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Recent Advances in Tomato Breeding and Production

Edited by Seloame Tatu Nyaku and Agyemang Danquah

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and **Agyemang Danquah**

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Notice

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Meet the editors

Dr. Seloame Tatu Nyaku's research interests are in host-plant interactions and application of integrated control measures for management of nematode and fungal pathogens on plants, including indigenous crop species. His other areas of expertise include designing Real-Time PCR assays, and analyzing data from multiple sources including complex whole genome, transcriptome, and population genomics through the use of bioinformatics tools available from numerous public and private sources. His current research focuses on the application of grafting techniques for tomatoes, utilizing nematode-resistant root-stocks, together with imploring useful rhizosphere microorganisms for nematode and fungal control.

Dr. Agyemang Danquah is the Head of Tomato Research at the West Africa Centre for Crop Improvement (WACCI), University of Ghana, and Coordinator of Teaching Programmes and Postgraduate Curriculum Development. His research focus is primarily on using Demand-Led Plant Breeding approaches to develop and deliver improved varieties of tomatoes to Farmers in Ghana. His current works include developing resistance to tomato yellow leave curl virus, fusarium wilt, extended shelf-life and processing type tomatoes for the local industry.

Contents

Foreword

Globally, tomato improvement has traversed a pathway spanning breeding for increased yield in the 1970s, extended shelf life in the 1980s, and enhanced organoleptic properties in the 1990s. Current efforts still include all these as well as nutritional quality and resistance to biotic and abiotic stress factors of the environment.

In most developing regions of the world, tomato breeding efforts are fragmented, uncoordinated, and poorly documented, leading to overlaps and duplications, resulting in only moderate gains compared to achievements in the more technologically advanced regions. The moderate gains in developing regions have been achieved using limited inputs by way of skilled personnel, infrastructure, and funds.

Recent Advances in Tomato Breeding and Production documents efforts by scientists working in typical developing country environments, using basic and widely tested methods and simple techniques the results of which are applicable and/or adaptable to similar environments. The focus is work carried out mostly in Ghana, but contributions from Brazil, Indonesia, and Iraq give this compilation an international/interregional flair that should appeal to a wide readership. The knowledge shared in this book is relevant to current tomato breeding and production efforts and will fill the gap as a useful reference material for undergraduate and graduate students and researchers working especially in related environments.

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Preface

Tomato production is limited by abiotic and biotic factors (fungi, bacteria, viruses, and nematodes). There are however various methods currently employed to address these challenges. This book "Recent Advances in Tomato Breeding and Production" focuses on two main themes: (i) disease and pest management in tomato production, and (ii) breeding tools and improvement of the tomato. These themes will be expanded on to include tomato breeding/production methods e.g., application of grafting techniques for disease control, where a scion of a susceptible plant is grafted onto a resistant root-stock against a biotic agent, the use of integrated management methods, e.g., good agronomic practices (GAPs), application of plant botanical extracts with fungicidal properties, and biological control agents such as *Trichoderma harzianum* to manage damping-off in tomato seedlings. Plant growth promoting Rizobacteria (PGPR) e.g., *Pseudomonas s*pp. and *Bacillus* sp. enhance growth and development of tomato plants and also provide protection against plant pathogens. Other chapters will focus on germplasm collection and screening, through morphological and molecular characterization for identification of resistance to biotic and abiotic stress. Modern-day tomato cultivation makes use of soilless media and controlled environments e.g., hydroponics, simple high tunnel structures, and automated screen and greenhouses. Marker assisted selection (MAS) is a conventional breeding tool where molecular markers linked to specific traits are identified. Other strategies include marker assisted backcrossing and recurrent selection for tomato breeding against stress. These studies can be complemented with understanding of the genotype x environment interactions for varietal development. I believe the chapters will be useful to university students and researchers.

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Section 1

Disease and Pest Management in Tomato Production

Chapter 1

Grafting: An Effective Strategy for Nematode Management in Tomato Genotypes

Seloame Tatu Nyaku and Naalamle Amissah

Additional information is available at the end of the chapter

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Abstract

Research focus currently relies on combinations of environmentally friendly approaches among which is grafting for pathogen management. Grafting has potential to provide resistance to multiple soilborne pathogens, for example, nematodes, after a susceptible plant (scion) is united with resistant rootstocks. Sources of resistant rootstocks include species from the same family or closely related species, hybrids, and weeds. This chapter focuses on the following themes: (1) grafting and cost implications, (2) rootstock selection and tomato grafting against root-knot nematodes, (3) grafting techniques and requirements and graft union formation, (4) fruit quality of grafted plants, and (5) screening of rootstocks against root-knot nematode and identification of markers linked to Mi gene in rootstocks. Tomato rootstock breeding efforts, if coordinated properly, can lead to production of rootstocks, which can be adapted to specific environments and abiotic stresses.

Keywords: grafting, root-knot nematode, tomato, management, rootstock

1. Introduction

Grafting is the deliberate joining together of a scion and rootstock, taken from different but compatible plants, which are taxonomically close, to produce a composite plant. The scion, which forms the top portion, is selected for its desirable attributes, such as better yields, bigger fruit sizes, or preferred flavor. The rootstock onto which the scion is grafted is selected for reasons such as its vigorous growth and resistance/tolerance to soilborne diseases and pathogens as well as its ability to withstand soil extremes [1]. The technique of grafting vegetables originated from Japan and Korea in the late 1920s. The first record of an interspecific graft for increased yield and pest and disease control was reported in Japan between

watermelons [*Citrullus lanatus* (Thunb.) Matsum and Nakai] as scion and squash (*Cucurbita moschata* Duch.) The watermelon grafting technique was then widely introduced to farmers in Japan and Korea between the 1920s and 1930s; later, the technique was extended to grafting of other vegetable crops *Cucumis sativus* L. [2] and *Solanum melongena* L. in the 1950s [2] and then to *Lycopersicon esculentum* Mill [1].

Vegetable grafting is implored to impart resistance to soilborne pathogens, for example, nematodes [1, 3] and increase yields [3] and tolerance to abiotic stress conditions [4–8].

Tolerance to soilborne diseases is one of the main reasons why vegetable grafting is practiced. Rootstocks are selected based on their tolerance to common vegetable production diseases caused by *Verticillium*, *Phytophthora*, *Fusarium*, and nematodes [3, 9–11].

Vegetable grafting has been shown to increase fruit yields of vegetables such as tomato and eggplants and enhances nutrient uptake together with improved water use efficiency [3, 12]. An improved water use efficiency and nutrient uptake enables grafted plants to withstand short dry spells and also increase photosynthetic activity. Eggplant rootstocks have the ability to withstand flooding conditions for several days [13].

2. Grafted tomato plants and cost implications

There are cost implications in any grafting venture, and these must be properly considered before beginning a grafting project. A positive or negative net return is mainly dependent on the cost of producing the grafted plants and the prevailing market price for the tomato fruits that will be produced [14]. Falling tomato prices coupled with high input cost for raw materials needed for grafting may result in some negative net returns. The net returns are also sensitive to the vigorousness of the rootstock and that the higher the marketable fruits, the higher the net returns. Costs of grafted plants (including seed, labor, and cost of other materials) have been estimated as $0.78 per grafted plant for 1000 plants per season in a small nursery [15]. Other investigators have also estimated the production costs of grafted and non-grafted seedlings at $0.67 and $0.15 per plant, respectively, in the production of fresh market tomato in Florida, USA [14].

Generally, labor cost represents a small proportion of the total cost of grafting, and the majority of the cost goes into the purchase of root stock seeds that are specially bred and forms 36% of the total cost [16]. However, apart from the cost of seeds, other inputs such as grafting clips and building a humidity chamber serve as additional cost.

Grafted transplants are more expensive to produce per plant than nongrafted plants. Therefore, a lower cost of rootstock can easily boost the rate at which farmers adopt this technology [15].

3. Rootstock selection and tomato grafting against root-knot nematode

Grafting a selected crop variety on to another is based on the genetic attributes of both crop varieties. Farmers select rootstocks with desirable genetic properties, for example, resistance

to nematodes, flooding, salinity, extreme temperatures, and increased yield production. Tomato and eggplants are the most grafted plants in the Solanaceous family, although crops of the cucurbitaceous family (melon) are also utilized [17].

The most common rootstocks used for commercial tomato grafting are hybrids (F1) or interspecific hybrids, which have been specifically bred for resistance against pathogens and other diseases such as nematodes, *Verticillium* wilt, and *Fusarium* wilt. Hybrids are produced by crossing selected tomato varieties with other wild *Solanum* species with the genetic ability to offer resistance to specific diseases and pathogen infection [18].

In Europe, tomato hybrids are used as rootstocks compared to other *Solanum* spp., because of their high level of genetic improvements [17]. There are other plants that share the same family with tomato (*Solanum torvum, S. aethiopicum*, and *S. macrocarpon*); these can serve as rootstocks for their tolerance to waterlogged and drought conditions, *Fusarium* wilt, and root knot nematode infestation [13]. Most eggplant lines utilized will graft successfully with tomato lines. Rootstocks selected should be resistant to bacterial wilt (caused by, for example, *Ralstonia solanacearum*) and other soilborne diseases. The Asian Vegetable Research and Development Centre (AVRDC) recommends eggplant accessions EG195 and EG203, which are resistant to flooding, bacterial wilt, root-knot nematode (*Meloidogyne incognita*), tomato *Fusarium* wilt (caused by *Fusarium oxysporum* f.sp. *lycopersici*), and southern blight (caused by *Sclerotium rolfsii*) [13]. Grafting of a tomato variety "Pectomec" onto *S. aethiopicum* and *S. macrocarpon* in the University of Ghana Farm, Legon provided resistance to *Fusarium* wilt caused by *Fusarium oxysporum*; however, nongrafted tomato plants had a disease intensity of 46% (**Table 1**) and were highly diseased [19] (**Figure 1**). Grafting success of the tomato variety "Pectomec" onto *S. aethiopicum*, *S. lycopersicon* "Mongal F1," and *S. macrocarpon* was poor with the rootstock *S. lycopersicon* "Mongal F1" [19] (**Table 2**).

An ideal rootstock for tomato grafting should not only be resistant to pathogens, but also have high compatibility with the scion of tomato, with the ability to express a high level of vigorousness and resistance to pest and diseases. Rootstocks with very high levels of vigorousness compared to the scion may result in the tomato grafts being more vegetative with less fruit yield and quality [20]. Rootstocks selected should be resistant to bacterial wilt and other soilborne diseases. The tomato line (Hawaii 7996) has a high level of resistance to bacterial wilt and *Fusarium* wilt and is a recommended variety by AVRDC [13].

In developing countries, the use of tomato hybrids as rootstocks is limited because of the costs of imported hybrid seeds. Therefore, the use of eggplants as rootstocks is the most common

Treatment	NRP	NDRP	DI (%)
Control	24	11	46
P/SM	24	0	0
P/SA	24	0	0

NRP = Number of recording plants; NDRP = Number of diseased recorded plants; DI = Disease intensity (%); P/SA = Pectomech grafted onto *Solanum aethiopicum*; P/SM = Pectomech grafted *Solanum macrocarpon*. Agyeman [19].

Table 1. *Fusarium* wilt disease intensity of grafted and nongrafted tomato plants onto solanum rootstocks.

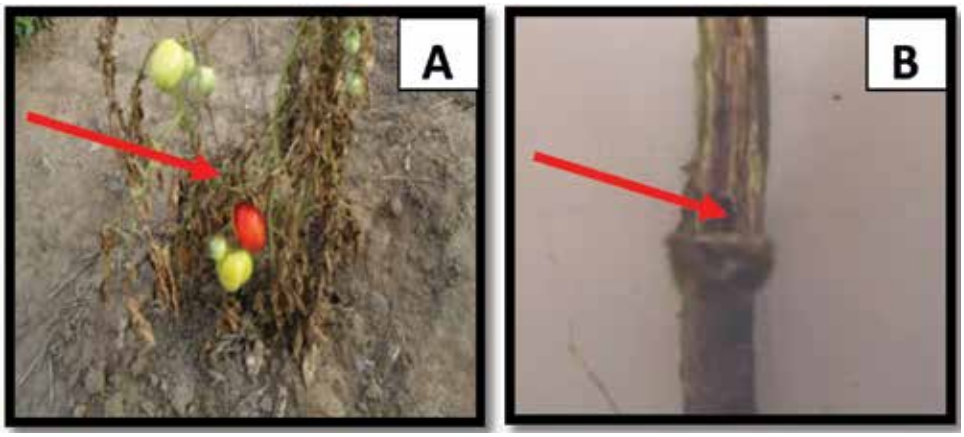

Figure 1. Symptoms of fusarium wilt disease of tomato variety "Pectomech". (A) Advanced symptoms (browning and wilting of leaves—red arrow), (B) Browning of tomato vascular tissues (red arrow).

Rootstocks	Number of grafted plants	Graft success	Percentage (%) graft success
P/M	196	2	1
P/SM	196	184	94
P/SA	196	185	94

P/M = Pectomech grafted onto *Solanum lycopersicon "*Mongal F1"; P/SA = Pectomech grafted onto *Solanum aethiopicum*; P/SM = Pectomech grafted onto *Solanum macrocarpon*. Agyeman [19].

Table 2. Grafting success of Pectomech onto three *Solanum* rootstocks.

method, of choice with *S. torvum, S. macrocarpon,* and *S. aethiopicum* being the most selected eggplants [21]. In rootstock selection, the eggplants are exposed to the biotic agent in pot or field evaluations, and tolerant or resistant rootstocks are selected for grafting experiments.

In a grafting study by Owusu et al. [22], against root-knot nematodes, five tomato cultivars were selected with "Big Beef," "Celebrity," and "Jetsetter" being resistant to *Verticillium* wilt, *Fusarium* wilt, nematodes, and tobacco mosaic virus (VFNT), which served as the nematode-resistant rootstocks, and "Tropimech" (VF) and "Power" (locally grown nematode-susceptible cultivar) served as scions. Grafted plants had the least nematode populations in the plant house. In field experiments, nematode population levels were lower in "Power" that had been grafted on Celebrity, Jetsetter, and Big Beef rootstocks, compared to self-grafted or ungrafted "Power". Fruit yields were also higher in the grafted plants utilizing resistant rootstocks than nongrafted plants.

In another study, grafting for root-knot nematode management in heirloom tomato production was undertaken. Susceptible heirloom tomato cultivars (*S. lycopersicum* "Brandywine" and *S. lycopersicum* "Flamme") were grafted onto two hybrid rootstocks (*S. lycopersicum* "Multifort" and *S. lycopersicum* "Survivor"); the non-grafted and self-grafted plants served

as controls. Results revealed that root damage or galling significantly reduced by 81% in the hybrid rootstocks, compared to the controls. There were, however, no clear correlations between root galling and total tomato yields [15].

Tomato grafting onto a resistant rootstock of wild brinjal (*S. sisymbriifolium*) under farmers' field conditions at Hemza of Kaski district against root-knot nematodes was undertaken. The root system of the grafted plants was free from gall formations; however, nongrafted plants had an average of 7.5 gall index (GI). Fruit yields significantly ($P > 0.05$) increased by 37% in the grafted plants compared with the nongrafted plants [23]. Eight wild *Solanum* rootstocks and two tomato hybrids were screened against root-knot nematode infection. Results revealed that the *S. sisymbriifolium*, *Physalis peruviana,* and *S. torvum* had the least galls per 10 g root (6, 5, 5) and females per g root (2, 2, 2), respectively, and showed the highest level of expression of phenolics and defense-related enzymes viz., peroxidases, polyphenol oxidases, phenylalanine ammonia lyase, and acid phosphatase from leaf samples, compared to the susceptible tomato scion (US-618) [24]. In a previous study, two garden egg rootstocks *S. torvum* and *S. aethiopicum* were poor hosts of *M. javanica* and *M. incognita* [25].

4. Grafting techniques

A successful grafting technique is one that would unite the scion and rootstock and enable both sections to grow together as a composite plant. The scion could be a small piece of shoot with several buds or a single bud that has been removed from an existing plant. The rootstock on the other hand forms the lower portion of the graft that forms the plant's root system.

Several grafting techniques are used by farmers for various tree crops and vegetable production generally. In grafting of vegetables, methods such as the splice, whip and tongue, hole insertion, and pin and cleft grafting methods can be used. However, the splice/tube grafting and cleft/wedge grafting are most commonly used because of the relative ease and strong vascular connection formed between scion and rootstock. It can also be used on seedlings with age ranging from 3 to 4 weeks [26].

With the splice grafting method, slanting cuts are made on both the scion and the rootstock at an angle of 45°, and the cut surfaces are then joined together to ensure the cambium layers of the scion and the rootstock, which are properly aligned. The joined surfaces are held firmly in place with the help of a grafting clip or tube.

The cleft graft method on the other hand, involves making a clean horizontal cut on the rootstock 5 mm below the cotyledon; a 4-mm vertical incision is then made in the middle of the root stock. The scion is then sharpened in the form of a wedge and gently inserted into the incision made in the rootstock.

The selection of a particular grafting method or technique depends on the skill of the person carrying-out the grafting and the ease with which the technique can be carried out. Other factors such as the type of vegetable crop and the sowing period of the rootstock and the scion are also considered. For instance, some farmers prefer using the whip and tongue technique

when grafting cucumbers because the seedlings of cucumber are large (hypocotyl length and diameter), making the grafting process easy [27].

The tube grafting method also has a high percent graft rate. The grafting of two tomato cultivars ("PG3" and "Beaufort") using the tube and the cleft graft methods resulted in a high-percentage graft rate (79–100%), an indication of the suitability of both methods for tomato grafting [28].

5. Requirements and graft union formation

There are five requirements critical to achieve a successful graft union: (1) the scion and rootstock should be compatible, (2) proper cambial alignment between scion and rootstock, (3) enough pressure to keep the cut surfaces firmly together, (4) avoidance of desiccation by maintaining high humidity around the cut surface, and lastly (5) both plants should be at the proper physiological stage for grafting to occur [29]. Good craftsmanship is an important requirement that brings the five requirements together. Graft union formation in compatible species involves a number of stages. In the first stage, parenchymatous cells are formed on the cut surfaces of the scion and rootstock followed by the interlocking of the callus between scion and rootstock leading to the formation of a callus bridge. This is followed by the differentiation of cells and the formation of the vascular cambium across the callus bridge between the scion and the rootstock and the eventual connection between phloem and xylem of the scion and rootstock to form a composite plant. The vascular connection lays the foundation for the transport of nutrients and water [30]. In tomato grafting, the formation of the xylem and phloem vessels occurs 8 days after grafting is performed [31].

Graft incompatibility refers to the inability of a graft union to form or grow properly between a scion and a rootstock, because of certain physical or chemical characteristics of the scion and rootstock. This leads to major setbacks in grafting operations, which may have economic implications in terms of grafting percentage and fruit yield. The response of Solanaceous plants to graft incompatibility may differ based on the combination of the scion and the rootstock selected. Severe incompatibilities have been observed in, for example, tomato/pepper (scion/rootstock) grafts, while moderate incompatibilities have been observed in eggplant and tomato (scion/rootstock) grafts. This is related to yield and the number of grafted plants that survived after grafting [32].

Rootstock regrowth, also referred to as "suckering" or adventitious bud growth, usually occurs about 14 days after grafting success. The regrowth becomes vigorous and occurs beneath the graft union on the rootstock. Usually both rootstocks (*S. macrocarpon* and *S. aethiopicum*) exhibit adventitious bud regrowth (**Figure 2**).

Monocotyledonous plants cannot be grafted because they lack the ability to form cambium layers, compared to dicotyledonous plants. Temperature and relative humidity levels are crucial environmental factors for graft union formation, and acclimatization of grafted plants. The regulation of these post-grafting factors will influence the survival rates of the grafted plants, grafting success, and yield. Generally, a higher relative humidity in the grafting chamber tends to favor grafted tomato plants, as grafted plants do not lose moisture at higher

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Figure 2. Grafted tomato plants showing adventitious bud regrowth (red arrow). Picture by Charles Agyeman.

rates [33]. High humidity within the grafting chamber can be achieved by misting the chamber regularly with water; the use of plastic polythene to cover the grafting chamber acts as an insulator, which shields the plants from the changes in temperature and other weather conditions.

An ideal post-grafting operation should therefore include the maintenance of an ideal air temperature and relative humidity of 25–28°C and 80–90%, respectively, which will promote a higher survival rate and quality of grafted seedlings [34]. In situations where temperature levels have exceeded 30–32°C, the leaf weights (dry weight and fresh weight) have been reported to reduce significantly in watermelon [35].

6. Fruit quality of grafted plants

Quality has become the hallmark of consumers who purchase vegetables as part of their daily dietary requirements; consumers therefore use certain visual and nonvisual attributes to determine the quality of vegetables and fruits in general. Consumers determine the quality of tomato fruits based on their appearance (size, color, and shape) and texture (firmness, mealiness, and juiciness) as well as their flavor and nutritional content [36]. However, different

market players along the vegetable value chain their standard for quality. The quality of tomato is based on soluble solids, acidity, sugars, pH, and shelf life [37].

Vegetable farmers and traders prefer tomato cultivars which exhibit firmness and can withstand mechanical damage, whilst in transit to various market centers [38]. The term fruit quality, which can be defined based on the visual and sensory properties such as color and sweetness, has been found to be controlled by certain inherent genes in some plant cultivars; some of these genes or genetic traits can be bred into new genotypes from other wild species [39].

Conflicting reports on the influence of grafting on fruit quality in vegetables exist. Positive and negative influences of grafting have been documented [40]. In their review of the impact of grafting on fruit quality in vegetables, Rouphael et al. [40] attributed these conflicting results to the differences in environments, production methods, scion/rootstock combinations, and harvest dates.

In an experiment conducted by Matsuzoe et al. [41], where tomatoes (Momotaro) were grafted on three *Solanum* species (*S. torvum, S. toxicarum* and *S. sisymbriifolium*), there were, however, no significant differences in the quality of grafted and ungrafted tomatoes in relation to the amount of sugars and their organic acid contents.

7. Screening of *Solanum* rootstocks against root-knot nematodes

Traditionally, field and pot screening have been used to identify plant cultivars that are resistant to root-knot-nematodes as screening of rootstocks against root-knot nematodes is essential for every grafting program, because this informs the selection of the right rootstock for grafting. In a field experiment to evaluate the performance of grafted eggplant cultivars on wild *Solanum* rootstocks against root-knot nematodes, results revealed that the wild *Solanum* rootstocks *S. torvum*, *S. sisymbriifolium,* and *S. khasianum* were resistant to root-knot nematode when inoculated with 1000 nematode juveniles [42]. The non-grafted plants generally flowered before the grafted plants, a situation which is attributed to the cut back of the leaves of the scion to reduce transpiration which slowed down the rate of growth. Thirty-three tomato genotypes screened for root-knot nematode resistance under five inoculum levels (100, 500, 1000, 1500, and 2000) showed increasing inoculum level with corresponding increase in gall score and fresh root weight [43]. Among the 33 tomato genotypes tested, Mongal F1 T-11 had the lowest mean gall score of 3.25 and "Beef Master" had a value of 3.75 with reproductive factors of 0.71 and 0.53, respectively. Tomato cultivars that are resistant to root-knot nematodes have a reproductive factor less than one, which implies that the plant is able to suppress the reproduction cycle of the organism once it gains entry into the roots [44]. In a grafting study by Agyeman [19], significant differences were not observed among total soluble solids (TSS), pH, and titrable acidity (TA) for the tomato variety "Pectomech" grafted onto *S. aethiopicum* and *S. macrocarpon* after infection to 500 and 1000 nematodes per pot (**Table 3**).

