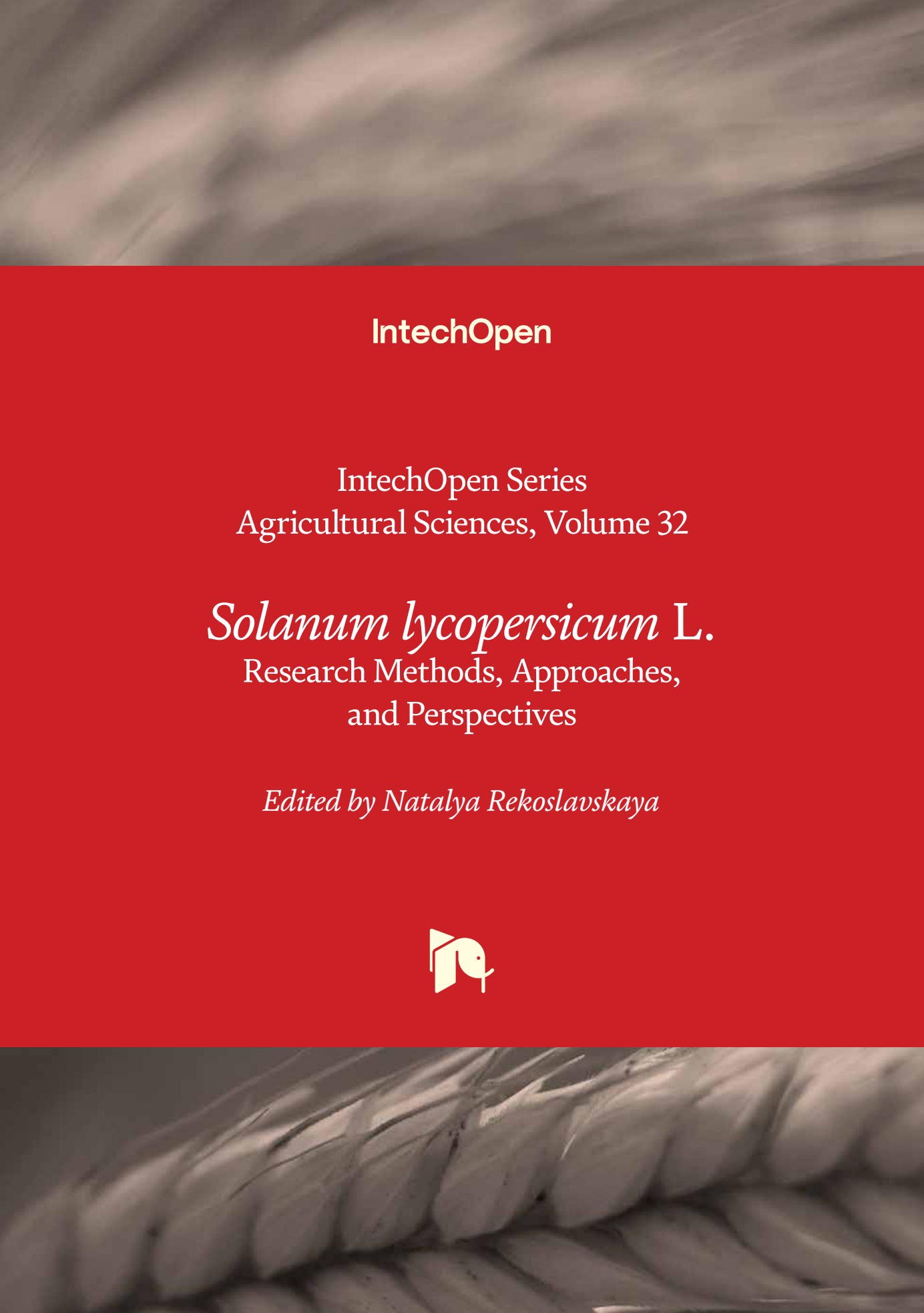




IntechOpen

IntechOpen Series
Agricultural Sciences, Volume 32

Solanum lycopersicum L.
Research Methods, Approaches,
and Perspectives

Edited by Natalya Rekoslavskaya



Solanum lycopersicum L.
- Research Methods,
Approaches, and
Perspectives

Edited by Natalya Rekoslavskaya

Published in London, United Kingdom

Solanum lycopersicum L. – Research Methods, Approaches, and Perspectives

<http://dx.doi.org/10.5772/intechopen.1006258>

Edited by Natalya Rekoslavskaya

Contributors

Abdi Najoua, Abiola O. Oke, Araceli Minerva Vera-Guzmán, Ayodeji O. Aduloju, Ben Ahmed Hela, Ben Hassine Abir, Charles O. Adetunji, Dorcas O. Ibitoye, Esther A. Adesegun, Esther T. Akinyode, Firdaus Bello, Hongyou Zhou, Irina Mokschnova, Irina Sotnikova, Jianxiu Hao, José Cruz Carrillo-Rodríguez, José Luis Chávez-Servia, Jun Hu, Mónica Lilian Pérez-Ochoa, Natalya Igorevna Rekoslavskaya, Olalekan A. Akinbo, Olawale Arogundade, Pamela E. Akin-Idowu, Qiaoxia Shang, Roseline I. Joseph, Ruiying Chen, Rurik Salyaev, Shakirat O. Ajenifujah-Solebo, Tatyana Kopytina, Valentine O. Ntui, Victoria O. Adedeji, Wasti Salma, Xin Wang, Xinyuan Wang, Yetunde O. Falana, Yufeng Wang, Zhen Wang, Zhe Yan

© The Editor(s) and the Author(s) 2026

The rights of the editor(s) and the author(s) have been asserted in accordance with the Copyright, Designs and Patents Act 1988. All rights to the book as a whole are reserved by INTECHOPEN LIMITED. The book as a whole (compilation) cannot be reproduced, distributed or used for commercial or non-commercial purposes without INTECHOPEN LIMITED's written permission. Enquiries concerning the use of the book should be directed to INTECHOPEN LIMITED rights and permissions department (permissions@intechopen.com).

Violations are liable to prosecution under the governing Copyright Law.



Individual chapters of this publication are distributed under the terms of the Creative Commons Attribution 4.0 License which permits commercial use, distribution and reproduction of the individual chapters, provided the original author(s) and source publication are appropriately acknowledged. If so indicated, certain images may not be included under the Creative Commons license. In such cases users will need to obtain permission from the license holder to reproduce the material. More details and guidelines concerning content reuse and adaptation can be found at <http://www.intechopen.com/copyright-policy.html>.

Notice

Statements and opinions expressed in the chapters are those of the individual contributors and not necessarily those of the editors or publisher. No responsibility is accepted for the accuracy of information contained in the published chapters. The publisher assumes no responsibility for any damage or injury to persons or property arising out of the use of any materials, instructions, methods or ideas contained in the book.

First published in London, United Kingdom, 2026 by IntechOpen

IntechOpen is the global imprint of INTECHOPEN LIMITED, registered in England and Wales, registration number: 11086078, 167-169 Great Portland Street, London, W1W 5PF, United Kingdom

For EU product safety concerns: IN TECH d.o.o., Prolaz Marije Krucifikse Kozulić 3, 51000 Rijeka, Croatia, info@intechopen.com or visit our website at intechopen.com.

British Library Cataloguing-in-Publication Data

A catalogue record for this book is available from the British Library

Solanum lycopersicum L. – Research Methods, Approaches, and Perspectives

Edited by Natalya Rekoslavskaya

p. cm.

This title is part of the Agricultural Sciences Book Series, Volume 32

Topic: Agronomy and Horticulture

Series Editor: W. James Grichar

Topic Editors: Murat Helvacı and Olga Panfilova

Print ISBN 978-1-83634-695-1

Online ISBN 978-1-83634-694-4

eBook (PDF) ISBN 978-1-83634-696-8

ISSN 3029-052X

If disposing of this product, please recycle the paper responsibly.

IntechOpen Book Series

Agricultural Sciences

Volume 32

Aims and Scope of the Series

The importance of agriculture cannot be overstated. It helps sustain life, as it gives us the food we need to survive and provides opportunities for economic well-being. Agriculture helps people prosper around the world and combines the creativity, imagination, and skill involved in planting crops and raising animals with modern production methods and new technologies. This series includes two main topics: Agronomy and Horticulture, and Animal Farming. This series will help readers better understand the intricacies of production agriculture and provide the new knowledge that is required to be successful. The success of a farmer in modern agriculture requires knowledge of events happening locally as well as globally that impact input decisions and ultimately determine net profit.

Meet the Series Editor



W. James Grichar has been employed with Texas A&M AgriLife Research for over 45 years with an emphasis on research in agronomy, plant pathology, and weed science. He obtained his BS from Texas A&M in 1972 and his Masters of Plant Protection in 1975. He has published 195 journal articles, over 330 research reports and briefs, 11 book chapters, and over 300 abstracts of profession meetings. He also directs research in many crops including corn, grain sorghum, peanuts, and sesame. He has held various positions in different professional societies including the American Peanut Research and Education Society, Southern Weed Science Society, and Texas Plant Protection Conference in addition to being Associate Editor for Peanut Science and Weed Technology. Significant accomplishments have included spearheading efforts to determine the optimum planting time for soybean production along the upper Texas Gulf Coast. These efforts have shown growers that soybean yields can be improved by 10 to 20% by following a late March to early April plant date. He also has been instrumental in developing a herbicide program for peanut production in the south Texas growing region. Through the development and use of herbicides that are effective against major weed problems in the south Texas region, peanut yields have increased by 25 to 30%.

Meet the Volume Editor



Natalya Rekoslavskaya was born in Irkutsk on August 5, 1950. In 1966, she joined the Siberian Institute of Plant Physiology and Biochemistry (SIPPB) of SB RAS. She defended her Candidate's degree in 1977 in Moscow at the Institute of Plant Physiology, and later her Doctor's degree in 1991 at the same institute. In 1991, she was invited to Michigan State University, where she joined the Laboratory of Plant Growth and Development, headed by Professor Robert S. Bandurski, and worked there for two years. During this period, she received grants from the National Science Foundation (NSF): DSB 88-05148 (1991), DSB 61-2060 (1992), and IBN 92077 (1992). Between 1996 and 2001, she collaborated with the Milan Istituto Biochimica e Agricoltura and obtained grants from C.N.R. (Italy), as well as a Guest Fellowship No. 52 grant from NATO-C.N.R. in 1996–1997. From 1997 to 2002, she served as the Head of the Laboratory of Phytohormone Biochemistry. For approximately 26 years, she also served as a Professor at the ISU Department of Plant Physiology, Cell Biology, and Genetics, where she lectured on modern genetics and molecular biology and conducted practical exercises. From 2001 to 2007, she worked with the State Scientific Centre of Virology and Biotechnology (“Vector”) under grant 2176p of ISTC (USA), focusing on the development of plant-made vaccines against HIV and Hepatitis B. She also received grants from the Russian Foundation for Basic Research in 1997, 1999, 2003, and 2019, as well as funding from G. Soros and the Council of Ministers during the 1990s. Between 2011 and 2016, she was invited by a pharmaceutical company in Irkutsk to develop vaccines against cancers caused by human papillomaviruses (HPV). She is the author of about 300 articles, several monographs, and practical materials for students.

Contents

Preface	XIII
Chapter 1	1
Green Prevention and Control Technologies for Common Tomato Main Diseases and Pests	
<i>by Jianxiu Hao, Hongyou Zhou, Zhe Yan, Yufeng Wang, Zhen Wang, Ruiying Chen, Jun Hu, Qiaoxia Shang, Xin Wang and Xinyuan Wang</i>	
Chapter 2	19
Salicylic Acid Mitigates the Negative Effects of NaCl in <i>Solanum lycopersicum</i> L. by Improving Growth Rate and Biochemical Parameters	
<i>by Wasti Salma, Ben Hassine Abir, Abdi Najoua and Ben Ahmed Hela</i>	
Chapter 3	29
Tomato Crop Improvement Efforts in Nigeria: Past, Current and Future Perspectives	
<i>by Shakirat O. Ajenifujah-Solebo, Pamela E. Akin-Idowu, Ayodeji O. Aduloju, Victoria O. Adedeji, Esther T. Akinyode, Dorcas O. Ibitoye, Olawale Arogundade, Abiola O. Oke, Esther A. Adesegun, Valentine O. Ntui, Olalekan A. Akinbo, Charles O. Adetunji, Yetunde O. Falana, Roseline I. Joseph and Firdaus Bello</i>	
Chapter 4	61
Variation in Agromorphological Traits and Phenolic Compounds, Vitamin C Contents, and Antioxidant Activity in the Fruits of Mexican Tomato Landraces	
<i>by Araceli Minerva Vera-Guzmán, Mónica Lilian Pérez-Ochoa, José Cruz Carrillo-Rodríguez and José Luis Chávez-Servia</i>	
Chapter 5	81
The Experience in Planting <i>Solanum lycopersicum</i> : Organic Cultivation in East Siberia, Transgenesis and the Connection with Plasticity of Tomato Genome Expression	
<i>by Natalya Igorevna Rekoslavskaya, Rurik Salyaev, Tatyana Kopytina, Irina Sotnikova and Irina Mokschonova</i>	

Preface

For centuries, tomatoes (scientific name *Lycopersicon lycopersicum*, meaning “wolf peach plum”) have been present on our tables, especially in summer. The tradition of eating fresh tomatoes in a salad or using tomato sauce for spaghetti originated in southern Italy and then spread worldwide, thanks in part to pizza. This is a berry that originated in Peru and was brought by the Spanish. The Aztecs called it xitomatl (“plump fruit with a navel”). The first tomatoes were small, golden in color, and eaten in wedges. Over time, through selection, they became red.

