
Review

Citron watermelon potential to improve crop diversification and reduce negative impacts of climate change

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Abstract: Citron watermelon (*Citrullus lanatus* var. *citroides*) is an underexploited and under-researched crop species with potential to contribute to crop diversification in sub-Saharan Africa and beyond. The species is commonly cultivated in the drier parts of Southern Africa, mainly by smallholder farmers who maintain a wide range of landraces. Understanding the molecular and morpho-physiological basis for drought adaptation of Citron watermelon in these dry environments can aid in screening local germplasm, identification of suitable traits for crop improvement and improving food system resilience among smallholder farmers by adding to crop diversification. This paper reviews literature on drought adaptation of *C. lanatus* spp. (C3 xerophytes), using the systematic review approach. The review discusses; (i) the potential role of citron watermelon in adding to crop diversification, (ii) alternative food uses and potential by-products that can be processed from citron watermelon and (iii) the role of Sub-Saharan farmers as key actors in conserving citron watermelon germplasm and biodiversity. Finally, the review provides a summary of significant findings and identifies critical knowledge gaps for further research.

Keywords: crop diversification, C3 xerophytes, food security, underutilized crops, drought adaptation strategies

1. Introduction

Citron watermelon belonging to the Cucurbitaceae family originated in Southern Africa [1]. It is a facultative xerophyte following the C3 photosynthetic pathway [2, 3]. The citron watermelon plant is a vine creeper with herbaceous stems up to 3 m long. Young stems and leaves are densely woolly, while the older parts become hairless. The leaves are herbaceous, sometimes unlobed, but usually 3-lobed. Both female and male flowers are on the same plant (monoecious) [4]. The fruits are formed in different shapes (subglobose, indehiscent globose, ellipsoid or oblong) and can be up to 200 mm in diameter. The rind of ripe fruit is hairless and smooth with different colours, usually mottled with irregular longitudinal bands. The flesh is firm and white, green-white or yellowish. The seeds are dicotyledonous, and typically red, white or mottled in seed coat colour.

Citron watermelon is mainly produced in Southern Africa [3]. Clustered data FAOSTAT [5] on melons (including cantaloupes) production show that production has declined in Southern Africa from 1990 to 2017 by approximately 44%. The decline in production is attributed to (i) pests and diseases, (ii) drought and (iii) poor agronomic practices. Although, until the beginning of the 1980s, citron watermelon was specific to countries in Southern Africa, since then, other regions have understood the potential and benefits of this plant. Consequently, both the research and production of citron watermelon have been growing steadily worldwide [4].

The young tender leaves and fruits of citron watermelon can be cooked as green vegetables, while the mature fruit flesh is mixed with maize meal to prepare porridge [6].

The flesh has a bitter taste when eaten fresh; however, it can be used to make preserves with sugar. The fleshy pulp contains pectins (natural gelatin), which is processed to make perfect preserves. Citron watermelon is a valuable stock feed during drought [7]. The seeds can be dried, roasted and eaten or ground into flour to make condiments. However, despite being a source of nutrition, farmers habitually discard citron watermelon seeds, sparing a few to plant in the next season.

Promoting the production and use of under-researched crops such as citron watermelon could offer potential solutions to mitigate the negative impacts of climate change (crop failure, hunger and malnutrition). This will contribute towards achieving the Sustainable Development Goals (SDGs) of the 2030 agenda, such as SDG 2 (zero hunger) and other interconnected goals such as SDG 1 (no poverty) and SDG 13 (climate change) [8]. The plant species has the potential of adding to crop diversity, boosting food security and local economies, strengthening rural development and promoting sustainable land-use. The inclusion of measures aimed at promoting crop diversification among smallholder farmers (who focus on growing few crops), is crucial in ensuring a broad food base and balanced nutrition for populations (both rural and urban) in developing countries. Therefore, crop diversification beyond over-reliance on a few food crops is vital in achieving food security.

Despite its potential contribution to food security, citron watermelon and other local/indigenous crops have been overlooked by both national and international research systems because (i) governments and policy-makers do not see their value as food or cash crops, and (ii) consequently, governments do not provide resources (funds) to promote their research [9]. The impact of having policy and government support for agricultural research is evident from the support given to the staple food crops (rice, wheat, maize and beans) which dominate human diets and have had their yields and nutritional values boosted over the years by breeding programmes. For example, these staple food crops have had their genomes mapped to the level of individual base pairs [10]. There is a need to focus attention on local/indigenous crops that have been previously neglected by research programmes because of their potential to add value and contribute to food security and improved livelihoods for smallholder farmers.

Research on previously neglected indigenous crops is increasingly being recognized and is receiving continental attention in recent times. For example, in 2011, the New Partnership for Africa's Development (NEPAD) committed to lead a consortium of companies, scientific and government bodies to sequence, assemble and annotate the genomes of 100 important Africa's neglected food crops. This consortium, African Orphan Crops (AOC) (africanorphancrops.org), aimed to train African scientists in plant breeding, techniques to improve these newly sequenced crops. The AOC worked to make more widely available genomes that are already sequenced. The knowledge and availability of these orphan crops allow African farmers to grow highly nutritious, productive, and robust crops, creating surpluses for the market.

