

INSIGHTS ON THE POTENTIAL OF RNA-SEQ ON IMPROVING POMOLOGICAL TRAITS OF AFRICAN INDIGENOUS FRUIT TREES: A MINI REVIEW

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Abstract

Fruit tree improvement has taken great strides by roping in improved and efficient biotechnological tools to increase fruit yield and quality to meet local and export demands. For the past decade, the RNA-Seq tool has successfully been used in fruit tree improvement programs to identify genes, dissect complex traits, and understand different molecular pathways and differential expression of genes. However, despite their growing importance in food and nutrition security, medicinal uses, and climate change mitigation strategies, very little has been done to improve the pomological traits of African indigenous fruits, especially at the molecular level. African indigenous fruit trees exhibit unexplained variation in flowering, fruit load, fruit size, fruit ripening, fruit taste, fruit nutritional composition and shelf-life. The booming local commercial companies and export markets are demanding consistent quality indigenous fruits. This has necessitated the need for fast and effective tools that will hasten the understanding and improvement of fruiting qualities. The improvement of fruiting and fruit qualities will go a long way in accelerating the domestication and commercialization of African indigenous fruit trees. This review paper gives molecular biology insights on how RNA-Seq has been successfully used in fruit improvement of exotic fruits through gene identification, comparative transcriptome analysis under different conditions, and understanding molecular pathways that influence important pomological traits. The review article also unearths opportunities where RNA-Seq can improve our knowledge and improvement of undesirable traits common in African indigenous fruits.

Keywords: RNA-Seq, indigenous fruit trees, Africa, pomological traits, fruit quality.

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1. Introduction

African indigenous fruit trees are gaining global attention and recognition because of their potential role in hunger and poverty alleviation. Most indigenous fruit trees exhibit biotic and abiotic tolerance, particularly to dry and hot conditions, characteristic of most African drylands, which occupy over 43 % of the continent's surface [1]. These indigenous fruit trees are an important food source for inhabitants of drier marginal areas where exotic fruit trees hardly survive, making them ideal for climate change mitigation strategies. In addition, they have a big role to play in improving the food and income security of most rural livelihoods in Sub-Saharan Africa [2–6]. Wild indigenous fruit trees make up 20 % of the rural people's forest resources [7], where indigenous fruits are often collected in season and consumed either fresh or processed [8].

Although most African indigenous fruits are nutritive, antinutritive factors and compounds often derail their optimum utilization and full acceptability, such as trypsin, protease inhibitors, phytates, and

tannins [9, 10]. Because of some of these negative attributes, there is less preference for African indigenous fruits favouring exotic ones like grapes, strawberries, and apples, as reported by [11]. In addition, several studies have revealed much tree-to-tree and location-to-location variation in flowering, ripening, fruit size, colour, sweetness, and shelf-life. Such inconsistencies make it difficult to use indigenous fruits for commercial processing or sell them at export markets. Data from several studies suggest that many factors heavily influence the quantity and quality of chemical metabolites, notably environmental conditions [12].

Traditional knowledge of processing many African indigenous fruits into value-added products such as cakes, porridge, juices, and wines is widespread among local indigenous groups. However, there is a lack of scientific information on the underlying causes of the negative fruit attributes [13–15]. The lack of information on data that pertains to genetic characterization and the underlying genetic basis for the noted differences in fruiting and fruit qualities is possibly the primary reason for underutilization and lack of evidence on the commercial processing of these fruits in many African countries [16, 17]. Selection of valuable pomological traits (fruit shape and size, taste, flavour, suitability for processing to wine, juice, and other beverages) and resistance to abiotic and biotic stresses through systematically and scientifically outlined selection and breeding methods is lacking. Research on indigenous species is lagging despite this potential, especially molecular work. It is not reassuring, considering they have been a part of the African culture since time immemorial. Recognising their role in food and nutrition security in Africa, the African Orphan Crops Consortium (AOCC) took the initiative to sequence 101 orphaned crops to speed the breeding process [18]. Of the 101 African orphaned crops, only five fruit trees have been fully sequenced and curated. These are Marula trees (*Sclerocarya birrea*) [19], jackfruit (*A. heterophyllus* Lam), breadfruit (*A. altalis* (Parkinson, Fosberg) [20], Olive tree (*Olea europaea*) [21], and Argan (*Argania spinosa*) [22]. Continuous efforts towards similar work will provide valuable genetic data, such as the draft genomes of many African orphaned crops.