In a pot culture experiment conducted by Dhivya et al. [45], 10 *Solanum* plant genotypes (*S. torvum*, *S. incanum*, *S. xanthocarpum*, *S. aethiopicum*, *S. sisymbrifolium*, *S. viarum*, *S. violaceum,*

Treatments	Inoculum levels	TSS	TSS/TA	pH	TA
P/SA	0	5.42	3.04	4.47	1.87
P/SM	0	5.99	4.02	4.36	1.65
P/SA	500	6.27	4.01	4.55	1.67
P/SM	500	6.33	4.40	4.79	1.62
P/SA	1000	6.67	4.27	4.42	1.65
P/SM	1000	5.78	6.44	4.72	1.22
P/SA	5000	6.3	4.25	4.45	1.45
P/SM	5000	6.28	3.81	4.43	1.66
LSD(P = 0.05)		ns	ns	ns	ns

P/SA = Pectomech grafted onto *Solanum aethiopicum*; P/SM = Pectomech grafted onto *Solanum macrocarpon*; TSS = Total soluble solids; TA = Titrable acidity; LSD = Least significant difference; ns = no significant difference. Agyeman [19].

Table 3. Comparison of grafted rootstocks and inoculum level interaction on TSS, TSS/TA, pH, and TA.

Physalis peruviana, and TNAU Tomato Hybrid CO-3 and US-618) consisting of eight wild species and two F1 cultivars were evaluated for their resistance to root-knot nematode over a 60-day period, and the results showed that *S. sisymbrifolium* rootstock had the highest shoot fresh weight and dry weight of 103.87 and 10.44 g, respectively.

The rootstocks, *S. sisymbrifolium, Physalis peruviana*, and *S. torvum* recorded the least nematode population of 39, 40 and 43 per 200 cc of soil and a reproductive factor of 0.71, 0.74, and 0.84, respectively. *Solanum sisymbrifolium*, *P. peruviana,* and *S. torvum* were resistant to root-knot nematode (*Meloidogyne incognita*), and *S. incanum* and *S. aethiopicum* were found to be moderately resistant to *Meloidogyne incognita*.

8. Screening of rootstocks for the Mi gene using molecular markers

The resistance offered by plants to the damage caused by root-knot nematodes have been well researched and attributed to the presence of a single dominant gene (Mi gene). The Mi gene confers resistance to various root-knot nematode species (*M. incognita*, *M. javanica,* and *M. arenaria*) in addition to whiteflies and aphids [46]. *Solanum* spp., for example, *Lycopersicon peruvianum* and *S. torvum* have been reported to have this resistant gene, which enables the plant to tolerate the feeding activities and the reproductive abilities of root-knot nematodes [47]. The Mi gene was first discovered in an accession of a wild *L. peruvianum* in South America from which commercial F1 varieties were introgressed with the gene [48]. This process involves the extraction and detection of the gene using DNA markers and subsequent isolation of the gene for introgression. In other related research conducted using the positional cloning approach to isolate gene with linked traits and the subsequent sequencing of the DNA, Kaloshian et al. [49] reported that the

sequencing analysis showed two genes, which were identical to each other (Mi-1.1 and Mi-1.2), which also confers resistance to three species of root-knot nematodes namely *M. arenaria, M. javanica,* and *M. incognita.*

Several DNA markers have been developed for the detection of the Mi gene in plants using polymerase chain reaction (PCR) amplifications. Devran et al. [50] screened for the Mi gene using gene specific primers C1/2 (5′-cagtgaagtggaagtgatga-3′) and C2S4 (5′-ctaagaggaatctcatcacagg-3′) for screening F2 tomato plants for the root-knot nematode resistance gene. A 1.6 kb amplification product was amplified in these containing the Mi-1.2 gene in the 3′ region; however, it was found to be absent in the susceptible F2 plants.

Similarly, in another study, the Mi-1.2 gene was introgressed into *S. melongena* to confer resistance to *M. javanica* and aphids. The study revealed that the transgenic eggplant was able to confer resistance to *M. javanica* but not aphids [51]. In confirming the presence of the Mi-1.2 gene in the transgenic eggplant, a reverse-transcription polymerase chain reaction assay with the Mi specific primers C2D1 (5′-ctagaa agtctgtttgtgtctaacaaagg-3′) and C2S4 (5′-ctaagaggaatctcatcacagg-3′) amplified a single PCR band of 915 bp, which was present but absent in the nontransgenic *S. melongena.*

A study in Morocco by Mehrach et al. [52] to detect the Mi-1.2 gene in 14 begomovirus-resistant breeding lines with known resistance was also undertaken using a two-step PCR approach. The primer pairs PM3Fb/PM3Rb and REX primers used in a multiplex PCR amplified a band of 720 bp for both susceptible and resistant varieties; however, the resistant varieties (Motelle and Better Boy) showed an additional band of 500 bp, indicating the presence of the Mi gene in those cultivars.

In distinguishing between heterozygous and homozygous plant cultivars with the Mi-1.2 gene, the primer pairs of PMiF3/PMiR3 amplified a single unique band of 350 bp for the susceptible cultivars (Moneymaker and Daniella). However, 550 and 350 bp fragments for both the homozygous and heterozygous plant resistant cultivars "Motelle" and "Better Boy" were amplified, respectively.

9. Conclusions

Farmers are the ultimate beneficiaries of grafted plants; therefore, healthy grafted seedlings production is important at affordable prices. The high costs involved in the grafting process are due to high labor requirements, grafting input costs, and seeds of rootstock. These associated costs therefore limit the usage of grafted plants by growers or farmers. Grafting costs can be reduced through training of selected farmers from farmer groups, who will in turn train other farmers (trainer of trainers). Information related to this technology can be passed on to farmers and other interested stakeholders through extension programs, for example, workshops, fairs, field days, and on-farm trials. There is also the need for undertaking extensive disease diagnosis in specific areas and feedback given to farmers. Tomato rootstock breeding efforts can lead to production of rootstocks to specific environments, pests and diseases, and other abiotic stresses.

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Chapter 2

PGPR (*Plant Growth Promoting Rizobacteria*) Benefits in Spurring Germination, Growth and Increase the Yield of Tomato Plants

I Ketut Widnyana

Additional information is available at the end of the chapter

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Abstract

There are microbes that are beneficial to plants. Among these, rhizobacteria, which functions as *plant growth promoting rhizobacteria* (PGPR) such as *Pseudomonas* spp. and *Bacillus* sp., can serve as fertilizer. These organisms have proven to accelerate germination and improve the yield of tomato plants. Colonization of rhizosphere by PGPR results in acceleration of plant growth and protection against plant pathogens. Soaking tomato seeds with *Pseudomonas* spp. and *Bacillus* sp. suspension accelerated germination by 2–3 days than the control without immersion with both bacteria. Soaking tomato seeds for 10–30 min in the suspension of *Pseudomonas* spp. yielded the same effect in tomato germination. Soaking in *Bacillus* sp. tends to cause faster growth as compared to immersion in *Pseudomonas* spp. suspension. Mixing these two bacterial suspensions had no significant effect in accelerating the germination of tomato seeds. Soaking tomato seeds for 20 min with a suspension of *Pseudomonas* spp. and *Bacillus* sp. at densities of 4×10^5 CFU and 8×10^5 CFU showed significant differences ($p < 0.05$) in plant height, leaf number, root length, number, and weight of tomato fruits. The highest fruit weight using *Pseudomonas* spp. and *Bacillus* sp. at 8×10^5 CFU was 491.7 g tomato plant^{-1} while the control average fruits weight was 100.0 g tomato plant^{-1}.

Keywords: *PGPR*, *Pseudomonas* spp., *Bacillus* sp., soaking, germination, yield

1. Tomato and plant growth promoting rhizobacteria

Tomato is a potential horticultural crop for cultivation due to its high economic value. The production of the crop in Indonesia was 864,798 t/ha in 2008–2011, with an average productivity of 21.5 t/ha, which is below production levels of 100 t/ha in the United States and Europe.

Rhizobacteria of *Pseudomonas* spp. group are beneficial for plants, improving soil fertility, and function as biological control agents for plant pathogens and have the potential of increasing plant resistance (induced systemic resistance; ISR) [1]. Rhizobacteria plays an indirect role as a biological fertilizer and biological stimulant through the production of plant growth hormones, such as indole acetic acid (IAA), gibberellins, cytokinins, ethylene, and solubilizing minerals. These organisms also indirectly function to inhibit pathogenic microorganisms, through the formation of siderophores and antibiotics [1, 2].

Rhizobacteria, such as *P. fluorescens*, *P. putida*, and *P. aeruginosa*, are beneficial to plants as plant growth promoting rhizobacteria (PGPR), with the ability to control plant diseases [3, 4]. Research on the benefits of *Pseudomonas* spp. still continues to better understand its mechanism in spurring plant growth.

Bacillus sp. is a Gram-positive bacteria used in controlling root disease. These bacteria produce spores that can be stored for long periods and are easily inoculated into the soil. Previous research has shown that the bacteria *Bacillus* strains PRBS-1 and AP-3 proved to inhibit the growth of pathogenic fungi (*Rhizoctonia solani*, *Colletotrichum truncatum*, *Sclerotinia sclerotiorum*, *Macrophomina phaseolina*, and *Phomopsis* sp.) in soybean seeds and enhanced the growth of plants [5].

Rhizobacteria can be used as a bioprotectant that can suppress the development of plant pests/diseases, as a biostimulant that for production of indole acetic acid (IAA), cytokines, and gibberellin, and as a biofertilizer for increasing nutrient availability to plants [6].

2. Concentration levels of *Pseudomonas* spp. and *Bacillus* sp. in germination of tomato seeds

Soaking of tomato seeds in *Pseudomonas* spp. at a concentration of 8×10^8 CFU produced the highest germination percentage that of 91.7%, while germination in distilled water was at 41.6%. Concentrations of *Pseudomonas* spp. and *Bacillus* sp. significantly influenced tomato seed germination (**Figure 1**).

Soaking tomato seeds with bacterial suspension *Pseudomonas* spp. and *Bacillus sp*. gives a significant effect when soaked for 10–20 min at a concentration from 4×10^5 CFU, 8×10^5, and 12×10^5 CFU (**Figure 2**). Tomato seeds soaked in a mixture of bacterial suspension of *Pseudomonas* spp. and *Bacillus* sp. showed significant effect when compared to distilled water. A previous study conducted by Widnyana et al. [7] involving the soaking of swamp cabbage (*Ipomoea reptans* Poir) seeds for 20 min with suspension of *P. alcaligenes* TrN2 resulted in 25% faster germination and increased fresh weight of stems up to 67.07%, compared to soaking of seeds in distilled water.

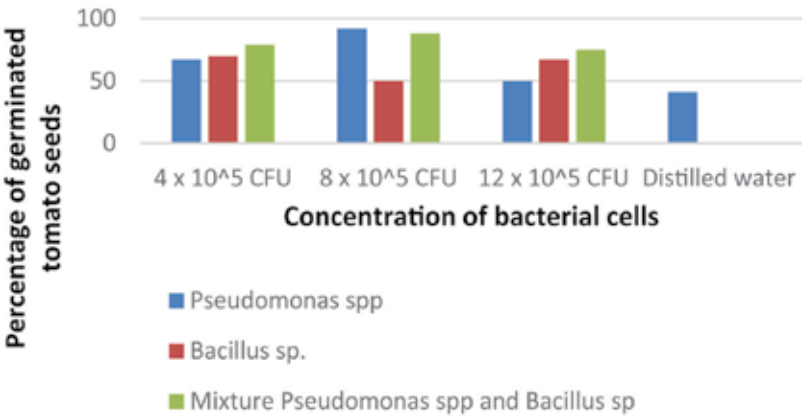

Figure 1. Percentage of tomato seed germination at different concentrations of *Pseudomonas* spp. and *Bacillus* sp.

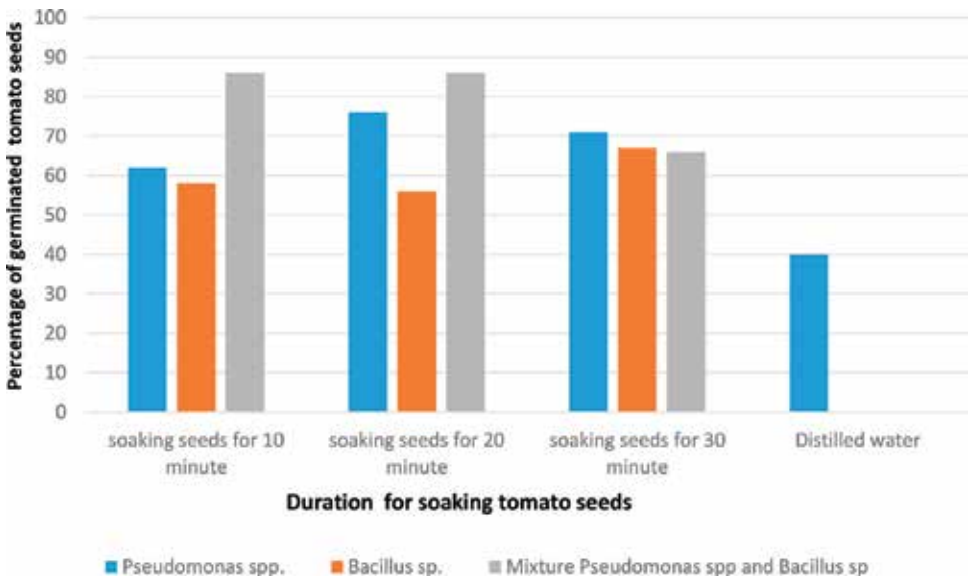

Figure 2. The percentage of tomato seeds germinated after soaking in bacterial suspensions of *Pseudomonas* spp. and *Bacillus* sp.

3. Effect of immersion of tomato seeds in *Pseudomonas* spp. and *Bacillus* sp. on plant height and number of leaves

Soaking tomato seeds with *Pseudomonas* spp. suspension and *Bacillus* sp. can increase the growth of tomato plants. This is evidenced in **Table 1**, with the increase in plant height followed by the increase in number of tomato plant leaves. The positive effect of soaking the tomato seeds is obtained on population density of *Bacillus* sp. and *Pseudomonas* spp. which is

a minimum of 4×10^5 to 12×10^5 CFU. The application of *Pseudomonas* spp. suspension with concentration of 5×10^5 CFU through seed immersion showed significant difference in tomato plant height, with average tomato height in the first and fourth week at 2.7 cm and 8.5 cm, respectively [8] (**Table 2**).

Tomato plants treated with rhizobacteria have higher productivity caused by the ability of PGPR in spurring plant growth and inhibiting the growth of pathogens. This is in accordance with Hatayama et al.'s [9] study that plants treated with PGPR bacteria have higher yields than controls. One of the PGPR product compounds that inhibit the growth of pathogens is siderophore. Siderophore serves as a systemic booster of plant resistance by inducing plants to form salicylic acid at higher level. Mukaromah [10] stated that salicylic acid acts as a signal transduction gene that activates the systemic inducing receptor in plant tissue. *Bacillus* sp. and *Pseudomonas* sp. are antagonistic microorganisms that are able to suppress soil pathogens by forming antibiotic compounds such as chitinase enzymes that can hydrolyze fungal cell walls and form siderophores and other antibiotics [11, 12].

The growth of tomato seedlings after the soaking treatment with suspensions of *Pseudomonas* spp. bacteria, *Bacillus* sp., and suspense mixture of both types of bacteria with different soaking time for 10, 20, and 30 min are presented in **Figures 3–5**. It appears that immersion with sterile water provides the smallest seed growth as compared to other treatments. Soaking tomato seeds for 20–30 min in the suspensions gives better growth for

Seedling height	Control average	Treatment average	95.00% confidence	t	df	p-value	Significance
1st week	0.5	2.7	1.8	8.589	49.714	0.000	Significant
2nd week	3.0	5.0	1.6	8.596	41.209	0.000	Significant
3rd week	4.3	6.1	1.2	5.612	27.993	0.000	Significant
4th week	7.8	8.4	0.2	2.363	30.688	0.012	Significant

Table 1. T-test results of the higher tomato seedlings on control and soaking treatment with suspensions of *Pseudomonas* spp. and *Bacillus* sp.

Leaves of seedlings	Control average	Treatment average	95.00% confidence bound	t	df	p-value	Significance
1st week	0.5	1.5	0.6	4.923	32.166	0.000	Significant
1st week	2.5	2.7	−0.2	0.740	25.716	0.233	Nonsignificant
1st week	3.9	3.9	−0.2	−0.204	32.195	0.580	Nonsignificant
1st week	5.2	5.1	−0.2	−0.437	30.990	0.667	Nonsignificant

Table 2. T-test results of the number of leaves of tomato seedlings on control and soaking treatment with suspensions of *Pseudomonas* spp. and *Bacillus* sp.

tomato germination. This indicates that the soaking of tomato seeds with suspensions of bacterium *Pseudomonas* spp. and *Bacillus* sp., or suspense mixture of both types of bacteria is very useful in spurring the growth of tomato seeds when the soaking treatment lasts 20–30 min.

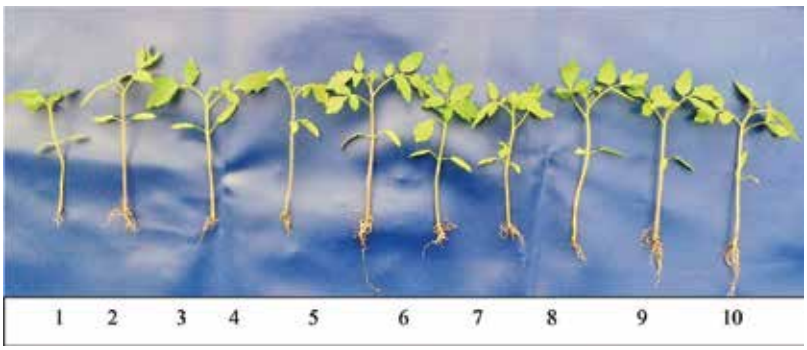

Figure 3. Growth of tomato seeds with *Bacillus* sp. suspense at different seed soaking time periods. *Note*: 1: seeds soaked in distilled water for 20 min; 2–4: seed soaked in *Bacillus* sp. suspension for 10 min; 5–7: seed soaked in *Bacillus* sp. suspension for 20 min; 8–10: seed soaked in *Bacillus* sp. suspension for 30 min.

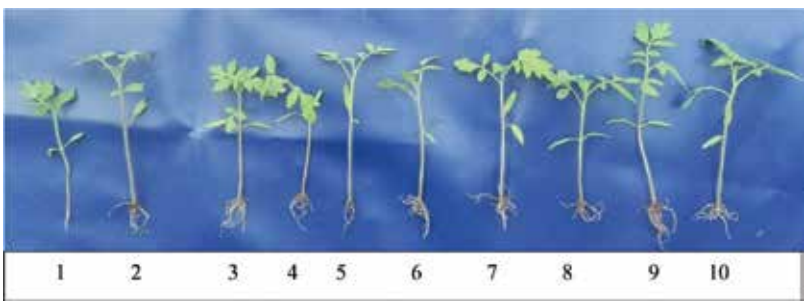

Figure 4. Growth of tomato seeds with *Pseudomonas* spp. suspension at different seed-soaking time periods. *Note*: 1: seed soaked with distilled water for 20 min; 2–4: seed soaked *Pseudomonas* spp. suspension for 10 min; 5–7: seed soaked *Pseudomonas* spp. suspension for 20 min; 8–10: seed soaked *Pseudomonas* spp. suspension for 30 min.

Figure 5. Growth of tomato seeds with a suspense mixture of *Bacillus* sp. and *Pseudomonas* spp. in different seed soaking times. *Note*: 1: seed soaked with distilled water for 20 min; 2–4: seed soaked in *Bacillus* sp. + *Pseudomonas* spp. suspension for 10 min; 5–7: seed soaked in *Bacillus* sp. + *Pseudomonas* spp. suspension for 20 min; 8–10: seed soaked in *Bacillus* sp. + *Pseudomonas* spp. suspension for 30 min.

4. Tomato seed immersion treatment on growth and yield of tomato plants

Treatment of tomato seeds with *Pseudomonas* spp. bacterial suspension in addition to spurring the germination of tomato seeds also has an impact on the growth and yield of tomato fruit [13]. Significant differences were observed ($P \leq 0.01$) among plant height and leaf numbers for *P. alcaligenes* bacteria isolate and the application method used (**Table 3**). Also significant differences were observed ($P \leq 0.01$) among fruit number, total fruit weight per plant, and weight per tomato fruit for *P. alcaligenes* bacteria isolate and the application method used (**Table 4**).

Soaking tomato seeds with *P. alcaligenes* suspension yielded a significant effect on the number of tomato leaves, where the number of leaves reached 192.11 strands on immersion with *P. alcaligenes* TmA1, followed by *P. alcaligenes* TrN2 where the number of leaves reached 182.4 strands. There were 161.6 strands on soaking the seeds with *P. alcaligenes* KtS1, whereas in soaking the seeds with distilled water, the number of leaves was only 78.6 strands. Soaking tomato seeds with *P. alcaligenes* suspension also yields a significant effect on tomato plant height. The highest tomato plant reached 120.4 cm in tomato seed immersion with suspension *P. alcaligenes* TmA1, followed by 116.3 cm with *P. alcaligenes* TrN2, and 114.1 cm with *P. alcaligenes* KtS1, while in soaking the seeds with distilled water, tomato plant height was

Treatment	Application method	Plant height (cm)	Leaf number (leaf)
Distilled water (control)	Root dipping	36.1d	78.6f
	Seed soaking	36.1d	78.6f
	Seedling watering	36.1d	78.6f
P. alcaligenes KtS1	Root dipping	87.7c	109.2e
	Seed soaking	114.1ab	167.6b
	Seedling watering	98.5c	150.1bc
P. alcaligenes TrN2	Root dipping	97.6c	118.4de
	Seed soaking	116.3a	182.4a
	Seedling watering	104.5bc	149.8bc
P. alcaligenes TmA1	Root dipping	98.3c	129.4cd
	Seed soaking	120.4a	192.1a
	Seedling watering	105.5bc	157.7b

Notes: Values followed by the same letter in the same column are not significantly different at 5% DMRT.

Table 3. *Pseudomonas alcaligenes* isolate treatment and the application method on plant height and leaf number of tomato plants.

Treatment	Application methods	Fruit number	Fruit weight/plant (g)	Average weight per fruit (g)	Fruit weight/ha (tons)
Distilled water (control)	Root dipping	30.6c	84.0e	2.8d	3.8e
	Seed soaking	30.6c	84.0e	2.8d	3.8e
	Seedling watering	30.6c	84.0e	2.8d	3.8e
P. alcaligenes KtS1	Root dipping	41.9b	231.6e	5.1bc	10.4e
	Seed soaking	55.0a	278.3d	5.1bc	12.5d
	Seedling watering	48.8b	241.0d	5.0bc	10.8d
P. alcaligenes TrN2	Root dipping	58.8a	237.2d	4.1cd	10.7d
	Seed soaking	70.7a	393.1b	5.9ab	17.7b
	Seedling watering	62.9a	330.4c	5.3bc	14.9c
P. alcaligenes TmA1	Root dipping	54.9b	259.4d	4.8bc	11.7d
	Seed soaking	64.3a	451.9a	7.2a	20.3a
	Seedling watering	58.9a	376.3b	6.7ab	16.9b

Notes: Values followed by the same letter in the same column are not significantly different at 5% DMRT.

Table 4. *Pseudomonas alcaligenes* isolates and the application method on yield of tomato plants.

only 36.1 cm. The abovementioned data indicate that the seed-soaking treatment is the best application method when compared to soaking the roots of the seedlings or watering the tomato seeds (**Table 3**)

Soaking tomato seeds with *P. alcaligenes* suspension has a significant effect on the number of fruits per plant, fruit weight per plant, average weight per fruit unit, and fruit weight in hectare. On the weight parameters of tomato per plant, the average weight per fruit unit, and the weight of tomato per hectare, it was found that soaking the tomato seeds with a suspension of *P. alcaligenes* TmA1 had a significant effect and was significantly different with all other treatments. The highest weight of tomatoes per plant, weight per fruit unit, and fruit weight per hectare was found in tomato seed immersion treatment with *P. alcaligenes* TmA1 suspension that are 451.9, 7.2, and 20.3 tons, respectively. This value differs significantly with all other treatments (**Table 4**).