Citron watermelon has received relatively little research attention as one of the neglected crops on the AOC list. Therefore, the current knowledge on citron watermelon's potential to improve crop diversity and contribute to improved livelihoods in smallholder farming systems, and in particular within the context of climate change effects is reviewed. Firstly, factors associated with citron watermelon adaptation to drought at morpho-physiological and molecular level and how this relates to yield performance are revised with a systematic review approach. Secondly, the potential role of citron watermelon in adding to crop diversification in the smallholder farming systems is presented. Thirdly, alternative food uses and potential by-products that can be processed from citron watermelon for small-scale processing and value-addition are discussed. Fourth, the role of Sub-Saharan farmers as key actors in the perpetuation of citron watermelon biodiversity is reviewed. Finally, the review provides a summary of the significant findings and identifies critical knowledge gaps for further research.

2. Materials and Methods

A systematic review approach was used, which aims to map the existing literature supporting the broad research question of the topic. The methodology for the systematic review was based on the framework outlined by Koutsos, Menexes [11]. The review included the following six steps: (i) scoping, (ii) planning, (iii) identification/search (iv) screening (v) eligibility/assessment and (vi) presentation/interpretation (Figure 1).

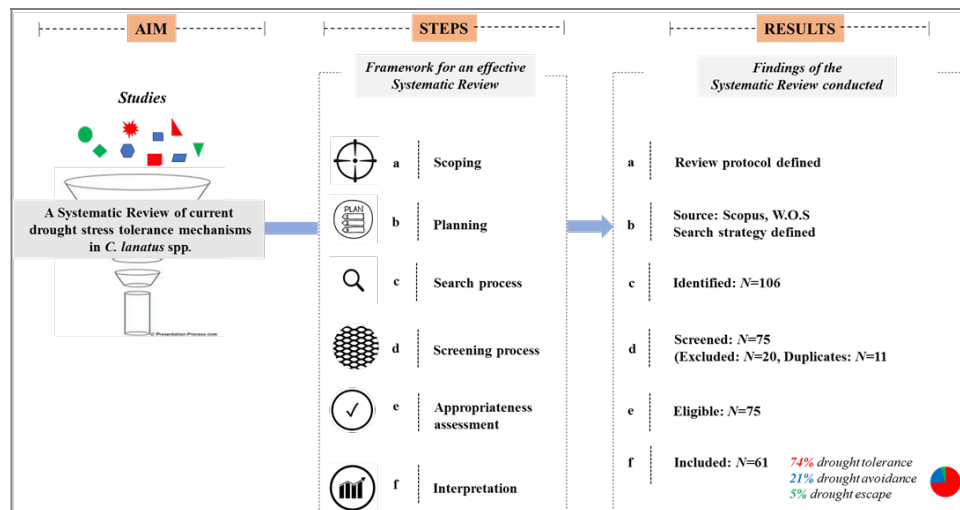


Figure 1: Framework used to perform a systematic review for current drought stress tolerance mechanisms in *C. lanatus* spp. [Adopted: Koutsos, Menexes [11]]

Research question

This review was guided by the question, “What is the current understanding of drought stress tolerance mechanisms in *Citrullus lanatus* spp.? Citron watermelon is a C3 plant which is known to be less photo efficient. It is worthy to know how this species deal with the problem of Rubisco having an affinity for oxygen at low CO₂ concentrations.

Data sources and search strategy

The search was implemented in five electronic databases: (i) Scopus (www.scopus.com), (ii) Web of Science (www.webofknowledge.com), (iii) Science Direct (www.sciencedirect.com), (iv) Science.gov (www.science.gov) and (v) Google Scholar (scholar.google.com). These databases were selected to be inclusive and cover disciplines in agriculture sciences. Limits on database search included peer-reviewed literature published from 1 January 1995 to 31 December 2019. The date range limitation was chosen in order to focus on contemporary literature on drought tolerance mechanisms. The search strategy employed broad search terms (Table 1) to ensure publications were not overlooked.

Table 1: Search strategy with Boolean operators for each database to identify peer-reviewed articles examining drought stress tolerance mechanisms in *C. lanatus* spp.

Database(s)	Main term(s)	Expanded term(s)
Scopus Web of Science Science Direct Science.gov Google Scholar	Drought stress	“water stress” OR moisture stress OR water deficit OR water shortage OR “water scarcity” AND
	<i>C. lanatus</i> spp.	watermelon OR citron watermelon OR desert watermelon OR wild watermelon OR melon OR muskmelon AND
	Mechanism(s)	“adaptation strategy” OR avoidance OR escape OR tolerance

Citation management

Citations were imported into the DistillerSR (Evidence Partners Incorporated, Ottawa, ON, Canada) web-based application and duplicate citations were removed using the duplicate removal function of DistillerSR. Subsequently, the title and abstract relevance screening and data characterisation of complete articles were carried out using DistillerSR.

Relevance screening and eligibility criteria

A two-step screening relevance technique was employed. For the first step of screening, the titles and abstracts of the articles were examined for relevance. Next, all citations considered relevant after the title and abstract screening went through a review of the full-text. Studies were eligible for inclusion if they were original articles on citron watermelon or *C. lanatus* spp. relevant to drought stress tolerance.

Data charting

The data collection categories included: author, year of publication, drought adaptation strategy, and key results. The data were compiled in a spreadsheet using the DistillerSR report function and subsequently imported into Microsoft Excel 2016.

Summarizing and reporting

A narrative synthesis approach was used to provide an overview of the existing literature. Firstly, a summary of the study findings was combined, considering the variations that may affect the generalization of drought tolerance mechanisms. Then, study results were organized into categories (drought avoidance, drought tolerance and drought escape) using thematic analysis techniques [12].