Ribose nucleic acid sequencing (RNA-Seq) is a powerful and useful tool for transcriptome analysis through deep sequencing technologies [23]. RNA-Seq is mainly employed for identifying, quantifying, annotating, and differentially expressing transcripts from different plant parts and environments. RNA-Seq technology has been an essential tool in sequencing species without reference genome information [24], which will be helpful for most African indigenous species, whose majority has not been fully sequenced yet. Identifying genes that influence a particular trait, either positively or negatively, is one approach to selecting plants with improved traits. As a result, important genes have been identified that are actively involved in the development and ripening of fruits [25].

2. Materials and methods

This systematic review focused on unveiling undesirable fruiting and fruit characteristics associated with edible African indigenous fruit trees and fruits. How these similar fruiting and fruit characteristics have been deeply understood and improved using RNA-Seq technology and how the same technology can be deployed to improve these undesirable characteristics.

Scientific literature on the undesirable fruiting and fruit traits of African indigenous fruit tree, how RNA-seq technology was used to understand fruiting and fruit traits of fruit trees exotic to Africa was sourced through relevant and established data bases such as Google scholar, Scopus, Directory of Open Access, Web of Science, ResearchGate, Science Direct, PubMed Central and African Journals Online. The search was optimised and narrowed down to variation in fruit and fruiting traits of African indigenous fruit trees, use of RNA-Seq on fruiting and fruit traits with particular attention to fruit trees exotic to Africa. Literature results were screened by title and abstract as reasons for inclusion, full texts reading was also done to remove material and studies that did not meet the inclusion criteria.

The results of the search are presented in the results and discussion section as a comparative study exposing undesirable fruiting and fruit traits found in indigenous fruit trees and how they can be deeply understood and solved using RNA-Seq tools, examples being cited.

3. Results and Discussion

African indigenous fruits' nutritional and health benefits have made them more attractive to the US and EU markets. A tangible example has been the authorisation of African baobab fruit

products into the European food market [26]. Opening such lucrative market opportunities fuelled a renewed interest in African indigenous fruits. Recent developments in export markets and organic, indigenous food-based industries have necessitated the quest for fruit yield and quality consistencies through cultivar development [27]. To fast-track cultivar development in African indigenous fruit trees, there is an imminent need to use powerful molecular biology tools such as RNA-Seq to understand molecular mechanisms underlying inconsistencies noted in flowering, fruiting, ripening, quality, shelf-life, and postharvest deterioration. Furthermore, to identify and discover putative and unigenes that control these traits of economic importance.

However, there has been relatively little or no literature published on RNA-Seq on African indigenous fruit trees or fruits to improve pomological traits. This lack of documented studies has created many research opportunities that await to be tapped. In addition, there are many grey areas where mechanisms that control certain important traits and behaviour are not fully understood or have not been studied yet. Therefore, this review section looks at some pomological challenges common to indigenous African fruit trees and examples of how RNA-Seq was used on fruits that are exotic to Africa to understand similar traits.