5. Conclusion

1. Soaking tomato seeds in a suspension of *Pseudomonas* spp. and *Bacillus* sp. can accelerate germination by 2–3 days than when not being immersed in both bacterial suspensions.

2. Soaking the tomato seed for 10–30 min in *Pseudomonas* spp. suspension yields the same effect on the speed of germination of tomato seeds.

3. Soaking of tomato seeds in *Bacillus* sp. tends to cause tomato growth faster than soaking in *Pseudomonas* spp. suspension.

4. Soaking the tomato seed for 20 min with *Pseudomonas* spp. suspension and Bacillus sp. at a population density of 8×10^5 CFU can increase the weight of tomatoes to 490% compared to controls.

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Chapter 3

Tomato Breeding for Insect-Pest Resistance

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Additional information is available at the end of the chapter

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Abstract

The tomato is susceptible to pest attacks that can lead to damages throughout the crop cycle. Pest control is carried out, mainly, by insecticide and chemical acaricide spraying. However, the use of chemical pest control can cause severe damage to the environment, biological imbalances and deleterious effects on farmers and consumer health, as well as increased production costs. An interesting alternative to minimizing the problems arising from the agrochemical application and maintaining pest populations below the economic damage level is the development of tomato plants displaying resistance to insect and arachnid pests. In this context, the main purpose of this chapter is to provide a review of the techniques applied in this regard, major progresses to date and future prospects for tomato pest-resistance breeding. This chapter is divided into five sections: (1) wild pest-resistant tomato species, (2) allelochemicals that confer pest resistance, (3) techniques used for the introgression of pest resistance genes (4) overview, challenges and prospects for pest-resistant tomato breeding and (5) final considerations.

Keywords: *Lycopersicon* sp., allelochemicals, genetic resistance, insects, mites, wild species

1. Introduction

Tomato breeding, from the characterization of wild accessions to the development and release of new technologies, has contributed considerably to increases in tomato productivity. It is possible that tomatoes cultivation for fresh consumption and processing will become even more competitive in the next years. Therefore, investments are required for the development

of new strains or hybrids, which, allied to productive potential, present pathogen, insect and pest-resistant characteristics and adaptations to adverse climatic cultivation conditions. In addition, measures that improve production techniques, as well as the transportation and commercialization logistics of the final product, are also relevant [1].

Although they display great productive potential, tomato crops are one of the most susceptible to pest attack throughout the crop cycle. Even in protected crops, pest occurrence can cause heavy losses. In general, the main pests that attack this crop in the productive regions worldwide are the biotype B whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aphididae), the aphids *Myzus persicae* and *Macrosiphum euphorbiae* (Thomas) (Hemiptera: Aphididae), the thrips *Frankliniella schultzei* (Trybom) (Thysanoptera: Thripidae), the tomato leafminer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), the leafminer fly *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae), the corn earworm *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidade), the tomato fruit bearer moth *Neoleucinodes elegantalis* (Guenée) (Lepidoptera: Crambidae), the caterpillar *H. armigera* and the arachnids *Tetranychus urticae* (Koch) and *evansi* (Baker; Pritchard) (Acari: Tetranychidae) [2–4].

Chemical control by insecticide and acaricide spraying is still the main approach used to control tomato crop pests. However, the use of these products as the sole or main management method can cause severe damage to the environment, such as biological imbalance, deleterious effects on rural and consumer health, as well as increased production costs [5–7].

In order to minimize chemical control problems and maintain pest populations below the level of economic damage, alternative control tactics have been sought for joint use in integrated pest management. Among these, insect and arachnid plant resistance developed by breeding programs is considered ideal, due to relatively low costs, allowing pests to be maintained below the level of economic damage and in balance with their natural enemies. In addition, this technique does not pollute the environment and, above all, does not endanger human health [8–10].

Although cultivated tomato species show great morphological diversity, they present a narrow genetic base due to their domestication having occurred outside South America, which is their center of origin. Therefore, the genetic diversity present in wild tomato species has been explored for the crop breeding. Although these species do not present commercial value due to unfavorable characteristics, such as small and usually pubescent fruits, they display pest-resistant characteristics [11–14].

2. Pest-resistant wild tomato species

In addition to the cerasiform variety, the cultivated tomato *Solanum lycopersicum* L. comprises several wild species, with which it has greater or less interspecific cross-compatibility (**Table 1**) [11, 15]. These species are native to regions located along the western South America coast, encompassing mainly the Andes in Ecuador, Peru and northern Chile, as well as the Galapagos Islands. Thus, these are species that have developed in a variety of habitats, from

Section	Group	Species	Geographical distribution
Lycopersicon	Lycopersicon	*S. lycopersicum*	Cultivated worldwide
		S. pimpinellifolium	Coast of Ecuador to Chile
		S. cheesmaniae	Galapagos Islands
		S. galapagense	Galapagos Islands
	Neolycopersicon	*S. pennellii*	Western Andean slopes from Peru to Chile
	Eriopersicon	*S. habrochaites*	Mountains of Ecuador and Peru
		S. huaylasense	Callejón de Huaylas, Peru
		S. corneliomulleri	Western Andean slopes of southern Peru
		S. peruvianum	Coast of Peru to the north of Chile
		S. chilense	Chilean coast and southern Peru
	Arcanum	*S. Arcanum*	Northern Peru, inter-Andean and coastal valleys
		S. chmielewskii	South of Peru
		S. neorickii	Ecuador to Peru, inter-Andean valleys
Lycopersicoides	—	*S, lycopersicoides*	Southern Peru and northern Chile
		S. sitiens	Southern Peru and northern Chile
Juglandifolia	—	*S. juglandifolium*	Colombia, Ecuador and Peru andes
		S. ochranthum	Ecuador and Peru andes

Adapted from Peralta et al. [11].

Table 1. Recognized ***Solanum*** tomato species and their geographical distribution.

sea level in the Pacific Coast to 3300 m of altitude in the Andean mountains of Ecuador, in climates that range from arid to rainy [16].

Genetic diversity between species is expressed through different morphological, physiological and sexual characteristics [17–20]. It is very probable that Andean geography, with its diverse ecological habitats and different climates, contributed significantly to tomato diversity [16].

Wild tomato species are valued for use in breeding programs because they present resistance genes to pests, phytopathogens and abiotic stresses, as well as higher nutritional quality [12–14, 21–27]. During evolution, wild plants underwent selection pressure in order to survive and guarantee their reproduction in their center of origin conditions, developing resistance mechanisms against the most adverse conditions present in their natural environment [20].

The following wild species display resistance to pest insects and arachnids: *S. pennellii*, *S. habrochaites* var. *hirsutum* e var. *glabratum*, *S. galapagense*, *S. peruvianum*, *S. pimpinellifolium*,

S. cheesmaniae and *S. chmielewskii* [12–14, 28–33]. Research has demonstrated the efficiency of these species in the transmission of genes that express certain desirable characteristics, such as the production of glandular trichomes that, in most cases, exude chemical compounds, called allelochemicals [14, 34].

3. Allelochemicals

Allelochemicals are natural chemicals mainly present in higher plants that act as nutritional, antinutritional, herbal, medicinal and pest- and disease-resistance factors. The chemical substances responsible for plant resistance to pest insects and arachnids can be classified into three categories: substances that act on pest behavior (glycosides, alkaloids, terpenes, phenols and essential oils); those that act on pest metabolism, such as secondary metabolites (including some alkaloids and quinones, among others); and antimetabolites, which make essential nutrients unavailable to pests, causing nutritional imbalances [2].

The most important allelochemicals found in wild tomato species are acyl sugars, sesquiterpenes and methyl ketones [28, 35–37]. Acyl sugars (AA), such as acylglycosis and acylsucrose, are found in *S. pennellii* [14, 36, 38, 39] and *S. galapagense* accession [40] leaf trichomes. Sesquiterpenes, mainly zingiberene (ZGB), are found in *S. habrochaites* var. *hirsutum* [35] accessions, while methyl ketone, 2-tridecanone (2-TD), is found in *S. habrochaites* var. *glabratum* accessions [28, 41–43].

3.1. Leaf trichomes

The *Solanum* genus presents seven types of trichomes. Their classification is based on the length of the trichome, the presence or absence of the gland at the apical end and the number of cells that make up the gland, when present. Trichomes are classified into two types, non-glandular trichomes (II, III, V), which are quite similar to each other, differing only in length, and glandular trichomes (I, IV, VI, VII), capitated, with the head, in most cases acting as the allelochemical secretory region [44].

Wild tomato accessions display an abundance of type I, IV and VI trichomes. In contrast, cultivated tomato display mostly type V trichomes, with the rare presence of types I and VI [33]. On the other hand, types I, IV and VI, due to the presence of allelochemicals, are considered to be of major importance in pest resistance (**Figure 1**).

Trichomes, besides acting as chemical barriers, can also act as physical barriers, limiting pest insect and arachnid access to the plant surface, due to trichome density and length [37].

3.2. Acylsugars

Acylsugars (AA) are glucose or sucrose esters containing acyl groups (**Figure 2**) present in type IV glandular trichomes [45]. In *S. pennellii* accession 'LA 716', the main AA is 2,3,4-tri-O-acyl-glucose. Its resistance character is presumably due to the fact that it confers a sticky

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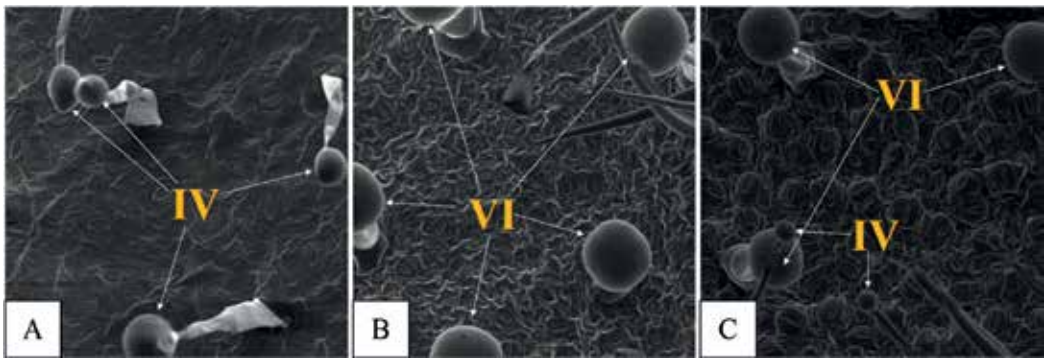

Figure 1. Scanning electron microscopy micrographs of glandular trichomes on the abaxial leaf surfaces of wild tomato species: type IV trichome in *S. pennellii* (A), type VI trichome in *S. habrochaites* var. *glabratum* (B) and type IV and VI trichomes in var. *hirsutum* (C).

Figure 2. Chemical structure of acylsugars.

appearance to leaf surfaces, which acts as a natural trap, avoiding pest insect oviposition, feeding or even causing deleterious effects on their development [13, 46, 47].

3.3. Zingiberene

Zingiberene (ZGB) is another naturally occurring, biologically active allelochemical that confers pest insect and arachnid resistance to [48]. ZGB is a monocyclic sesquiterpene consisting of three isoprene units, with the molecular formula $C_{15}H_{24}$ (**Figure 3**).

ZGB is present in type IV and VI glandular trichomes, found in the wild species *S. habrochaites* var. *hirsutum* [22]. Accession 'PI-127826', rich in ZGB, is resistant to the mite *T. urticae* [49], to the tomato moth [50] and to other pests [32].

3.4. 2-Tridecanone

The allelochemical 2-tridecanone (2-TD) (**Figure 4**) is a sticky liquid that both binds insects to the plant and accumulates in the insect labium, leading to difficulty in feeding [37]. 2-TD is found on the heads of type VI trichomes, mainly in accession 'PI134417', referring to var. *glabratum* [51]. This insect-toxic substance is found at higher levels (72-fold) in *glabratum* compared to *S. lycopersicum* [52].

Several studies have observed the association of pest resistance in *S. habrochaites* var. *glabratum* and the presence of the methyl ketone 2-TD [53–55].

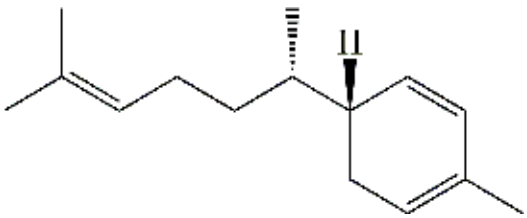

Figure 3. Chemical structure of zingiberene.

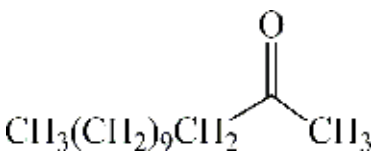

Figure 4. Chemical structure of 2-tridecanone.

4. Techniques used for introgression of pest-resistance genes

To initiate genetic breeding programs aiming at pest insect and arachnid resistance, it is necessary to work with the crop of economic interest and its main pests, in order to select resistance sources, determine the mechanisms/types of resistance involved and structure the program breeding. Regarding the latter, almost all breeding methods can be used, and the choice will depend on the reproduction mode of the plant and the type of gene action that conditions the characters attached to the resistance. Other important aspects should also be considered, such as the need for a large numbers of insects and arachnids for plant infestation/evaluation in replicate experiments, the need for representative pest occurrence conditions, trained personnel to perform the evaluations and method feasibility [56, 57].

Tomato breeding programs aimed at obtaining pest-resistant cultivars have adopted the strategy of incorporating genes responsible for the production of glandular allelochemicals and/or trichomes [58–67]. This strategy has succeeded because the selection for high allelochemical content and, in some cases, glandular trichomes, has led to correlated responses regarding increased resistance to key tomato pests. Breeding programs have commonly performed the hybridization method between pest-resistant wild-type accessions and commercial crops of suitable agronomic value and highly productive traits, followed by backcrossing to the commercial *S. lycopersicum* cultivar (**Figure 5**). This technique is promising with regard to obtaining lines displaying higher pest insect and arachnid resistance levels [38, 39, 58–60, 64–66].

4.1. Resistance introgression with acylsugars

The first selection of pest-resistant plants in generations descended from interspecific crosses between *S. lycopersicum* and *S. pennellii* accession 'LA-716' (high AA content) took

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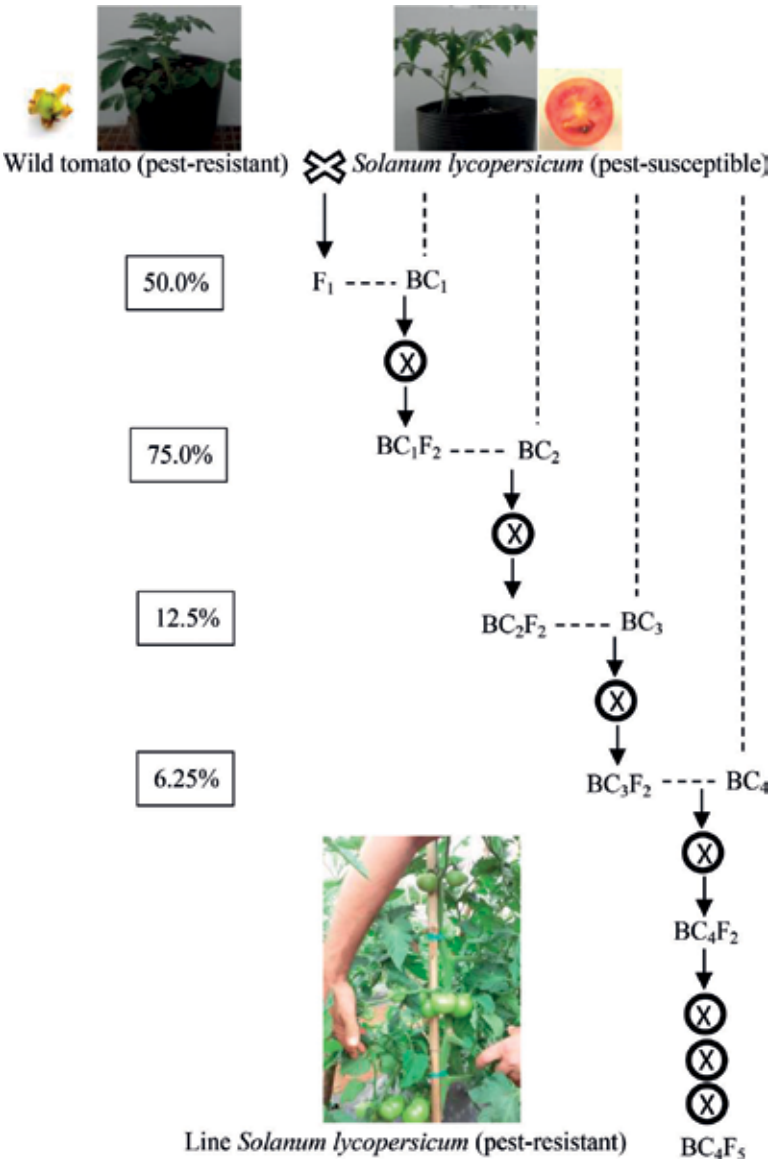

Figure 5. Hybridization (F_1) method between pest-resistant wild-type access and *Solanum lycopersicum*, followed by backcrossing (RC) to the commercial *S. lycopersicum* cultivar until obtaining lines with desirable agronomic characteristics and resistance to pests.

into account morphological and physiological characteristics of plants to identify resistance [13, 68]. These authors also recommend that, for the efficient selection of tomato plants, it is necessary to expose the plants to the pest infestation, allowing for breeding in the quality of the initial evaluation and leading to selection of plants displaying much higher levels of resistance.

When evaluating tomato F_2 genotypes selected for high AA content from interspecific crossbreeding *S. lycopersicum* x accession 'LA-716', high levels of resistance to whitefly were obtained, with a lower oviposition index and 100% of adults trapped in exudates [58]. Thus, resistance evaluations led to the detection of allelochemical efficiency regarding resistance of tomato breeding lines to mites, tomato moths [12], whiteflies [64, 69] and western flower thrips (*Frankliniella occidentalis*) [69]. It was further verified that plants descendants of the crossing between 'LA716' and *S. lycopersicum* are resistant to aphids [13, 61].

Experiments were performed with plants selected for high and low AA content in the F_2 population of the crossing between *S. lycopersicum* 'TOM-584' and accession 'LA-716' and the F_2 population of the first backcrossing for *S. lycopersicum* [59, 60, 69, 70]. These plants were submitted to *T. evansi* mite and whitefly and tomato moth repellency assays, alongside the parent plants, and positive AA effects on mite repellency and the control of other pests were observed. In an experiment with AA-rich tomato genotypes, an even lower oviposition rate of tomato moths and lower damage levels to the plants were observed when compared to genotypes with low allelochemical levels [24].

When studying the inheritance of the AA content character of the 'LA716' accession, an estimate of 1.36 for the number of genes involved is obtained, suggesting a monogenic inheritance [39]. These authors observed a relatively high value for AA content heritability in the broad sense (0.48), indicating that much of the F_2 generation plant variations were genetic in nature. When evaluating AA content inheritance in other studies, the authors observed similar results [24, 71]. Normally, when measured directly, resistance heritability toward insect pests does not present high values, in contrast to what was observed for AA content (which is an indirect selection criterion). These characteristics are due to the difficulty of the environmental control of a direct resistance evaluation system that covers not only the plant and the environment, but also the pest [13].

In the advances made by the breeding programs using the accession 'LA716' as a donor parent, it is verified that AA implies in a variety of interactions between the plant and the pests, including feeding deterrence and changes in pest reproductive potential [13, 68, 69, 70]. As a result of the efforts of breeding programs, tomato lines with high potential to resist pests were developed. The tomato line CU071026, containing high content of AA, was bred from *S. pennellii* accession 'LA716' and contains five introgressions from 'LA716' [64]. In addition, the AA-rich lines TOM-687, TOM-688 and TOM-689 exist [12, 55] and pre-commercial hybrids obtained from an AA-rich tomato inbred line [72].

Studies using *S. galapagense* as an AA source are more recent when compared to *S. pennellii*. As in *S. pennellii*, the presence of AA in *S. galapagense* is closely associated to the presence of type IV glandular trichomes [73]. These authors, when investigating the inheritance of type IV glandular trichome density and its association with whitefly resistance, identified high estimates for heritability, both broadly and in the narrow sense. They suggested that this character displays a relatively simple inheritance and that resistance is associated to a higher density of type IV glandular trichomes. The authors also identified molecular markers for two higher-effect quantitative trait

loci from the *S. galapagense* accession 'LA1401' (one locus located on chromosome 2 and one on chromosome 3), associated to high density of type IV trichomes.

The *S. galapagense* 'PRI9500/PY-8027' accession has been noted as providing higher resistance levels to whitefly by non-preference mechanisms for oviposition and antibiosis [74]. These authors observed a high correlation between higher resistance levels and high density of type IV trichomes, which possibly produce AA and make leaves stickier.

When resistance to the *Helicoverpa armigera* caterpillar (Lepidoptera: Noctuidade) was evaluated in tomatoes obtained from the interspecific cross of *S. lycopersicum* × *S. galapagense*, the F_2 population genotypes, presenting a high density of type IV glandular trichomes, displayed higher resistance levels, both by antibiosis and antixose, than genotypes presenting low glandular trichome density [40].

4.2. Zingiberene resistance introgression

Higher ZGB content is associated with higher resistance levels to mites in populations originating from the cross between *S. lycopersicum* and *S. hirsutum* var. *hirsutum* [22]. Proof of the effectiveness of ZGB regarding whitefly resistance were observed in F_2 generation genotypes of interspecific crosses between *S. lycopersicum* 'TOM-556' and *S. habrochaites* var. *hirsutum* accession 'PI-127826'. Plants containing high ZGB content presented higher resistance levels to pest insects than the commercial tomato *S. lycopersicum* 'TOM-556' (low ZGB content) [75].

A positive genetic correlation between ZGB content and type IV, VI and VII trichome density for an interspecific intersection of *S. lycopersicum* x accession 'PI-127826' was observed [75]. In addition, that study also observed that ZGB content can be explained, in large part, by the action of a single main gene locus, where the var. *hirsutum* allele that conditions high ZGB content is recessive (incompletely) on the *S. lycopersicum* allele. However, the action of another epistatic locus for type IV and VI trichomes was also evidenced.

When investigating ZGB content inheritance in the interspecific intersection between *S. lycopersicum* and *S. habrochaites* var. *hirsutum* accession 'PI-127826', it was observed that leaf ZGB content is controlled by two genes with incomplete dominance in the sense of lower content, presenting greater heritability in the broad sense (81.9%) [26]. When evaluating the synergistic effect between high AA and ZGB leaf content, heterozygous genotypes were used for both characters [6], and the authors observed that the fact that heterozygous double genotypes show the same behavior as the heterozygotes only for ZGB or AA indicates that, although allelochemicals act similarly on the resistance of these genotypes to whitefly, they do not present a synergistic effect in this case. However, in relation to the isolated presence of ZGB or AA, the simultaneous presence of ZGB and AA promoted an increase in the resistance level to tomato moths.

4.3. 2-Tridecanone resistance introgression

The selection of tomato plants containing high 2-TD levels is effective as an indirect screening criterion for pest resistance [41]. However, these authors observed that 2-TD heritability

regarding resistance to pest-arachnids in a segregating generation of the interspecific cross-breeding between *S. lycopersicum* and *S. habrochaites* var. *glabratum* (high 2-TD content) does not fit into a simple additive-dominant model, thus demonstrating a complexity not elucidated in the genetic control of character.