3. Results

Overview of studies identified

The review resulted in three main themes explaining drought adaptation mechanisms in *C. lanatus* spp. The three main mechanisms are drought avoidance (DA), drought tolerance (DT) and drought escape (DE). Table 2 summarize 61 studies from a systematic review on drought adaptation mechanisms conducted in the past 24 years (1995-2019). The drought tolerance (DT) mechanism had the highest number of articles (74%), followed by (DA) 21% and (DE) 5% (Figure 2).

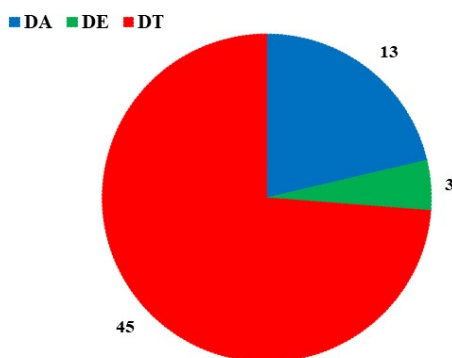


Figure 2: Pie chart summarizing studies on drought tolerance mechanisms in *C. lanatus*

In the past 24 years, scientists have investigated the morphology, genetic and molecular mechanisms of drought response to enhance the drought tolerance in *C. lanatus* spp. Drought tolerance mechanisms (45 articles) were more often investigated rather than DA (13 articles) and DE (3 articles). Drought tolerance studies in *C. lanatus* spp. included change in gene expression [13-23] and accumulation of osmolytes (citrulline,

glutamate, arginine) in leaves and roots [24-31]. Drought avoidance studies include reduced leaf water loss [32-35], enhanced water uptake [36-39] and accelerated transition from vegetative growth to reproductive growth to avoid complete abortion at the severe drought stress stage [35, 40]

Table 2: Summary of studies on drought adaptation strategies in *C. lanatus* spp. [DA: drought avoidance DT: drought tolerance DE: drought escape]

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Author	Title	Research summary	DA	DT	DE
[41]	Expressed sequence tag-based gene expression analysis under drought stress in wild watermelon	Changes in gene expression in roots within 6 h water stress. Genes involved in oxidative stress (glutathione peroxidase, glucose-6-phosphate-dehydrogenase, and ascorbate peroxidase) were demonstrated to be regulated by water stress.		✓	
[42]	Analysis of drought-induced metallothionein in wild watermelon	Gene (<i>CLMT2</i>) of the same homology with type-2 metallothionein contributed to the survival of wild watermelon under severe drought		✓	
[43]	Agrobacterium-mediated transformation system for the drought and excess light stress-tolerant wild watermelon (<i>Citrullus lanatus</i>)	Experimental basis for molecular studies of wild watermelon genes to help understand their contribution to stress tolerance in this plant.		✓	
[13]	Potent hydroxyl radical-scavenging activity of drought-induced type-2 metallothionein in wild watermelon	Gene (<i>CLMT2</i>) of same homology with type-2 metallothionein contributed to the survival of wild watermelon under severe drought		✓	
[44]	Functional analysis of DRIP-1, a drought-induced polypeptide in wild watermelon	Wild watermelon accumulates high concentrations of citrulline, glutamate and arginine in its leaves during drought		✓	
[45]	Dynamic changes in the leaf proteome of a C ₃ xerophyte, <i>Citrullus lanatus</i> (wild watermelon), in response to water deficit	Defense response of wild watermelon involves orchestrated regulation of functional proteins, of which HSPs play a pivotal role in the protection of the plant under water deficit		✓	
[46]	Molecular responses of wild watermelon to drought stress	Rapid accumulation of HSPs in stressed melons		✓	
[32]	Potential involvement of drought-induced Ran GTPase CLRan1 in root growth enhancement in a xerophyte wild watermelon	Ran GTPase (CLRan1), which is expressed in the roots of drought-resistant wild watermelon, functions as a positive factor for maintaining root growth under osmotic stress.	✓	✓	
[47]	Drought mediated physiological and molecular changes in muskmelon (<i>Cucumis melo</i> L.)	Increased activity of catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), and guaiacol (POD). Under drought stress, muskmelon elevates the abundance of defence proteins and suppresses catabolic proteins	✓	✓	
[14]	Identification, molecular characterization and expression analysis of RPL24 genes in three Cucurbitaceae family members: cucumber, melon and watermelon	Ribosomal protein L24 (RPL24) is responsible for stabilization of the peptidyl transferase activity. Increased expression of CmRPL24-01 genes in melon leaf tissue at 3 h upon polyethylene glycol treatment.		✓	
[48]	Identifying sources of water stress tolerance from wild species of the family <i>Cucurbitaceae</i> in vitro culture	Evaluating water stress tolerance capacity using the calus recuperation after dehydration under a laminar flux hot until a loss of 50% of their fresh weight as a basis.			
[15]	Genome-wide identification and comparative expression analysis of LEA genes in watermelon and melon genomes	Induction of LEA genes in root and leaf tissues after drought application		✓	
[49]	Foliar Application of Abscisic Acid and Sulfonamide Compounds Induced Drought Tolerance in Watermelon	Sulfacetamide and Sulfasalazine improve drought resistance like ABA, by increasing levels of proline, glycine betaine and malondialdehyde and the activity of ascorbate peroxidase.		✓	
[33]	The Apocarotenoid beta-Cyclocitric Acid Elicits Drought Tolerance in Plants	Volatile compound β -Cyclocitral (β -CC) in plant leaves when converted to β -cyclocitric	✓	✓	