3. 1. Flowering dynamics

Successful sexual reproduction and fruit and seed setting in fruit trees depend on proper flower development. [28, 29] reported cases of monoecy, mostly in the *caffra* subspecies of *Sclerocarya birrea*. However, it is known as a dioecious species. In the unimodal areas flowering in the subspecies *birrea* and *caffra*, the woodland begins when the dry period is about to end, but it is less marked in the bimodal equatorial areas [30]. *Uapaca kirkiana* has been recorded to bear an unusually heavy fruit load every second year, possibly because of cyclic environmental stress or a condition known as alternate bearing [31]. Several researchers have deployed the RNA-Seq tool to decipher flowering dynamics on other fruits, [32] studied the flowering of the Chinese cherry (*Prunus pseudocerasus*) by performing a *de novo* transcriptome profiling of its flower buds. The study results identified APETA-LA3-like, MADS-box, and AGAMOUS-like as the genes related to the release of flower bud dormancy. [33] analysed the continuous flowering trait of Longan (*Dimocarpus longan*) using RNA-Seq. They identified candidate genes involved in regulating flowering, giving new insights into the molecular pathways involved in regulating the flowering time of woody plants. Finally, [34] used RNA-Seq to identify genes responsible for plums' early fruit and stone development (*Prunus domestica*). The study results are a testament that RNA-Seq data can be used for standard gene identification, thus providing reference genes for a specific experiment or tissues under study.

3. 2. Fruit ripening

The fruit ripening process brings major changes in the composition and content of phenols. Through these changes, fruits become sweet and good tasting. [35] reported significant variability in first fruiting in *Dacryodes edulis*, ranging from 3 to 22 years in Nigeria. Most *Uapaca spp.*, when left on the tree, fruits ripen unevenly [31]; 85 % of harvesters or users of *Adansonia digitata* have to climb the tree to harvest because the baobab fruits do not easily abscise when ripe [36]. Previous researchers have successfully used the RNA-Seq technique to understand fruit ripening dynamics on fruits exotic to Africa. First, [37] studied red-colouration pigments (anthocyanins) in plums (*Prunus salicina* Lindl.) using the RNA-Seq technique during fruit ripening. The study revealed 13 differentially expressed genes and transcription factors like bHLH and MYB, which may be involved in anthocyanin biosynthesis. Next, [38] studied fig fruit (*Ficus carica* L) ripening dynamics of tree-ripe and commercial-ripe harvesting stages. They highlighted that fruit quality is determined by the succulent receptacle, which serves as the edible part of the fruit and protective structure. Finally, [39] sequenced Chinese bayberry (*Myrica rubra* Sieb. and Zucc) using the RNA-Seq to examine changes that occur during ripening which affect fruit quality. The annotated unigenes provide a future platform for functional berry genomic research. In addition, the study provided a reference for future research on complex metabolism in non-model perennial species. The results from these studies show that the RNA-Seq technique can be successfully used to understand fruit ripening dynamics.

3. 3. Fruit size and yield

Fruit size plays a key role in determining the market or economic value of the fruit, African indigenous fruit trees exhibit a lot of fruit variation. Amarula tree (*Sclerocarya birrea*) exhibits big variations in fruit yield between trees in the forest compared to the cultivated ones [40], and tree-to-tree fruit yield variations were also noted on trees growing in the same native environment [41–43] also reported significant tree-to-tree differences in fruit loads in *Sclerocarya birrea*. Variations in fruit load and size in *U. kirkiana* species in the wild and fruit loads of up to 6,000 fruits per plant were recorded [44]. Most indigenous fruit tree yields are subject to season variations [31]. The genetics underlying fruit yield is more complex than earlier thought [45]; it differs from other fruit traits.

In the quest to understand genes influencing fruit size, [46] studied the regulatory mechanism that controls the fruit size of an apple (*Malus domestica*) using two varieties through RNA-Seq. KEGG analysis revealed that the phytohormone pathway was most enriched and that most DEGs were related to auxin signalling. They concluded that the findings suggest that auxins play an important role in fruit size development. [47] researched fruit size and shape in two *Cucurbita pepo* cultivars (small-fruit and large-fruit) through RNA-Seq technology. They reported that TUBULIN and KINESIN genes linked with the microtubules that influence cell expansion and cell division are highly upregulated in the cultivar with large fruits. Finally, [48] studied fruit size and shape variation in *Cucumis Sativus* L.; from the results, QTL and gene expression analyses showed variation in *Cucumis sativus* L. fruit shape and size. The study identified genes and molecular pathways influencing cell expansion and division and suggested candidate gene factors. The results from these examples show that variation in fruit size and yield of African indigenous fruit trees can be explained by using the RNA-Seq tool.