The “golden apple” spread across Europe in the late 16th century. In Italy, it was already known in the second half of the 1500s. Evidence of this is a mention in a scientific treatise by the Siena physician Pietro Andrea Mattioli (1500–1577): “Now in Italy they grow fruits similar to pink apples, divided into segments, green at first, and golden when ripe, which are used for food”.

The earliest recipe for the sauce, “salsa di pomodoro alla espanola”, is found in Antonio Latini’s 1694 cookbook, *Lo Scalco alla Moderna*. It was made from roasted and peeled tomatoes with onions, thyme, marjoram, and vinegar.

Botanically, a tomato is a fruit. Cucumbers, peppers, pumpkins, peas, and eggplants are also fruits, as they develop from a flower and contain seeds.

According to the International Trade Centre database, global tomato exports in 2020 reached 14.9 million tonnes, with a FOB value of US\$16.8 billion (FOB-free on board: free on board).

This book presents the latest research methods, approaches, and perspectives on *Solanum lycopersicum* L., offering comprehensive insights into its biology, cultivation, and improvement strategies. It brings together 5 advanced studies on disease management, stress physiology, crop improvement, genetic plasticity, and nutritional traits, thereby serving as a valuable reference for researchers, plant breeders, and agricultural practitioners.

Selected Chapters

1. Green Prevention and Control Technologies for Common Tomato Main Diseases and Pests
2. Salicylic Acid Mitigates the Negative Effects of NaCl in *Solanum lycopersicum* L. by Improving Growth Rate and Biochemical Parameters
3. Tomato Crop Improvement Efforts in Nigeria: Past, Current and Future Perspectives

4. Variation in Agromorphological Traits and Phenolic Compounds, Vitamin C Contents, and Antioxidant Activity in the Fruits of Mexican Tomato Landraces
5. The Experience in Planting *Solanum lycopersicum*: Organic Cultivation in East Siberia, Transgenesis and the Connection with Plasticity of Tomato Genome Expression

Natalya Igorevna Rekoslavskaya

The Siberian Institute of Plant Physiology and Biochemistry,
The Siberian Branch of Russian Academy of Sciences,
Irkutsk, Russia

Chapter 1

Green Prevention and Control Technologies for Common Tomato Main Diseases and Pests

Jianxiu Hao, Hongyou Zhou, Zhe Yan, Yufeng Wang, Zhen Wang, Ruiying Chen, Jun Hu, Qiaoxia Shang, Xin Wang and Xinyuan Wang

Abstract

Tomato (*S. lycopersicum* L.), an important and popular vegetable among people, is grown in fields and greenhouses in almost all countries in the world. With the continuous improvement of living standards, the people's demand for fresh fruits and vegetables is also increasing day by day. Nevertheless, tomato production worldwide remains highly vulnerable to both abiotic and biotic stresses. In particular, infection, feeding, and competitive growth of some pathogenic microorganisms, pests, and weeds have significantly reduced tomato production, severely limiting development of the tomato industry and impacting the supply–demand balance. Over 200 species of tomato pathogens have been identified as causing production problems. Approximately 100 insect pests and 25 non-insect pests attack tomatoes. The heavy use of chemical pesticides has led to plant resistance to diseases and pests, leftover pesticide residues, and environmental damage, all of which pose risks to food safety and human health. Therefore, strategies to reduce pesticide use and the implementation of environmentally friendly control measures for plant diseases and pests must be explored. In this chapter, we review the major tomato diseases and pests and their prevention and control measures, thereby providing theoretical support for the green and sustainable development of the tomato industry.

Keywords: tomato (*S. lycopersicum* L.), diseases, pests, prevention and control measures, tomato industry

1. Introduction

Tomato (*Solanum lycopersicum* L.) is one of the most widely grown vegetable crops in the world, after potato and sweet potato [1]. It is known for its sweet and slightly sour taste, and is believed to help cool the body, remove toxins, and lower blood pressure. Tomatoes belong to the Solanaceae family and are cultivated in almost every country, both in open fields and in greenhouses [2]. Originally from

the Andes region of South America, the tomato was introduced to Europe in the sixteenth century and later distributed throughout eastern and southern Asia, the Middle East, and Africa [3]. Tomato fruits are usually eaten fresh in salads or cooked in soups, sauces, fish, or meat dishes, and are frequently also processed into juices and purees. They are essential ingredients in Italian cuisine, particularly in the production of pizzas. In India, tomatoes are popular additives due to their flavor. In China, they can be used as both vegetables and fruits, and can be eaten raw or cooked, which is very popular among people. Moreover, products such as dried and canned tomatoes also have high economic value, as these products represent an affordable way to buy tomatoes when the production is poor or during off-seasons [4–6].

With the continuous improvements in living standards, the people's demand for fresh fruits and vegetables is also increasing day by day. As a nutrient-rich fruit and vegetable gardening crop, tomatoes have become a staple daily food [3]. In 2023, the global planting area of tomatoes reached 6,540,956 ha, with China being the top producer (planting area of 2,316,831 ha; <https://data.fao.org/?lang=en>). However, the global tomato fruit harvest can be greatly impacted by both abiotic and biological stresses. In particular, infection, feeding, and competitive growth of some pathogenic microorganisms, pests, and weeds have significantly reduced tomato production, severely limiting development of the tomato industry and impacting the supply–demand balance [7].

Tomatoes are frequently affected by diseases and pests throughout all growth stages, which can cause significant yield losses and occasionally complete crop failure [8]. Over 200 species of tomato pathogens have been identified that cause production problems. Fungi, bacteria, and viruses are common causes of numerous tomato diseases [7]. Early blight can cause fruit yield losses of 50–86% [9], late blight can induce losses of 20–70% [10], and vascular wilting can reduce yields by 30–40% [11, 12], although yield losses can increase to 80% under certain weather conditions. Moreover, bacterial leaf spots can reduce tomato yields by 20–50% [13], whereas viral diseases such as bud necrosis/spotted wilt, leaf curl, and mosaic (Tobamovirus) cause yield losses of 45%, 35%, and 18%, respectively [14]. The other most severe and widespread tomato disease is root knots, produced by the nematode *Meloidogyne incognita* (Kofoed & White), which causes annual crop losses of 11–35% [15]. This disease also makes tomato plants more susceptible to other fungal and bacterial diseases [16].

Approximately 100 insect pests and 25 non-insect pests attack tomatoes [17]. These pests feed from germination to harvesting and significantly affect the number and quality of fruits [17]. Whitefly, thrips, and American serpentine leaf-miner lead to tomato yield losses of 45% and 23% respectively [18]. Farmers commonly use a variety of fungicides and pesticides to rapidly control diseases and pests. However, according to the Food and Agriculture Organization of the United Nations, total pesticide use is increasing globally, reaching more than two million tons in 2020 [19]. Extensive chemical pesticide use has led to plant resistance to pathogenic bacteria and pests, excessive pesticide residues, and environmental pollution, all of which threaten food safety and human health [20]. Therefore, strategies to reduce pesticide use and implement greener prevention and control measures for plant diseases and pests must be explored. In this chapter, we review the major tomato diseases and pests and their prevention and control measures, thereby providing theoretical support for green and sustainable development of the tomato industry.

2. Common tomato diseases and pests and control measures

2.1 Common diseases and control measures

2.1.1 Tomato early blight

Early blight is a common disease in tomatoes that becomes more severe and harmful with increasing humidity. In countries such as the United States, Canada, and India, tomato production has decreased by as much as 79% owing to early blight infections [21]. The disease often begins in the early stages of fruiting and the peak fruiting period. Old leaves are primarily affected, whereas young leaves are less impacted. The causes of early blight include improper cultivation and management, insufficient fertilization, poor plant growth, poor disease resistance, and severe disease occurrence. Moreover, the occurrence and prevalence of early blight in tomatoes are closely related to the field temperature and humidity, plant growth status, and degree of disease resistance. Under certain conditions, that is, temperatures of 20–25°C, high humidity, and foggy and rainy weather, the disease develops rapidly and is more prone to spreading [22].

Early blight is caused by the facultative parasitic pathogen *Alternaria solani*, which destroys the cell walls, cytoplasm, and other related metabolic enzymes of host cells, as well as mediating the pathogenic activities of the host [23]. The pathogen overwinters in diseased residues in the soil or seeds, then becomes the primary source of infection during the production season [24]. Overwintering pathogen sources produce asexual propagules at the disease spots in the second year, which spread to the leaves *via* rainwater splashes, air currents, or agricultural operations, re-infecting the leaves and causing disease. Under suitable conditions, disease spots can form in 2–3 days, and a large number of asexual spores can be produced on the disease spots within 4–5 days; repetition of this cycle can lead to substantial spreading of the disease if not controlled [25].

The prevention and control of early blight includes the following measures.

Select disease-resistant tomato varieties, such as Green Tomato, Zhongshu no. 5 and no. 6, which are relatively resistant to early blight [26]. Clean up the countryside, after pulling seedlings, residual plants, fallen leaves, fallen fruits, etc. In addition, Rotation with *non-solanaceous* crops, such as corn, sunflower, wheat, and melons, for 2–3 years has a remarkable effect on disease prevention [7]. Moreover, treating the leaves of tomato seedlings with a certain concentration of *Bacillus lateralis* can effectively reduce the infection degree of the pathogen in tomato plants. Additionally, the control effect of spraying and root irrigation with *B. pilirensis* on early blight in tomatoes reached 91.96% and increased the tomato yield. *Trichoderma spinosporum* fermentation liquid can also inhibit the growth and development of early blight fungi in tomatoes [26–28].

2.1.2 Tomato late blight

Late blight is a highly prevalent disease in tomatoes. If scientific preventive measures are not implemented in a timely manner, late blight can develop rapidly and become difficult to control, causing large-scale destructive harm. This disease is caused by *Phytophthora infestans*, which parasitizes a living host to survive, mainly overwintering on tomatoes, eggplants, and stored potatoes [29]. The plant that initially develops the disease is called the “central disease plant,” which produces a

large number of sporangia. Both seedlings and adults can be infected. The seedlings are infected, and dark green water-stained lesions appear on the leaves, which rapidly expand to the petioles and stems, causing them to thin and brown necrosis, and the seedlings wilt and die. Adult plants are diseased, mainly affecting leaves, petioles and stems, and in severe cases, they are also harmful to green fruits. When conditions are suitable, overwintering pathogens produce sporangia on their overwintering hosts, which spread to tomatoes *via* air currents or rainwater, causing the disease to rapidly expand and spread in all directions [30].

The prevention and control measures of late blight are as follows:

1. Select disease-resistant varieties, including Shengmei, Fenbeili no. 9, and Jiayue 9015 [31].
2. Implement reasonable cultivation management measures, including planting tomatoes far from potatoes and eggplants and maintaining reasonable planting densities, formula fertilization, organic fertilization, and watering [32].
3. Improve field investigations to promptly identify the central disease plants for chemical control. The field control effect of the new fungicide on tomato late blight was significant, such as 30% fluopyramide-cyanoglutazole suspension 600 mL/hm², 170 g/L fluthiazole, acetopyritone-azoxystrobin suspension 350 mL/hm², 32% pyraclostrobin flupyramidamine suspension 750 mL/hm² [33].

2.1.3 Tomato gray mold

Gray mold is an important disease affecting tomato production. In China, which has the largest tomato planting area and highest yields in the world, the rapid spread of tomato gray mold in recent years poses a particularly serious threat to production. Inadequate prevention and control measures can cause significant losses [34, 35]. Tomato gray mold disease has an incidence rate in the field of approximately 30% and typically results in yield reductions of 20–30%; however, this can increase to 50% or even termination of production in serious cases [36, 37]. Gray mold is caused by the pathogen *Botrytis cinerea*, with the tomato flowering period representing the peak period of infection [38]. *B. cinerea* infection often begins in the petals and stigma of tomatoes and continues to spread to other parts, such as the fruit stem and navel, causing symptoms in both growing and non-growing tomato plants, although the pathogen is dormant in non-growing plants [39]. The disease often occurs during the transportation of ripe harvested fruits owing to the low storage temperature and high humidity. High-temperature, rainy, and humid environments, as well as cool and shady conditions, provide favorable conditions for the occurrence of tomato gray mold. Continuous rainy weather can significantly increase field humidity, which also creates favorable conditions for disease spread [40].

There were several measures to control gray mold:

1. Clean fields by promptly removing diseased leaves, flowers, and fruits. In particular, removing the remaining diseased petals of tomatoes as early as possible after fruit setting can effectively prevent the occurrence of tomato gray mold disease, with a prevention efficiency of over 90% and control temperature and humidity additionally [41]. Besides, implement some biological control methods. Some antagonistic fungi and bacteria can be utilized to prevent and control

gray mold in tomatoes. Currently, widely studied and applied biocontrol fungi include *T. harzianum* and *T. mucilage*. Common biocontrol bacteria include *B. subtilis* and *Pseudomonas fluorescens* [42, 43].

2.1.4 Tomato canker

Tomato canker is a bacterial disease caused by gram-positive bacterial pathogens that seriously endangers tomato production [44]. Tomato canker was first discovered in Michigan, USA, in 1909, and then became widely distributed in various tomato production areas in the United States, as well as Mexico, Canada, and other places, gradually becoming a global plant disease. The disease broke out on a large scale in the UK from 1943 to 1946, seriously affecting the tomato-canning industry. Since then, tomato canker disease has been reported in more than 600 countries, including the United States, Europe, Africa, and Oceania [45]. In 1985, tomato canker was discovered in the Pinggu and Yanqing counties of Beijing, China, and now occurs in many provinces and cities, such as Beijing, Xinjiang, Hebei, Anhui, and Shanghai, affecting tomato production to varying degrees in many areas [46]. Owing to its wide transmission routes and strong harmful effects, this disease is regarded as one of the most destructive and economically significant tomato diseases worldwide, which affects both the yield and quality of tomatoes. It is now listed as a quarantine disease in many countries [47].