		acid (β -CCA) it signals drought tolerance		
[50]	Assessment of watermelon accessions for salt tolerance using stress tolerance indices	GMP and STI indices indicated that G04 G14 and G21 could be prominent sources to develop drought tolerance.		✓
[40]	Effect of water stress on the carbohydrate metabolism of <i>Citrullus lanatus</i> seeds during germination	Stressed seeds lower the rate of $^{14}\text{CO}_2$ release from $[2-^{14}\text{C}]$ acetate, $[1-^{14}\text{C}]$ glucose, and $[6-^{14}\text{C}]$ glucose	✓	✓
[34]	Physiological responses of two contrasting watermelon genotypes exposed to drought and nitric oxide	Drought stress decreased fresh and dry weights of shoots and roots and lengths drought-sensitive genotype KAR 147	✓	
[51]	Biochemical effects of drought stress on two Turkish watermelon varieties are different and influenced by nitric oxide	MDA (a marker of oxidative damage on lipid membranes), was increased due to drought in watermelon genotypes and NO treatment slightly reduced the contents of MDA under drought stress.		✓
[16]	Expression Analysis of Five Arabidopsis PDLP5 Homologous in Watermelon Subjected to Biotic and Abiotic Stresses	Plasmodesmata-located protein 5 (PDLP5) controls cell-to-cell communication and defence signalling		✓
[36]	Establishment of a transgenic hairy root system in wild and domesticated watermelon (<i>Citrullus lanatus</i>) for studying root vigour under drought	A powerful tool for the comparative study of the molecular mechanism underlying drought-induced root growth in desert plants	✓	✓
[52]	Watermelon (<i>Citrullus lanatus</i>) late-embryogenesis abundant group 3 protein, CILEA3-1, responds to diverse abiotic stresses	A representative group of LEA proteins CILEA3-1 (Cl017745) can be used as an abiotic stress marker gene in watermelon		✓
[17]	Abiotic stress and tissue-specific reference genes for quantitative reverse transcription PCR analysis in Korean native watermelons, <i>Citrullus lanatus</i> 'Black-King' and 'Speed-Plus-Honey'	Reference genes (CIACT and CIEF1 α) were expressed in flowers, leaves, tendrils, stem, and roots after drought treatment		✓
[35]	Preferential decay of the CF1 epsilon subunit induces thylakoid uncoupling in wild watermelon under drought stress	Selective decomposition of epsilon subunit induces uncoupling of thylakoid membranes under drought, and contributes to the avoidance of over-acidification in the thylakoid lumen under excess light conditions.	✓	
[18]	Expression analysis of beta-glucosidase genes that regulate abscisic acid homeostasis during watermelon (<i>Citrullus lanatus</i>) development and under stress conditions	Beta-glucosidase genes regulate ABA content during drought stress		✓
[37]	Water relations and Abscisic-Acid levels of watermelon as affected by rooting volume restriction	ABA act as a signal for reduced growth of plants under Rooting volume restriction (RVR) conditions.	✓	✓
[53]	Comparative effects of ethylene inhibitors on Agrobacterium-mediated transformation of drought-tolerant wild watermelon	Controlling ethylene level during co-cultivation and shoot formation using the <i>cad's-harboring</i> Agrobacterium, enhances drought tolerance		✓
[54]	Proteomic analysis of avoidance and defence mechanisms to drought stress in the root of wild watermelon	Defence response of wild melons involves orchestrated regulation of functional proteins	✓	✓
[55]	Co-expression of cytochrome b_{561} and ascorbate oxidase in leaves of wild watermelon under drought and high light conditions	Levels of cDNA (CLb561A) mRNA and protein were elevated in the leaves during drought		✓
[56]	Genome-wide expression profiling of leaves and roots of watermelon in response to low nitrogen	Under abiotic stress, leaf tissues are more sensitive compared with root tissues. 9598 genes were differentially expressed, out of which 4533 genes were up-regulated and 5065 genes were down-regulated		✓