3. 4. Fruit quality

Fruit quality plays a major role in determining shelf-life and attracting consumers. However, there is much variation in fruit quality, especially regarding the nutritional composition of fruits from the same species in most African indigenous fruits. For example, [49] noted biochemical composition and pulp colour in baobab fruits from plants on different soil types, while [50] noted variation in fruit vitamin C content, pulp fraction, and weight in baobab fruits from areas that receive different rainfall regimes. Several studies also noted these variations in Mali's baobab fruit morphology, sugar and Vitamin C content [51–54] also observed variations in the fruit pulp chemical composition of *Uapaca kirkiana* fruit pulp from different places in Zimbabwe. Mng'omba et al. [55] also noted fruit taste and colour variations in *Uapaca kirkiana* species within Malawi and Zambia. There are also numerous reports of some trees of *Sclerocarya birrea* being exceptionally sweet compared to others in the same location [44]. [35] also observed large-quality variability in Nigeria's *Dacryodes edulis* H.J. Lam fruits. [56] conducted research to study Jujube (*Ziziphus jujube* Mill), comparing it with wild and cultivated jujubes (*Ziziphus jujube* var. *spinosa*) through comparative analysis. They identified key genes responsible for controlling sugar content and organic acid metabolism. The study offered valuable insights and provided important genomic resources for jujube improvement.

Apart from the variation in fruit quality, some indigenous African fruits also have volatile and antinutritive compounds that hamper their utilisation. The astringency, pungency, and volatile compounds in *Parinari curatellifolia* seem to have eclipsed the nutritional and health benefits of the fruit. Some indigenous fruits of importance in Africa, like baobab and marula, have substantive antinutritive compounds such as tannins, phytates, and oxalates [57]. In the quest to understand the genetic pathways responsible for these characteristics, several researchers deployed the RNA-Seq tool. [58] studied persimmon (*Diospyros kaki*) fruit, which is widely known for its unique astringent taste in mature fruits because of its hyper-accumulation proanthocyanidins during the fruit development stage. They did a comparative genomic analysis against *Diospyros oleifera*, a diploid persimmon species. The study sought to unveil the potential biochemical pathways responsible for astringency removal (proanthocyanidin insolubilisation) and development (proanthocyanidin biosynthesis). The study provided fundamental insights into the development and removal of astringency at the transcriptome level, which will be useful in persimmon fruit breeding programs. [59] studied the after-ripening process in Avocados (*Persea americana* Mill.) analysing flavonoids, fatty acids, tannins, and phenolics and screening for transcripts associated with after-ripening parameters. Their research study generated and screened transcription factors involved

in the after-ripening process in avocados. The information is important in controlling after-ripening and maintaining avocado fruit quality during storage. The examples show that the biochemical pathways and underlying genes responsible for astringency and tannins can be identified and understood.

3. 5. Shelf-life and postharvest quality

Postharvest management is critical for maintaining fruit quality. The arduous search for consistency in desirable fruit yields and quality for the current and upcoming food industries increased the quest for improved cultivars of African indigenous fruit trees [60]. However, the postharvest deterioration rate negates indigenous fruits' popularity and commercial value, as most succulent indigenous fruits in Africa are highly perishable. Fifty to seventy-five per cent of indigenous fruit marketers attributed fruit perishability as one of their biggest constraints [8]. [61] noted that *Uapaca kirkiana* fruits usually experience postharvest darkening in October because of higher temperatures, sunlight intensities, and low relative humidity. The same is also true for other subtropical fruits like *Litchi chinensis*. Although, *U. kirkiana* fruit skin gets soft when fully ripe [62], fruit ripening, darkening, sugar content, and fruit weight are affected by harvesting time [61, 63]. Postharvest quality deterioration under different conditions has also been reported in *Strychnos* species [64].