During disease progression, the seedlings become diseased, the true leaves wilt from the bottom to top, the vascular bundles turn brown after stem cutting, the pulp becomes empty, the stems rot, and the plants die. In the adult stage of the disease, symptoms appear during the fruiting stage, with plant leaves wilting from bottom to top. Some leaves first show patchy necrosis, then gradually wilt and die. When the stem of a wilted plant is cut open, the vascular bundles have turned brown. When cut horizontally and squeezed by hand, yellow purulent substances can be squeezed out, representing bacterial pus. The fruit is invaded on the surface, resulting in a central dark brown scar-like bulge and white “bird’s eye”-shaped spots along the edge [48].

Tomato canker is caused by *Clavibacter michiganensis* subsp. *Michiganensis* (Cmm), which can infect other plants of the tomato genus such as chili peppers, solanums, and split-leaf *solanums* [49]. Cmm is an aerobic gram-positive bacterium, short rod-, stick-, or wedge-shaped, without flagella or spores [50]. Moreover, the cells generally exist in single or paired forms and can induce hypersensitivity reactions in non-host tobacco plants [50]. The pathogen can overwinter inside and outside seeds, as well as on diseased and dead plants, and can survive in the soil for 2–3 years along with diseased and dead plants [51]. The pathogen mainly invades root wounds, harming the root system, but can also directly invade local areas through the hairy bodies of leaves and the epidermis of young fruits, causing disease [51]. Long-distance transmission relies primarily on the transport of infected seeds, seedlings, and unprocessed fruit; close-range transmission mainly occurs through rainwater and water [50]. Agricultural operations can also spread this disease. The occurrence and prevalence of this disease are related to the bacterial carrier rate, quantity of seeds, and number of diseased and dead overwintering plants. Warm and humid conditions, frequent overcast and rainy days, and heavy rain are conducive to disease onset [48].

Prevention and control measures:

2. Focus on eliminating seed-carrying bacteria using disease-free seeds and performing appropriate treatments. Strict quarantine of seeds should be imple-

mented, and transportation of seedlings from epidemic areas must be prohibited. And implement a rotation of more than 3 years with non-*solanaceous* vegetables, adopt ridge cultivation, and apply fertilizers reasonably to enhance disease resistance in plants [52].

3. Disinfect and sterilize seeds by soaking in warm water at 55°C for 30 min, sterilizing with dry heat at 70°C for 72 h, or soaking in 1% hydrochloric acid solution for 5–10 h or 1.05% sodium hypochlorite for 20–40 min. The samples can be germinated after thorough washing with clean water [53].
4. Biological control. Treating tomato seeds with *Pseudomonas* and *Bacillus* strains can improve their quality and reduce the incidence of bacterial canker diseases. *Streptomyces* sp. strain HL-12, *T. harzianum*, and *Rhodosporidium diobovatum* also inhibit Cmm [54–57].

2.1.5 Tomato bacterial spot disease

Tomato bacterial spot disease was first discovered in the United States in 1933 and has since spread across all continents [58]. The incidence rate of bacterial spot disease in tomatoes can reach 100%, leading to yield reductions of 5–75%. Accordingly, this disease is included in the list of harmful organisms for entry–exit quarantine in China [59].

Tomato bacterial spot disease mainly affects the leaves and infects the stems, petioles, and fruits. The leaves become densely covered with small, irregularly shaped spots of varying sizes, ranging from grayish-white to grayish-brown [60]. These spots, which are slightly sunken with darker edges and an oily luster, join together to form large, irregularly shaped necrotic spots with a dark brown color [61]. Infection of the petioles and stems produces amorphous brown depressed necrotic spots. Infected fruit, which mostly comprises young and tender fruits, shows slightly raised small spots, which later turn into brown scab-like spots; the tissues around the lesions delay red ripening [58].

Tomato bacterial spot disease is caused by *Pseudomonas syringae* tomato, which is short, rod-shaped, does not produce spores, has no entrapment, and has one or more flagella [61]. The fungus overwinters on seeds, diseased carcasses, and soil. The pathogen can survive for several years on dried seeds, and the environmental conditions are often suitable for infecting plants at the seedling stage. Seedlings are infected by sowing infected seeds, and become diseased after planting; the disease then spreads through rainwater splashing, agricultural operations, and irrigation water. Susceptibility to tomato bacterial spotting disease varies diurnally, with nighttime susceptibility being stronger than daytime susceptibility [62].

Prevention and control measures:

1. Select disease-free seeds or soak seeds in warm water at 55°C for 30 min, in a 200× dilution of 30% copper succinate solution for 60 min, or in 1% potassium permanganate solution for 20 min [63].
2. Implement crop rotation with non-*Solanaceae* vegetables for more than 3 years, adopting ridge cultivation and reasonable fertilization to improve disease resistance in plants. In addition, implement chemical control. In the early stages of the disease, chemicals should be administered in a timely manner for prevention and control. Spray with 47% Spring-Wang copper wettable powder (800×

dilution), 77% copper hydroxide wettable powder (500× dilution), neomycin (4000× dilution), 3% Zhongshengbin wettable powder (600–800× dilution), or 50% succinate copper wettable powder (400–500× dilution) [63].

2.1.6 Common tomato virus diseases

Common tomato viral diseases include mosaic, fern leaf, strip spot, and rolled leaf. During production, these diseases often occur in a mixed infection, causing the plants to shorten, the internodes to shorten, the leaves to rise, the leaf color to pale, and the yield and quality to decline. The main symptoms are as follows. (1) Fern leaf disease: top leaves are slender, the mesophyll is atrophied and twisted, middle and lower leaves curl upwards, and the internodes shorten [1]. (2) Stripe disease: irregular necrotic spots ranging from yellowish-brown to blackish-brown are scattered on the upper and middle leaves, which spread to the petioles, presenting as brown stripes. The stems are initially dark green, with irregularly sunken short streaks, which later turn into dark brown, oily necrotic streaks of varying lengths [1]. (3) Mosaic disease: affected plants show a pale leaf color, slow growth, and the appearance of net-like mottled leaves or irregular yellowish-green patches on the leaves [1]. (4) Leaf curl disease: yellowing between the veins of the leaves, the edges of the leaves curl upwards, small leaves are spherical and twisted into a spiral deformity, the entire plant atrophies, and occasionally grows in clusters [1]. The major viruses causing tomato diseases include tomato yellow leaf curl virus, cucumber mosaic virus, tomato spotted wilt virus, and southern tomato virus (**Table 1**).

Prevention and control measures:

At present, no effective agent exists for the treatment of viral diseases, and only a few types of virus passivators are available to alleviate the disease [1]. Therefore, the prevention and treatment of viral diseases should be based on all aspects of cultivation and management, improving disease resistance in plants, and implementing drug control like this [1].

1. Select disease-resistant varieties according to local conditions and viruses.
2. Before sowing, pre-soak the seed in water for 3–5 h, then soak the seeds in 10% trisodium phosphate solution for 20 min.
3. Strengthen field management, ensure timely watering in high-temperature and dry seasons, apply foot fertilizers, consider the combined application of nitrogen, phosphorus, and potassium fertilizers, and appropriately increase potassium fertilizers.
4. Control aphids, whiteflies, and thrips can control disease development.

2.2 Common tomato pests and control measures

2.2.1 *Tuta absoluta*

Tuta absoluta (Meyrick) eggs are typically laid on the front or back of young leaves. The insects are divided into four instar stages, and the developmental period is approximately 20 days. After hatching into larvae, the mesophyllous-eating insects form irregular insect passages on the affected leaves, and the leaves are transparent

Serial number	Virus type	Virus characteristics	Transmission medium	First reported	Infestation symptoms
1	Tomato yellow leaf curl virus, TYLCV	A single-stranded DNA virus belonging to the genus <i>Begomovirus</i> .	Whiteflies	Israel in 1931 [64]	Yellowing leaves, thickening and shrinking, curling and wrinkling, dwarfization of diseased plants, delayed growth, flower and bud drop, reduced fruit setting, and fruit stiffness.
2	Cucumber Mosaic virus, CMV	Positive single-stranded RNA virus; a typical member of the genus <i>Cucumovirus</i> .	Aphids	Michigan, USA, in 1916 [65]	Infected leaves initially develop “bright veins”, which then become dull. The plant is dwarfed and deformed, and the leaves will appear mosaic and necrotic, with yellow-green mottled spots, and thinning in severe cases. Some diseased leaves will have shrunk edges and curls, and some will narrow their tips to form a “rat tail”. Can also may be asymptomatic when occurring later in plant development.
3	Tomato spotted wilt virus, TSWV	Negative-strand RNA viruses belonging to the <i>Orthospovirus</i> .	Thrips	Australia in 1915 [66]	At the seedling stage of diseased plants, the leaves are wilted or severely dwarfed, the leaf veins and dorsal are purple, the leaf texture is not stretched and gradually becomes brittle, and many irregular small black spots form. Infected stem appears brown, necrotic streaks appear, and the fruit shows a greenish ring and brown necrosis.
4	Tomato chlorosis virus, ToCV	A double-stranded RNA virus belonging to the genus <i>Crinivirus</i> .	Whiteflies	Florida in 1998 [67]	Infected tomatoes grow slowly throughout the growth period, with yellowing of the top leaves and mild greening at the bottom of mature leaves.
5	Southern tomato virus, STV	A double-stranded RNA virus belonging to the genus <i>Amalgavirus</i> .	A strictly species- borne virus, with no reports of insects as its transmission mediator	California, USA in 1984 [68]	It usually manifests as a compound infection. Infected plants are whitish, exhibiting greening, plant decline, fruit size reduction, etc.. Currently no clear expression of symptoms after the STV virus alone infects tomato plants.

Table 1.
Major viruses infecting tomatoes.

and paper-thin, with window shapes and accumulations of black excrement. The larvae can also eat the fruit and form holes, making the fruit susceptible to infection by pathogens, resulting in fruit rot. As the larvae progress through the pupal stage, they darken and are often covered with a white silk cocoon. Adults have light gray or grayish-brown silvery-gray scales [69].

Prevention and control measures:

1. Strengthen field management with non-Solanaceae vegetable crops to reduce the number of tomato leaf-miner host plants. Remove insects from the field in a timely manner, burying impacted leaves and fruits deeply. Strengthen water and fertilizer management and ensure appropriate application [70].
2. Implement physical control measures such as sex pheromone trapping, which is an important method of controlling adult tomato leaf-miners during production. The traps attract and capture adult males during the courting period through the use of blue colors and synthetic pheromones [70].

2.2.2 *Liriomyza sativae*

The *L. sativae* is a polyphagous pest. Although both the adults and larvae can cause harm, the larvae are the main pests. Female adults stab the leaf epidermis with an ovipositor, feed on the sap, and lay one egg in each wound hole. After hatching, the larvae begin to feed on the mesophyll, and the affected leaves exhibit white irregular channels. Black excrement occurs in the insect tunnels in the shape of broken threads. This insect bites through the leaf epidermis to pupate on foliar or ground surfaces. Pathogenic microorganisms invade wound holes, leading to the occurrence and spread of disease, the transmission of various viruses, and enhanced damage to plants [71].

Prevention and control measures:

1. Agricultural control. As different tomato varieties exhibit different selectivity, resistant varieties can be planted to reduce damage to *L. sativae*. Moreover, timely irrigation and deep tillage in protected areas and sheds can eliminate pupae falling onto the surface [72].
2. Physical control. In July and August, the stubble should be changed at high temperatures, greenhouses should not be ventilated day or night, and greenhouse residues should be removed after insecticide treatment to prevent the spread of insect sources. Insect nets should be installed in the vents of the facility to prevent the exchange of insect sources in the open field and within the facility. As the adults exhibit a certain tropism for yellow, they can be trapped by hanging yellow plates [73].
3. Pharmaceutical preventive measures. Specifically, alternate the application of biopesticides, such as fly amines, avermectin, ethyl spinosad, and matrine, to reduce their harmful effects. In the early stages of insect infestation, 2.5% cypermethrin EC and 10% cyantranamide can be applied. Oil suspensions and 16% perchlorine insecticidal monoemulsions should be used in strict accordance with the manufacturer's instructions, and the dosage should not be increased [72].

2.2.3 *Spodoptera exigua*

The cotton bollworm, also known as *Spodoptera exigua*, is one of the main burrowing pests, with tomato plants mainly eaten by the larvae. Adults are grayish-brown, diurnal, and nocturnal, and exhibit phototaxis and chemotaxis [73]. The eggs are mostly laid at dusk and at night, typically on the tips of tomatoes, young leaves, and young shoots. Newly hatched larvae bite the tips of young leaves, and the second and third instar larvae spin silk and droop to eat the buds, flowers, and fruits. This leads to fruit decay, with young fruits eaten completely or allowed to rot and fall off. Ripe fruit is eaten by part of the pulp, and the fungus invades the borer and causes fruit rot, resulting in a significant reduction in yield. The flower buds turn yellow-green after damage and withered after 2–3 days [73].

Prevention and control measures:

1. Agricultural control. At the peak of adult oviposition, topping and pruning should be performed in time to reduce the number of eggs laid. When an insect is found in the field, it should be removed in a timely manner to reduce the number of insects laid [73].
2. Physical control. As adults are attracted to the smell of poplar branches, prior to the peak moth period, farmers can plant poplars at a density of 300 trees per hectare, with 75–105 branches on each tree; the adults can then be collected early in the morning with the dew and killed [74]. Additionally, black light lamps and high-pressure mercury lamps can be installed in the field to trap male adults, exploiting their phototaxis. This also reduces the number of eggs laid by female moths [75].
3. Pharmaceutical prevention and control. After the peak oviposition period of adults, a bollworm karyopolyhedrovirus suspension of 20 billion PIB/mL or *B. thuringiensis* wettable powder can be sprayed at a concentration of 32,000 IU/mg for larval control. The resulting larvae do not moth the fruit [74]. Alternatively, a 2% emamectin benzoate emulsifiable concentrate, 14% chlorantranilide perchlorofluorine microcapsule suspension, or 10% cyantraniliprole dispersible oil suspension can be used for prevention and control [74].

