics that are processed into biodegradable straws and cutlery. In 2018 the Biofase Company in Mexico was using 15,000 kg of avocado seeds per day in making bioplastics which were exported to Peru, Colombia, Canada, United States and Costa Rica. In Tanzania, the locals use avocado branches and old stems in making wood for cooking and timbers that are processed into furniture. Dried avocado leaves are used in making tea which is thought to have several health benefits that include removing free radicals in the body, breaking kidney stones, lowering blood pressure and glucose levels and reducing convulsions caused by seizures.

Tanzania's economy relies heavily upon agriculture which has given employment to approximately 65% of the labour force, most of them being engaged in small scale agriculture. Avocado, a cash crop which has gained much attraction in recent years, has been grown in the country for decades. Most of the avocados are being sold on the local unstable market and only a small quantity is exported, hence limiting the possibility to earn foreign currency. Despite the crop's long cultivation history and its significance in providing employment to farmers and traders and securing the government's revenue, few studies have been executed in Tanzania for revamping its production and trade. Therefore, the current research aimed to assess the crop's diversity, production and marketing in the country, particularly the Southern Highland area.

For the purpose of identifying different aspects of avocado production and trading a sum 275 avocado growers, 231 traders and 16 key informers were interviewed. As for the diversity study, a sum of the 226 seed-originated avocado trees were sampled in eight districts and their diversity was studied using 14 morphological characteristics and 10 microsatellites (SSR).

Analyses of the respondent answers showed that the growers in the different districts produced avocado fruits at an average of 52 to 156 kg per tree. Growers of commercial cultivars generally received a higher price, 0.45 US$ kg^{-1}, compared to growers of local avocado cultivars, 0.30 US$ kg^{-1}. The growers' average earnings, in US$ $tree^{-1}$, varied from 24.38 to 74.88 between districts. The growers that only grew commercial avocado cultivars earned less, 25.63 US$ $tree^{-1}$, compared to the ones that grew only local cultivars, 46.47 US$ $tree^{1}$. The procuring capacity of the traders, (during approximately one week), varied from 14 to 349 kg between districts. The female traders, due to their limited capital, showed lower capacity (64 kg/about a week) than the males (212 kg/about a week). The avocado fruit quality and the value chain was affected by a series of factors ranging from farmers' improper orchard management and harvesting, through poor transportation, to the traders' improper fruit storage. The losses in the different districts ranged from 9 to 33%. Approximately 28 and 79% of the growers and traders were content with the earnings from the avocado trading. About 98 and 100% of the growers and traders, respectively, mentioned challenges affecting the crop yield and value chain. These challenges included limited extension services, drought, diseases/pests, poor marketing environment, and the short shelf life of the fruits. Resolving them is the key towards improvement of the earnings and the lives of the farmers and traders, of all crops in general and of avocado in particular, as the other crop industries do face similar challenges.

The sampled trees showed great variation in the evaluated morphological features like shapes of leaves, mature fruits and seeds. As for the genetic characteristics, statistical evaluations showed considerable diversity at the 10 DNA sites investigated. However, genetic variation was comparatively low among the districts (9.89), with the variation among individuals within district being 5.28% and the within individual variation recorded as 84.83%. Most of the observed morphological and genetic characters were not unique for a particular area as revealed by "district/region-free" clustering pattern of the trees using different multivariate approaches. Introductions of highly similar (overlapping) germplasm to more than one districts and cross-transfer of the seeds/propagules among the districts/regions might be the reason for the observed sharing of characteristics.

Populärvetenskaplig sammanfattning

Avokadofrukter konsumeras över hela världen, färska, i sallad eller som juice. På grund av det höga näringsinnehållet och olika hälsofördelar är avokado en viktig handelsvara globalt. I Mexiko används avokadofrön för att tillverka biobaserad plast för framställning av biologiskt nedbrytbara sugrör och bestick. År 2018 använde Biofase Company i Mexiko 15 000 kg avokadofrön per dag för att göra biobaserad plast som exporterades till Peru, Colombia, Kanada, USA och Costa Rica. I Tanzania använder lokalbefolkningen avokadogrenar och stammar som bränsle vid matlagning och som råvara vid möbeltillverkning. Torkade avokadoblad används för att göra te som tros ha flera hälsofördelar inklusive oskadliggörandet av fria radikaler i kroppen, nedbrytning av njurstenar, sänkning av blodtryck och glukosnivå och dämpning av krampanfall.