[38]	Mycorrhizal inoculation affects arbuscular mycorrhizal diversity in watermelon roots but leads to improved colonization and plant response under water stress	Plant inoculation with mycorrhizal fungi was related to the response of plants to water stress conditions by improving WUE	✓
[39]	Ectopic expression of Arabidopsis H ⁺ -pyrophosphatase AVP1 enhances drought resistance in bottle gourd (<i>Lagenaria siceraria</i> Standl.)	Wild-type plants showed minimal growth while the AVP-1 expressing plants resumed rapid growth displaying longer ramified primary roots	✓
[19]	Molecular cloning and in silico analysis of DREB-like gene in watermelon	DREB genes were identified from watermelon related to drought tolerant genes.	✓
[57]	Factors Affecting Germination of Citron melon (<i>Citrullus lanatus</i> var. <i>citroides</i>)	Citron melon can grow in a wide range of climatic conditions	✓ ✓
[58]	Vegetable grafting: a toolbox for securing yield stability under multiple stress conditions	Movement of mRNA through the phloem from rootstock to scion regulate plant growth and adaptation to drought stress	✓
[24]	Phytohormones regulate accumulation of osmolytes under abiotic stress	Osmolytes (proline, glycine-betaine, polyamines, and sugars) are accumulated to safeguard the cellular machinery. Phytohormones (abscisic acid, brassinosteroids, cytokinins, ethylene, jasmonates, and salicylic acid) modulates the accumulation of osmolytes	✓
[20]	Cloning and expression analysis of the Ccrboh gene encoding respiratory burst oxidase in <i>Citrullus colocynthis</i> and grafting onto <i>Citrullus lanatus</i> (watermelon)	Drought responsive gene <i>Ccrboh</i> is functionally important during the acclimation of plants to stress and it's promising for improving drought tolerance of other cucurbit species	✓
[59]	Gene expression changes in response to drought stress in <i>Citrullus colocynthis</i>	During drought, stress-responsive genes and plant hormones are involved in an extensive cross-talk	✓
[25]	Biochemical and molecular characterization of glutamate N-acetyltransferase involved in citrulline accumulation in wild watermelon during drought/strong-light stresses	Exogenous acetylene triggers the accumulation of citrulline to maintain the plant membrane structure	✓
[26]	Regulation of metabolic pathways for the massive accumulation of citrulline during drought/strong light stress in wild watermelon	Rapid accumulation of citrulline in leaves and shoot under drought stress	✓
[21]	Comparative identification, characterization, and expression analysis of bZIP gene family members in watermelon and melon genomes	Genes (ClabZIP and CmbZIP) were expressed in leaf and root tissues after the drought was imposed	✓
[22]	Comparative analysis of Calcium-Dependent Protein Kinase in Cucurbitaceae and expression studies in watermelon	The study provides insights into the evolutionary history of gene families in Cucurbitaceae, and indicate a subset of candidate genes for functional characterizations	✓
[27]	Glycinebetaine biosynthesis in response to osmotic stress depends on jasmonate signalling in watermelon suspension cells	Osmotic stress-induced glycinebetaine biosynthesis occurs via JA signal transduction and contributes to osmotic stress hardening	✓
[28]	Genome-Wide Identification and Expression Analysis of NF-Y Transcription Factor Families in Watermelon (<i>Citrullus lanatus</i>)	The study provides a foundation for further functional analysis of NF-Y proteins during watermelon development and responses to drought stress. The results will be valuable for evolutionary analysis of the NF-Y family in <i>Cucurbitaceae</i> species.	✓
[60]	Identification and expression analyses of WRKY genes reveal their involvement in growth and abiotic stress response in watermelon (<i>Citrullus lanatus</i>)	A total of 63 putative WRKY genes in watermelon were reported to regulate respective target genes	✓
[29]	Citrulline and DRIP-1 protein (ArgE homologue) in drought tolerance of wild watermelon	Wild watermelon accumulates high concentrations of citrulline, glutamate and arginine in its leaves during drought	✓

[30]	Programmed proteome response for drought avoidance/tolerance in the root of a C ₃ xerophyte (wild watermelon) under water deficits	Defence response of wild watermelon involves orchestrated regulation of functional proteins, of which HSPs play a pivotal role in the protection of the plant under water deficit	✓
[61]	Proteomic analysis of drought/strong light stress responses in wild watermelon leaves	DREB genes were identified from watermelon related to drought tolerant genes.	✓
[62]	Identification of drought-responsible proteins in the root of wild watermelon by proteomic analysis	DREB genes were identified from watermelon related to drought tolerant genes.	✓
[63]	Regulation of the root development mechanism involved in Ran GTPase of wild watermelon under drought stress	Ran GTPase genes function in watermelon development, as well as in response to abiotic stress and hormones	✓
[23]	Genome-wide identification and expression analysis of CILAX, CIPIN and CIABCB genes families in <i>Citrullus lanatus</i> under various abiotic stresses and grafting	Expression genes (CILAX, CIPIN and CIABCB) under drought helps to understand the roles of auxin transporter genes in watermelon adaptation to environmental stresses	✓
[31]	Antioxidant enzymes activities in leaves and yield analysis of different ecological types watermelon under drought stress	The content of proline, the activity of SOD, POD, CAT was genotype related	✓ ✓ ✓
[64]	Identification and characterization of the glutathione peroxidase (GPX) gene family in watermelon and its expression under various abiotic stresses	CIGPX genes function in watermelon development, as well as in response to abiotic stress and hormones	✓

4. Discussion

In response to water deficits or drought stress conditions, desert xerophytes have evolved a series of mechanisms at morphological, physiological, and molecular levels to proceed with normal plant function and metabolism. The mechanisms Figure 3 includes drought escape (DE) through early completion of a plant life cycle, drought avoidance (DA) through improved capacity of water absorbance by improved root system and shedding of leaves. Drought tolerance (DT) occurs through altering the metabolic pathway (for example, increased antioxidant metabolism).