High 2-TD levels present in leaflets provide resistance to *T. urticae* and *ludeni* mite species [43], and it is possible to induce an increase in the level of repellency to *T. urticae* from the backcrossing between *S. lycopersicum* and genotypes containing high 2-TD levels [76]. These authors have identified that mite repellency is related to the presence of higher type VI trichome densities, where 2-TD is concentrated.

When evaluating genotypes presenting different 2-TD leaf concentrations, results indicate that plants containing high 2-TD levels as compared to those with low content are less preferred for feeding and oviposition by the tomato moth [42]. In addition, high 2-TD content is an effective indirect resistance selection criterion when the relationship between 2-TD content in selected genotypes and resistance levels to tomato moth is evaluated [52]. The high 2-TD levels of the BC_2F_4 generation are linked to non-preference oviposition and feeding type resistance mechanisms in tomato moths.

When comparing the degree of resistance to whitefly in tomato lines containing high levels of AA, ZGB and 2-TD, lines containing high 2-TD levels were as effective as those containing high AA and ZGB content [54]. Moreover, when evaluating resistance to aphids (*M. persicae*) in genotypes with different 2-TD, AA and ZGB levels in leaflets [55], the authors observed that TOM-687 and TOM-688 (containing high AA content) and BPX-365G-899-07-04-02 and BPX-367E-238-02 (containing high 2-TD levels) both present antibiosis resistance. The allelochemical 2-TD also displays potential against *T. vaporariorum* [77] and other pest-arachnids.

4.4. *S. peruvianum*, *S. pimpinellifolium*, *S. cheesmaniae* and *S. chmielewskii*

Some *S. pimpinellifolium* [78], *S. cheesmanii*, *S. galapagense* [33], *S. chmielewskii* and *S. chilense* accessions also demonstrate pest resistance [51]. However, the reasons for the resistance of most of these species have not yet been well elucidated.

4.5. Allelochemical quantification techniques

It is necessary to emphasize that genetic tomato breeding programs regarding pests, in general, apply relatively inexpensive colorimetric methodologies to quantify allelochemical content in leaflets and, consequently, identify plants that display the greatest resistance. These techniques allow for acceleration of the selection process and for a large number of plants from a segregating population to be evaluated in a short time. On the contrary, if all the plants of a population were to be exposed to pests to measure resistance, the process would be very laborious.

An efficient methodology proposed by Resende et al. [38], based on a rapid colorimetric method, allows for the nondestructive quantification of AA content in the leaflets of a large number of tomato plants. This reference methodology shows high potential for indirect genotype selection, because it presents low costs and facilitates the non-destructive selection

of individual plants in segregating generations, and is currently being applied by several authors for tomato breeding regarding pests [14, 23, 24, 34, 60]. Moreover, this methodology stands out when compared to new AA content quantification methods in leaflets [79].

Quantification of ZGB content in tomato plants by means of ZGB retention time obtained by gas chromatography and mass spectroscopy has been proposed [80]. However, these techniques do not allow for the evaluation of a high number of plants in a short period of time. Considering this, a rapid, low-cost spectrophotometric methodology was established for ZGB quantification in tomato leaves [81]. This method is now routinely applied in tomato breeding programs regarding pest insects and arachnids [22, 26, 82, 83].

Regarding 2-TD, quantification can be performed through gas chromatography and high performance liquid chromatography [84]. As for ZGB, colorimetric quantification methodologies have been developed that, when compared to chromatographic techniques, allow for the evaluation of a greater number of plants in less time [41, 42, 85]. However, 2-TD quantification through colorimetry in the selection of resistant tomato plants has been shown to be a less efficient technique than those applied in the quantification of AA and ZGB due to the fact that 2-TD content is a more complex genetic inheritance.

Morphological and physiological characteristics can also be used for the selection of tomato plants presenting high allelochemical levels [68]. The main characteristic is the identification and quantification of foliar trichomes based on the quantification of the number of glandular and nonglandular trichomes in leaflets [37]. On the other hand, estimating resistance level regarding pests and associated allelochemicals based on morphological characteristics tends to be more laborious, allowing for the evaluation of a smaller number of plants when compared to colorimetric methodologies.

In general, regardless of the applied technique, it is necessary, at some point, to expose plants identified as containing high allelochemical levels to insect and/or arachnid infestations, in order to efficiently select pest-resistant tomatoes, which allows for confirmation if the selected genotypes actually display good resistance levels.

5. Current overview, challenges and prospects for pest-resistant tomato breeding

In recent years, major transformations in the breeding scenario for several crops have occurred, and this is currently the new reality [85]. In the last 15 years, science and technology investments have taken place that enable training of human resources in the area of plant biotechnology. Classical breeding is still imperative for the development of new cultivars, but new biotechnology techniques using molecular markers can accelerate the selection process. Regarding tomato pest-resistance, many specific molecular markers have not yet been developed. However, this technique may significantly aid in the selection process. Very useful markers have been developed for the identification of plants with high type IV glandular trichome density and high AA content in populations derived from crossings with *S. galapagense* 'LA1401' [73, 86].

Relevant studies have identified quantitative trait loci (QTL) of *S. pennellii* that affect the AA chemistry [64–66, 87–89]. It was observed that some QTL alter the chemotype of AA accumulation in tomato lines descendants of the accession 'LA 716' [87]. It is considered that the addition of QTL that alter AA chemotype in tomato line could provide a means of generating AA with stronger resistance [90].

The two main pest tomato breeding programs in the world are under the leaderships of Martha A. Mutschler and Wilson R. Maluf, respectively.

Dr[a]. Mutschler is a professor in the Department of Plant Breeding, College of Agriculture and Life Sciences, Cornell University. The Cornell University tomato breeding program conducts important works in relation to the crossed *S. pennellii* accession 'LA716' with cultivated tomato to then derive tomato breeding lines with resistance to pests AA-mediated. As a result of these works, the benchmark AA breeding line was developed, CU071026, which produces ~15% of the AA levels of 'LA716' but with a different composition [64–66, 69].

Dr. Maluf is a professor at the Department of Agriculture, Federal University of Lavras (UFLA), Brazil and a partner at Hortiagro Sementes SA, a company that maintains a mutual cooperation agreement with UFLA in the breeding and production of vegetable seeds research area. Their work resulted in the obtaining of tomato lines with high foliar levels of AA, ZGB and 2-TD and resistant to pests [6, 12, 55].

The pest insect and arachnid breeding study, coordinated by Dr. Maluf, mainly applies colorimetric methodologies developed or adapted for the quantification of allelochemical content in leaflets and the selection of resistant strains, contributing to pest control and minimizing the intensive use of chemical insecticides in tomato crops. Following Dr. Maluf's legacy, Dr. Juliano Tadeu Vilela de Resende, a professor at the Department of Agronomy at the Central-West State University (UNICENTRO), Brazil, has also dedicated himself to improving tomato plants regarding pest resistance.

However, other than the research conducted by the Cornell University, UFLA and UNICENTRO research groups, few researchers have developed breeding aimed at obtaining new pest-resistant tomato cultivars. Considering these aspects, it is necessary to stimulate agronomy students to follow the career of the classic tomato pest-breeding, thus avoiding the extinction of committed professionals in this line of research, in a not so distant future.

6. Final considerations

In general, *Solanum lycopersicum* genotypes containing high levels of allelochemicals are promising in the context of advancements aiming at creating lines adequate for both table and processing and displaying pest insect and arachnid resistance. They represent a favorable condition for integrated pest management because they facilitate pest control, reducing the amount of chemicals applied to the crops and, simultaneously, contribute to decreased production costs.

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Section 2

Breeding Tools and Improvement of Tomato

Chapter 4

Review on Tomato (*Solanum lycopersicum*, L.) Improvement Programmes in Ghana

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Abstract

Tomato is an important component of every Ghanaian meal, and its cultivation contributes significantly to livelihood improvement. The demand for tomato in Ghana outstrips supply, and therefore local production is augmented by imports from neighbouring countries. Despite the importance of tomato in Ghana, past tomato-breeding programmes have been unsystematic and had not led to the development of new varieties that meet the needs of consumers as well as environmental stresses. This review outlined tomato production trends, constraints and past tomato improvement programmes in Ghana, which mainly focused on germplasm collection, morphological and agronomic characterization, molecular evaluation, diversity study, as well as screening germplasm against biotic and abiotic stresses. The established variability and the outcomes of the evaluations against the various biotic and abiotic stresses have not been utilized in the development of new varieties. This work will serve as a reference for developing future tomato-breeding programmes.

Keywords: tomato, unsystematic, breeding programmes, agronomic, morphological, molecular

1. Introduction

Tomato (*Solanum lycopersicum,* L.) belongs to the *Solanaceae* family also called Nightshades, which include more than 3000 species [1]. Other examples of crops within the Nightshade family include pepper, potato, eggplants and tobacco. Tomato originated from the Andean region,

which is modern day Chile, Bolivia, Ecuador, Colombia and Peru; however, the original site of domestication is unclear [2]. Two hypotheses have been expressed for the original site of tomato domestication: one stipulates Peru and the other Mexico. It is, however, presumed that Mexico is probably the site of domestication and Peru is the centre of diversity [3]. Originally, tomatoes were pea-sized berries but domestication and plant breeding have resulted in increased fruit sizes [4].

Tomato continues to be the most important vegetable in the world due to increasing commercial and dietary value, widespread production as well as model plant for research [5]. Tomato is utilized as a fresh crop or processed into various forms such as paste, puree and juices. Tomato is a rich source of vitamins (A and C), minerals (iron, phosphorus), lycopene, Beta-carotene, high amount of water and low calories [6]. The five leading producers of tomato in the world are China, India, United States of America, Turkey and Egypt [7]. The world's tomato production in 2014 was 171 million tonnes with an average yield of 37 tonnes per hectare [8].

According to Norman [9], tomato (*S. lycopersicum*) was introduced into the geographical area considered modern day Ghana in the sixteenth century. Although the cultivation of tomato remains a subsistent farming activity, its cultivation and trade contributes significantly to livelihoods improvement [10]. Schippers [11] asserts that tomato is the most important vegetable in Ghana, compared to all the other vegetables. This view can be justified with the continuing increase in the demand for fresh and processed tomatoes in Ghana. With an average yield of about 8.1 tonnes per hectare in 2013, an estimated 340,218 tonnes of fresh tomatoes were produced locally and 5,945 tonnes was imported. In addition, 109,513 tonnes of processed tomatoes were imported within the year 2013 [12]. In the ensuing year, reported tomatoes statistics showed that there were increases in the local production volumes (366,772 tonnes), marching the increase in output per hectare of 8.6 t/ha [13]. The high volumes of tomato produced locally as well as imported are an indication of the importance of tomato in every Ghanaian meal.

Despite the importance of tomato in Ghana, tomato-breeding programmes over the years have not been systematic and therefore had not led to the development of new varieties that meet the needs of consumers as well as biotic and abiotic stresses [14]. The major goals of tomato breeding worldwide are increasing yield, tolerance to biotic and abiotic stresses and improvement in sensory and nutritional value of the crop [15]. Consequently, past Ghanaian plant breeders have focused on germplasm collection, evaluation of imported and local accession for morphological and agronomic traits as well as screening accessions for their reactions to biotic and abiotic stresses. Nonetheless, there have been little published breeding programmes in the past that focussed on improving fruit-quality traits or introgression genes that will make cultivars resilient to both biotic and abiotic stresses. In 2014, the Ghana National Tomato Federation stated that the union has been pushing government to support research in the development of high yielding and quality tomato variety suitable for local and export market [16]. This chapter therefore highlights tomato production trends in Ghana, tomato production constraints, past tomato-breeding programmes in the country and future tomato-breeding objectives, which will serve as a locus for developing future tomato-breeding programmes.

2. Tomato production trends and constraints in Ghana

Tomato is mostly produced in seven out of the 10 regions in Ghana. These production regions include Upper East region, Northern region, Brong Ahafo region, Ashanti region, Eastern region, Greater Accra region and Volta region. The demand for both fresh tomato and tomato products is year round although tomato production in Ghana is seasonal due to the differences in the rainfall patterns as well as water availability. In the exception of the Upper East Region where tomato is produced during the dry season under furrow irrigation system and some parts of the Greater Accra region, tomato production is generally rain fed. During the rainy season, harvest is abundant, leading to glut and wastage even though there is scarcity during the dry season. The abundance of tomato during the rainy season results in low prices and low return on investment. Tomato produced during the rainy season is supplied to the market from May to October but the varieties produced during this period are poor in colour, watery, acidic and have a shorter shelf life, making them unsuitable for processing. Due to the unavailability of processing tomato varieties, all the three state-owned tomato-processing factories had to shut down. Tomato varieties that are currently grown by Ghanaian farmers are mostly imported varieties and farmers selected varieties. A very important open-pollinated variety (OPV) grown in Ghana particularly in the Brong Ahafo region is the Power Rano (a cross between Power and Laurano varieties) which was identified by the National Research Institute (NRI) researchers in the 1990s based on its good production and local processing qualities [17].

Dry season production in Ghana on the other hand is challenging, and demand is in excess of supply. This period partially coincides with the Christmas season when demand for tomato is at its peak. In order to meet the dry season demand, there is heavy importation of fresh tomato from neighbouring countries, particularly Burkina Faso to augment local supply. Some parts of the Greater Accra region such as Ashiaman, Tema and Weija grow tomato under irrigation system and mostly supply tomato unto the market from September to December, and the Upper East region then continues tomato supply from January to April**. I**mported tomato from Burkina Faso supplements local production 5–6 months of the year [18] with a peak supply from February to April [19]. It has been established that, with the availability of water and favourable night temperatures, the highest quality and fruit yield of tomato is obtained in the dry season [20]. In Ghana, the capacity for dry season tomato production lies in the savannah zones, particularly the Upper East, Volta and the Greater Accra regions since water for dry season irrigation is not a limiting factor in these regions. Tomato production halted in the Upper East region in 2002 due to Tomato Yellow Leaf Curl Disease (TYLCD) and a complex of fungal pathogens [21]. In addition, over 600 tomato farmers in the Agotime-Ziope District of the Volta region were reported to have lost virtually all their investment following the TYLCD infection (in 2014) of over 1000 hectares of tomato farms in the area [22]. A high night temperature, a high prevalence of TYLCD and inadequate irrigation facilities to channel the available water are characteristics of dry season production of tomato in the Greater Accra region. Ghana's inability to produce tomato during the dry season therefore has been attributed to a lack of irrigation facility, a high incidence of Tomato Yellow Leaf Curl Disease [23, 24] as well as high night temperatures [25].

3. Past tomato-breeding programmes in Ghana

Tomato-breeding programmes in Ghana can be traced to the 1950–1978 when cultivars like OK, MH and Wosowoso were developed. A major tomato-breeding programme led by the National Research Institute (NRI) in UK also carried out a study from 1994 to 2000. Post 2000, tomato improvement programmes focussed mainly on screening tomato germplasm for both biotic (particularly the TVLCD) and abiotic stresses as well as mutation breeding; however, none has led to the release of varieties. Robinson and Kolavalli in 2010 stated that since the NRI tomato-breeding work ended in 2000, there have been no breeding programmes and no systematic seed multiplication in the country [26]. Again, a 2013 publication indicated that the varieties developed during the 1950 to 1978 together with farmers' selection in tomato-growing areas have led to the development of large tomato ecotypes in Ghana [27].

3.1. Germplasm collection and genetic diversity studies

Germplasm is required for the commencement of any breeding programme. Consequently, the Council for Scientific and Industrial Research-Plant Genetic Resources Research Institute (CSIR-PGRRI) and the National Agriculture Research Programme periodically collected a number of tomato accessions from all the 10 regions in Ghana. The 2012 tomato germplasm collection by the Council for Scientific and Industrial Research-Crops Research Institute of Ghana (CSIR-CRI) included accessions from two districts in Burkina Faso (Kougoussi and Yako), Asian Vegetable Research Development Centre (AVRDC), Rural Development Administration (RDA), National Institute of Horticulture and Herbal Science (NIHHS) and Republic of Korea. This was funded by the Korea Africa Food and Agricultural Cooperation Initiative (KAFACI) project [28]. Recently, 13 accessions were also collected from Afari, Akumdan and Akuawu in the Ashanti region. The recent germplasm collected included accessions such as 'Atoa', 'Daagyine', 'Local 1', 'Power', Pectofake 1, Petomech, 'Akoma', Pectofake 2, Powerano, 'Bolga', 'Dwidwi' (cherry), 'Local 2' and Rano [29]. Most of the locally collected germplasm and introduced accessions have been evaluated for various agronomic and morphological traits as well as the establishment of genetic variation that exists within this germplasm. The Savanna Agricultural Research Institute evaluated three tomato varieties (ICRISIND, Petomech and Tropimech) for various agronomic traits. Variations were observed in plant height, days to flowering, number of fruits, fruit size and fruit weight [30]. Again in 2013, SARI evaluated the following accessions: S 22, Naywli, Bebi yereye, LBR 7, Keneya, LBR 17, Abhijay and Petomech for variability in various agronomic traits [31].

S. pimpinellifolium possesses some desirable traits that can be utilized to improve cultivated varieties; however, the size of the fruit is a hindrance to domestication. In order to improve on the size and other desirable traits, a group of researchers at the Biotechnology and Nuclear Agriculture Research Institute (BNARI) of the Ghana Atomic Energy Commission (GAEC) irradiated the seeds of *S. pimpinellifolium*. The variability of the elemental composition of five mutation-induced variant lines (M3 population; BV-27, BV-40, BV-21, BV-23, BV-10/27) of *S. pimpinellifolium* and the parental line was studied using Instrumental Neutron Activation Analysis (INAA). The results showed a significant variation in the concentration of elements (Na, K, Ca, Mg, Cu, Mn and V) in the pericarp, pulp and seeds of the variant lines and the

parental line [32]. The five induced variant lines used in the previous study were also analysed for lycopene, total antioxidant properties and other quality factors such as pH, total soluble solids (TSS) and total solids. Similarly, 10 F5 tomato-breeding lines were characterized for variability in physico-chemical properties (colour, pH, total titratable acidity (TTA), TSS and vitamin C). The lines used include wosowoso (parent variety), cherry yellow, roma variant (a prolific trait), wosowoso variant (stripped, prolific and big fruit), roma variant (bicoloured fruit), *S. pimpinellifolium* parent, roma variant (hardened and big fruit), roma variant (yellow skin), roma variant (red skin) and wosowoso variant (big fruit, and deep red color). The lines varied in the various physico-chemical properties measured [33]. In addition, fruits of F4 lines derived from crosses between some varieties of *S. lycopersicon*, cherry red, cherry yellow and roma, and wosowoso with a wild tomato, *S. pimpinellifolium,* were analysed for physico-chemical properties, and variation was seen among the lines for the traits studied [34].

In 2014, five introduced fresh market tomato varieties from the USA and Crops Research Institute of Ghana (CRI) were evaluated for genetic variability, adaptability in Ghana as well as plant and fruit attributes. The varieties included Heinz, Shasta, Op-B149, Op-B155 and CRI-P00. With the advent of molecular markers, this study used 15 Simple Sequence Repeat (SSR) primers (**Table 1**) to determine the genetic diversity existing among the five introduced fresh market tomato varieties [35]. In order to establish the genetic diversity that exists in the germplasm collected in 2015, all the accessions (in exception of Rano) were evaluated in field as well as molecularly characterized using 12 SSR primers. The SSR primers include Tom 8–9-F, Tom 11–28-F, Tom 55–56-F, Tom 59–60-F, Tom 67–68-F together with seven primers listed in **Table 1** [36]. In the same year, 20 tomato genotypes were evaluated in the greenhouse as well as the field at the University of Ghana Forest and Horticultural Crops Research Centre (FOHCREC), Okumaning-Kade in the Eastern Region of Ghana to determine the genetic variability in agronomic and fruit-quality traits. There was variability in almost all the traits studied [37].

The various findings of the germplasm evaluation for morphological and agronomic traits together with the variability that exists in the germplasm can be explored in the development of new varieties.

3.2. Breeding for fruit quality

Cultivars such as OK, MH series [38] and Wosowoso [39] were developed in the 1950s. Agble [40] also began breeding for processing quality traits, shelf life and heat tolerance lines by making crosses between local accessions with heat-tolerant and nonripening gene (nor^A) from exotic accessions. Nonetheless, due to lack of continuity, no variety was released despite the positive outlook [41].

The NRI focused on pure line selection of local landraces in the Brong Ahafo region of Ghana with the aim of releasing pure lines of good open-pollinated varieties. Six varieties consisting of three local and three introduced varieties were used in that study. These varieties were selected based on farmers and traders (fruit quality, good taste and longer shelf life) preferred traits. As part of this project, a tomato breeder seed production trial was then established at Wa in the Upper West region with the five selected varieties. The research was, however, not very successful because there was no long-term impact due to lack of sustainable seed distribution systems to ensure that the resource-poor farmers have access to the developed varieties [42].

Marker no.	Primer sequence (5′-3′)	Number of bases
TGS0001F	GCGACCCTCTATTGAACTTGAAGAC (F)	25
	ACAAATCAAAGGAACAATTTCAA (R)	23
TGS0002F	GCAAACGTGTTCGAGTTCGTG (F)	21
	CCACACAATAAAGACAGAAAAATG (R)	24
TGS0003F	ATGCATGCGTGTGTGTTGTA (F)	20
	GTGTGTGTGTGTGTGTGTGTGT (R)	22
TGS0004F	GCAATTTATTTTCATTTGTTATACCGGA (F)	28
	ACCGAGACTCCTGGCTCATA (R)	20
TGS0005F	GACAAAAATTTTCCACACGGC (F)	21
	TCTCTTATAATTTTGTTGAGTCTCTGA (R)	27
TGS0006F	GTCGCATAAATATGGACAACGA (F)	22
	TTTTTAAAATACCATTCCAGAAAAA (R)	25
TGS0007F	GTGGATTCACTTACCGTTACAAGTT (F)	25
	CATTCGTGGCATGAGATCAA (R)	20
TGS0008F	GCGGTGTGAAATACAACAAGACG (F)	23
	CTCGACAAGCTAATTTCTGGG (R)	21
TGS0009F	GCGAAGCAAAAGAAAATTGGG (F)	21
	CACCACGAAGGCTGTTGTTA (R)	20
TGS0010F	TTGAAAAGCTGAAAAGTCAATCA (F)	23
	GAGAGGTGCCACATCACCTT (R)	20
TGS0012F	GTCCCTACCCCACAAATTGAA (F)	21
	AGGTACAACTCACCTCCCCC (R)	20
TGS0013F	GGTGGACATATGAGAAGACCTTG (F)	23
	TCATTTTCCAATGGTGTCAAA (R)	21
TGS0014F	GTGAAGACGAAAAACAAGACGA (F)	22
	CCTTCCCCTTTTGTCTCTCC (R)	20
TGS0020F	TCTTTCAACTTCTCAACTTTGGC (F)	23
	GCCGACTTCAAAAACTGCTC (R)	20
TGS0023F	GTCCAAATTAAAAACTAACCGCA (F)	23
	TTTCCAAAATGACCTAGCGG (R)	20

NB: F: forward primer, R: reverse primer.

Table 1. Tomato microsatellite markers used in DNA fingerprinting among five tomato accessions.

From 2011 to 2013, pure line selection was used to advance a locally identified cultivar commonly called petofake. From the segregating population collected from farmers, 12 progenies (P002, P005, P011, P020, P026, P035, P057, P068, P074, P077, P082 and P085) were selected based on their fruit shape, size, color, surface and yield [43]. Trials are ongoing to release these lines.

Dried seeds of SP 300/30.4.2.4, a variant line selected from second generation (M2) following the irradiation of *S. pimpinellifolium* at 300 Gy, were used for a study. Also, seeds (2000) of SP 300/30.4.2.4 were re-irradiated at 150 and 300 Gy and included in the study. From the study, it was found that the irradiation led to a reduction in plant height and a larger fruit size. Variation was also observed in color, plant height, architecture, number of days to flowering and fruiting. This variation can be explored in future breeding programmes [44].