2.2.4 *Bemisia tabaci*

B. tabaci larvae and adults swarm on the back of the young leaves, sting and suck the sap of the leaves, which turn green and yellow, wilt and dry; in severe cases, the entire plant withers and dies [76]. Adults and nymphs secrete large amounts of honeydew, which causes black sooty stains on leaves and fruits. Adults can also transmit viral diseases when they suck leaves [77].

Prevention and control measures:

1. Physical control. Before the tomato facility is planted, an insect net can be installed in the vent to prevent adults from entering the shed. Silver-gray plastic film can be used as the mulch film to repel whiteflies and effectively reduce the number of whiteflies in the greenhouse. As the insects are attracted to yellow colors, previous control measures have included hanging 375–450 yellow plates

per hectare after tomato planting, with the lower edge of the yellow plate placed 10–15 cm from the plant. The artificial release of the natural enemies of whitefly, including aphid wasps, new pasteur mites, and heterochromatic ladybugs, can also be used for control [78].

2. Pharmaceutical prevention and control, such as the application of 5% d-limonene dissolvable agent, 17% flupyradone dissolvable solution, 22% spirachlor-ethiacaprid suspension agent, or 20% spirafen propylene dispersible oil suspension [79].

3. Conclusions

Tomatoes are important vegetables with strong consumer demand. However, the frequent occurrence of pests and diseases seriously affects their yield and quality. With higher consumption levels and greater attention to food safety, the effective prevention and control of pests and diseases has become increasingly important in tomato production. Prevention and control should combine agricultural practices, biological control measures, physical control measures, and the selective use of chemical agents. Considering these requirements, the green prevention and control of tomato diseases and pests is vital for guaranteeing tomato quality and promoting the sustainable development of the tomato industry.

Acknowledgements

Thanks for the funding: “Reform and construction project of grassroots agricultural technology extension system (RK2400002392)” and Monitoring and control of crop diseases, insects, weeds, and rodents.

Conflict of interest

The authors declare no conflict of interest. “The funders had no role in the design of the study; in the writing of the manuscript, or in the decision to publish the chapter”.

Author details

Jianxiu Hao¹, Hongyou Zhou^{1*}, Zhe Yan², Yufeng Wang³, Zhen Wang³, Ruiying Chen³, Jun Hu¹, Qiaoxia Shang², Xin Wang¹ and Xinyuan Wang¹

1 College of Horticulture and Plant Protection, Inner Mongolia Agricultural University, Hohhot, China

2 College of Plant Sciences and Technology, Beijing University of Agriculture, Beijing, China

3 Ulanqab Agricultural and Forestry Science Research Institute of Inner Mongolia, Ulanqab, China

*Address all correspondence to: hongyouzhou2002@aliyun.com

IntechOpen

© 2025 The Author(s). Licensee IntechOpen. This chapter is distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. 

References

- [1] Mao X. Identification and Green Prevention and Control Technology of Tomato Virus Disease in Ningxia [Thesis]. Yinchuan: Ningxia University; 2022. DOI: 10.27257/d.cnki.gnxhc.2023.001191
- [2] Gebhardt C, Montecchi-Palazzi L, Quondam MX. The historical role of species from the *Solanaceae* plant family in genetic research. Theoretical and Applied Genetics. 2016;**129**:2281-2294. DOI: 10.1007/s00122-016-2804-1
- [3] Dan Z, Lv W, Wang W, Ma J, Yang L, Mu W. Production status, recommended cultivars and trend analysis on winter and spring tomato of Southwest China. Journal of Changjiang Vegetables. 2021;**6**:1-3
- [4] Singh P, Goyal GK. Functionality of pizza ingredients. BFJ. 2011;**113**:1322-1338. DOI: 10.1108/00070701111179960
- [5] Tiwari JK, Behera TK, Rai N, Yerasu SR, Singh MK, Singh P. Tomato breeding for processing in India: Current status and prospects. BFJ. 2022;**49**:123-132
- [6] Kaur C, Walia S, Nagal S, Walia S, Singh J, Singh BB, et al. Functional quality and antioxidant composition of selected tomato (*Solanum lycopersicon* L.) cultivars grown in Northern India. LWT-Food Science and Technology. 2013;**50**:139-145. DOI: 10.1016/j.lwt.2012.06.013
- [7] Panno S, Davino S, Caruso AG, Bertacca S, Crnogorac A, Mandić A, et al. A review of the most common and economically important diseases that undermine the cultivation of tomato crop in the mediterranean basin. Agronomy. 2021;**11**:2188. DOI: 10.3390/agronomy11112188
- [8] Toševski I, Jović J, Mitrović M, Cvrković T, Krstić O, Krnjajić S. *Tuta absoluta* (Meyrick, 1917) (Lepidoptera, Gelechiidae): A new pest of tomato in Serbia. Pesticidi i fitomedicina. 2011;**26**:197-204. DOI: 10.2298/PIF1103197T
- [9] Kamlesh Mathur KM, Shekhawat KS. Chemical control of early blight in kharif sown tomato. Indian Journal of Mycology and Plant Pathology. 1986;**16**:235-238
- [10] Nowicki M, Kozik EU, Foolad MR. Late blight of tomato. In: Varshney RK, Tuberosa R, editors. Translational Genomics for Crop Breeding: Biotic Stress. 1st ed. Chichester: Wiley; 2013. pp. 241-265. DOI: 10.1002/9781118728475.ch13
- [11] Nirmaladevi D, Venkataramana M, Srivastava RK, Uppalapati SR, Gupta VK, Yli-Mattila T, et al. Molecular phylogeny, pathogenicity and toxigenicity of *Fusarium oxysporum* f. sp. *Lycopersici*. Scientific Reports. 2016;**6**:21367. DOI: 10.1038/srep21367
- [12] Sidharthan VK, Aggarwal R, Surenthiran N, Shanmugam V. Selection and characterization of the virulent *Fusarium oxysporum* f. sp. *lycopersici* isolate inciting vascular wilt of tomato. International Journal of Current Microbiology and Applied Sciences. 2018;**7**:1749-1756. DOI: 10.20546/IJCMAS.2018.702.212
- [13] Kavitha R, Umesha S. Prevalence of bacterial spot in tomato fields of Karnataka and effect of biological seed treatment on disease incidence. Crop Protection. 2007;**26**:991-997. DOI: 10.1016/j.cropro.2006.09.007
- [14] Nagendran K, Venkataravanappa V, Chauhan NS, Kodandaram MH, Rai AB,

- Singh B, et al. Viral diseases: A threat for tomato cultivation in Indo-Gangetic eastern plains of India. *Journal of Plant Pathology*. 2019;**101**:15-22. DOI: 10.1007/s42161-018-0124-9
- [15] Kumar A, Razi R, Singh A, Das H. Res-VGG: A novel model for plant disease detection by fusing VGG16 and ResNet models. In: Bhattacharjee A, Borgohain S, Soni B, Verma G, Gao XZ, editors. *Machine Learning, Image Processing, Network Security and Data Sciences*. 1st ed. Singapore: Springer; 2020. pp. 383-400. DOI: 10.1007/978-981-15-6318-8_32
- [16] Ashraf MS, Khan TA. Integrated approach for the management of *Meloidogyne javanica* on eggplant using oil cakes and biocontrol agents. *Archives of Phytopathology*. 2010;**43**:609-614. DOI: 10.1080/03235400801972434
- [17] Lange WH, Bronson L. Insect pests of tomatoes. *Annual Review of Entomology*. 1981;**26**:345-371
- [18] Al-Kazafy H, Abd-El Rahman TA, Abolmaaty SM. Influence of some new insecticides on sweetpotato whitefly, *Bemisia tabaci* and American serpentine leafminer, *Liriomyza trifolii* and their residues in cucumber fruits. *IJAR*. 2015;**3**:1874-1881
- [19] Sharma A, Kumar V, Shahzad B, Tanveer M, Sidhu GPS, Handa N, et al. Worldwide pesticide usage and its impacts on ecosystem. *SN Applied Sciences*. 2019;**1**:1446. DOI: 10.1007/s42452-019-1485-1
- [20] Boudh S, Singh JS. Pesticide contamination: Environmental problems and remediation strategies. In: Bharagava R, Chowdhary P, editors. *Emerging and Eco-Friendly Approaches for Waste Management*. 1st ed. Singapore: Springer; 2019. pp. 245-269. DOI: 10.1007/978-981-10-8669-4_12
- [21] Patel SJ, Subramanian RB, Jha YS. Biochemical and molecular studies of early blight disease in tomato. *Phytoparasitica*. 2011;**39**:269-283. DOI: 10.1007/s12600-011-0156-6
- [22] Qu Z. Studies on the Influence of Soil Amendments to Soil Microbes, Tomato Early Blight and Greenhouse Whitefly [Thesis]. Beijing: China Agricultural University; 2004
- [23] Kang Z, Jiang L, Luo Y, Liu C, Li X. The research advances of mechanism of pathogenicity of *Alternaria* phytopathogenic fungi. *CBLS*. 2013;**25**:908-914. DOI: 10.13376/j.cbbs/2013.09.009
- [24] Li M. The occurrence and control technology of tomato early blight. *CCV*. 2014;**27**:73-74. DOI: 10.16861/j.cnki.zggc.2014.04.030
- [25] Gao Z, Li S, Dai S, Zhu D, Zhang W, Feng L. A new variety of medium-ripe disease-resistant tomato, Zhongshu No. 5 and Zhongshu No. 6. *China Vegetables*. 1990;**39**:4-6. DOI: 10.19928/j.cnki.1000-6346.1990.03.002
- [26] Sun Y, Liu Z, Li H, Zheng Z, Ji C, Guo Q, et al. Biocontrol effect and mechanism of *bacillus laterosporus* Bl13 against early blight disease of tomato. *Chinese Journal of Applied Ecology*. 2021;**32**:299-308. DOI: 10.13287/j.1001-9332.202101.036
- [27] Chen Y, Yao A, Ru B, Li X, An T, An D. Study on the control of tomato early blight by *Bacillus pilereensis* BC39. *China Plant Protection*. 2017;**37**:65-68
- [28] Yang S, Sun L, Deng S, Yuan B, Su J, Wang Z, et al. Effects of *Trichoderma asperellum* fermentation broth on antioxidant system and lipid peroxidation of *Alternaria solani* Sorauer. *Chinese Agricultural Science Bulletin*. 2017;**33**:90-94

- [29] Li M. Prevention and treatment of tomato late blight. *Vegetables*. 2020;**4**:69-72 +86+85
- [30] Whisson SC, Boevink PC, Wang S. The cell biology of late blight disease-science direct. *Current Opinion in Microbiology*. 2016;**34**:127-135. DOI: 10.1016/j.mib.2016.09.002
- [31] Chen H, Zhou L. Introduction and screening experiment of new tomato cultivars. *Vegetables*. 2023;**11**:66-69
- [32] Peralta IE, Spooner DM. History, origin and early cultivation of tomato (*Solanaceae*). In: Razdan MK, editor. *Genetic Improvement of Solanaceous Crops Volume 2*. 1st ed. Boca Raton: CRC Press; 2006. p. 24. DOI: 10.1201/b10744
- [33] Zhng Q. Field control effect of different new fungicides on tomato late blight. *Modern Agricultural Science and Technology*. 2023;**21**:96-98
- [34] Bao H, Li K, Zhong K, Hao Z. Inhibitory effect of piperine on *Botrytis cinerea* and its mechanism. *Journal of China Agricultural University*. 2022;**27**:117-124
- [35] Pan X, Li Z, Shi X, Lin S, Li J, Tian Y. Screening, identification and biocontrol effects of antagonistic bacterial strain XF and preliminary exploration of biocontrol factors. *Acta Agriculturae Boreali-Occidentalis Sinica*. 2019;**28**:1888-1895. DOI: 10.7606/j.issn.1004-1389.2019.11.018
- [36] Williamson B, Tudzynski B, Tudzynski P, van Kan JA. *Botrytis cinerea*: The cause of grey mould disease. *Molecular Plant Pathology*. 2007;**8**:561-580. DOI: 10.1111/j.1364-3703.2007.00417.x
- [37] Bi K, Liang Y, Mengiste T, Sharon A. Killing softly: A roadmap of *Botrytis cinerea* pathogenicity. *Trends in Plant Science*. 2023;**28**:211-222. DOI: 10.1016/j.tplants.2022.08.024
- [38] Cantu D, Blanco-Ulate B, Yang L, Labavitch JM, Bennett AB, Powell AL. Ripening-regulated susceptibility of tomato fruit to *Botrytis cinerea* requires NOR but not RIN or ethylene. *Plant Physiology*. 2009;**150**:1434-1449. DOI: 10.1104/pp.109.138701
- [39] Shao W, Zhao Y, Ma Z. Advances in understanding fungicide resistance in *Botrytis cinerea* in China. *Phytopathology*. 2021;**111**:455-463. DOI: 10.1094/PHYTO-07-20-0313-IA
- [40] Wang Y, Yu T, Xia J, Yu D, Wang J, Zheng X. Biocontrol of postharvest gray mold of cherry tomatoes with the marine yeast *Rhodospiridium paludigenum*. *Biological Control*. 2010;**53**:178-182. DOI: 10.1016/j.biocontrol.2010.01.002
- [41] Bello GD, Rollán MC, Lampugnani G, Ronco L, Larrán S, Mónaco C. Biological control of leaf grey mould of greenhouse tomatoes caused by *Botrytis cinerea*. *International Journal of Pest Management*. 2011;**57**:177-182. DOI: 10.1080/09670874.2011.561887
- [42] Yao B, Wang A, Li J. Study on the inhibition of *Trichoderma harzianum* on four tomato pathogenic fungi. *Journal of Northeast Agricultural University*. 2009;**40**:26-31. DOI: 10.19720/j.cnki.issn.1005-9369.2009.05.006
- [43] Zhuang J, Sun G, Gao Z, Liu X, Chen J. Selection of biocontrol agents to *Botrytis cinerea*. *Journal of Shenyang Agricultural University*. 2005;**36**:33-36
- [44] Francis I, Holsters M, Vereecke D. The gram-positive side of plant-microbe interactions. *Environmental Microbiology*. 2010;**12**(1):1-12. DOI: 10.1111/j.1462-2920.2009.01989