Several studies have shown that RNA-Seq can be successfully deployed to understand the underlying genetic mechanisms influencing postharvest deterioration. [65] researched mechanisms underlying pericarp browning and fruit senescence litchi fruit in (*Litchi chinensis* Sonn.) fruit by combining long-read sequencing and RNA-Seq. It was discovered that the expression of the isoforms linked to stress response and senescence was notably upregulated during the 'senescence onset' stage, and the expression of the isoforms linked to disease response, cell wall degradation, and oxidation was significantly upregulated during the 'browning' stage. [66] studied mechanisms underlying the controlled environment effect on mealiness in nectarines. RNA-Seq analysed samples under different conditions. The results showed that firm fruits had more differentially expressed genes (DEGs) than soft fruits, suggesting that the most important changes occur during cold storage. [67] conducted a research to identify genes responsible for fruit softening in the flesh of nectarines using quantitative trait loci (QTL) and expression quantitative trait loci (eQTL). The findings noted the over-expression of genes linked to auxin biosynthesis in the high soft rate (HSR) group, which translates to higher accumulation and expression of auxin, which triggers fast softening. Auxin homeostasis might clarify the low softening rate (LSR) linked with low auxin levels being altered. This research study explained the underlying genetic mechanisms behind the flesh-softening rate in nectarines and peaches, leading to molecular marker development.

To fully decipher and understand gene expression and interaction, there is a need to deploy powerful sequencing techniques like RNA-Seq as a big step towards improving the productivity of indigenous fruit trees in Africa. The examples above show a need to deploy transcriptomics using RNA-Seq to identify putative or unigenes responsible for such traits and fully understand gene expression and biochemical pathways influencing fruit qualities under different environments and physiological conditions. Improving these prohibitive traits and inconsistencies through cultivar development will hasten commercialization and utilization of indigenous fruits in Africa.

3. 6. Sequencing costs and training

The major constraints in using high throughput sequencing platforms for crop improvement have been the exorbitant sequencing costs and lack of training in bioinformatics, especially for many African institutes and scientists. With the advent of Oxford Nanopore and Pacific Biosciences (PacBio) sequencing technologies, the sequencing costs for the past five years took a significant knock [68]. Also, the constantly growing published genomic information is tangible evidence of plummeting costs [69–71]. The formation of the African Orphan Crops Consortium (AOCC) is intensively training the next crop of plant breeders. It comprises 116 plant breeders from 28 countries who have been extensively trained by the African Plant Breeding Academy (AFPBA) and are leading research in different institutions [18]. The increase in collaboration between African and international universities has helped secure international funding for competitive crop improvement Ph.D. programmes. As a result, the standard of education and expertise in crop improvement has significantly increased in several African countries [72]. Most bright African students also have a better chance of securing international scholarships at world-class

universities outside the continent to secure quality education. These training platforms are a testament that African scientists are now capacitated to be research leaders in improving indigenous fruit trees.

4. Conclusions

This review paper deciphered a powerful molecular tool that uses deep sequencing technology (RNA-Seq) for identification, discovering, and profiling putative and unigenes responsible for controlling fruiting and fruit quality traits to quicken the cultivar development. The review paper also unveiled potential research opportunities for RNA-Seq technology by citing major factors hampering the full uptake, utilisation, and domestication of African indigenous fruits. A comprehensive analysis of how RNA-Seq technology was effectively used in identifying and discovering genes, gene expression analysis, and understanding molecular pathways influencing important traits of many exotic fruits using tangible and recent examples. After a thorough review, it can be concluded that the RNA-Seq technology can be very useful in understanding underlying genetic mechanisms controlling important pomological traits of African indigenous trees and opening opportunities for fruit tree improvement programmes in Africa. The onus is now on researchers to exploit these opportunities presented by this powerful and effective RNA-Seq tool and improve the quality of African indigenous fruits. The review urges researchers to embrace and utilise this molecular tool, speed up indigenous fruit improvement in Africa, and close the gap in cultivar development between exotic fruits and indigenous fruits.

Conflict of interest

The authors declare that there was no conflict of interest in relation to this research, whether on authorship, personal or financial that could affect the research paper results.

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Data availability

The manuscript has no associated data.

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