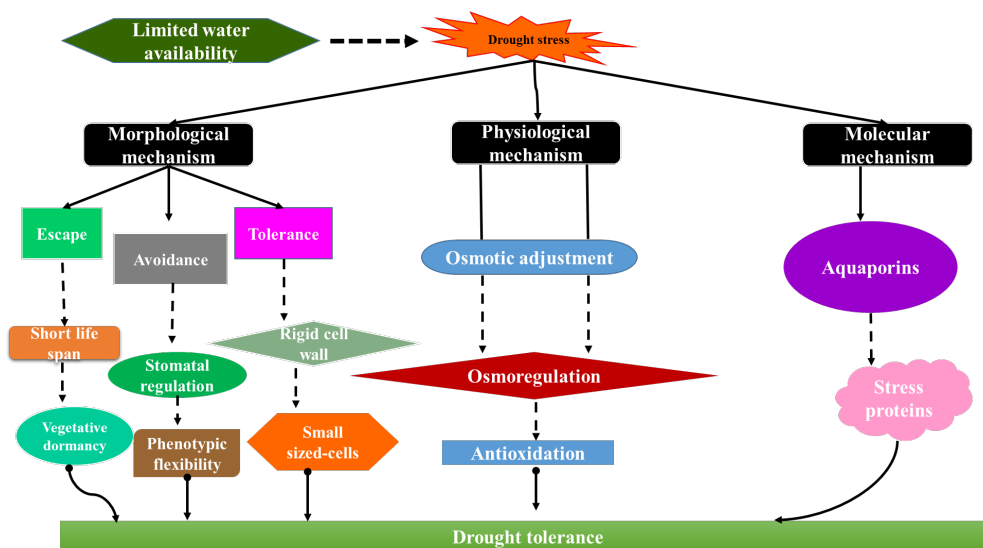


Figure 3: Plants adopting morphological, physiological and molecular behaviour under drought stress

Citrullus lanatus spp. have the capability to minimize water through transpiration by maintaining basic physiological processes under drought stress conditions, that is, adjusting morphological features (hairy leaf surface and shedding leaves) [65, 66]. Primarily DA is characterized by the maintenance of high plant water potentials under water stress conditions [67]. *Citrullus lanatus* spp. has been reported to respond to drought using the following DA mechanisms: (i) reducing water loss by partial closure of stomatal pores, leaf rolling [68], and wax accumulation on the leaf surface [69, 70]; (ii) enhancing water uptake ability through a well-developed ramified root system. [39], and (iii) accelerating/decelerating the transition from vegetative growth to reproductive growth to avoid complete abortion under severe drought stress [35].

Citron watermelon escapes drought by adjusting its growth period [71]. Plant phenology has a decisive effect on yield under water stress conditions. Early maturity in wild watermelon [32] was found to be correlated with root length density to leaf area ratio, which translates to the plant's ability to maintain high leaf water potential under soil moisture stress. Plants that escape drought, such as the desert ephemeral (*Alyssum alyssoides*), exhibit early flowering, short plant life cycle, and developmental plasticity [72]. Wild watermelon was reported to escape drought through early flowering rather than avoid drought through increased water-use efficiency [62]. While a short growth period is correlated with reduced yield potential, if the specified cultivar's target environment represents a definitive stress area, then the early genotype gain under stress outweighs its yield potential deficiency.

From the systematic review results, it is evident that our understanding of the molecular mechanisms underlying drought tolerance in *C. lanatus* spp. is limited to the accumulation of abscisic acid (ABA) and heat shock proteins (HSPs). Literature has not explained the role of phytosterols (a group of hormones that are essential for the regulation

of plant development and morphogenesis) under drought stress in citron watermelon. Future genome-scale studies involving stress signalling pathways in *C. lanatus* spp. are necessary, given that drought response is dependent on species and genotype. Data obtained from such experiments can be applied to build network models, which can then be used to establish link between phenotypic traits with regulatory mechanisms. In addition to this, current and future generation DNA sequencing technology, high throughput phenotyping platforms, and improved informatics resources, expediting gene discovery. Once this is achieved, a number of new genetic targets will be available for manipulation using transformation technologies in economically important plants.

Citron watermelon a C3 xerophyte has the ability to survive absolute moisture stress [73-75]. Despite its potential utility as source of genes for drought tolerance, functional genomics of *C. lanatus* spp. has been limited due to the lack of genetic approaches and complexity of the phenomenon, and there is a need to bridge this gap. However, with the realization of "omics" technologies it is possible to provide a comprehensive description of changes on the transcript, proteome, and metabolome levels during drought stress. The combination of the data should lead to a systems biology approach and identify target genes and critical metabolic pathways. The complete elucidation of this process would enable interpreting the incredible nature of C3 xerophytes (drought tolerance) and enable creation of a platform that is an alternative sustainable genetic resource for drought tolerant and less water-intensive agricultural systems.

Citron watermelon: potential contribution to human nutrition and health

Citron watermelon could potentially fulfil nutritional requirements while supplying compounds with health-promoting properties. In watermelon seeds (same family with citron watermelon), four proteinogenic amino acids (phenylalanine, threonine, tryptophan, and valine) have been identified, and proteins are accumulated in quantities higher than those found in cereals (10-15%). Watermelon seeds also contain vitamins A, C, D, E, and K and several antioxidants such as flavonoids [76]. Populations consuming flavonoids-enriched foods reveal low cancer frequency [77]. In addition, lactating mothers eating citron watermelon seeds can produce higher quality milk as seen in animal models fed with isoflavone-rich fodder [78]. Flavonoids can inhibit degenerative diseases like coronary heart disease, atherosclerosis, cancer, diabetes and Alzheimer's disease through their antioxidant activity and/or by modulating multiple protein functions [79]. In addition, the absence of gluten in citron watermelon seeds offers alternative nourishment for the celiac population (people with reaction to eating gluten), and it could counteract the increasing problems of obesity in the developed world. In less developed countries, citron watermelon could make a great contribution towards reducing malnutrition and death by hunger.