3.3. Breeding for biotic stress

Post 2000 has seen some breeding efforts made in screening tomato accessions against biotic stresses. However, most of these programmes focussed on the most devastating tomato disease (TYLCD).

3.4. Screening germplasm for tomato yellow leaf curl disease resistance

TYLCD is a major tomato disease in Ghana and Africa as a whole and can lead to a massive yield loss and consequent impact on livelihood if the vector of the disease (whitefly) is not controlled and infection starts at an early stage of the plant growth [45]. The Tomato Yellow Leaf Curl Virus (TYLCV) causes the TYLCD. It was reported that the USAID West African Regional Programme identified research on Virus resistance (VR) as a priority, and Ghana was included in seven members' regional investigation of tomato virus complex [46]. The Agricultural Biotechnology Support Project II (ABSPII) aimed to improve agriculture production in the developing countries through Biotechnology, and that is why this project was initiated in 2005 to address tomato production in West Africa. This project was a partnership among researchers from AVRDC, Cornell University and University of California-Davis (UC Davis). The ABSII established the Regional Vegetable Germplasm Trailing Network that evaluated 100 putatively TYLCD-resistant tomato varieties that were adaptable to the growing conditions of West Africa which Ghana was a part from 2005 through 2008. In the 2005–2006 growing season, only 40 varieties were evaluated (**Table 2**). The resistant varieties used for the entire trial were mainly F1 hybrids since they were sourced from commercial seed companies and some breeding lines from breeding institutions. Based on the TYLCD scoring scale, at the end of the 2007–2008 multilocational trail, varieties such as Lety F1 scored below 1, Yosra scored 1, and Atak, Bybal and Gempride scored between 1.0 and 2.0 in Ghana (Navrongo and Technimanitia). The lower score was an indication of tolerance under the disease pressure. It was noted that the varieties suffered under farmers' field compared to research stations under comparable disease pressure. At the various trial locations, farmers preferred Lety F1, Yosra, Atak and Bybal. Due to the competitive nature of the tomato-breeding industry in developed world, some of the selected varieties were no longer in use in the countries where they were originally bred [47].

Seed source	Variety name	Resistance source
AVRDC	CLN 2123A Ty-2	Ty-2
	CLN 2460E Ty-2	Ty-2
	CLN 2468A Ty-2	Ty-2
	CLN 2498E Ty-2	Ty-2
	CLN 2545A Ty-2	Ty-2
	CLN 2545B Ty-2	Ty-2
	PT 4722A Ty-2	Ty-2
	TLCV 15 Ty-2	Ty-2
Cirad Guadeloupe	O4 108	
	O4 240	
	O4 495	
	O4 498	
	O4 501	
De Ruiter Seeds	Bybal	
	Industry DR 10403	
	Lety F1	
	Realeza	
	Thoriya	
Enza Zaden	Bybal	
	Industry DR 10403	
	Lety F1	
	Realeza	
	Thoriya	
Enza Zaden	Atak	
	Chenoa	
	Ponchita	
	Yosra	
Harris Moran	FTC 6231	*Ty-1*
	FTC 6236	*Ty-1*
	FTC 7088	*S. chilense* LA 1969, *S. habrochaites* H24
	FTC 7127	*Ty-2*, *S. habrochaites* H24
	FTC 7351	*S. chilense* LA 1969 and LA2779
	FTC 7483	*S. pimpinellifolium*
	HMX 4810	*S. chilense* LA 1969
Hazera	HA 3060	
Hebrew University	Favi 9	Ih902

Seed source	Variety name	Resistance source
Seminis	GemPride	*Ty-1*
	PS 43316	
Seminis—India	Sasya 0202 F1	
Syngenta	Cheyenne E448	
	Nirouz TH 99806	
	Yassamen TH 99802	
Takii	TY 75	*Ty-2*
Tropicasem	F1 3019 Galina	F1 3019 Galina
	Nadira	Nadira
	Roma VF	Susceptible check

Table 2. Forty varieties evaluated in 2005–2006 TYLCD resistance trails.

In 2008, three distinct isolates of the TYLCD virus were identified in Ghana from infected tomato plant samples collected from the Ashanti region in Ghana. The three strains of virus identified are the Tomato Yellow Leaf Curl Ghana Virus, Tomato Yellow Leaf Curl Kumasi Virus and the Tomato Yellow Leaf Curl Mali Virus [48].

Fifteen tomato accessions (collected from AVRDC-Taiwan and CSIR-Crops Research Institute, Ghana) that have been reported to be resistant to TYLCD as well as susceptible checks were screened against the TYLCD in a greenhouse at the Kwame Nkrumah University of Science and Technology (KNUST) in Kumasi (**Table 3**). These 15 accessions were later on evaluated in the field at Afari (hot spot) in the Ashanti region. The whiteflies used for the greenhouse inoculation were collected from infested tomato plants at Akumadan, Agogo and Afari. The incidence and severity of TYLCV were scored 30, 45 and 60 days after transplanting using the severity scale 0–4 developed by Lapidot and Friedmann in 2002. At 60 days after transplanting in the greenhouse, accessions A2 (FLA456-4), G14 (WSP2F7 (3) PT.3) and G15 (WSP27F7 (3) PT.3) expressed moderate symptoms in terms of incidence of the TYLCD while accessions A8 (99S-C-39-20), A9 (H24), G13 (WS273.3LARGE) and G12 (WSP2F1PT.3) also showed mild symptom of the disease. A1 (TY52), A3 (FLA478-6-3-0), A6 (TLB111) and A7 (LA 1969) expressed slight severity to the TYLCD. Accessions G11 (PIMPILIFOLIUM) and A1 (FLA505) had the lowest incidence rate compared to accessions A10 (CLN2026D), G13 (WS273.3LARGE) and A4 (FLA653-3-1-0) that had the highest incidence of TYLCV infection in the field. At 60 days after transplanting only accession, A1 (FLA505) showed no TYLCD symptoms [49].

Again, 30 accessions (including the 15 accessions that were screened in the greenhouse and the field in 2010) were screened against the local strains of virus in Afari in the Ashanti region (**Table 4**). Some of these accessions were reported to be resistant in other countries. Only two accessions (Local Rano and Petomech-Ghana/France) out of the 30 accessions expressed mild symptoms whilst accessions WSP2F1pt.3 and Tomato Red Cloud expressed moderate symptoms after 60 days of transplanting. In order to confirm the resistance or susceptibility

Accessions	Resistance source	Origin
TY52 (A7)	LA 1969	D. Zamir, Hebrew University
'FLA456–4 (A2)	Tyking, LA2779 (*L. chilense*)	J. Scott, University of Florida
FLA505 (A1)	LA1969, Tyking, Fiona	J. Scott, University of Florida
FLA496–11–6-1-0 (A5)	LA1932	J. Scott, University of Florida
FLA478–6–3-0 (A3)	LA1938 (*L. chilense*), Tyking	J. Scott, University of Florida
FLA653–3–1-0 (A4)	LA2779 (*L. chilense*), Tyking	J. Scott, University of Florida
99S-C-39-20 (A8)	Unknown	Namdhari Seeds, India
H24 (A9)	*L. hirsutum* f.sp. *glabratum*	G. Kalloo, India
TLB111 (A6)	H24	AVRDC
CLN2026D (A10)	Susceptible check	AVRDC
WSP2F1PT.3 (G12)	Unknown	CSIR-CRI
WS273.3LARGE (G13)	Unknown	CSIR-CRI
WSP2F7 (3) PT.3 (G14)	Unknown	CSIR-CRI
PIMPILIFOLIUM (G11)	Unknown	CSIR-CRI
WSP27F7 (3) PT.3 (G15)	Susceptible Check	CSIR-CRI

Table 3. Tomato accessions used for the TYLCD screening in both the greenhouse and the field.

observed in the field, six viral detection primers were used to screen all the 30 tomato accessions (**Table 5**). From the results obtained in that study, none of the primers amplified viral DNA in Tomato Red Cloud. For WSP2F1pt.3, only one of the six primers (PAL/PAR) amplified the viral DNA. Only MF/MR primer amplified the viral DNA in Local Roma. For Petomech (Ghana/France), two primers (GHF/GHR and KR/KF) amplified the viral DNA. None of the 30 accessions was considered resistant since none of them showed no symptom in the field as well as no TYLCV DNA amplification [50].

Again, between 2010 and 2011, seven tomato varieties (**Table 6**) were grown in the fields against the TYLCD in the University of Ghana and the Volta region of Ghana. The symptom expression of the varieties against the TYLCV was confirmed in the laboratory using the set of primers in **Table 5** in addition to Beta 01/02. The study also identified Ty-3 gene in tomato that confer resistance to TYLCV using the primers in **Table 7**. From the field screening, it was found that Burkina (obtained from farmers in the Volta region) had the highest TYLCD incidence, followed by Petomech and the susceptible check. However, Petomech expressed higher severity than Burkina. Both severity and incidence were lower in the hybrids in exception of F1 Thorgal that showed no symptom. AC1048/AV494 detected the most viral DNA in the samples collected. The primer set T0302-F/T0302-R did not amplify the Ty-2 gene in any of the varieties evaluated. However, Primer P6-25-F/P6-25-R amplified a band size of approximately 400 bp in F1 Jaquar, F1 Nadira and *S. pimpinellifolium* [51].

Entries	Code	Resistance source	Origin
FLA 505	A1	LA 1969 (*L. chilense*)	J. Scott, Univ. Florida
FLA 456–4	A2	Tyking, LA2779 (*L. chilense*)	J. Scott, Univ. Florida
FLA 478–6–3-0	A3	LA1938, Tyking, Fiona	J. Scott, Univ. Florida
FLA 653–3–1-0	A4	LA2779 (*L. chilense*), Tyking	J. Scott, Univ. Florida
FLA 496–11–6-1-0	A5	LA1932 (*L. chilense*), Tyking	J. Scott, Univ. Florida
TLB 111	A6	H24	AVRDC
TY52	A7	LA 1969 (*L. chilense*)	D. Zamir, Hebrew Univ.
99S-C-39-20-11-24-17-0	A8	Unknown	Namdhari Seeds, India
H24	A9	*L. hirsutum* f.sp. *glabratum*	G. Kallo, India
CLN2026D	A10	Susceptible check	AVRDC
Pimpinellifolium	G11	Unknown	CSIR-CRI
WSP2F1pt.3	G12	Unknown	CSIR-CRI
WS273.3 Large	G13	Unknown	CSIR-CRI
WSP2F7 (3) pt.3	G14	Unknown	CSIR-CRI
2641A	B16	Unknown	AVRDC
Tomato Money Maker	B17	Unknown	USA
Tomato Roma-Jam Vf	B18	Unknown	Burkina Faso
Parona	B19	Unknown	Local
Local Roma	B20	Unknown	Local
Rando	B21	Unknown	Local
Tomato Slumac	B22	Unknown	Holland
Tomato Tima	B23	Unknown	France
Tomato Red Cloud	B24	Unknown	Holland
Tomato Rio Grande	B25	Unknown	Holland
Petomech (Ghana/France)	B26	Unknown	France
Tomato Roma VF	B27	Unknown	USA
Petomech (Ghana/Burkina)	B28	Unknown	Burkina Faso
Petomech (Ghana)	B29	Unknown	Ghana
Tomato Ventura F	B30	Unknown	USA

Table 4. A list of tomato accessions screened against the tomato yellow leaf curl disease in Afari.

Between 2011 and 2012, a group of researchers also evaluated the susceptibility of 10 accessions to TYLCD under field conditions. The accessions include *S. pimpinellifolium*, Wosowoso, Cherry red, Roma, Hyb−1 (Wosowoso × *S. pimpinellifolium*), Hyb-2 (Roma × *S. pimpinellifolium*), Hyb-3

Marker name	Primer sequence	Source
PARc1496/PAL1v1978	F:5′GCATCTGCAGGCCCACATYGTCTTYCCNGT R: 5′AATACTGCAGGGCTTCTRTACATRGG	Rojas et al. (1993)
AV494/AC1048	F: GCCCATGTATAGAAAGCCAAG R: GGATTAGAGGCATGTGTACATG	Wyatt and Brown (1996)
PTYv787/PTYc1121	F: 5-GTTCGATAATGAGCCCAG-3 R: 5-ATGTAACAGAAACTCATG-3	Zhou et al. (2008)
GHF/GHR	F: GCCCGAAAGCTTCGTTGTT TTCCCGCT R: ACGGATGGCCGCTTTGGGT ATTCG	Osei et al. [48]
KF/KR	F: GGACCCGGCGCACTATTTAT GTTGGC R: ACCCCATTACCCCAATACCA	Osei et al. [48]
MF/MR	F:TGGCCGCGCCCTTCCTTTTGT R: ACCAATGGCTCCCCAAAGCGT	Osei et al. [48]

NB: F: Forward primer, R: Reverse primer.

Table 5. A list of primers used in TYLCV DNA detection.

(Cherry red × *S. pimpinellifolium*), BC-1 (Wosowoso × (Wosowoso × *S. pimpinellifolium*)), BC-2 (Roma × (Roma × *S. pimpinellifolium*)) and BC-3 (C-Red x (C-red × *S. pimpinellifolium*)). The observed TYLCD symptoms on *S. pimpinellifolium* were no visible symptom to slight yellowing of margins of apical leaflets.

The observed symptoms on the hybrids together with the backcrosses were slight yellowing of margins of apical leaflets and moderate yellowing and slight curling of leaflet tips. The results from the phenotypic screening were verified with a molecular marker detection of

Varieties	Resistance	Source
F1 Jaguar	TYLCV	Technisem (AgriSeed Company Ltd.)
F1 Nadira	TYLCV	Technisem (AgriSeed Company Ltd.)
F1 Thorgal	TYLCV	Technisem (AgriSeed Company Ltd.)
Petomech	Unknown	University of Ghana
Burkina	Unknown	Farmer variety
Solanum pimpinellifolim	Reported resistance to TYLCV	Farmers
CLN2026D	Susceptible check	AVRDC

Table 6. Tomato germplasm used for field screening against TYLCD in Volta region and University of Ghana.

Primer	Primer sequence	Reference
T0302-F/T0302-R	F: TGGCTCATCCTGAAGCTGATAGCGC	Ji and Scott (2006)
	R: AGTGTACATCCTTGCCATTGACT	
P6–25-F/P6–25-R	F: GGT AGT GGA AAT GAT GCTGCTC	Ji et al. (2007)
	R: GCT CTG CCT ATT GTC CCA TAT ATA ACC	

Table 7. Primer pairs and sequences for TYLCV gene detection.

the viral DNA among the accessions. This work also deployed both triple antibody sandwich enzyme-linked immunosorbent assay (TAS-ELISA) and PCR method (using the primers in **Table 5**) for the TYLCV detection in order to recommend a better way of detecting TYLCV in infected samples. A TAS-ELISA kit with a known TYLCV-infected *Nicotiana benthamiana*-positive control was used for the study. The study confirmed the superior sensitivity of the PCR technique as a TYLCV detection method compared to the TAS-ELISA technique. There were no observable TYLCV symptoms on the BC-3 (C-Red × (C-red × *S. pimpinellifolium*)) in the field and both methods did not detect viral DNA in the leaf samples. BC- 1 (Wosowoso × (Wosowoso × *S. pimpinellifolium*)) behaved similarly like BC-3 in the field but there was amplification of viral DNA by the AV494/AC1048 primer set. In addition, two PCR primers detected viral DNA in the *S. pimpinellifolium* even though there was no TYLCV symptom observed in the field.

Recently, there was a phenotypic evaluation of 36 local tomato genotypes (**Table 8**) for the source of resistance against TYLCD in two locations (University of Cape Coast and Asuansi) in Ghana. The results showed that five accessions (K005-Petomec, K100-Local 3, K213-AVTO 9804, K116-Ashanti 2 and K042-Tomatose) out of the 36 genotypes were selected for mild severity, two genotypes showed severe symptoms (K027-Local, K202-AVTO 0102) and one genotype (LV-Fadzebegye) showed moderate severity. In order to confirm the infection or otherwise of the eight tomato accessions selected for mild and severe symptom expression, two of the viral detection primers (AV494/AC1048 and PTYv787/PTYc1121) were used for the detection of the virus in infected plant samples (**Table 5**). The primer pair AV494/AC1048 amplified the viral DNA in all the eight genotypes (K100, K027, K116, K005, K202, LV, K213 and K042) in the University of Cape Coast and six out of the eight genotypes in Asuansi (K100, K027, K116, K005, K202 and K042) (**Table 8**). The primer pair PTYv787/PTYc1121 on the other hand amplified viral DNA in all the samples from both locations [53].

3.5. Molecular screening of tomato germplasm for root knot nematodes resistance

This study involved the use of primer Mi23/F//Mi23/R to detect the presence or absence of *Mi* genes in twenty eight (28) tomato cultivars (**Table 9**). The primer amplified the homozygous resistant genotypes (*Mi*/*Mi*) in cultivars VFNT, FLA 505-BL 1172, 2641A, "Adwoa Deede" and Terminator FI while the heterozygous resistant genotypes (*Mi*/*mi*) were amplified in cultivars Tima and 2644A [54].

Codes	Genotype names	Source
K116	Ashanti 2	Ghana (Ashanti region)
K045	Tomatose	Ghana (Volta region)
K042	Tomatose	Ghana (Volta region)
K100	Local 3	Ghana (Upper East)
K074	Local 6	Ghana (Northern region)
K144	BK-Dotvert Yako	Burkina Faso (Burkina Faso)
K124	Local 1	Ghana (Ashanti region)
K005	Petomec	Ghana (Eastern region)
K214	AVTO 9001	Taiwan(AVRDC)
K138	BK-Koly zy	Burkina Faso
K146	BK-Kong-L6	Burkina Faso
K194	Magmet	Korea
K087	5(K)	Ghana (SARI)
K084	1R	Ghana (SARI)
K188	Madiso	Korea
K027	Local	Ghana (Volta region)
K098	Local 1	Ghana
K088	Local1	Ghana (Upper East)
K205A	AVTO 1006	Taiwan (AVRDC)
K197	REX	Ghana (Eastern region)
P077	Local 9	Ghana (Northern region)
K213	AVTO 9804	Taiwan (AVRDC
K083	6(A)	Ghana (SARI)
K050	Asante tomato	Ghana (Western region)
K011	Ntose	Ghana (Eastern region)
K106	Local 2	Ghana (Upper East)
P085	21(B)	Ghana (SARI)
K200	2001 heat tolerant	Ghana (Eastern region)
K191	Dyune	Korea
K186	Superdotaerang	Korea
K190	Orange carl	Korea
K006	Power Rano	Ghana (Eastern region)
K202	AVTO 0102	Taiwan (AVRDC)
P009	Mmoboboye	Ghana (Eastern region)
K206	AVTO 1008	Taiwan (AVRDC)
L.V	Fadzebegye	Ghana (Central region)

Table 8. Code, name and sources of 36 tomato genotypes screened against TYLCD.

Cultivar	Source/origin
FLA 505-BL1172	AVRDC, Taiwan
2641A	AVRDC, Taiwan
Wosowoso	Commercial, Ghana
FLA 496–11–6-0	AVRDC, Taiwan
Adwoa Deede	Commercial, Ghana
TLB111	AVRDC, Taiwan
Terminator F1	Green seeds, India
3008A	AVRDC, Taiwan
Roma-JAM VF	Commercial, USA
Burkina Petomech	Commercial, France
Roma VF	Commercial, B. Faso
Ventura F	Commercial, France
Slumac	Commercial, Holland
Red	Commercial, Holland
Rando	Commercial, Ghana
Akoma	Commercial, Ghana
Ghana Petomech	Petomech Commercial, France
Floradade	Commercial, USA
FLA 478–6–3-0	AVRDC, Taiwan
Money maker	Comm. South Africa
Tima	Commercial, France
Rio grande	Commercial, Holland
Parona	Commercial, Ghana
Biemso	Commercial, Ghana
Power	Commercial, Ghana
2644A	AVRDC, Taiwan
VFNT (Resist. check) TGRC, V. Williamson	VFNT (Resist. check) TGRC, V. Williamson
UC82 (Suscept. check) TGRC, V. Williamson	UC82 (Suscept. check) TGRC, V. Williamson

Table 9. Tomato cultivars evaluated for nematode resistance.

3.6. Screening for abiotic stress

Another important tomato-breeding objective is breeding for abiotic stress; nonetheless, there is limited published work on screening of tomato against abiotic stresses in Ghana. It was reported that 19 tomato cultivars (**Table 10**) were screened for adaptation to high temperature,

Tomato cultivar	Origin
'Petomech'	Monarch Seed, Holland
'Rio Grande VF'	Griffaton Producteur Grainier, France
Tomato Rockstone VF'	Griffaton Producteur Grainier, France
'Caracoli'	Griffaton Producteur Grainier, France
F1 Ninja'	Technisem, France
'Tropimech'	Technisem, France
'Petomech VF II	Improved Petoseed Seminis, Netherlands
'Moneymaker'	Griffaton Producteur Grainier, France
King 5'	Japan
Queen'	Japan
'18I (CLN 2318 F)'	AVDRC
14IR Island Red'	Samoa Island
'8S Selected SM1'	Samoa Island
'5C Roma'	Samoa Island
'17I (CLN 2443B)'	AVDRC
'Nkansah'	Forest and Horticulture Crops Research Centre, Kade, University of Ghana
'DV-2962'	Seminis Monsanto, Thailand
'Champion'	Crop Science Department, University of Ghana
Wosowoso'	Crop Science Department, University of Ghana

Table 10. Tomato cultivars used for the heat stress.

and it was found that Nkansah, King 5, 181 (CLN 2318 F) and DV 2962 cultivars were better adapted to heat stress [55].

The outcome of these various screening programmes can be utilized in a hybridization programme by crossing genotypes expressing mild symptoms to the TYLCV and nematodes as well as genotypes that are tolerant to heat with locally adapted accessions that are susceptible to these stresses to develop resilient varieties.

3.7. Potential tomato breeding objectives

Tomato varieties currently grown in Ghana are generally acidic, watery, poor in color, poor shelf life and susceptible to TYLCV as well as intolerant to heat. Future tomato-breeding programmes should focus in the short-term on introgression of Tomato Yellow Leaf Curl Disease Resistant genes into locally adapted varieties and improving the shelf life of these locally adapted tomato varieties. These will address the major constraints facing the tomato industry in Ghana. Long-term tomato-breeding objectives should encompass the improvement of fruit color, increasing brix, improving rainy season varieties with good fruit-quality traits, increasing variability through

irradiation, resistance to other biotic and abiotic stresses as well as sensory and nutritional value. Due to the pressing nature of these short-term breeding objectives, students of the West Africa Centre for Crop Improvements (WACCI), University of Ghana, are currently breeding for TYLCD-resistant varieties and prolonged tomato shelf life. Other students of the same institution are also working on breeding for processing quality and Bacteria Wilt-resistant tomato varieties.

4. Conclusion

Tomato is indispensable in all Ghanaian recipes and contributes significantly to the economy of Ghana. Ghana has the potential to meet the country's tomato demand; however, low yield, unavailability of quality tomato varieties, pests and diseases have hindered this potential. This review presented tomato production trends in Ghana, past tomato-breeding programmes that have been carried out as well as some potential tomato-breeding objectives. Ghana will achieve self-sufficiency in tomato production if the government, Universities, Research Centres and National Research Institute (NRI) will invest more resources into tomato breeding to achieve both the short- and long-term-breeding objectives. This review will serve as a reference for improving tomato in the country.