- [45] Gleason ML, Gitaitis RD, Ricker MD. Recent progress in understanding and controlling bacterial canker of tomato in eastern North America. *Plant Disease*. 1993;77:1069-1076
- [46] Luo L, Zhao T, Li J, Zhang L, Li Y, Bolkan H. Progress in research on bacterial canker of tomato caused by *Clavibacter michiganensis* subsp. *michiganensis*. *Scientia Agricultura Sinica*. 2004;8:1144-1150
- [47] Anderson PK, Cunningham AA, Patel NG, et al. Emerging infectious diseases of plants: Pathogen pollution, climate change and agrotechnology drivers. *Trees*. 2004;19(10):535-544. DOI: 10.1016/j.tree.2004.07.021
- [48] Wang Y, Deng S, Li Z, Yang W. Advances in the characterization of the mechanism underlying bacterial canker development and tomato plant resistance. *Horticulturae*. 2022;8:209. DOI: 10.3390/horticulturae8030209
- [49] Nandi M, Macdonald J, Liu P, Weselowski B, Yuan Z. *Clavibacter michiganensis* ssp. *michiganensis*: Bacterial canker of tomato, molecular interactions and disease management. *Molecular Plant Pathology*. 2018;19:2036-2050. DOI: 10.1111/mp.12678
- [50] Hassan MF, Qutb AM, Dong W. Prediction and activity of a cationic α -helix antimicrobial peptide ZM-804 from maize. *International Journal of Molecular Sciences*. 2021;22:2643. DOI: 10.3390/ijms22052643
- [51] Peritore-Galve FC, Tancos MA, Smart CD. Bacterial canker of tomato: Revisiting a global and economically damaging seedborne pathogen. *Plant Disease*. 2021;105:1581-1595. DOI: 10.1094/PDIS-08-20-1732-FE
- [52] Sen Y, van der Wolf J, Visser RGF, van Heusden S. Bacterial canker of tomato: Current knowledge of detection, management, resistance, and interactions. *Plant Disease*. 2015;99:4-13. DOI: 10.1094/PDIS-05-14-0499-FE
- [53] Han Y, Yang J, Li J, Li X, Zhang Y, Qiao N, et al. Comprehensive control measures for tomato canker disease in Bayannur city. *Modern Agriculture*. 2017;6:51. DOI: 10.14070/j.cnki.15-1098.2017.06.039
- [54] Amkraz N, Boudyach EH, Boubaker H. Screening for fluorescent pseudomonades, isolated from the rhizosphere of tomato, for antagonistic activity toward *Clavibacter michiganensis* subsp. *michiganensis*. *World Journal of Microbiology and Biotechnology*. 2010;26:1059-1065. DOI: 10.1007/s11274-009-0270-5
- [55] Kasselaki AM, Goumas D, Tamm L, Fuchs J, Cooper J, Leifert C. Effect of alternative strategies for the disinfection of tomato seed infected with bacterial canker (*Clavibacter michiganensis* subsp. *michiganensis*). *NJAS*. 2011;58:145-147. DOI: 10.1016/j.njas.2011.07.001
- [56] Yuan H, Min H, Lv Z, Li Z. Antimicrobial activity of isolate HL-12 against *Clavibacter michiganensis* subsp. *michiganensis* in the presence of cadmium. *Ecotoxicology*. 2009;18:447-454. DOI: 10.1007/s10646-009-0299-0
- [57] Utkhede R, Koch C. Biological treatments to control bacterial canker of greenhouse tomatoes. *BioControl*. 2004;49:305-313. DOI: 10.1023/B:BICO.0000025373.69584.08
- [58] Turgut A, Basim H. Sensitivity of tomato (*Solanum lycopersicum*) cultivars from Turkey to bacterial speck (*Pseudomonas syringae* pv. tomato).

- African Journal of Biotechnology. 2013;**12**:15. DOI: 10.5897/AJB12.2740
- [59] Byrne JM, Dianese AC, Ji P, Campbell HL, Cuppels DA, Louws FJ, et al. Biological control of bacterial spot of tomato under field conditions at several locations in North America. Biological Control. 2005;**32**:408-418. DOI: 10.1016/j.biocontrol.2004.12.001
- [60] Liang P. The occurrence and prevention of the main diseases of cherry tomatoes in Tianyang District, Baise City. Modern Agricultural Science and Technology. 2021;**5**:143-144
- [61] Fan X, Yang C, Qiu S, Hu F. Identification of biocontrol bacterial strain and its antagonistic activity to tomato bacterial speck and colonizing ability in tomato. Journal of Fujian Agriculture and Forestry University. 2013;**42**:337-341. DOI: 10.13323/j.cnki.j.fafu(nat.sci.).2013.04.010
- [62] Yang Y, Wang M, Yin Y, Onac E, Zhou G, Peng S, et al. RNA-seq analysis reveals the role of red light in resistance against *Pseudomonas syringae* pv. Tomato DC3000 in tomato plants. BMC Genomics. 2015;**16**:1-16. DOI: 10.1186/s12864-015-1228-7
- [63] Si T, Xue L, Sang Y, Yang D. Screening of fungicide for controlling tomato bacterial speck disease and its resistance identification. Northern Horticulture. 2016;**22**:127-130
- [64] Czosnek H, Laterrot H. A worldwide survey of tomato yellow leaf curl viruses. Archives of Virology. 1997;**142**:1391-1406. DOI: 10.1007/s007050050168
- [65] Doolittle SP. A new infections mosaic disease of cucumber. Phytopathology. 1916;**6**:145-147
- [66] Latin RX, Ruhl GE, Nameth ST. First report of tomato spotted wilt virus (TSWV) on field-grown peppers in the Midwest. Proceedings of the Indiana Academy of Science. 1988;**98**:117-120
- [67] King AM, Adams MJ, Lefkowitz E. Family astroviridae BT-virus taxonomy: Ninth report of the international committee on taxonomy of viruses. In: Virus Taxonomy: Ninth Report of the International Committee on Taxonomy of Viruses. Vol. 10 (12). Amsterdam: Elsevier; 2011. pp. 581-586
- [68] Laemmlen FF, Vanmaren AF, Endo R-M, Valverde RA. A tomato decline of unknown etiology in Imperial Valley. Phytopathology. 1985;**75**:1287-1287
- [69] Zhang Z, Wu S, Lei Z. Occurrence and prevention of tomato leaf miner, a new agricultural invasive organism in Ningxia. China Cucurbits and Vegetables. 2022;**35**:111-116. DOI: 10.16861/j.cnki.zggc.20221121.001
- [70] Terzidis AN, Wilcockson S, Leifert C. The tomato leaf miner (*Tuta absoluta*): Conventional pest problem, organic management solutions? Organic Agriculture. 2014;**4**:43-61. DOI: 10.1007/s13165-014-0064-4
- [71] Johnson MW, Oatman ER, Wyman JA. Natural control of *Liriomyza sativae* [dip.: Agromyzidae] in pole tomatoes in southern California. Entomophaga. 1980;**25**:193-198. DOI: 10.1007/BF02374320
- [72] Yadav SPS, Pokhrel S, Poudel A, Anju P, Devkota S, Katel S, et al. Evaluation of different insecticides against *Liriomyza sativae* (Diptera: Agromyzidae) on cucumber plants. Journal of Agriculture and Food Research. 2024;**15**:100987. DOI: 10.1016/j.jafr.2024.100987

[73] Juvik JA, Shapiro JA, Young TE, Mutschleret MA. Acylglucoses from wild tomatoes alter behavior and reduce growth and survival of *Helicoverpa zea* and *Spodoptera exigua* (Lepidoptera: Noctuidae). Journal of Economic Entomology. 1994;**87**(2):482-492. DOI: 10.1093/jee/87.2.482

[74] Murphy ST, LaSalle J. Balancing biological control strategies in the IPM of New world invasive *Liriomyza leafminers* in field vegetable crops. Biocontrol News and Information. 1999;**20**:91N-104N

[75] Frattini A, González-Martínez RM, García JM, Minchev Z, Pozo MJ, Flors V, et al. Constitutive and inducible tomato defenses contribute to *Bacillus thuringiensis* lethality against *Spodoptera exigua*. Biological Control. 2024;**198**:105624. DOI: 10.1016/j.biocontrol.2024.105624

[76] Edde PA. Principal insects affecting tobacco plants in the field. Beiträge zur Tabakforschung International. 2018;**28**:117-165

[77] Palumbo JC, Horowitz AR, Prabhaker N. Insecticidal control and resistance management for *Bemisia tabaci*. Crop Protection. 2001;**20**:739-765. DOI: 10.1016/S0261-2194(01)00117-X

[78] Gerling D, Alomar Ò, Arnò J. Biological control of *Bemisia tabaci* using predators and parasitoids. Crop Protection. 2001;**20**:779-799. DOI: 10.1016/S0261-2194(01)00110-7

[79] Sharaf N. Chemical control of *Bemisia tabaci*. Agriculture, Ecosystems & Environment. 1986;**17**:111-127. DOI: 10.1016/0167-8809(86)90032-0

Salicylic Acid Mitigates the Negative Effects of NaCl in *Solanum lycopersicum* L. by Improving Growth Rate and Biochemical Parameters

*Wasti Salma, Ben Hassine Abir, Abdi Najoua
and Ben Ahmed Hela*

Abstract

Tomato is the most important vegetable in the world and also the one with the highest economic value. However, it is frequently exposed to multiple environmental stresses, especially salinity. Salt tolerance is susceptible to be ameliorated by genetic and physiological ways. Salicylic acid controls signaling pathways whose role in resistance is the best established. The objective of this study is to examine the effect of exogenous application of (0.01 mM SA) on the salt tolerance (100 mM NaCl) of cultivated tomato cvs. Moneymaker, Super Marmande, and Marmande. This evaluation includes assessing growth, pigment level, and metabolic parameters in the plant during the first month of development.

Keywords: tomato, salinity, salicylic acid, photosynthetic pigments, proline, sugar content

1. Introduction

Climate change is becoming increasingly restrictive for the growth and development of plants, particularly in semi-arid and arid areas throughout the world [1, 2]. Soils are classified as saline where the electrical conductivity of a pulp extract saturated at 25°C (CE_{eps}) is 4 dS m⁻¹ or higher (USDA- ARS. 2008), which is approximately equivalent to 40 mM NaCl, generating an osmotic pressure of around 0.2 MPa (FAO 2008) [3].

The main causes of salt accumulation in plants are irrigation with salt water and the excessive use of fertilizers. Additionally, severe climatic conditions such as temperature increases and drought contribute to the rise in salt concentration in the soil [4].

The tolerance of plants to salinity varies from one species to another, and each crop has its own physiological and/or biological tolerance to different levels of salinity [5]. Indeed, some crops thrive very well in salt soil, but this is not the case for others. However, the development of methods to improve the salt tolerance of cultivated plants is essential and receives considerable attention. The cultivated tomato is currently the most consumed vegetable in the world. Due to its importance in terms of food, the tomato has received significant attention. It is classified as a plant with medium tolerance, exhibiting intraspecific variability. Salt tolerance can potentially be improved through genetic, biotechnological, or physiological means. The use of salicylic acid represents a recent approach in improving plant tolerance to salinity. SA is a phenolic phytohormone, naturally synthesized by the plant in response to various stresses, to be involved in acquired systemic resistance (ASR) and participate in the regulation of physiological processes [6]. Thus, it is considered to activate most of the plant defense responses against biotic and abiotic stresses [7, 8]. SA is considered a molecule involved in many physiological processes in plants and it is also a compound naturally found in plants. Gharbi et al. [9] reported that 0.01 mM SA improved the growth of aerial parts in *Solanum lycopersicum* cv. Ailsa Craig as well as its wild, salt-resistant relative, *Solanum chilense*. Additionally, Mimouni et al. [10] observed that applying 0.01 mM SA recovered the content of photosynthetic pigments (Chl and caro) in plants exposed to salinity.

To encourage crop production and rapidly increase the agricultural yield of currently available cultivated lands under abiotic constraints at the national level, it is necessary to understand the physiological and biochemical responses to these limiting conditions. In this context, this work is a contribution to the study of physiological behaviors of tomato subjected to 100 mM NaCl and to evaluate the effect of root application of 0.01 SA on the tolerance of three contrasting tomato cultivars to salt stress.