The preservation of citron watermelon biodiversity

Citron watermelon seeds of different accessions are currently being conserved in several seed banks around the world (*ex-situ* conservation). However, preserving agrobiodiversity means preserving also the associated culture, that of indigenous farmers living in the SSA region [80]. The importance of seed banks in the conservation of biodiversity is well known, and the success of future conservation and breeding programs hinges on the preservation of this diversity on-farm. Moreover, the transfer of indigenous knowledge and associated practices will help to adapt citron watermelon to new regions. Citron watermelon is a crop of family heritage; knowledge is acquired from the parents who have cultivated it since their childhood [81] Mujaju, Zborowska [82] pointed out that, the SSA farmers are a valuable resource because (i) they preserve the genetic diversity of citron watermelon in their fields, and (ii) they have the expertise for the agronomic management of their own accessions.

Industrial development is causing migration from rural areas to the cities [83]. In addition to the increasing demand for daily calories, this social and economic situation is changing land use and increasing the genetic homogeneity of the crop (few genotypes are

grown for commercial purposes). Due to better profits from staple crop exports and higher incomes from commercial farmers, small farmers are migrating, putting their cultural and agro-biodiversity heritage at risk [84]. It is, therefore, of primary importance to preserve small-scale farming where the greatest genetic diversity of citron watermelon and associated human culture is found [85]. In Southern Africa, citron watermelon is still grown in the major historical areas of cultivation (the province of Limpopo, the province of Matabeleland and the region of Omaheke), which remain an integral part of rural cultural heritage and identity [86, 87]. Citron watermelon is a promising crop in a broader context, but scientists and stakeholders must do all they can to preserve the heritage of citron watermelon so that this crop can continue to be cultivated in a sustainable way while contributing to food quality and security in the SSA region and worldwide.

5. Future research perspectives

Building on the literature examined, we identify six priority areas for research (summarized in Figure 4) and make recommendations for the short-and long-term development of citron watermelon as a crop species that could potentially contribute to food security under the changing climatic conditions.

Synchronization of research and methods

According to the Global Biodiversity Information Facility (GBIF) (<https://www.gbif.org/>), citron watermelon research and germplasm record include researchers from at least 10 institutions in 13 countries. Currently, despite positive national and international collaborations [88], citron watermelon research is still disconnected with interesting and relevant research programmes running in isolation [4, 89]. Partly, this review aims to draw together many disparate aspects of citron watermelon research to facilitate a body knowledge and collaboration by researchers. Also, we relate the experience of the BamNetwork (<http://bambaragroundnut.org/>), the online representation of the international research community on Bambara groundnut (*Vigna subterranea*), which sought to bring together the expertise and enable close collaboration, the sharing of materials, resources, data and technology. It is our view that citron watermelon research and food security in SSA could benefit from such an approach, with equitable and appropriate access and benefit-sharing agreements in place. Here, the suggestion is to develop a web database, which will act as an open repository for data emerging from citron watermelon research programmes.

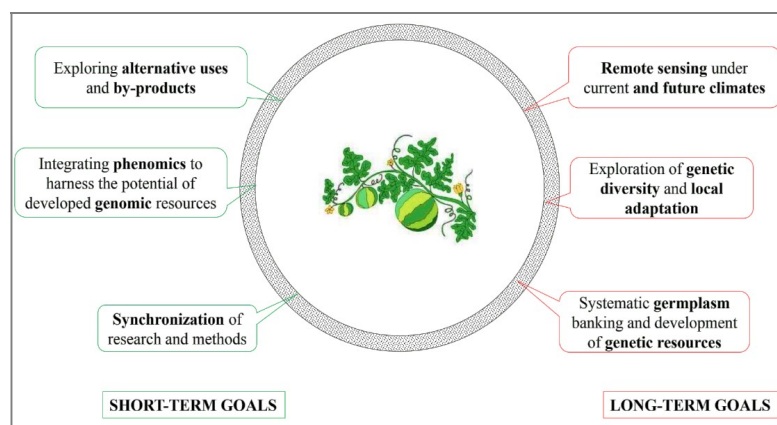


Figure 4: Roadmap for the sustainable development and exploitation of citron watermelon for food security and to support livelihoods

Integrating phenomics to harness the potential of developed genomic resources

The most productive farming land is facing biotic/abiotic stresses (fungal and bacterial diseases, heat, salinity, and drought stresses) [90]. All these biotic and abiotic

stresses exert tremendous survival pressure on crop germplasm. Under the prevailing conditions and available resources, new plant varieties with desired traits (drought tolerance) and high yield potential need to be developed. This can be achieved through a better understanding of the genetic makeup of plants (genomics) and their phenotype (phenomics) and the interaction between the two in different environments.

In this era of phenomics, high-throughput precise phenotyping helps to amass high-quality, accurate phenotyping data. The high-quality phenotypic data is useful for meaningful genetic dissection and genomics assisted breeding for drought stress. The earlier use of destructive plant phenotyping methods now gives way to high-throughput non-destructive, precise imaging techniques. Several phenomics platforms (<https://www.plantphenomics.org.au/>) are now available with facilities allowing scientists new windows into the inner machinery of living plants [91]. These facilities embrace (i) infrared cameras to scan temperature profiles/transpiration, (ii) incandescent microscopy to measure photosynthesis, (iii) 3D camera to record precise changes in growth responses after crop plants are exposed to stresses, (iv) lidars (light detection) to measure growth rates, and (v) magnetic resonance imaging (MRI) to examine root/leaf physiology.