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Chapter 5

Genotype × Environment Interaction: A Prerequisite for Tomato Variety Development

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Additional information is available at the end of the chapter

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Abstract

Tomato (*Solanum lycopersicum* L.) is the second most important vegetable crop in the world due to its high level of nutrition particularly in vitamins and antioxidants. It is grown in several ecologies of the world due to its adaptability and ease of cultivation. Besides field conditions, tomatoes are grown in controlled environments which range from hydroponics and simple high tunnel structures to highly automated screen houses in advanced countries. However, the yield and quality of the fruits are highly influenced by the environment. This results in unpredictable performances in different growing environments in terms of quality, a phenomenon known as genotype by environment (G × E) interaction which confounds selection efficiency. Various approaches are employed by plant breeders to evaluate and address the challenges posed by genotype by environment interaction. This chapter discusses various field and controlled environments for growing tomatoes and the effect of these environments on the performance of the crop. The various types of genotype × environment interactions and their effect of the tomato plant are discussed. Finally, efforts are made to suggest ways and methods of mitigating the confounding effects of genotype × environment interaction including statistical approaches.

Keywords: tomato (*Solanum lycopersicum* L.), adaptability, field conditions, controlled environments, genotype × environment interaction

1. Introduction

The rise in population and the ensuing increase in the demand for agricultural produce are expected to be greater in Africa where production is not adequate. The need for increase in

agricultural production cannot be overemphasized. This embodies challenges to forming systems, and must come mainly from increased yield per unit area, given the limited scope for extension of cultivated land worldwide. To meet this requirement, numerous crop improvement programs all over the world have been initiated. In every crop improvement program, promising genotypes are tested for their performance each year at a number of sites, representing the major growing area of the crop. This is to identify genotypes which possess the dual qualities of high-yield sustainability to adverse changes in environment condition. It is observed that a specified difference in environment may produce disparity outcome on genotype. This interplay of genetic and nongenetic effects causing differential relative performances of genotypes in different environments is called genotype × environment interaction (GEI). A genotype × environment interaction thus may perhaps be a change in the relative performance of a character of two or more genotypes measured in two or more environments. There have been early efforts made to classify genotype-environment interactions into four groups [1]. The first group, although was not an interaction, was later observed as a nonadditive relationships between genotype and environment [2].

2. Origin of genotype × environment interaction

There are two different conceptions of the origin of gene × environment interaction (GEI). The two concepts are referred to as biometric and developmental interaction [3] or statistical and common sense interaction [4]. Fisher introduced the biometric concept of GEI, whereas Lancelot Hogben introduced the developmental concept of GEI [3]. The biometric (statistical) concept of GEI has its origins in research programs that seek to measure the relative proportions of genetic and environmental contributions to phenotypic variation within populations. Biometric gene × environment interaction has particular importance in population genetics and behavioral genetics [3]. Developmental GEI is a concept more commonly used by developmental geneticists and developmental psychobiologists. The developmental interaction is not seen merely as a statistical phenomenon, but manifested in the causal interaction of genes and environments in producing an individual's phenotype [5]. Most of the subsequent history of research on GEI has largely been based on the Fisher and Lancelot Hogben's concepts [3].

3. Tomato genome and genetic variation

Tomato (*Solanum lycopersicum* L.) is the second most important vegetable crop in the world, and an important model plant for genetics and genomics studies, because of its relatively short reproductive cycle and small genome size. Moreover, the continued importance of tomato as a vegetable is reflected by the large volume of research on almost all aspects of the crop. Its genotype determines the characters expressed by the crop. The tomato genome has been translated by plant geneticists who discovered that the crop contains 31,760 genes after mapping its genetic makeup. The tomato's genome is, however, closer to that of a potato. As a crop plant, tomato is one of the best-characterized plant systems. It has a relatively small genome of

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0.95 pg or 950 Mb per haploid nucleus [6] and features such as diploidy, self-pollination, and a relatively short generation time make it amenable to genetic analysis. The tomato genome at the DNA level consists of approximately 78% single-copy sequences, as evaluated under high stringency hybridization conditions [7]. The remaining part of the tomato sequences is repetitive DNA of which four major classes have been characterized. Ribosomal DNA represents the most abundant repetitive DNA family and comprises approximately 3% of the tomato genome. Both 5S and 45S rRNA genes are tandemly repeated with 1000 and 2300 copies and map to single loci on chromosomes 1 and 2, respectively [8]. Tomato chromosomes can easily be identified by pachytene analysis. With the development of trisomics, monosomics, and translocations through chromosome engineering, tomato cytogenetic research has become one of the most advanced areas in the field of agriculture. Tomato crosses with its wild relatives with varying degrees of difficulty; thus, wild relatives can and have been used as sources of genes for crop improvement. Wild species are interesting resources of genetic variation for introgression breeding and comprise exclusive sources of many resistance genes for cultivated tomatoes [9]. Higher plant densities have increased yield in tomatoes and it is influenced by the genotype [10–16].

4. Tomato growth and environment

Tomato is grown under various environments ranging from field conditions such as gardens and under controlled environments. Growing tomatoes under field conditions is the cheapest option for most smallholder farmers due to the low resource requirements. Farmers rely on the rainfall pattern with supplementary watering particularly during the dry season. The crops cultivated this way are exposed to the diverse environmental conditions that may prevail in the area [17]. Intensive crop management such as pruning and staking is always difficult under these conditions. Due to harsh environmental conditions in most parts of the tropics, most tomato growers prefer to grow tomato under controlled environments. The main objective of such operations is to attain the full potential of the crop in terms of yield and nutrient content. Growing tomatoes under controlled environments facilitates improved management such as pruning and staking that could improve the yield of tomatoes. Studies have shown that high temperatures particularly in the tropics affect the quality and nutrient content particularly lycopene of field-grown tomatoes [18, 19]. However, growing tomatoes under controlled environments requires more resources that increase the cost of production and make it difficult for smallholder farmers to engage in it.

5. Field conditions

Tomato is mostly cultivated in moderate climates around the world but can thrive well in a wide range of climatic conditions. The vegetative and reproductive processes of the tomato are adversely affected by high temperature stress, resulting in a reduction in fruit quality and yield [20]. In temperate regions, the crop does well within daily average temperature range of 18°C

and high of 25°C, while the warm season temperatures average low of 26°C and a high of 32°C. Significantly higher or lower temperatures can have negative effects on fruit set and quality. Studies have shown that temperatures above 32°C for more than 3 hours a day can induce abortion of flowers resulting in low fruit yield [21]. In Ghana and most parts of West Africa, it is cultivated in the open field under field conditions, or in controlled environments such as greenhouse. The productivity of the tomato crop depends on the yield potential of the genotype, the soil as well as agronomic and management practices that are carried out. Tomatoes can be produced on a wide range of soils varying from deep, medium textured sandy loam or loamy, fertile, well-drained soils [22]. The site for growing tomatoes should be carefully selected based on the topography, soil type, soil structure, and soil management and the cropping history of the land (fields previously cropped to solanaceous crops should be avoided). Tomato plants depend on the soil for adequate nutrient and water supply as well as anchorage for physical support. For this reason, land preparation should be adequately done to ensure proper plant establishment and to provide the best soil structure for root growth and development. Tomatoes require soils that are rich in nutrients but most soils in Sub-Saharan Africa are low in nutrients due to continuous intensive cultivation without adequate application of soil amendment measure [23, 24]. The potential of organic and inorganic fertilizers can provide the needed solution for intensive tomato cultivation, but this is limited due to scarcity, cost implications, and problems with high acidity associated with over application of such fertilizers [25]. The application of green manure can also provide a viable alternative for maintaining soil fertility but its use is limited among tomato farmers in Ghana [26].

5.1. Controlled environments

In most parts of the tropics, tomato production is weather dependent and highly seasonal. This had led to fluctuations in glut during peak harvest and scarcity during the unfavorable periods of the season. This scenario often affects the pricing and revenue of the growers as well as consumer satisfaction [27]. The use of controlled environment in tomato cultivation can address the challenges faced by tomato farmers to provide suitable environment for growing tomatoes during the off-season and meet consumer demands. Several controlled environments are used in tomatoes cultivation.

6. Screenhouse/greenhouse

Greenhouse tomato production utilizes techniques that are not used in the open field or other intensive cropping systems. In the greenhouse, water, carbon dioxide, artificial lighting, soilless growth medium such as hydroponics and heating systems are provided to simulate the growing conditions that occur in the open field [28]. Most greenhouses are used in association with drip irrigation systems that regulate and save the amount of water that will be required to produce the optimum yield. In some cases, only 25% of the water required in the open field is used to produce the same quantity in the greenhouse [29]. This is very useful in areas that are faced with extreme temperatures and water scarcity [28] and will be crucial in crop production

especially with the imminent shortage of water that will be associated with climate change and variability. The use of greenhouse technology in tomato cultivation combines market-driven quality parameters with the production system that enhances the quality and quantity of the final product. Provision of the necessary intensive plant care is possible without the excessive use of chemical pest management. This is because better protection is achieved through the use of integrated pest management strategies that are more effective under controlled environments than in open field [30]. Cultivation of tomato under this system ensures that the high profit margins due to premium prices offered the good-quality products obtained because in addition to higher yield, the production is also free from dust, insect, disease, and pest [31]. Greenhouse-grown round and cluster tomatoes were found to contain higher levels of lycopene than field-grown tomatoes. However, the opposite was the case with cherry tomatoes which recorded lower levels of lycopene under greenhouse conditions compared with open-field cherry tomatoes. These reports suggested the presence of genotype by environment interaction effect [18]. Therefore, careful varietal selection should be done when utilizing the greenhouse technology in tomato cultivation. Besides careful varietal selection, energy consumption is also one area that needs to be considered critically when deciding the type of technology to be used for maximum profit [32].

6.1. High tunnel

Tomatoes are well adapted to the growing conditions within a high tunnel. A high tunnel often called *hoophouse* is a solar-heated, manually controlled vented structure cold frame that is covered with plastic (single or double layer) for cultivation of many horticultural crops with the purpose of lengthening the growing season. Though similar in appearance to some greenhouses, they lack some features of greenhouses such as electricity for temperature and humidity regulation, and thus require no electrical connections for ventilation and supplemental heat [33–35]. However, most high tunnels have roll-up sidewalls and detachable end walls for temperature and humidity management. High tunnels can significantly increase the average daily temperature and protect the crop from wind, rain, insects, and diseases. Crops are grown directly in the soil using raised beds or mulch [36, 37]. Since high tunnels exclude natural rainfall so water must be applied through irrigation. Drip irrigation significantly improves the marketable yield and overall quality and is the best form of irrigation for tomatoes grown under high tunnels. It ensures uniform application of water to help reduce fruit cracking and other physiological problems such as blossom end rot. In most intensive cultivation using the high tunnel technology, both water and nutrients are supplied to the crops during the growing season with drip irrigation [38]. When tomatoes are cultivated in high tunnels they can be trained to grow vertically by the use of trellis or staking (**Figure 1**).

6.2. Hydroponics

Hydroponic tomatoes are grown in a nutrient solution rather than soil. The plants are typically placed in a nonsoil material known as substrata that can support their roots and hold the nutrients. In some cases, hydroponic system utilizes absorbent substrata such as coconut fiber, perlite, rock wool, vermicompost, and their combinations [39, 40] together with a drip-irrigation

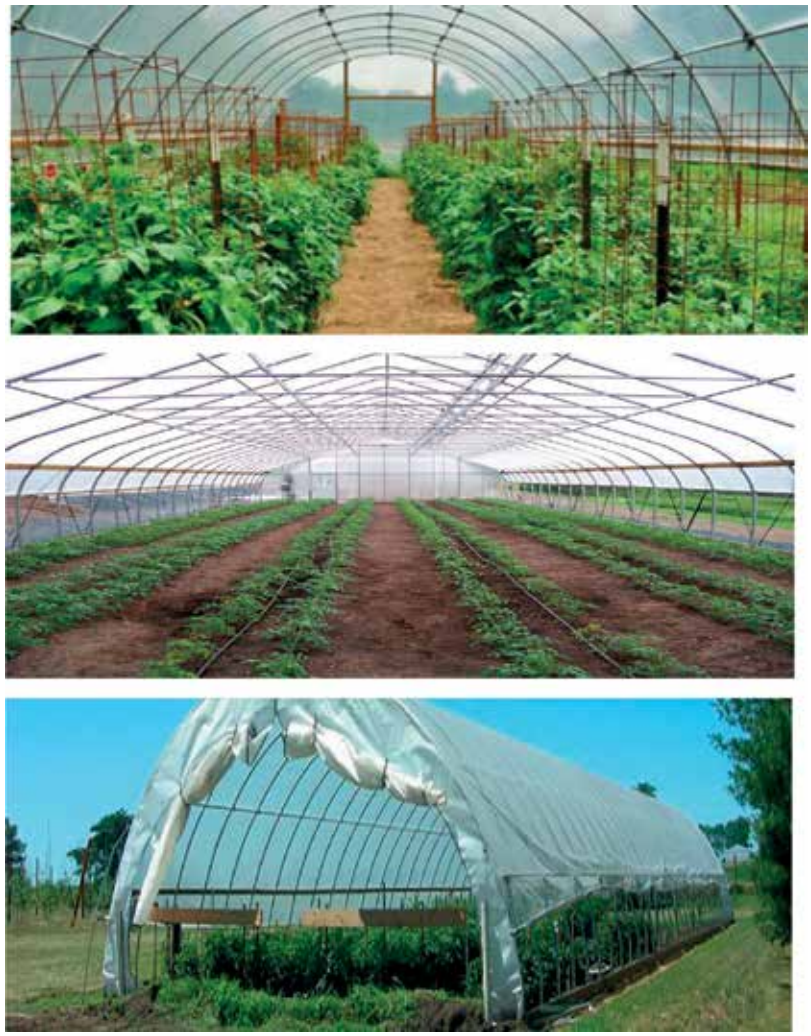

Figure 1. Interior and exterior features of high tunnels for controlled vegetable cultivation.

system which supplies water at low tension and high frequency to create optimum environment for growth of the vegetable [41, 42]. By avoiding soil medium, the use of hydroponics enables the grower to prevent diseases and soil-borne pests, such as nematodes, that are difficult to control [43]. Tomato production under protected systems such as hydroponics allows cultivation in regions inappropriate for conventional agriculture by efficiently using natural resources particularly water and soil [44]. Hydroponic systems provide regulation of harvesting, avoiding crop rotation, better fruit quality, better crop handling, and better control over nutritional needs and environmental conditions. Growing tomatoes under hydroponic system allows the grower to raise them under a controlled environment with less chance of disease, faster growth, and greater fruit yield. This offers several advantages in terms of the quantity and quality of products obtained per unit land area over cultivation in soil [45].

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However, hydroponic gardening is labor-intensive and requires skilled training for efficient water and nutrient management under large-scale production. It has been suggested that one of the major problems of using the hydroponics systems for tomato cultivation is its requirement for highly specialized technical support in order to properly replenish the nutrient solution in all the growing phases of the crop [43] (**Figure 2**).

6.3. Irrigation

The tomato plant like most vegetable crops requires a lot of water for optimum growth and development. Moisture stress causes abortion of flowers and young fruits, and young fruit, sun scalding, and dry rot of fruit. Water is required at most critical stages of growth of the

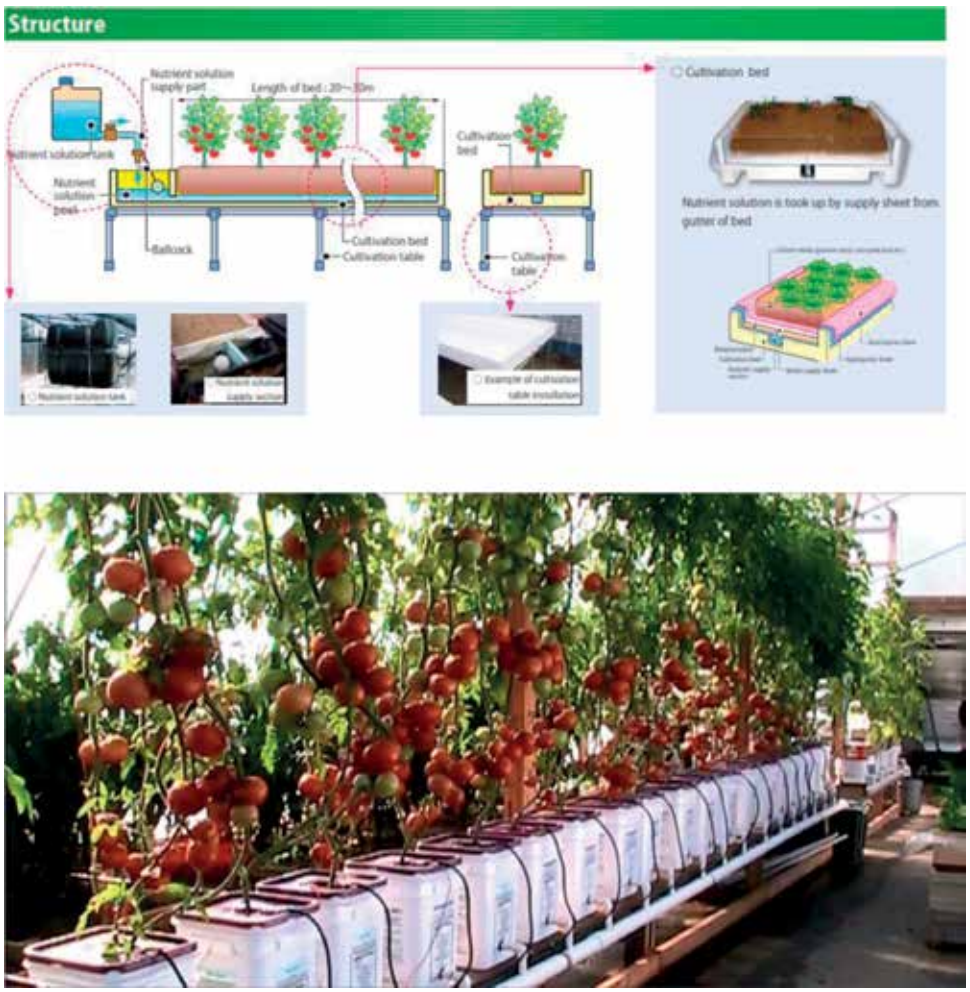

Figure 2. Dutch bucket hydroponic system for cultivating tomatoes (https://www.google.com.gh/search?tbm = isch&sa = 1&q = hydroponics+tomatoes&oq = hydroponics+tomatoes&gs_l = psy-ab.3..0j0i5i30k1j0i24k1l6.202616.205468.0.206233.9.9.0.0.0.0.384.1735.2-5j1.6.0….0…1.1.64.Psy-ab..3.6.1732…0i67k1.0.HQe-PNKGI6I#imgrc = gjqgs0WVSaQvuM).

tomato plant particularly at transplanting, flowering, and fruit development. Adequate supply of water is very essential for attaining the full potential of tomato plants under cultivation [31, 32]. However, agricultural activities in most parts of the tropics are mostly rainfed resulting in short supply of water for farming activities during the dry season. Rainfall amounts are often erratic even during the main growing season resulting in poor crop performance especially in areas where tomatoes are grown in soils with low water holding capacity. The use of irrigation schemes provides the needed water required for crop production. This makes supplemental irrigation essential for commercial tomato production to sustain consistent yields of high-quality tomatoes during the off-season to meet demand of consumers. Studies have shown that irrigation increases annual tomato yields by an average of at least 60% over dryland production [32, 33]. The quality of tomatoes cultivated under irrigation has also been found to be better than nonirrigated fields [20].

7. Types of irrigation in tomato cultivation

7.1. Sprinkler irrigation

These systems include center pivot, linear move, traveling gun, permanent set, and portable aluminum pipe with sprinklers that supply the irrigation water in sprays to the crops. The idea is to mimic the natural rain drops. Sprinkler systems used in tomato production are normally adjusted to deliver at least an inch of water every 4 days. The system is also designed to supply the water in such a way that runoff is prevented [41]. The type of soil is also considered in adjusting the speed of the sprinkler irrigation system. Whereas faster speed (3 inches per hour) is preferred in sandy soils, slower speed is preferred in loamy soils (1 inch per hour). High level of application uniformity is essential every plant is covered to ensure uniform growth and development throughout the field [42].

7.2. Drip irrigation

Drip irrigation has become the standard practice for tomato production. Although it can be used with or without plastic mulch, its use is highly recommended with plastic mulch culture. One of the major advantages of drip irrigation is its water use efficiency. When used in conjunction with plastic mulch, the tubing can be installed at the same time the plastic mulch is laid. In drip irrigation system, water is delivered to each plant usually done with tubes and emitters that carry water from main lines to the base of each plant. In some cases, fertilizer is included in the irrigation water in a system appropriately called “fertigation” [41, 46]. The important thing to note is that water is supplied in such a way that the plants do not wilt. Studies have also shown significant yield increases with drip irrigation and plastic mulch when compared with sprinkler-irrigated tomatoes. The most dramatic yields have been attained by using drip irrigation and plastic mulch, and supplementing nutrients by injecting fertilizers into the drip system. This observation is due to judicious utilization of the water and nutrient resources that are supplied to each plant which is not the case with sprinkler irrigation system. The incidences of weeds also less of a problem, since only the rows are watered and

the middles remain dry. Another advantage of drip irrigation is obtained when used in within a high tunnel which is equipped with the ability to inject water-soluble nutrients through the drip lines as the plant needs them.

8. Genotype × environment interaction

Multilocation trials are usually performed by researchers to evaluate new or improved genotypes across multiple environments (locations and years), before they are promoted for release and commercialization. This is systematic approach undertaken to increase yield stability of new crop varieties in stress-prone environments [47]. Data generated from such trials are important for (i) accurate estimation and prediction of yield based on limited experimental data; (ii) determining yield stability and the pattern of genotypes response across environments; and (iii) providing reliable guidance for selecting the best genotypes or agronomic treatments for planting in future years and at new areas [48]. However, the performances or ranking of the genotypes in such experiments are usually not the same in the different environments. This is because of interactions between the genotypes and the environments [49, 50]. This type of interaction is known as genotype × environment interaction (GEI), and may complicate the selection and recommendation of genotypes evaluated in diverse environments [51, 52]. The importance of GEI in genotype evaluation and breeding programs has been demonstrated in almost all major crops [53–57]. The GEI reduces the association between the phenotypic and genotypic values and leads to bias in the estimation of gene effects and combining ability for various characters that are sensitive to environmental fluctuations less reliable for selection [57].

Genotype × environment interactions can be classified into three broad types (**Figure 3**) (i) "no" GEI, (ii) non-crossover interaction, and (iii) crossover interaction [58]. The number of environments (E) and the number of genotypes (G) determine the number of GEI possible and that, the higher the number of environments and genotypes the greater the number of possible G × E interactions. Thus, with two genotypes and two environments, and with only a single criterion, at least four different types of interactions are possible. With 10 genotypes and 10 environments, 400 types of interactions are possible, which would undoubtedly make their implications and interpretation more difficult to comprehend [59, 60].