2. Materials and methods

2.1 Plant material and growth conditions

Three genotypes of tomato (*Solanum lycopersicum* L.,) were used (cv. Moneymaker, cv. Super Marmande, and cv. Marmande). Seeds were surface-sterilized by soaking in a 5% (v/v) sodium hypochlorite solution for 15 min followed by three washes with sterile distilled water. Seeds were then germinated in Petri dishes with moistened filter paper and incubated under fluorescent light ($90 \mu\text{mol m}^{-2} \text{s}^{-1}$ with a 16 h photoperiod at 25°C). Ten days after sowing, seedlings were transferred to growth chamber ($25^{\circ}\text{C}/70\%$ relative humidity during the day and $20^{\circ}\text{C}/90\%$ relative humidity during the night; photoperiod: 16 h daily with a light irradiance of $150 \mu\text{mol m}^{-2} \text{s}^{-1}$). They were grown in a continuously aerated hydroponic Hoagland nutrient solution containing the following chemicals: 5 mM KNO_3 , 1 mM $\text{NH}_4\text{H}_2\text{PO}_4$, 0.5 mM MgSO_4 , 5.5 mM $\text{Ca}(\text{NO}_3)_2$, 10 μM H_3BO_3 , 1 μM MnSO_4 , 1 μM ZnSO_4 , 0.25 μM CuSO_4 , 10 μM Na_2MoO_4 , and 0.34 g/L Fe-EDDHA [ethylenediamine-N,N'-bis (2-hydroxyphenyl)acetic acid] [11]. After 7 days of acclimatization in control conditions, the seedlings were exposed to four treatments (**Table 1**). Fifteen days after

	Nutrient solution	Salicylic acid (0.01 mM)	NaCl (100 mM)
C	+	—	—
SA	+	+	—
S	+	—	+
S + SA	+	+	+

C - Control, SA - Salicylic acid, S - Salt (NaCl), SA + S - salicylic acid + NaCl.

Table 1.
 Different treatments applied to tomato seedling. (+) indicates presence and (-) absence of considered solution.

treatment, plants were collected and separated into leaves, stems, and roots for the assessment of physiological parameters.

2.2 Dry weight determinations

For plant growth, 10 independent dry matter measurements were performed on separated leaves, stems, and roots. Dry weight (DW) was determined after desiccation at 80°C for 48 h.

2.3 Chlorophyll and carotenoid analysis

Pigments were extracted from leaf disks in 80% acetone. Chlorophyll and carotenoid concentrations were quantified spectrophotometrically based on the method outlined by Lichtenthaler [12] employing the following equations:

$$C_a = 12.25A_{663} - 2.79A_{645}$$

$$C_b = 21.50A_{645} - 5.10A_{663}$$

$$C_{a+b} = 7.15A_{663} + 18.71A_{645}$$

$$C_{x+c} = [1000A_{470} - 1.82C_a - 85.02C_b] / 198$$

where C_a = chlorophyll a; C_b = chlorophyll b; C_{a+b} = total chlorophyll; C_{x+c} = carotenoids, A_λ = absorbance at λ (nm).

2.4 Proline and total soluble sugar contents

Proline concentration (g/FW) was measured using the method described by Bates et al. [13]. Proline was extracted from approximately 200 mg of fresh weight (FW) organ samples with 10 mL of 3% sulfosalicylic acid at 70°C for 30 minutes. After adding acid ninhydrin and glacial acetic acid to the extracts, the mixture was heated in a water bath at 90°C for 1 hour. The mixture was extracted with toluene, and the absorbance of the toluene fraction was measured spectrophotometrically at 520 nm.

Total soluble sugars were estimated using the anthrone reagent method, with glucose as the standard, according to Yemm and Willis [14].

3. Results

3.1 The effect of SA on growth parameters of tomato plants

It is observed, in our study, that salinity negatively affects plant growth of all the genotypes (**Figure 1**). Salt treatment (S) caused a significant reduction in whole plant dry mass in cvs. Moneymaker, Super Marmande, and Marmande by 53, 46, and 32%, respectively, compared to the control plants. In tomato grown in the presence or in the absence of NaCl, root application of 0.01 mM SA stimulates biomass production. The root system is not very sensitive to NaCl, and its growth is stimulated by SA. Thus, SA improves plant growth in saline environments by stimulating root system growth and promoting the development of aerial organs. The results showed that the beneficial effect of exogenous SA application in mitigating NaCl-induced growth inhibition was particularly pronounced especially in the cultivar (cv. Marmande) (**Figure 1**).

3.2 The effect of SA on photosynthetic pigments of tomato plants

There was a significant alteration in the photosynthetic pigments, chlorophyll (Chl) and carotenoid content (carot), under salinity stress in the three genotypes when compared to the control plants (**Table 2**). Under saline treatment, the photosynthetic pigment content in cv. Marmande decreased by 42% for carotenoid and 30% for chlorophyll. On the other hand, the SA + S treatment significantly increased chlorophyll and carotenoid levels by 27 and 28%, respectively, compared to plants treated only with NaCl for the same cultivar (cv. Marmande). Application of SA alone or in combination with salt-stressed plants did not significantly improve chlorophyll concentrations in cv. Super Marmande (**Table 2**).

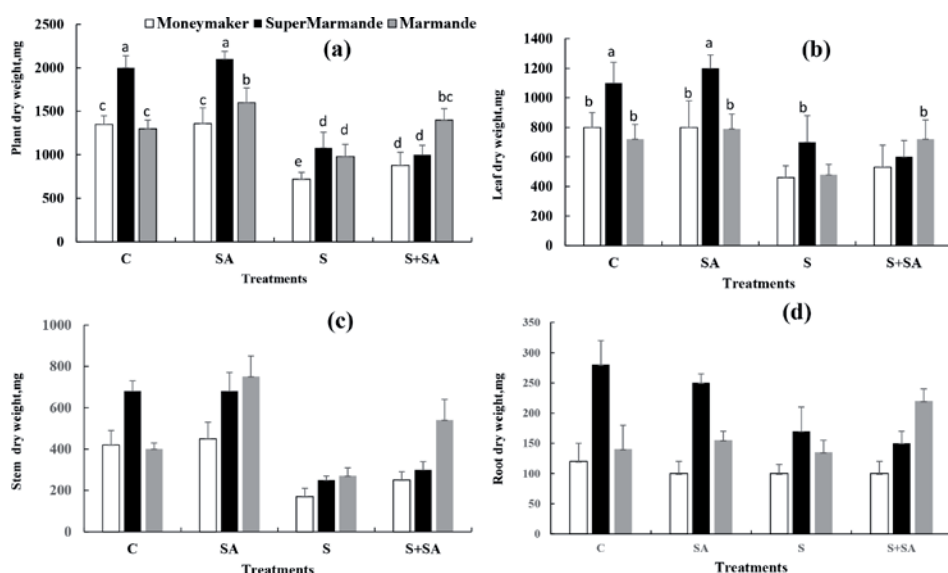


Figure 1.

NaCl effect on dry weight of different tomato cultivars with/without SA application after 15 days of growth. Each value represents the mean of 12 replicates. Bars indicate $\pm$ standard error ($P \leq 0.05$). C - control, SA - salicylic acid, S - salt (NaCl), SA + S - salicylic acid+NaCl.

	C	SA	S	S + SA
cv. Moneymaker				
Total Chl (mg g ⁻¹ FW)	2.81 ± 0.41a	1.52 ± 0.09c	1.62 ± 0.66c	1.80 ± 0.21b
Carot (mg g ⁻¹ FW)	0.35 ± 0.03a	0.34 ± 0.05a	0.15 ± 0.02b	0.18 ± 0.01b
cv. Super Marmande				
Total Chl (mg g ⁻¹ FW)	2.10 ± 0.19a	1.92 ± 0.26a	1.16 ± 0.07b	1.28 ± 0.10b
Carot (mg g ⁻¹ FW)	0.33 ± 0.03a	0.30 ± 0.03a	0.18 ± 0.02b	0.20 ± 0.04b
cv. Marmande				
Total Chl (mg g ⁻¹ FW)	1.53 ± 0.08a	1.43 ± 0.06a	1.12 ± 0.10b	1.35 ± 0.05c
Carot (mg g ⁻¹ FW)	0.25 ± 0.01a	0.22 ± 0.02a	0.13 ± 0.01b	0.17 ± 0.02c

Each value represents the mean of five replicates. Bars indicate ± standard error ($P \leq 0.05$). C - control, SA - salicylic acid, S - salt (NaCl), SA + S - salicylic acid + NaCl.

Table 2.
NaCl effect on pigments (total chlorophyll and carotenoid) of different tomato cultivars with/without SA application after 15 days of growth.

3.3 The effect of SA on proline content of tomato plants

After 15 days of treatment, the increase in proline content in plants treated with 100 Mm NaCl was significant in leaves and roots compared to control plants (**Figure 2a, b**). The content of proline increased particularly in roots, especially for cultivars Moneymaker and Super Marmande under saline conditions. Exogenous

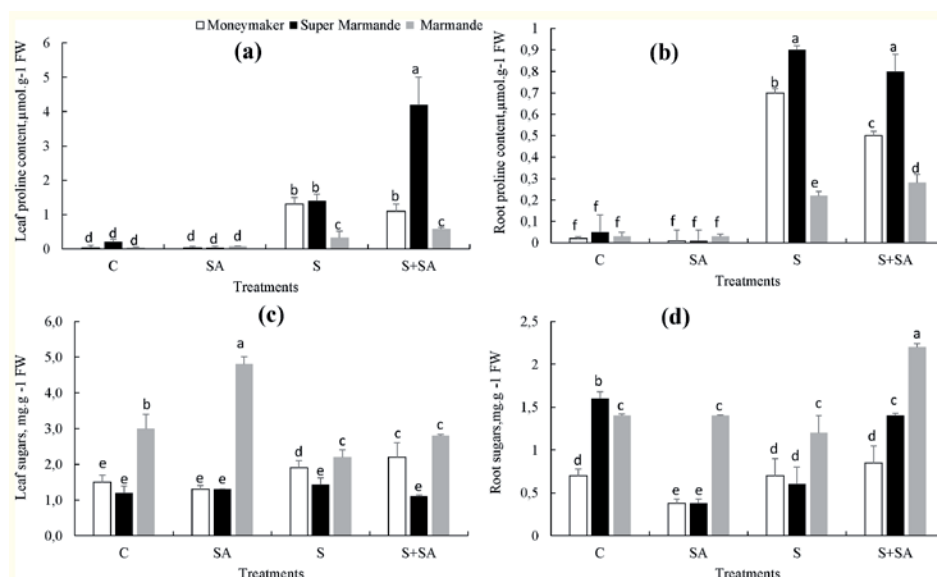


Figure 2.
NaCl effect on proline (a, b) and sugars (c, d) of different tomato cultivars with/without SA application after 15 days of growth. Each value represents the mean of five replicates. Bars indicate ± standard error ($P \geq 0.05$). C - control, SA - salicylic acid, S - salt (NaCl), SA + S - salicylic acid + NaCl.

application of SA via root medium enhanced proline content in both organs of cv. Marmande, with an increase of about 22% in leaves and 33% in roots compared to salt treatment (S) (**Figure 2a, b**).

3.4 The effect of SA on sugar content of tomato plants

In our study, the sugar level evaluated in leaves of cv. Marmande treated with NaCl was reduced by 27% compared to control plants (**Figure 2c**). However, plants treated with SA show increased sugar content in the leaves and roots of tomatoes grown in a saline medium with 35 and 39%, respectively, compared to those grown only in a saline medium (S) (**Figure 2c, d**).

Cultivars exposed to salt exhibited a reduction in their root soluble sugar content. For instance, NaCl decreased root sugar concentration by 56% compared to control for cv. Super Marmande (**Figure 2d**). The addition of SA mitigated this negative impact of salinity on root sugar levels. This effect was more pronounced in cv. Marmande, which increased sugar content by 52%, compared to salt treatment (S). In cv. Moneymaker, there was no significant change at 100 mM NaCl; however, adding salicylic acid increased the root sugar level slightly.

4. Discussion

The salinity of soils and water remains a major obstacle to plant growth. Indeed, the salts accumulated in the soil cause physiological and metabolic disturbances, leading to reduced growth of roots and aerial parts [6]. Indeed, the results obtained indicate that salinity caused a significant reduction in growth rate. **Figure 1** demonstrated that the growth parameter (dry mass) decreased with the addition of NaCl, compared to controls, which may be due to the reduction of leaf area. These findings were consistent with a previous study on tomato [15]. Thus, plants growing in saline conditions will face the challenge of salinity, which they must resist to survive. The exogenous application of growth regulators or compatible solutes can effectively help improve crop productivity under saline stress conditions [7]. Salicylic acid is known as a signaling molecule that induces responses to environmental stress [16]. This substance has attracted attention due to its ability to induce gene expression [17]. The exogenous application of salicylic acid enhances the growth of several species subjected to various types of abiotic stress, such as salt stress [9, 18]. The results showed that exogenous application of SA promoted tomato plant growth under both non-saline and saline conditions. Indeed, dry mass determination of the different organs of tomato indicated that the mitigation effect of SA was important in plants treated with NaCl compared to those grown in salt stress only (**Figure 1**). This data was similar to a previous study where plant growth and dry weight of rice were enhanced with 0.1 SA under salt stress (120 mM NaCl) [19].

The amount of chlorophyll and carotenoids in the leaves decreases under salt stress. Furthermore, if the stress period is prolonged, older leaves begin to develop chlorosis [20].

Chlorophyll, due to its green color, is the main pigment found in plants. It is essential for the plant's photosynthetic activity.

Under salt stress, chlorophyll is reduced due to several factors related to the physiological disturbances in plants. It damages cell membranes and proteins involved in chlorophyll synthesis [21].

Our results showed that 100 mM NaCl decreased the total Chl and carotenoids content in leaves of the three genotypes compared to control plants (**Figure 2**). Chlorophyll and carotenoid content in tomato leaves increases with exogenous application of SA (**Table 2**). Zhao et al. [22] demonstrated that the application of salicylic acid stimulates the photosynthetic machinery and increases the chlorophyll content in soybean.

Plants accumulate a small molecule that helps them to overcome salt stress by regulating internal osmotic balance and stabilizing proteins and other cellular structures [23].

The proline accumulates in plant cells to maintain water balance. It is one of the important components in the defense responses of plants to salinity by contributing to better tolerance to prolonged salt stress.

Sugars, such as sucrose, glucose, or fructose, act as osmotically active solutes. This helps maintain the plant's water balance counteracting the dehydration effects caused by excess salt. Also, sugars have antioxidant properties that help protect plant cells from damage caused by reactive oxygen species (ROS) [24].