Tanzanias ekonomi är beroende av jordbruket som ger sysselsättning till cirka 65% av arbetskraften. De flesta arbetar inom småskaligt jordbruk. Avokado, en avsalugröda som har fått mycket uppmärksamhet de senaste åren, har odlats i landet under flera årtionden. Majoriteten av skörden säljs på den lokala, instabila marknaden medan endast en mindre del säljs på exportmarknaden. Trots grödans långa odlingshistoria, dess betydelse för sysselsättningen inom jordbruk och handel, och dess värdefulla bidrag till statsinkomsterna, har få studier genomförts i Tanzania för att förbättra produktionen och handeln. Syftet med detta forskningsprojekt var därför att utvärdera grödans diversitet, produktion och handel i landet, med fokus på de södra höglandsområdena.

I syfte att belysa olika aspekter av avokadoproduktionen och handeln intervjuades 275 avokadoodlare, 231 handlare och 16 andra nyckelpersoner. Vad beträffar diversitetsstudien togs prover på 226 fröförökade avokadoträd i åtta olika distrikt och variationen studerades med hjälp av 14 morfologiska karaktärer och 10 DNA-markörer (SSR-markörer).

Analyser av intervjusvaren visade att odlarna i de olika distrikten producerade i genomsnitt 52 till 156 kg avokadofrukter per träd. De som odlade kommersiella sorter fick i allmänhet ett högre pris (0,45 US$/kg) än de som odlade lokala sorter (0,30 US$/ kg). Odlarnas medelinkomst per distrikt varierade från 24,38 till 74,88 US$ per träd. De som endast odlade kommersiella avokadosorter tjänade mindre per träd (25,63 US$), jämfört med dem som endast odlade lokala sorter (46,47 US$). Handlarnas upphandlingsförmåga under ca en vecka varierade från 14 till 349 kg. Kvinnor inom handeln visade på grund av sitt begränsade kapital en lägre kapacitet (64 kg/omkring en vecka) än män (212 kg/omkring en vecka). Frukternas kvalitet och värdekedjan inom produktionen påverkades av en rad olika faktorer, allt från jordbrukarnas felaktiga skötsel av odlingen och skördeteknik, via dåliga transportförhållanden, till avokadohandlarnas olämpliga lagring av frukterna. Förlusterna i de olika distrikten varierade från 9 till 33%. Ungefär 28% av odlarna och 79% av handlarna var nöjda med inkomsterna från avokadoproduktionen. 98% av odlarna och 100% av handlarna nämnde utmaningar som på olika sätt påverkar avkastningen och värdekedjan. Dessa utmaningar inkluderade begränsad rådgivningsservice, torka, sjukdomar och skadedjur, dålig marknadsföring samt fruktens korta hållbarhet. Att lösa dessa utmaningar är nyckeln till en ökad inkomst och förbättrade livsförhållanden för bönder och handlare. Detta gäller för alla grödor i allmänhet, och avokado i synnerhet, då produktionen av många olika grödor står inför liknande utmaningar.

De analyserade träden visade på en stor variation i morfologiska egenskaper som former på blad, plockfärdiga frukter och frön. Även de analyserade DNA-markörerna visade på en betydande genetisk diversitet. Dock var den genetiska differentieringen mellan distrikten låg (9,89%), medan differentieringen mellan individer inom distriktet var 5,28% och variationen inom individerna 84,83%. De flesta av de observerade morfologiska och genetiska karaktärerna var inte unika för ett specifikt område. Den begränsade differentieringen mellan de olika geografiska områdena kan förklaras av en introduktion av mycket likartat (över-lappande) genmaterial till mer än ett distrikt och utbyte av frön mellan olika distrikt och regioner.

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