9. No G × E interaction

When there is no GEI, the effects of each of the risk factors are similar across the levels of the other risk factors. A "no" GEI occurs when one genotype (G1) constantly performs better than the other genotype (G2) by approximately the same amount across both environments. **Figure 3A**, **B** shows that G1 and G2 perform similarly in two environments, because their responses are parallel and stable. The variations in trait expression across a range of environments for the two genotypes are therefore additive. Moreover, the intergenotypic variance

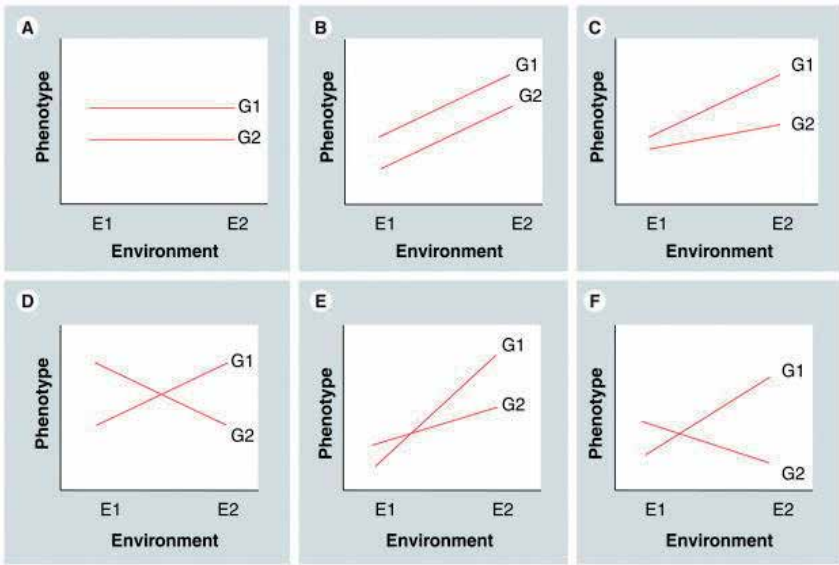

Figure 3. Graphical representation of the "no" interaction, non-crossover interaction, and crossover interaction types of genotype-environment interactions (Source: [58]).

remains unchanged in the two environments and the direction of environmental modification of genotypes is the same. In **Figure 3A**, there is a main effect of G, and in **Figure 3B**, there is a main effect of environment [58].

10. Non-crossover G × E interaction

Figure 3C signifies a non-crossover type of GEI. Unlike in **Figures 3A** and **3B**, the difference in performance is not similar across the environments. The G1 and G2 respond differently to the two environments but their ranks remain unchanged. The response of the two genotypes under different environments is therefore not additive, and the magnitude of intergenotypic difference increases. Moreover, the environmental modifications of the two genotypes are in the same direction [58].

11. Crossover G × E interaction

The different and inconsistent response of genotypes to diverse environments is regarded as crossover GEI, when the ranks of genotypes vary from one environment to another [1]. Crossover interaction suggests that no genotype is superior in multiple environments [61]. **Figure 3D** illustrates a crossover type of GEI where the direction of environmental modification of genotypes, G1 and G2 is opposite: the performance of G1 increases and that of G2 decreases. The genotypic ranks change between the two environments, but the magnitude of

intergenotypic variance remains unchanged. **Figure 3E** is also a representative of a crossover interaction as the genotypes change ranks between the two environments. There is also a change in magnitude of intergenotypic variance. Moreover, the difference between genotypes G1 and G2 in environment E1 is smaller than that in E2, and the direction of environmental modification of the two genotypes is the same. The illustration in **Figure 3F** is a crossover interaction with the environmental modification in opposite direction [58].

12. Multilocation trial for tomato production

Multilocation trials are conducted to evaluate yield stability performance of genetic materials under varying environmental conditions [55]. The relative performance of genotypes for quantitative characteristics, such as yield and other characteristics, influences yield to vary from an environment to another. To develop a genotype with high yielding ability and consistent performance, high attention should be given to the importance of stable performance for the genotypes under different environments and their interactions. This enables the breeding of better crop varieties that have buffered and can give stable and consistent performance across different environments and seasons [59]. To attain this, feat genotypes are evaluated in multienvironment trials (METs) by testing their performance across environments and selecting the best genotypes in specific environments. The main objective is to eliminate genotype by environment interaction results from differences in the sensitivities of genotypes to the conditions in the target environment [62]. This leads to inconsistent performances of genotypes across environments and limits the efficiency of selection of superior genotypes [56].

13. Tools/methods for genotype × environment interaction analysis

Analysis of GEI is important to obtain information on the performance of genotypes in terms of adaptability and stability. Analysis of variance is performed across environments in order to identify the presence of GEI in multilocation trials. When the GEI variance is found to be significant, then one of the various methods for measuring the stability of genotypes can be used to identify the most stable genotype(s). Several statistical methods have been proposed for analysis and interpretation of GEI [63–66]. The joint regression analysis [67–69] method has been widely used; nonetheless, several limitations of the method have been stated [70, 71]. For example, see [48]. The PCA method has the ability to overcome the limitations associated with the linear regression method by giving more than one statistic, that is, the scores on the principal component axes, to describe the response of a genotype. Another method which has been proposed for analysis of GEI is the cluster analysis which is a numerical classification technique that defines groups of clusters of individuals [48, 72]. Currently, the additive main effects and multiplicative interaction (AMMI) model [64, 71] and genotype main effect plus genotype × environment interaction (GGE) biplot methodology [66] are the two most powerful statistical tools used by many researchers for the analysis of multilocational trial data. The AMMI model combines the analysis of variance for the genotype and environment main

effects with principal component analysis of the genotype × environment interaction. It also provides a better prediction assessment and a valuable approach for understanding GEI and obtaining better yield estimates. The interaction is described in the form of a biplot display, where PCA scores are plotted against each other and provides visual inspection and interpretation of the GEI components. Integrating biplot display and genotypic stability statistics enable genotypes to be grouped based on similarity of performance across diverse environments. Similarly, the GGE biplot analysis enables visual (graphical) presentation of interaction estimate. This method also combines analysis of variance and PCA by partitioning together sums of squares of genotypes and sums of squares of GEI (which are relevant in genotype evaluation) using PCA method. The biplot technique is used for the presentation and estimation of genotypes in different environments [73]. The GGE biplot shows the first two principal components (PC1 and PC2) which are obtained by decomposition of singular values of multilocation trials yield data. GGE biplot analysis enables the identification of the genotypes with the highest yields in different environments, comparison of their performances in different environments, identification of ideal genotype, as well as mega-environments (model of regional distribution or target environment) [74, 75].

Several researchers have compared the efficiency of AMMI and GGE biplot for analyzing GEI. According to Yan and others, the major disadvantage of the AMMI model is that it is insensitive to the most important part of the crossover GEI [75]. Moreover, the AMMI model does not offer any advantage to the breeder for genotypic and site evaluation when analyzing METs data because there is no clear biological separation between the two terms, genotype and GEI. However, the GGE biplot is a powerful statistical model that takes care of some of the disadvantages of AMMI. The method is an effective statistical tool for identifying the best performing cultivar in a given environment and the most suitable environment for each cultivar, comparison of any pair of cultivars in individual environments, the best cultivars for each environment and mega-environment differentiation, average yield and stability of the genotypes, and the discriminating ability and representativeness of the environments [75–77]. Gruneberg and others indicated that AMMI was highly effective for the analysis of MET [78]. Kandus and others also revealed that the AMMI model is the best model for describing the GEI [79]. Stojaković and others [80] and Mitrovic and others [81] found that both models provided similar results. However, contrary to these reports, [75, 82, 83] concluded in their comparison of both models that the GGE biplot was superior to the AMMI biplot in mega-environment analysis and genotype evaluation.

14. Prospects and problems of G × E

The phenomenon of genotype × environment interaction refers to the differential performance of genotypes in different environments that affect the efficiency of selection in a breeding program. G × E interaction arises due to the differences in the sensitivities of genotypes to the different environmental conditions. In order to mitigate the effect of G × E interaction, crops need to be tested in several environments to assess their specific and broad adaptation [53, 76]. Though tomatoes do well in both tropical and temperate climates, its performance can vary with respect to the environments [18]. Prior to the release of every crop variety, multilocation

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trials are conducted to ascertain crop performance in a wide range of environments for adaptability and stability in performance [47].

14.1. Causes of genotype × environment interaction

Living organisms are made up of genes whose expression are subject to modification by the environment; therefore, genotypic expression of a phenotype is environmentally dependent [84]. This is because genotypes exhibit different levels of phenotypic expression under different environmental conditions resulting in crossover performances [85]. Crossover performances by genotypes in different environments result from differential genotypic responses under varying environmental conditions [63, 86]. This results in genotype by environment interaction where one genotype gives its maximum performance in one environment by performing poorly in another environment. In G × E interaction, the magnitude of the observed genetic variation changes from one environment to another and tends to be larger in better environments than poorer environments [87].

14.2. Problems of genotype × environment interaction effect on selection

The objective of most plant breeders is to develop new varieties that will perform consistently well across multiple environments. However, significant G × E interaction has been reported for most quantitative traits in tomato particularly for fruit yield and quality traits such as lycopene, total soluble solids, vitamin C, etc. [19, 88]. A tomato variety with improved fruit quality in one environment may not necessarily perform the same in another location due to differential responses to the different environmental conditions prevailing in the different locations. Environmental factors such as soil, moisture, temperature, light intensity, humidity, rainfall, photoperiod, and agronomic practices play important role in the expression of the genes controlling the trait of interest. This results in different phenotypic expression among locations. Genotype × environment interaction effect complicates the selection of suitable varieties by breeders because elite varieties developed for one location may not perform the same in different locations. In some cases, the quality of fruits of tomatoes is significantly influenced by genotype by environment interaction. Such interactions confound the selection of the superior cultivars by altering their relative productiveness in different environments. For instance, see [89]. Other studies [90] also reported significant G × E interaction effect on total sugars among six tomato varieties grown under field and screenhouse conditions. This problem implies that tomato varieties that were developed and selected under field conditions may not perform to its full potential when farmers grow them under controlled environments. Therefore, the extent of G × E interactions effect for most traits of economic importance needs to be taken into account during the selection process in order to obtain crop varieties that will give consistent performance across environments and seasons.

14.3. Elimination of genotype × environment interaction

Breeding of crops involves different attributes of the genetic materials that are subject to variation in environmental conditions [91]. In some cases, direct selection is slow due to low heritability, polygenic control, epistasis, and significant G × E interaction on the trait of interest

[92]. To mitigate the confounding effect of G × E interaction on selection efficiency, plant breeders have devised strategies to ensure progress in selection efficacy. For this reason, genotypes are tested in diverse environments to assess their adaptability and stability [85]. After this sound, analyses are carried out using the appropriate software to assess the extent of G × E interaction effect. Genotypes whose G × E effects are not significant are considered to be stable and therefore selected [62].

Stability analysis is performed to estimate the performance of genotypes as linear function of the level of productivity in each environment [93]. Eberhart and Russell suggested joint regression analysis to estimate the average performance of a genotype in different environments relative to the mean performance of all genotypes in the same environment [68]. The use of multiplicative models which include the additive main effect and multiplicative interaction (AMMI) model has also been used to assess the stability of other crops [94, 95]. The AMMI model allows fitting of the sum of several multiplicative terms rather than only one multiplicative term in dissecting the performance of genotypes in different environments [93]. Yan also suggested the use of the genotype and genotype × environment interaction (GGE) biplot to graphically visualize genotypic performance across several environments [96]. The use of these strategies will enable the breeder to make informed decisions in where to place which variety based on their adaptability for optimum performance.

15. Conclusion

The pounding prominence of tomato as a vegetable is reflected by large volume of research on almost all aspects of the crop. In every crop improvement program, promising genotypes are tested for their performance for some years at a number of sites, to identify genotypes which possess the dual qualities of high-yield sustainability to adverse changes in environment condition. This interplay refers to genotype by environment interaction. A genotype × environment interaction is a change in the relative performance of a character of two or more genotypes measured in two or more environments. Its origin is linked to two concepts: biometric and developmental interaction. Interactions may therefore involve changes in order for genotypes between environments and changes in the absolute and relative magnitude of the genetic, environmental, and phenotypic variances between environments. These can further be classified as no GEI, non-crossover interaction, and crossover interaction. Complex quantitative traits, such as yield, with multiple contributing traits are highly influenced by environment interaction effects. Tomato production, though weather dependent and highly seasonal, can be grown under both field and greenhouse conditions (controlled environment). Researchers perform multilocational trials to evaluate new or improved genotypes across multiple environments (locations and years), before they are promoted for release and commercialization. This organized approach helps increase yield stability of new crop varieties in stress-prone environments. To obtain information on the performance of the genotypes in terms of adaptability and stability, an analysis of the GEI is paramount. Even though several statistical methods have been proposed for analysis and interpretation of GEI, the joint regression analysis method has been widely used; nonetheless, it has numerous limitations. Many other researchers have also found AMMI and GGE biplot efficient for analyzing GEI. A major

problem of GEI is that its effect thwarts the selection of suitable varieties by breeders because elite varieties developed for one location may not perform the same in different locations. In some cases, the quality of fruits of tomatoes is significantly influenced by genotype by environment interaction. Such interactions confuse the selection of the superior cultivars by altering their relative productiveness in different environments. Though tomatoes do well in both tropical and temperate climates, its performance can vary with respect to the environments.

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Chapter 6

Marker-Assisted Selection (MAS): A Fast-Track Tool in Tomato Breeding

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Abstract

Marker-assisted selection (MAS) is a complementary tool for conventional breeding where a molecular marker linked to a trait is indirectly selected. Many studies conducted have been able to identify and develop markers for traits such as disease and pest resistance and other abiotic stresses. Despite the availability of these markers, the technology has been extensively used in tomato breeding for the identification of some economic traits in particular disease resistance. In developed countries, MAS is utilized routinely in breeding programs, but this cannot be said for developing countries such as Africa. It is high time Africa as a continent looks at the importance of the technology and invests in it. In addition to MAS, other strategies such as marker-assisted backcrossing and recurrent selection have also been employed for breeding in tomato. The use of MAS in crop improvement will not only reduce the cost of developing new tomato varieties but will also increase the precision and efficiency of selection in the breeding program as well as lessen the number of years required to come up with a new crop variety.

Keywords: tomato, crop improvement, molecular marker, indirect selection, efficiency, variety

1. Introduction

Tomato, *Solanum lycopersicum* L., is the second most important vegetable after potato. Indisputably, it is the most popular vegetable crop in the world [1]. Though a tropical plant, the crop is cultivated virtually all over the world [2]. In most West African countries especially Ghana, the crop is consumed in almost every household daily [3]. Tomato provides vitamins A and C as well as vital

minerals and other nutrients [4]. That notwithstanding, both the fresh and processed tomatoes are the richest sources of the dietary antioxidant lycopene, which debatably protects cells from oxidants linked to cancer [5]. Tomato is also a source of other compounds with antioxidant activities such as rutin, tocopherol, chlorogenic acid, plastoquinones and xanthophylls [6]. Tomato has been commonly used not merely as food, but also as research material. The tomato plant possess many interesting features such as fleshy fruit, compound leaves and a sympodial shoot, which are lacking in other model plants (e.g., *Arabidopsis* and rice). Moreover, tomato belongs to an enormous family Solanaceae, which is closely interrelated with many commercially important plants such as garden eggs, eggplants, peppers, potato and tobacco [7]. Information or knowledge obtained from studies conducted on tomato can be easily applied to these plants, hence making tomato an important research material. For this reason, tomato functions as a model organism for the family Solanaceae and especially for fleshy-fruited plants. Phenotypic selection coupled with traditional breeding was used to develop most commercial cultivars of tomato. Currently, tomato breeding has entered into a new era following the introduction of molecular markers and marker-assisted selection (MAS) technology. Tomato was one of the first crops for which molecular markers were suggested as indirect selection criteria for breeding purposes [8–10]. Molecular markers have been used extensively for genetic mapping as well as identification and characterization of genes for many agriculturally important traits in tomato. The technology also has been utilized for marker-assisted breeding for several economically important traits. The actual use of MAS in tomato breeding began approximately 30 years ago with the use of the isozyme marker acid phosphatase (*Aps-11* locus) as an indirect selection criterion for breeding for nematode resistance [11]. Paradoxically, this isozyme marker is still being used in many private and public tomato-breeding programs for selecting for nematode resistance. However, more recently, with the development of new molecular markers and maps in tomato, MAS has become a routine practice in many tomato breeding programs, in precisely in the private sector. MAS is often used to assess hybrid purity from overseas production by screening seed lots with a panel of molecular markers [12]. MAS is used effectively for quick germplasm screening for disease resistance or fruit quality. Often, a panel of linked markers is used on individual selections or pools of seed or tissue from early generation populations to "index" breeding populations. This aids breeding efforts by informing the breeder about which disease resistances or fruit quality traits are segregating or fixed in a given population. MAS is employed for marker-assisted backcrossing (MAB) after reliable linkages between markers, and simple traits of interest are discovered. Such traits include, but not limited to, disease resistance, fruit color and carotenoid content (e.g., lycopene and β-carotene), fruit-ripening-related traits (various genes including *Rin* and *Nr*), jointless pedicel (*j2*) and extended shelf life using various genes such as *alcobaca, nor and rin* [12]. MAS is not only faster than phenotypic selection but also cheaper and more effective. However, the extent to which MAS has been employed in public and private tomato breeding programs has not been clearly determined. This chapter gives a review of the application of MAS in tomato and assesses the current and potential use of MABC in tomato breeding programs.

2. Breeding history of tomato

Domestication of tomato has activated a wide range of morphological and physiological traits that differentiate domesticated crops from their wild ancestors. At the end of the nineteenth

century, numerous cultivars of tomato were available in different colors and for different purposes. Since these cultivars require no cross-pollination, growers especially tomato farmers get access to seeds effortlessly for the next planting. For the reason that tomato has only 4% chance of outcrossing, tomato produces plants that show resemblance to the parents. As a matter of fact, previous or former tomato cultivars that were carefully chosen and innate in a family got the name heirloom. Heirloom tomato varieties though open-pollinated are unique in shape, size and color [13]. These cultivars could be considered as landraces and products of domestication. The collection, description, propagation and distribution of genetic materials are of the utmost importance in tomato breeding. The Tomato Genetics Resource Center in Davis, California (TCRC) during the latter half of the twentieth century assembled and maintained thousands of wild Solanum species accessions coupled with producing large proportion of monogenic mutants and various genetic stocks of tomato. Currently, the most Solanaceae species in the world were collected and maintained by the Botanical and Experimental Garden (http://www.bgard.science.ru.nl/) in the Netherlands [14] (http://zamir.sgn.cornell.edu/mutants/), which is an isogenic tomato "mutation library" containing a total of 13,000 M(2) families derived from treatment with ethyl methane sulfonate (EMS) and fast-neutron mutagenesis.

Systematic breeding for improvement of the overall horticultural characteristics of tomato actually started in the 1930s. Tomato breeding gained prominence at the beginning of twentieth century in the public institutions predominantly in the USA. Later private companies were formed and engaged in commercial breeding that led to hybrid development. Hybrids give a good combination of characters from both parents. Growers preferred to buy hybrid seeds at higher prices following their enormous benefits over the open-pollinated cultivars. The first hybrid tomato cultivar, which developed through a single cross, was released in 1946 [15].

Currently, most tomato varieties whether fresh market tomato or processed tomato are hybrids. The breeding process involves recognizing and combining certain traits to create a novelty for each market. The final product could be sold in a wide range of shapes such as pyriform, high round, cylindrical, oval and sizes from small cherry tomato to very large beef tomatoes. The breeders' law allows breeders to make new crosses either with their own materials or cultivars of their competitors [16]. To avoid taking many generations to remove deleterious genes, breeders often dodge using wild germplasm to introduce new traits. Crosses are, however, made to produce test hybrids i.e., hybrids developed through F4 to F6 with fixed parental lines. These hybrids then go for testing at on station (breeders site) and finally to the farmers' sites after which the best hybrids are selected for commercial usage. Recently, a number of tomato breeding companies are major players in the world market. It is, therefore, important that seed companies continue to develop new cultivars with added value [17]. It takes approximately 5 years for commercial tomato cultivars to turn over time. As a matter of fact, breeding companies can get return on their investments if prices are high for their seeds. This is typical of the fresh tomato market as the yearly value of worldwide tomato seed market is approximately half a billion euros especially for fresh market.

The goals of public and private tomato breeding programs vary widely depending on location, need and resources. In general, breeding goals in tomato have gone through four phases: breeding for yield in the 1970s, for shelf life in the 1980s, for taste in the 1990s and for nutritional quality currently. To be successful, growers must produce a high yield of high-quality

fruit, while holding production costs as low as possible. Therefore, many of the breeding goals focus on characteristics that reduce production costs or ensure reliable production of high yields with high-quality fruits. The genetics of a quantitative trait is hard to study, since the effect of each gene is small and often influenced by environment or by the interaction with other genes (epistasis). Many important tomato traits as described above are genetically controlled by a combined action of QTLs with favorable alleles often present in the wild species [18–20]. To introgress the wild favorable allele into cultivated tomato, marker-assisted selection plays an important role and the map positions and markers linked to the QTLs provide a basis for breeders to design optimal breeding strategies. To map QTLs in tomato, interspecific populations have been extensively used. However, in an interspecific cross, multiple segregating QTLs at the whole genome level often tend to mask the effects of one another [21, 22].

3. Development of genetic markers

An alternative approach to improving selection efficiency in tomato is to discover genetic markers that are associated through linkage or pleiotropy with genes that control the trait(s) of interest. Genetic markers are biological features that can be transmitted from one generation to another. They can be used as experimental probes or tags to track an individual, a tissue, a cell, a nucleus, a chromosome or a gene. The value of genetic markers as indirect selection criteria has been known to breeders since early 1900s. Genetic markers can be classified into two categories namely classical markers and DNA markers [23, 24]. Classical markers comprise morphological markers, cytological markers and biochemical markers. DNA markers such as restriction fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP), rapid amplified polymorphic DNA (RAPD), simple sequence repeats (SSR), single nucleotide polymorphism (SNP), etc. have been developed. These DNA markers have developed into many systems based on different polymorphism detecting techniques or methods including northern and southern blotting of nucleic acid hybridization, polymerase chain reaction (PCR), and DNA sequencing [25].

4. Classical markers

Breeders have used morphological markers to select for superior phenotypes for many decades. During the history of plant breeding, markers mainly used included visible traits such as flower color, leaf shape, seed shape, fruit shape, flesh color, stem length, etc. These morphological markers can easily be identified and therefore usually used in the construction of linkage maps. Some of these markers are also linked with other agronomic traits and thus can be used as indirect selection criteria in breeding. However, morphological markers available are limited, and many of these markers are not associated with important economic traits like yield and quality. In addition, some even have undesirable effects on the development and growth of the plant. In tomato, there are over 1300 morphological, physiological (e.g., male sterility, fruit ripening, and fruit abscission), and disease-resistance genes [26] of which only less than 400 have been mapped [27].

Cytological markers are represented by chromosome karyotype and banding patterns. These markers are not directly used in plant breeding but serve as landmarks on the chromosomes thereby used for identifying linkage groups and subsequently genetic maps are constructed. Biochemical markers or isozymes are alternative forms or structural variants of an enzyme with different molecular weights and electrophoretic mobility but have the same catalytic activity or function. The second generation of isozymes became more popular during 1970s and early 1980s. Although some 41 isozymic genes in tomato have been identified, characterized and mapped [28], these markers are few and less polymorphic [29].

5. DNA markers

In overcoming limitations associated with classical markers, development of DNA markers have proven to be of great significance in enhancing genetics and breeding of crop varieties [30]. A DNA marker is a fragment of DNA showing mutations/variations, which can be used to detect polymorphism between different genotypes in a population. These fragments are usually associated with a specific location within the genome and may be detected using modern molecular tools. In the past, different types of molecular markers have been developed and utilized. This includes both dominant and codominant markers. Dominant markers are markers that are unable to differentiate between homozygotes and heterozygotes, while codominant markers can differentiate between homozygotes and heterozygotes. A lot of molecular markers have been developed for tomato. Notable among them are RFLP markers; however, this marker is time and labor intensive and requires the use of large amount of DNA. As a result, RFLP markers have been replaced with PCR-based markers that are easy to handle (http://solgenomics.net). Other marker techniques that have been developed for tomato include random amplified polymorphic DNA (RAPD) and amplified fragment length polymorphism (AFLP) [30]. Large amount of sequence information have been released for tomato species and subsequently, SSR markers developed. These SSR markers are widely used because they are easy to handle and able to detect multiple alleles. Currently, over 20,000 SSR markers have been developed from expressed sequence tag (EST) and BAC-end sequences and used as genetic and genomic tools in tomato species [31]. Single nucleotide polymorphism (SNP), which is now the marker technology of choice, has also been discovered by a resequencing strategy, and several SNP genotyping methodologies have been developed for application in tomato research. As a result, this high-throughput SNP analysis can be performed effectively in a large number of samples by array-based assays as genotyping platforms and applied to the construction of high-density genetic linkage maps and performance of genome-wide association studies [32]. The diversity arrays technology (DArT) platform, which is one of the array-based methods, has also been used to develop polymorphic markers across introgression line (ILs) population of tomatoes [33].