Our data showed that the application of SA via root medium promotes proline and sugar content, especially in cvs. Super Marmande and Marmande in saline conditions. Shakirova et al. [6] showed that salicylic acid promotes the accumulation of proline in maize-stressed seedlings. In our study, tomato plants submitted to NaCl treatment showed a decrease in their root soluble sugar content in cv. Super Marmande and in their leaf soluble sugars in cv. Marmande. Salt stress (100 mM NaCl) induced a marked decrease in root sugar level by 56% compared to control in cv. Super Marmande (**Figure 2d**). However, SA treatment enhanced the sugar content accumulations in the roots and leaves of the three cultivars. This effect was more prominent in cv. Marmande. Salicylic acid (0.01 mM) stimulates the degradation of soluble sugars, thereby inducing the formation of new cells, resulting in improved growth. The hydrolysis of proteins provides a pool of compatible solutes necessary for osmotic adjustment in salt conditions [25].

5. Conclusion

In summary, our investigation into the effect of Salicylic acid on tomato under salinity reveals a promising avenue for enhancing tomato crops. SA is a phytohormone that plays several roles in plant growth including enhancing shoot and root growth. In our study, the analysis of growth parameters showed that the 100 mM NaCl concentration significantly reduced biomass production in tomato organs. The application of salicylic acid to tomato plants has shown a positive influence on growth parameters under saline and non-saline conditions. The efficiency of growth rate was associated with the stimulation of photosynthesis by promoting the accumulation of chlorophyll, the primary pigment responsible for capturing light, which improves the plant's ability to produce sugars under salt stress. The application of SA could significantly reduce salt damage, mainly by increasing the content of osmotic substances such as proline and sugars, enhancing photosynthesis, and promoting growth. Our study enhances the understanding of SA's role and serves as a reference for studying its mechanism in salt-resistant tomatoes, which requires further investigation.

Acknowledgements

I would like to especially thank Pr. Ben Ahmed Hela for her help and valuable suggestions during the writing of this article.

Disclosure

The authors declare that no conflicting interests exist.

Author details

Wasti Salma^{1,2*}, Ben Hassine Abir^{1,2}, Abdi Najoua² and Ben Ahmed Hela^{1,2}

1 Laboratoire Mixte Tuniso-Marocain de Physiologie et Biotechnologie Végétales et Changement Climatique LR11ES09, Faculté des Sciences de Tunis, Université de Tunis El Manar, Tunis, Tunisia

2 Laboratoire Interaction Plante Sol et Environnement (LR21 ES01), Faculté des Sciences de Tunis, Université de Tunis El Manar, Tunis, Tunisia

*Address all correspondence to: salma.wasti1@gmail.com

IntechOpen

© 2025 The Author(s). Licensee IntechOpen. This chapter is distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. 

References

- [1] Huang Y, Bie Z, He S, Hua B, Zhen A, Liu Z. Improving cucumber tolerance to major nutrients induced salinity by grafting on *Cucurbita ficifolia*. *Environmental and Experimental Botany*. 2010;**69**:32-38
- [2] Kurum R, Ulukapı K, Aydınxsakir K, Onus AN. The influence of salinity on seedling growth of some pumpkin varieties used as rootstock. *Notulae Botanicae Horti Agrobotanici*. 2013;**41**:219-225
- [3] FAO. Soaring food prices: Facts, perspectives, impacts and actions required. In: Document HLC/08/INF/1 Prepared for the High-Level Conference on World Food Security: The Challenges of Climate Change and Bioenergy, 3-5 June 2008. Rome: FAO; 2008
- [4] Raj M, Binoy S, Hanuman SJ, Parbodh CS, Nanthi SB. Soil salinity under climate change: Challenges for sustainable agriculture and food security. *Journal of Environmental Management*. 2021;**280**:111736
- [5] Ashraf M, McNeilly T. Salinity tolerance in brassica oilseeds. *Critical Reviews in Plant Sciences*. 2004;**23**:157-174
- [6] Sakhabutdinovas AR, Fatkutdinova DR, Bezrukova MV, Shakirova FM. Salicylic acid prevents the damaging action of stress factors on wheat plants. *Bulgarian Journal of Plant Physiology*. 2003;**21**:314-319
- [7] Ashraf M, Foolad MR. Roles of glycine betaine and proline in improving plant abiotic stress resistance. *Environmental and Experimental Botany*. 2007;**59**:206-216
- [8] Kovacik J, Klejdus B, Hedbavny J, Backor M. Salicylic acid alleviates NaCl induced changes in the metabolism of *Matricaria chamomilla* plants. *Ecotoxicology*. 2009;**18**:544-554
- [9] Gharbi E, Martínez JP, Benahmed H, Fauconnier ML, Lutts S, Quinet M. Salicylic acid differently impacts ethylene and polyamine synthesis in the glycophyte *Solanum lycopersicum* and the wild-related halophyte *Solanum chilense* exposed to mild salt stress. *Physiologia Plantarum*. 2016;**158**:152-167
- [10] Mimouni H, Wasti S, Manaa A, Gharbi E, Chalh A, Vandoorne B, et al. Does salicylic acid (SA) improve tolerance to salt stress in plants? A study of SA effects on tomato plant growth, water dynamics, photosynthesis, and biochemical parameters. *Omics Journal of Integrative Plant Biology*. 2016;**20**:180-190
- [11] Hoagland DR, Arnon DI. The water culture method for growing plants without soil. *California Agricultural Experiment Station*. 1950;**347**:1-32
- [12] Lichtenthaler HK. Chlorophylls and carotenoids: Pigments of photosynthetic biomembranes. *Methods in Enzymology*. 1987;**148**:350-382
- [13] Bates L, Waldren R, Teare I. Rapid determination of free proline for water-stress studies. *Plant and Soil*. 1973;**39**:205-207
- [14] Yemm W, Willis AJ. The estimation of carbohydrates in plant extracts by anthrone. *Biochemical Journal*. 1954;**57**:508-514
- [15] Adilu GS, Gebre YG. Effect of salinity on seed germination of some

tomato (*Lycopersicon esculentum* mill.) varieties. Journal of Arid Agriculture. 2021;7:76-82

[16] Senaratna T, Touchell D, Bunn E, Dixon K. Acetyl salicylic acid (aspirin) and salicylic acid induce multiple stress tolerance in bean and tomato plants. Plant Growth Regulation. 2000;30:57-161

[17] Metraux JP. Systemic acquired resistance and salicylic acid: Current state of knowledge. European Journal of Plant Pathology. 2001;107:13-18

[18] Gharbi E, Lutts S, Dailly H, Quinet M. Comparison between the impacts of two different modes of salicylic acid application on tomato (*Solanum lycopersicum*) responses to salinity. Plant Signaling & Behavior. 2018;13:e1469361

[19] Liqing S, Yating X, Dan W, Jiayi H, Tongyuan Y, Cong D, et al. Effects of salicylic acid on growth, physiology, and gene expression in rice seedlings under salt and drought stress. Plant Stress. 2024;11:100413

[20] Hernandez JA, Olmas E, Corpas FJ, Sevilla F, Del Rio LA. Salt induced oxidative stress in chloroplasts of pea plants. Plant Science. 1995;105:151-167

[21] Jaleel CA, Sankar B, Sridharan R, Panneerselvam R. Soil salinity alters growth, chlorophyll content, and secondary metabolite accumulation in *Catharanthus roseus*. Turkish Journal of Biology. 2009;32:79-83

[22] Zhao HJ, Lin XW, Shi HZ, Chang SM. The regulating effect of phenolic compounds on the physiological characteristics and yield of soybeans. Acta Agronomica Sinica. 1995;21:351-355

[23] Manaa A, Gharbi E, Mimouni H, Wasti S, Aschi-Smiti S, Lutts S, et al.

Simultaneous application of salicylic acid and calcium improves salt tolerance in two contrasting tomato (*Solanum lycopersicum*) cultivars. South African Journal of Botany. 2014;95:32-39

[24] Zhang F, Zhang H, Xia Y, Wang G, Xu L, Shen Z. Exogenous application of salicylic acid alleviates cadmium toxicity and reduces hydrogen peroxide accumulation in root apoplasts of *Phaseolus aureus* and *Vicia sativa*. Plant Cell. 2011;30:1475-1483

[25] Mahmoud MMR. Ameliorative effect of salicylic acid on growth, minerals and nitrogenous compounds of *Vicia faba* L. plants under salt stress. Egyptian Journal Botany. 2017;57:11-29

Tomato Crop Improvement Efforts in Nigeria: Past, Current and Future Perspectives

Shakirat O. Ajenifujah-Solebo, Pamela E. Akin-Idowu, Ayodeji O. Aduloju, Victoria O. Adedeji, Esther T. Akinyode, Dorcas O. Ibitoye, Olawale Arogundade, Abiola O. Oke, Esther A. Adesegun, Valentine O. Ntui, Olalekan A. Akinbo, Charles O. Adetunji, Yetunde O. Falana, Roseline I. Joseph and Firdaus Bello

Abstract

This chapter provides an overview of the tomato crop and efforts to improve its productivity within Nigeria's food value chain. It highlights the biotic, abiotic and physiological challenges which pose substantial threat to the economics and nutritional impact of tomato in Nigeria, with specific reference to selected previous and current research techniques applied to improve the crop. It discusses the application of conventional breeding, tissue culture and genetic engineering aimed at improving traits such as disease resistance, fruit quality and shelf-life, including the revolutionary CRISPR genome editing technology for precise trait modifications. Furthermore, the chapter outlines the current research landscape and capacity-building initiatives in Nigeria, focusing on the need for collaboration among researchers, farmers and policymakers. The conclusion presents recommendations for future research directions, advocating for increased investment in biotechnological innovations to complement conventional breeding to ensure sustainable tomato production in the face of evolving agricultural challenges, thus contributing to food security and economic development.

Keywords: tomato production, genetic improvement, in-vitro regeneration, policy, capacity building, biosafety regulations, CRISPR technology

1. Introduction

Tomato, *Solanum lycopersicum* L., is a widely cultivated vegetable crop in Nigeria and has significant economic importance for small-scale farmers and commercial

producers. Global production of tomatoes is about 186.82 million tonnes grown across 5 million hectares. Nigeria is estimated to produce 4.1 million tonnes of tomatoes and has been ranked as the 11th largest producing country in the world, placing her as the second largest producer in Africa after Egypt [1].

Among the various vegetables grown in Nigeria, tomato stands out as the most important in terms of both production scale and consumption levels [2]. The cultivation contributes to food security, income generation and employment opportunities in rural areas. It is an important source of nutrition accounting for about 18-20% of the average daily consumption of vegetables in Nigeria, significantly contributing to meeting the human recommended dietary allowance (RDA) of over 200 million Nigerians [3]. Due to its multi-purpose utility, popularity and low cost, it is constantly in high demand. The demand for tomatoes in Nigeria was \$11.5b in 2015 [4] and increasing. As of 2023, Nigeria's tomato processing industry alone was valued at over USD 1 billion [5]. Over 3 million people are employed across various stages of tomato production, from farming and harvest to post-harvest handling, transportation and marketing [6]. This sector is particularly vital for rural employment, with smallholder farmers representing the majority of those engaged in tomato farming. Moreover, women are often involved in tomato production, marketing and processing, providing a source of income and empowering local communities [7].

Tomato cultivation in Nigeria spans various agro-ecological zones, from the humid southern regions to the sub-humid middle belt and the semi-arid and arid north. The crop is predominantly grown in the northern regions, positioned between latitudes 7.5 and 13°N, where the temperatures range from 25 to 34°C, providing an optimal climate for tomato production. The cultivation of tomatoes is practiced by different ethnic tribes and farming communities across Nigeria. The major tomato-growing regions in Nigeria include the northern states such as Kano, Kaduna, Jigawa, Plateau, and Katsina, which are known for their favorable climatic conditions and large-scale commercial tomato production [8]. These regions have a dry season, thus allowing for both irrigated and rain-fed tomato cultivation. The southern states, including Oyo, Ogun, Osun and Lagos, also engage in tomato cultivation, albeit on a smaller scale, due to the presence of suitable agro-climatic conditions and market demand [9]. Open-pollinated and hybrid cultivars are cultivated, depending on the preferences of farmers and the market demands. Common tomato types grown in Nigeria include Roma, Cherry, Beefsteak and Saladette varieties [9]. The preferences are based on their adaptability to local conditions, disease resistance, fruit quality and market preferences.

However, reported rise in tomato production in Nigeria has been driven by expansion in area under cultivation, which has increased by 5% annually in the last decade [10], which is unsustainable in the face of climate change challenges. Despite being one of the largest producers in Africa, Nigeria struggles to meet domestic demand, which is growing steadily. The challenges faced in tomato cultivation in Nigeria are influenced by various factors, including pests and diseases, climate variability, limited access to quality inputs, post-harvest losses and inadequate infrastructure for storage and processing [11, 12]. Post-harvest losses are a major issue due to the physiological ripening of the crop in the warm and humid climate and its susceptibility to pests. Despite the availability of documented technologies for improvement, local tomato cultivars in Nigeria remain largely undeveloped, and 80% of the seeds planted by farmers are generic varieties of low quality with limited post-harvest shelf-life [13]. Nigeria has the capacity to lead in world exports of tomato and tomato products. However, it was reported that Nigeria records up to 50% of locally produced tomatoes in the country as annual loss [14].

Efforts to enhance tomato production and reduce post-harvest losses have led to the integration of biotechnology to address challenges in research for development. Biotechnological advancements aim to improve tomato yield, shelf life and resistance to pests and diseases. Research has focused on developing high-yielding, disease resilient tomato varieties and to extend the shelf life to reduce post-harvest losses. There are existing regulatory frameworks and policies in Nigeria [15] to oversee the development and deployment of biotechnological products in agriculture. The Act regulates the use of modern biotechnology to ensure safety for human health and the environment.