Exploring alternative uses

Citron watermelon has the potential to produce other valuable by-products. The leaves can be cooked as vegetables and seeds can be roasted as snacks, ground into a powder and used as a condiment. Exploring alternative uses requires the input of indigenous knowledge from the local farmers where the crop is grown through conducting ethnobotanical surveys. In India, high-value protein and oils are extracted from seeds of closely related species (Mateera Beej) [92]. The seeds contain 35-50% crude protein, 28-40% oil and minerals in significant quantities. Further, the oil contains more than 80% unsaturated fatty acids, with linoleic acid being the dominant fatty acid (68.3%). In citron watermelon, the chemical basis and nutrient composition have not been explored. Alka, Anamika [93] reported pharmacological activities (treatment of urinary tract infection, bed wetting, dropsy and renal stones) of *C lanatus*.

Remote sensing under current and future climates

Estimates of the land area under citron watermelon cultivation [94] and associated yields are highly variable. They have been hampered by (i) poor record-keeping and (ii) difficult access to remote areas. The short-term nature of citron watermelon cultivation, local differences in cultivated landraces, plant growth rates, agronomic practice and dependency on co-staple crop productivity in any given period make estimating citron watermelon production difficult. Therefore, standardized empirical analyses for both land area suitable for citron watermelon cultivation and area currently under cultivation, yield components and inter-annual trends are lacking.

Improvements in the resolution and accessibility of satellite data from National Aeronautics and Space Administration (NASA) products such as Moderate Resolution Imaging Spectroradiometer (MODIS) and Sentinel 2 are increasingly applied to vegetation and crop surveys [95, 96]. Therefore, in the near term, there may be a potential to use freely accessible satellite data to monitor citron watermelon production directly. Furthermore, this approach could be applied to mapping crop suitability of citron watermelon. Concomitantly, upgraded regional bioclimatic datasets (Worldclim2) and an improved network of climate stations and data loggers will allow better characterization of the citron watermelon environmental niche and stress conditions. The impact of climate change under a range of future scenarios is yet to be quantified for citron watermelon and will form an essential part of any future development strategy.

Exploration of genetic diversity and local adaptation

Citron watermelon genetic diversity distributed across different environmental conditions indicates that the process of domestication might have facilitated the adaptation of landraces to local conditions, and indeed to a wider range of conditions than its

wild progenitor. Since citron watermelon is propagated by seed, this represents a powerful system to investigate the genomic basis of drought adaptive traits. Key steps to achieve this would be the characterization of existing citron watermelon genetic diversity using high-resolution genomic markers, standardized methods to measure fitness and yield as well as robust monitoring of environmental conditions. Concurrently, assessing the risk of erosion to citron watermelon genetic diversity through the loss or decline of landraces should be a priority for future citron watermelon monitoring strategies. In the medium term, this could similarly be extended to monitoring of crop wild relative diversity. In the long term, with the prerequisite knowledge of germination biology, novel sexual breeding using mapping populations and pan-genomic sequencing may enable the development of improved genotypes, tolerant of disease, better adapted to current and future climates, with desirable yield and by-product attributes.

Systematic germplasm banking and development of genetic resources

In global *ex situ* germplasm collections, *Citrullus lanatus* species, and particularly citron watermelon landraces, are currently severely underrepresented [87]. This chronically reduces the potential for plant breeding and crop improvement. In the long term, under scenarios of habitat loss, agricultural intensification, disease spread, climate change and introduction of high-yielding genotypes, citron watermelon as an invaluable plant genetic resource is at risk of losing genetic diversity and consequently leading to the loss of genetic diversity.

While a large number of landraces are present among subsistence farmers in sub-Saharan Africa, citron watermelon germplasm management is vulnerable to outcrossing and poor documentation and needs commitment to proper maintenance [89]. Therefore, further exploration of the potential for germplasm banking from a wide range of spatial and environmental conditions is a crucial research objective. Conventional breeding and *ex-situ* seed conservation also require an understanding of desiccation, longevity of storage, and, essentially, the germination requirements. As with citron watermelon, much of this is not well understood. With appropriate access and benefit-sharing agreements, germplasm could be incorporated into established seed banks, benefiting research and sustainable exploitation, and also safeguard an essential tropical crop.

In Nepal, a digital information system is currently under development as part of the Nepal Seed and Fertilizer (NSAF) project, funded by the United States Agency for International Development (USAID) [97]. This system allows easy access to an electronic seed catalogue with features and sources of all registered varieties, at the same time, the balance sheet collects and shares information on seed demand and supply by all stakeholders in real-time.

6. Conclusion

Under the context of climate change and crop production, Citron watermelon is an interesting plant species whose capacity to tolerate adverse environmental conditions (water stress) and remarkable nutritional qualities warrant further research in all fields of plant biology, agronomy, and ecology. We projected short term and long-term goals integrating the fundamental factors that explain and determine the future of citron watermelon, in terms of food security, biodiversity conservation, and crop diversification. Additionally, smallholder farmers should be encouraged to rely on a wider range of genotypes in order to sustain small-scale crop production and their economic, social, and cultural interactions. This will reinforce local conservation dynamics and ensure the sustainability of citron watermelon locally and around the world.

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