6. Genetic maps in tomato

The first linkage map of tomato was reported in 1968. This linkage map was constructed based on both morphological and physiological markers [34]. The map was later improved

and was assigned to the 12 linkage groups in tomato [35]. This facilitated the development of other maps including the tomato isozyme linkage map that was published in 1980. Then in 1986, another map consisting of RFLP and isozyme loci was also generated. Since then, several interspecific genetic linkage maps have been generated with RFLPs incorporating cleaved amplified polymorphic sequences (CAPS), SSR and SNP markers. Varying number of markers ranging from 93 to 4491 have been used for constructing linkage maps with a coverage of about 50% of the genome. Other intraspecific maps were later constructed using SSR and SNP markers. Identification and construction of these markers and maps, respectively, will be helpful in identifying useful genes or QTLs that can be introgressed into desirable genetic backgrounds for marker-assisted breeding [36]. This may not only hasten the breeding process, but will also allow pyramiding of desirable genes and QTLs from different genetic backgrounds, which will serve as an effective complementary approach to substantial crop improvement.

7. Applications of marker-assisted selection (MAS) in tomato breeding

Marker-assisted selection (MAS) is a tool for crop improvement where an associated marker is used for indirect selection of a trait. In this case, you are selecting for a trait based on the genotype of an associated marker rather than the trait itself. It is a technique that has been extensively explored for a wide range of plant traits and can reduce the cost as well as increase the precision and efficiency of selection in breeding. With recent development of molecular tools and genetic maps, MAS has become more attractive and practical than before. Molecular markers are not affected by either genetic or environmental factors, making MAS a useful tool in crop improvement. Markers developed to be used for MAS must be tightly linked to the genes or QTLs. In recent years, it is widely accepted that QTL effects, QTL validation or fine mapping with high resolution is a requirement for MAS [37]. The most important issue in the application of molecular markers in plant breeding is that major effect QTLs or genes should be mapped with high accuracy. In addition, these genes should not have any negative effect on other traits. The use of MAS in tomato breeding started in the 1930s [35] much earlier than in many other crop species. It was employed for the improvement of many morphological, physiological, and disease resistant traits.

Although resistant genes or QTLs have been identified for many fungal diseases in tomato, only few of these are been used for MAS, while with the others, markers associated with resistant genes/loci have been identified, but there are no reports on PCR-based markers developed for resistance breeding. Typical examples are with Alternaria stem canker [38] and gray leaf spot [39] where RFLP markers have been reported, but no PCR-based markers developed; with anthracnose ripe rot, few RADP markers associated with QTLs [40] have been reported but not validated for MAS; with black mold, QTLs [39] have been identified, but there is no report for MAS; with corky root rot, RFLP markers have also been identified and converted to CAPS and additional RAPD markers identified [41], but there is no report of using these markers for MAS; with Fusarium crown root rot, a RAPD marker has been identified, which may be useful for MAS in tomato breeding [42]; with early blight, QTLs have been identified [43], but there is no

PCR-based markers reported; with powdery mildew, several QTLs [44] have been identified, but there are no PCR-based markers closely linked to these QTLs identified; and with Septoria leaf spot, there has been no report of genetic mapping studies for resistance breeding. MAS has, however, been successful for resistance breeding in tomato for Fusarium wilt, late blight, leaf mold and Verticillium wilt. Molecular markers associated with Fusarium wilt resistance *I*, *I-1*, *I-2* and *I-3* [45] conferring resistance to four different races of the pathogen were identified, and PCR-based markers developed for all with the exception of *I-1* and used effectively for MAS; markers associated for late blight resistance *Ph-1*, *Ph-2* and *Ph-3* [46] has also been developed and used for tomato breeding; several PCR-based markers linked to the *Cf* gene for leaf mold [47] and Verticillium wilt [48] has also been reported and widely used for MAS.

QTLs and molecular markers associated with resistance have also been identified in tomato for the various bacterial diseases; however, it is only markers that are tightly linked to RFLPs and PCR-based markers for gene *Pto* in bacterial speck [49] that have been used for resistance breeding via MAS. With the other bacterial diseases including the bacteria canker, bacterial spot and bacterial wilt, QTLs or RFLP markers have been identified and reported but are not commercially used for MAS. With bacterial canker, two QTLs [50] have been developed and could be useful for MAS. RFLP markers associated with *Rx-1* and *Rx-2* and Rx-*3* for bacterial spot have been reported [51], but *Rx-1, Rx-2* and Rx-*3* are independently associated with hypersensitive response in the greenhouse and are not polymorphic in most breeding populations and hence not useful for MAS breeding, while *Rx-3* is associated with both hypersensitive response and field resistance. CAPs markers have been developed for the gene *Rx-3* and used for MAS breeding. Several QTLs have also been identified for breeding for bacteria wilt resistance in tomato; however, two dominant markers associated with the gene *TRST-1* [52] have been suggested to be useful.

Although there has been reports on the identification of the resistant gene *Cmr* for the cucumber mosaic virus [53], *pot-1* gene for Potyviruses [54] and two QTLs associated with the tomato mottle virus, there are no reports of use of these markers in tomato breeding. With the tomato mosaic virus, PCR-based markers for *Tm-1*, *Tm-2*, and $Tm\text{-}2^2$-resistant gene have been reported to be used for MAS [55]. Several genes have also been reported to be resistant to the tomato spotted wilt virus; however, PCR-based markers for only resistant gene *Sw-5* have been reported to be developed and utilized by most tomato breeding programs [56]. With the tomato yellow leaf curl virus, PCR-based markers have been identified for and developed for *Ty-1*, *Ty-2*, *Ty-3* and *Ty-4*-resistant loci [57]; hence, these markers are not very consistent and hence the challenge in using them for MAS. In the early 1980s, linkage association between the gene *Mi* [58] controlling nematode (*Meloidogyne incognita*) resistance and $Aps\text{-}1^1$ locus was reported [59]. RFLP markers associated with the $Aps\text{-}1^1$ locus and PCR-based markers associated with the *Mi* gene [60] have been routinely used for the selection of root knot nematode resistance in tomato. The *Mi* gene has also been reported to be resistant to two biotypes of the whitefly *Bemisia tabaci*. Several studies have tried to identify genes or QTLs for insect resistance in tomato; however, there are fewer reports on the identification of these genes/QTLs [61]. This may be attributed to difficulties in phenotypic screening for insect resistance, linkage drag and ease of using pesticides for insect control. However, with the increasing crusade on integrated pest management and restrictions on the use of pesticides, new discoveries in marker development, it is expected

that more efforts will be devoted to the identification, development and use of markers for insect resistance improvement in tomato. In tomato, molecular markers have been used to map genes or QTLs for abiotic environmental stresses (such as salinity, drought and heat) and many flower and fruit-related characteristics including exerted stigma, petal and sepal characters, fruit size, shape, color, soluble solids content, pH, lycopene, acidity, flavor, ripening, and many others. However, there is very little indication of the use of MAS for manipulating QTLs for these complex traits, although attempts are being made to improve some quantitative traits. Although MAS is as an effective tool for crop improvement, most breeding programs especially in Africa are not using it routinely. It is imperative that MAS is employed in our breeding programs to enable us ripe the benefits.

8. Marker-assisted backcrossing approach in tomato breeding

8.1. Marker-assisted backcrossing

The backcrossing method has been used extensively in plant breeding to incorporate one or a few genes from one plant possessing a unique trait (donor parent) into a desired adapted or elite variety (recurrent parent) that lacks few qualities such as disease resistance. In most cases, the parent used for backcrossing has a large number of desirable attributes but is deficient in only a few characteristics [62]. The application of molecular markers in backcrossing has increased the efficiency of selection. Marker-assisted backcrossing involves the use of molecular markers to track either the target locus or the background of the recurrent parent. The outcome of such a process is a cultivar that contains only the major gene that is obtained from the donor parent, while the genome of the recurrent parent remains intact.

8.2. Marker-assisted backcrossing approaches

Whereas [63] proposed two types of selections (foreground and background selection) under marker-assisted backcrossing, [64] identified three levels of marker-assisted backcrossing (foreground selection, recombinant selection and background selection).

8.3. Foreground selection

In the foreground selection, target locus of the donor parent is tracked using the selected molecular marker of interest [65]. The objective is to maintain the target locus in a heterozygous state (one donor allele and one recurrent parent allele) until the final backcross is completed. This is done to ensure that the locus that is targeted for improvement remains in a state of heterozygosity in the progeny for both donor and recurrent parent. The progeny are then selfed to ensure segregation and recombination in the next generation. Individuals that are found to be homozygous for the allele of interest are identified and selected [66].

The foreground selection is an efficient method to introgress favorable alleles into farmer-preferred varieties and elite cultivars of crops including maize. This approach ensures that only the gene of interest is transferred, while the genetic background of the elite cultivar remains intact. The resulting variety is the same as the original recurrent parent except the

new gene. This prevents the need to promote the new variety [67]. This method is useful for traits that have laborious or time-consuming phenotypic screening procedures. It is also very effective for selecting reproductive traits at the seedling stage, so that only best plants are identified and tagged for backcrossing. Application of marker-assisted backcrossing enables the successful transfer of recessive alleles, which is difficult to do when using conventional approaches. Visscher et al. [68] reported that resistance in barley was improved following a successful tracking of a marker linked (0.7 cM) to the *Yd2* gene for resistance to barley yellow dwarf virus in the progeny population. They observed that BC_2 F_2-derived progenies containing the linked marker showed fewer leaf symptoms and gave much higher grain yield though they were together with progenies that lacked the marker (**Figure 1**). The method has also been successfully used to improve salinity tolerance in rice. This selection involved the use of markers tightly linked to salt tolerance in rice to screen BC_1F_1 progenies for the presence of salt tolerance QTL. They were able to successfully identify individuals that carried homozygous loci from the heterozygous ones though they were phenotypically the same. These heterozygous individuals were then selected for further evaluation in the program.

8.4. Background selection

The approach involves the use of flanking markers that are tightly linked to the genomic regions for recombinant selection and unlinked markers to select for the genomic background of the recurrent parent [69, 70]. Background markers are markers that are unlinked to the target gene. Therefore, these markers can be used to select against the donor genome. Individuals that are homozygous for as many alleles of the recurrent parent are selected for full recovery of the recurrent parent genome [71, 72].

The breeder selects the genome of the recurrent parent using marker alleles for all the genomic regions of the recurrent parent except the target locus. The target locus is then selected based on the phenotype. Sometimes, elite genes are colocated in the same genomic regions and may affect the final product if transferred together. Elimination of such regions is very difficult in conventional approaches. The application of marker-assisted backcrossing approaches using background selection enables the introgression of just the target locus. The background method of selection is important in eliminating such deleterious genomic regions of the donor parents that may negatively affect the final product. This is extremely useful because the recurrent parent recovery can be greatly accelerated. Conventional backcrossing takes a minimum of six backcross generations to recover the genome of the recurrent parent, with some fragments of the donor genome still remaining intact. However, the genome of the recurrent parent can be achieved at the BC_2, BC_3 or BC_4, thus shortening the process by two of the four backcross generations when markers are involved [69, 70, 72–74] (**Figure 1**).

8.5. Recombinant selection

This method of MABC approach is used to reduce the number of deleterious genes (linkage drag) that are transferred from the donor parent. It involves the simultaneous tracking of the genetic background of the recurrent parent and the allele of the donor parent in a heterozygous state [75]. Many undesirable genes that negatively affect crop performance may be linked to the target gene of the donor parent, and the rate of decrease of this undesirable

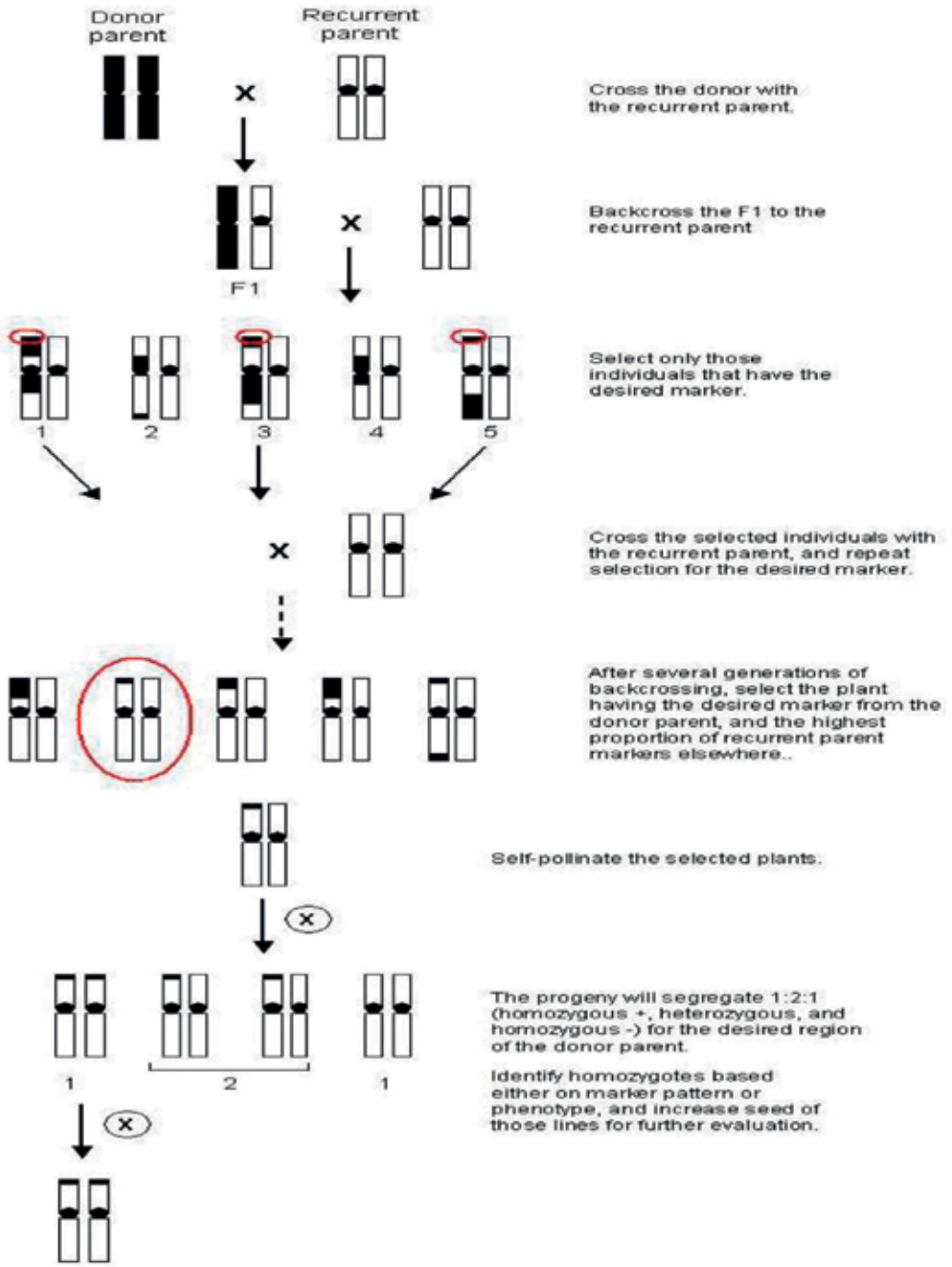

Figure 1. Flowchart of foreground and background selection scheme. Source: http://passel.unl.edu/Image/siteImages/MASFigure7Lg.jpg.

segment is slower than the unlinked regions [76]. After identification of individuals using foreground markers, single and double recombinant individuals carrying the donor alleles as well as the recurrent parents are selected [77, 78]. The use of flanking markers are able to greatly reduce the undesirable segment of the donor parent compared to the conventional

approaches that may carry large segments of the donor parent even after several generations [79, 80]. Compared with conventional backcrossing approaches, marker-assisted backcrossing enables faster recovery of the recurrent parent genome especially when foreground and background selection are combined. In practice, both foreground and background selections are conducted simultaneously in the same backcross program.

9. Progress and prospects of MAS in tomato breeding

In most developing countries such as Ghana, the development of new cultivars, for example tomato, maize, groundnut, cowpeas, has been achieved through conventional plant breeding method rather than transgenic breeding. It generally comprises of sequences of imbrications of three corresponding stages:

- Assembling germplasm like landrace, wild types, improved and/or exotic types of tomatoes as sources of genetic diversity for the major breeding activities to create different recombinants.
- Identification of superior recombinants through selection and testing. This comprise of the selection environment (e.g., promising against biotic and abiotic stresses), selection time (e.g., early against late generation), and the number of years and locations of testing.
- Releasing, distribution, and utilization of new cultivars [81–83].

This breeding method can take over five generations leading to increase in the number of years to develop an elite variety of a particular plant. Backcrossing is the breeding method, which involves transfer of alleles at one or more loci from a donor to an adapted variety or a desirable line [83, 84]. Recurrent backcrossing is the traditional backcrossing program based on the assumption proposed by [85] that the quantity of the recurrent parent genome is recovered at a rate of $[1–(1/2)^t + 1]$ where t is the number of generations of backcrossing. Thus, the expected recovery of the recurrent parent genome after six generations of backcrossing would be 99.2%, a situation called near-isogenic. An imperative objective of recurrent backcrossing is to reduce the effect of the donor genome, as the aim is to move just a few of its genes responsible for the target trait into the recurrent parent's genetic background. It is generally used to improve qualitatively inherited traits such as pests and diseases resistance, since the existence of target trait genes must be confirmed by individual phenotype in the successive cross-generations. Thus, individual phenotypic performance is a key indicator of the genotype, provided genes have a major effect on phenotypic performance and the phenotypic uncertainty is insignificant [86]. However, due to linkage between a target gene and nearby genes (which could code for economically undesirable traits) from the donor parent [87] and/or chance (stochastic or nonrandom positions of chiasmata), any specific backcross progeny will digress from this expectation. This digression has been experienced in couple of plants, for instance, where one tomato cultivar developed after 11 backcrosses still had the complete chromosome arm carrying the gene from the donor parent and introgressed fragments as large as 4 centimorgan (cM) found in tomato cultivars developed after 20 backcrosses, [88]. This was also found in a study conducted by [89] where the fragments around the introgressed genes in barleys diverse from about 1–14 cM in seven (7) generation backcrossed lines. Consequently, two main limitations of recurrent backcrossing approach have been identified:

- The number of generations, thus time, necessary to achieve the introgression objective
- The simultaneous transfer of other genes flanking the gene of interest of the donor parent i.e., linkage drag [90].

For the past three decades, an optimal number of molecular markers have been identified to be linked to traits of agronomic importance. These markers have been used as gene benchmarks to facilitate the introgression of genes of economic importance into elite varieties [91, 92]. Molecular markers are being used intensively to increase the efficiency of backcross breeding programs. This is what is termed as marker-assisted backcrossing (MAB) (also known as marker-assisted introgression, marker-assisted selection or molecular breeding). In the context of recurrent backcrossing, MAB amplified the pertinence of recurrent backcrossing at least in the following facets. Firstly, for traits that are simply inherited, but challenging or costly to identify phenotypically, and/or that do not have a reliable phenotypic expression under certain specific selection conditions, the efficiency of phenotypic selection is low. The use of markers for foreground selection makes the transfer of target genes feasible and economic. Secondly, quantitative traits, which are generally not targeted by a recurrent backcrossing approach, can be improved using recurrent backcrossing, if major quantitative trait loci (QTL) affecting the trait have been identified. Thirdly, markers provide an effective option to control linkage drag and to speed up the recovery of recurrent genome and make the use of genes contained in unadapted resources easier [93, 94]. Lastly, the number of backcross generations and the time required to eliminate unwanted fragments of donor parent genome to reach high level of similarity to the recurrent parent are lessened.

MAB is an accurate and an efficient process of introgression of major gene controlling a desired trait while retaining the vital features of the recurrent parent [95, 96]. MAB is the process of selecting an individual plant as the parent in a subsequent generation of a genetic improvement program using the results of DNA tests. Molecular markers used to perform DNA test are not influenced by the environment; hence, problems associated with conventional plant breeding (i.e., selection based on phenotype) are eliminated. Here, selection is concentrated on genes that control the desired traits directly and are detectable at all stages of plant growth. With the availability of an array of molecular markers [97] and genetic maps, MAB has become possible both for traits governed by single gene and quantitative trait loci (QTLs) [98]. The philosophy in marker development and implementation can be divided into three broad categories: genetic mapping [99], analyses of links between molecular markers and the trait of interest, and MAB [85, 94, 100].

Gene mapping is the method used to locate the locus of a gene and the distances between genes [101].

The closer a target gene is to another gene, the more likely they are inherited together [94, 100]. Therefore, the preferred condition for MAB is when a direct markers or gene assisted selection is used. This is a situation where molecular markers cosegregate or are closely linked with the desired trait [102]. The effective development of a marker that can be linked to a gene of interest leads to success of MAB. Hence, the assumption that the ideal distance between a molecular marker and a desirable gene initially isolated from wild germplasm be as close as 2 cM, while that of a marker and a target gene from elite into elite lines be close as 12 cM. This

reduces the required size of the backcross population and the time taken to obtain the desirable results [103, 104]. MAB has been effectively used to introgress disease-resistance gene and improve fruit quality in tomatoes [27].

The challenge associated with the utilization of MAB in the developing countries like Africa is the initial cost of developing the markers and the requisite laboratory equipment. For it to be welcomed and used effectively in these regions, the economic returns on their usage must far exceed the cost of using the conventional backcrossing. The initial cost could be funded with aids from donors [105].

10. Conclusion

Tomato breeding evolved from conventional breeding where breeders directly selected for the traits of interest, to the use of morphological and physiological traits, differentiated domesticated crops from their wild ancestors. The limitations of these morphological markers gave rise to more efficient approaches with the emergence of genetic marker technologies since the turn of the nineteenth century. The discovery of DNA markers that are closely associated with the desired phenotypes has been used to track tissue, cell, chromosome or a gene in individuals and increased selection efficiency. A DNA marker is a fragment of DNA that contains large amounts of sequence information and closely linked to traits of importance. The close association of DNA markers with morphological and physiological traits has facilitated the development of several linkage maps and enhanced the selection efficiency in marker-assisted tomato breeding programs. Marker-assisted selection has been explored to increase precision and efficiency of selection for many economic traits in tomato breeding. One classical marker-assisted approach in tomato breeding is marker-assisted backcrossing, which targets either the genetic background of the recurrent parent (background selection) or tracking the gene of interest (foreground selection) through the use of flanking markers. Marker-assisted backcrossing enables faster recovery of the recurrent parent genome compared with conventional backcrossing approaches. Due to the long duration of recurrent backcrossing approaches, adoption of marker-assisted backcrossing approaches will enhance selection efficiency and shorten the breeding process. The potential genetic and economic benefits of marker-assisted backcrossing need to be compared with conventional breeding programs to determine their viability.

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Tomato cultivation is a major economic activity in many countries of the world. Thus, strategic efforts should be directed towards mitigating production constraints that limit overall yields and quality. In addressing some of these constraints, researchers are developing and using varieties of modern and innovative techniques to improve local tomato germplasm, make rapid genetic gains, and breed for varieties with resistance to biotic and abiotic stress. This book focuses on recent advances in genomics and genetic improvement of the tomato crop, and production systems, and center around the following themes: (i) disease and pest management in tomato production, and (ii) breeding tools and improvement of the tomato.

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