Despite the importance of tomatoes, research and development (R&D) in this sector faces challenges, including limited funding, inadequate infrastructure and a shortage of skilled personnel, contributing to the decline in tomato production. Addressing these challenges is crucial for enhancing tomato production and reducing post-harvest losses in Nigeria.

This Chapter seeks to assess the tomato crop and the efforts that have been made to improve available cultivars, the technologies applied, expertise and institutional capabilities that can support research on the crop in Nigeria.

2. Challenges in tomato production

2.1 Biotic stresses: Pests and diseases

Tomato crops can be infected by bacterial, fungal and viral pathogens that can reduce yield, fruit quality, shelf-life and nutritional content. Every part of tomato plant including the leaves, stems, flowers and fruits are susceptible to insect pests and diseases.

2.1.1 Pests

Tomato production in Nigeria is constrained by insect pests such as the fruitworm *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae), cotton leafworm *Spodoptera littoralis* Boisduval (Lepidoptera: Noctuidae), leafminer flies *Liriomyza trifolii* Burgess (Diptera: Agromyzidae), tomato aphid *Myzus persicae* Sulzer (Hemiptera: aphididae), and the whitefly *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) [16, 17]. The recorded devastating invasion of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) in Nigeria caused 100% damage to tomato plants [18]. The prevalence and severity of insect infestations are projected to increase with global warming, as rising temperatures directly impact the growth, development and reproductive capabilities of insect pests [19]. Temperature fluctuations can exert direct effects on the physiology and biochemistry of insects, while also indirectly influencing their phenology [20]. The potential of *Tuta absoluta* to develop over a wide range of temperature: 10–30°C [21] and adaptability to high-temperature stress at 44°C during the egg stage without reduction in the fecundity of such emerged adults [22], has made it a pest of economic status on tomato in most invaded areas around the world.

2.1.2 *Fusarium wilt*

Out of the major diseases that affects tomato in Nigeria and other parts of the world is the attack of *Fusarium wilt* which is usually caused by *Fusarium oxysporium*

f. sp. lycopersicum. The fungus comes in three physiological races (1, 2 and 3) which is based on their pathogenicity on tester plants [23]. This disease causes great loss and reduction in tomato production globally, especially in warmer climates [24]. Fusarium wilt attack tomato plants at any growth stage, both under greenhouse and field conditions [25]. Control of this disease with fungicide has come with limitations and adverse effects like mammalian toxicity due to chemical residue, environmental pollution and lack of technical know-how. Therefore, the best way to control this disease is to develop improved varieties that are host-resistant for optimum tomato production and improve food and economic security for tomato farmers in Nigeria.

2.1.3 Bacterial wilt

Bacterial wilt (BW), caused by *Ralstonia solanacearum* (race 1 biovar 3), is one of the most devastating plant pathogenic bacteria [26]. *Ralstonia solanacearum* has a large host range comprising more than 200 plant species which include major crops such as tomato, potato and banana [27]. *Ralstonia solanacearum* is a soil-borne bacterium that enters plant roots, invades xylem vessels and spreads rapidly to parts of the plant through the vascular system where its high level of multiplication leads to wilting symptoms and ultimately plant death [28]. The bacterial wilt disease can cause up to 80% yield losses in tomatoes [29, 30]. Furthermore, BW disease has been associated with small fruit weight, bitter flavor, susceptibility to root-knot nematodes and other negative traits [31]. Temperature and soil moisture are the most important factors affecting host-pathogen interactions [32]. Maximum incidence of bacterial wilt of tomato has been reported at soil temperature of 30–35°C and soil moisture of 90% [33]. In addition to its lethality, the ability of *R. solanacearum* to survive in soils for many years and to form latent infections within indigenous weeds contributes to the difficult eradication of the bacterium [34]. Integrated strategies for the control of *R. solanacearum* are complex and involve chemical control which are potentially harmful to the environment and are not efficient to eradicate *Ralstonia solanacearum* species complex (RSSC). An alternative control strategy is to use biological control agents such as antagonistic bacteria or avirulent mutants of RSSC, but the promising results obtained under controlled conditions were not confirmed in the field [35]. Host resistance is the single most effective management strategy associated with BW and planting resistant cultivars is the cheapest, simplest and most environmentally friendly approach to limit losses [36]. Induction of systemic resistance by plant growth promoting rhizobacteria (PGPR) has been investigated as a possible practical way to use induced resistance in agriculture.

2.1.4 Overview of viruses of tomato Solanum lycopersicum L. in Nigeria

Worldwide, increase in the incidence of viral diseases of tomato has retarded the production of tomato. Most of these viruses are spread by insects such as whiteflies, beetles, aphids, thrips and leafhoppers, but some are spread mechanically through exposure of plant wounds to the infected sap. Tomato infecting viruses lead to various symptoms such as abnormal color patterns on leaves and fruits, irregular growth, stunted plants, decreased yields and even plant mortality [37]. In Nigeria, multiple viral diseases affecting tomatoes exist, either singly or in combination. Control strategies have been largely ineffective because of the tendency of the viruses to mutate at a high rate resulting in high genetic heterogeneity and increasing the ability of the viruses to spread fast. Numerous viruses infecting tomatoes have the ability to affect

Virus Species	Acronym	Genus	Family	Transmission
Tomato mosaic virus	ToMV	<i>Tobamovirus</i>	<i>Virgaviridae</i>	Mechanically, seeds, water and soil
Tobacco mosaic Virus	TMV	,	,	Mechanically, seeds, water and soil
Pepper mild mottle virus	PMMV	,	,	Mechanically
Tomato leaf curl virus	TLCV	<i>Begomovirus</i>	<i>Geminiviridae</i>	Whiteflies
Tomato yellow leaf curl virus	TYLCV	,	,	Whiteflies
Pepper yellow vein virus	PepYVV	,	,	Whiteflies
Betasatellite	DNA-β	<i>Betasatellite</i>	<i>Tolecusatellitidae</i>	Whiteflies
Tomato spotted wilt virus	TSWV	<i>Orthospovirus</i>	<i>Tospoviridae</i>	Thrips
Potato virus Y	PVY	<i>Potyvirus</i>	<i>Potyviridae</i>	<i>Myzus persicae</i> and other aphid species
pepper veinal mottle virus	PVMV	,	,	<i>Myzus persicae</i> and other aphid species
pepper mottle virus	PepMoV	,	,	<i>Myzus persicae</i> and some other aphid species
Cucumber mosaic virus	CMV	<i>Cucumovirus</i>	<i>Bromoviridae</i>	Seeds, <i>Myzus persicae</i> , <i>Aphis gossypii</i> and some other aphid species
Tomato aspermy virus	TAV	,	,	<i>Myzus persicae</i> and <i>Aphis gossypii</i>
Alfafa mosaic virus	AMV	<i>Alfamovirus</i>	,	<i>Myzus persicae</i> and some other aphid species
Tomato bushy stunt virus	TBSV	<i>Tombusvirus</i>	<i>Tombusviridae</i>	Seeds, pollen, propagative material, soil and water
Tomato Ringspot Virus	ToRSV	<i>Nepovirus</i>	<i>Secoviridae</i>	Mechanically. vegetative propagation, seeds and pollen
Tomato black ring virus	TBRV	,	,	<i>Longidorus</i> spp.

Table 1.
 Viruses associated with tomato in Nigeria.

a variety of other plant species. Emerging or re-emerging viral diseases of tomatoes in Nigeria along with their respective causative agents are presented in **Table 1** [38–40].

3. Control measure

Efforts to control the insect vectors using insecticides have typically been ineffective in mitigating virus diseases [41] as viruses exploit the resources of host plants

to reproduce. Identifying and eliminating the unique proteins in the tomato plant, utilizing the biological characteristics of the virus along with an RNAi approach, could serve as a potential method for control in the future [37]. Integrated pest management (IPM) strategy comprising the use of certified virus-free seeds and adequate field hygiene management, early detection and removal of symptomatic plants are essential to help reduce virus diseases. Planting of resistant variety is still the best option in the management of viral diseases [41].

3.1 Abiotic stresses: Heat and drought tolerance

Abiotic stresses caused by environmental factors adversely affect the growth and development of crops and crops respond with various modifications at morphological, cellular, physiological, biochemical and molecular level [42]. Among the abiotic stresses, drought and heat stress are two critical threats to crop growth and sustainable agriculture worldwide. Drought stress is as a consequence of insufficient rainfall or deficient soil moisture while heat stress is due to global warming which has consistently led to increase in temperature. Considering global climate change, incidence of combined drought and heat stress is likely to increase [42, 43]. Severe growth and yield reduction are imminent with increase in temperature and water deficit unless adaptation strategies are implemented. Consequently, heat stress and drought stresses reduce tomato productivity in the tropical and subtropical regions where tomato is mainly grown under open field-condition where growing conditions cannot be controlled [44, 45].

3.2 Ripening and postharvest losses

Tomatoes are a highly nutritious and economically valuable crop; however, significant post-harvest losses render the value chain unprofitable, negatively affecting food quality, pricing, and market competitiveness [46]. Fresh tomato losses are predicted to be about \$8.9 billion yearly due to huge post-harvest spoilage that result in the reduction of household income [18]. Postharvest losses are the resulting quantitative and qualitative losses, and food waste occurring from the point of harvest through to the final consumption stage [47]. Physiological changes, such as ripening, that continues after harvest can result in spoilage, reduced processing suitability and increased vulnerability to fungal and bacterial infections, thereby exacerbating post-harvest losses and diminishing the quality of produce available for value addition. Ripening in tomato involves a number of biochemical, morphological and physiological activities, including softening, pigment change, development of flavor components, autocatalytic ethylene production and climacteric respiratory behavior, which work together to make fruits ripen [48, 49]. The extent of fruit softening determines the shelf-life, palatability, resistance to post-harvest pathogen infection, consumer acceptability and stability during storage and transportation [50]. Ripening is, therefore, a major determinant of fruit quality and shelf-life of climacteric fruits like tomato, and the modification of the process may offer the opportunity of breeding new genotypes and phenotypes to enhance fruit quality and shelf-life. The improvement of fruit shelf life through the alteration of the ripening process has been investigated by many scientists in the past decades using conventional breeding and genetic modification. Biotechnology has made considerable progress in modifying metabolic pathways that delay the tomato ripening process and discovering complex networks of transcription factors that regulate ripening [50, 51]. The potential of known tomato ripening mutant genes to prolong the shelf life of tomato are also

being explored [52]. However, these mutant genes may produce undesirable pleiotropic effects on other components of tomato fruit quality [53] in the homozygous state, but in the heterozygote form, they develop acceptable color for marketing, ripe naturally and exhibit extended shelf life too [49]. The first genetically modified product approved for commercial cultivation by the United States (US) by the Food and Drug Administration (FDA) in 1994 was the transgenic “*flavr savr*” tomato modified to slow down the ripening process and reduce fruit softening after harvest. Products of genetic modification have, however, continued to experience the skepticism of consumers [54] and unstable government policies. However, the availability of genome editing tools offers new opportunities to overcome these drawbacks. The goal for tomato breeders is to specifically control the fruit softening process in tomato, while maintaining other aspects of its normal ripening.

4. Advances in breeding for resilience to biotic and abiotic stresses

4.1 Improving tomato for resistance to Fusarium wilt

Fusarium wilt is a major problem to tomato cultivation in Nigeria. The National Horticultural Research Institute (NIHORT) has been engaged in developing resistant varieties with increased yield and desirable fruit quality.

A total of 30 tomato lines were screened for resistance to Fusarium wilt, and selected 16 lines were selected for further analysis. F₁ hybrids generated using North Carolina II mating design of the parental lines were challenged with Fusarium wilt inoculum in the screenhouse. Pure line selection method was employed to advance from F₂ to F₆ generation. About 14 lines were selected and evaluated in on-station (three locations) trials while three lines were selected for on-farm (10 locations) trials under open field conditions. Additionally, evaluations on the nutritional and disease reactions for these lines were also carried out. During on-farm trial, a commercial check and farmers’ variety were added, making five tomato lines evaluated.

The result in **Table 2** shows HORTITOM3 had the highest fruit yield (25.93 t/ha) under disease infestation followed by HORTITOM1 (25.51 t/ha) and HORTITOM2 (24.17 t/ha). HORTITOM3 had the lowest disease incidence (5.84%) followed by HORTITOM2 (10.07%), while the farmers’ variety was the most susceptible with a mean incidence of 35.66%. Following all statutory evaluations of the improved lines, HORTITOM1, HORTITOM2 and HORTITOM3 (**Figure 1**) were registered and released in Nigeria in January 2023 as Fusarium wilt-resistant varieties.

Entry	Genotype	Yield (t/ha)	Disease incidence (%)	Rating
1	HORTITOM1	25.51	13.39	MT
2	HORTITOM2	24.17	10.07	MT
3	HORTITOM3	25.93	5.84	T
4	ONITYRE	21.35	28.32	S
5	FARMERS’ VAR.	17.37	35.66	S

MT = moderately tolerant; T = tolerant; S = susceptible.

Table 2.
Performance of improved tomato lines for yield and disease infestation.

**Figure 1.**

Three new tomato varieties having resistance to *Fusarium wilt*, released by NIHORT in Nigeria.

5. Efficacy of plant growth promoting rhizobacteria in the control of bacterial wilt of tomato in Southwestern Nigeria

Induction of systemic resistance by plant growth promoting rhizobacteria (PGPR) has been investigated as a possible practical way to induce host plant resistance to diseases in agriculture. The results on the use of PGPR formulation provided evidence that commercial PGPR formulations (Bioyield and Equity) reduced bacterial wilt incidence significantly in the screen house and field on Ibadan local (Ib) and 62-T/563/JM94/62 (JM96/62) cultivars of tomato [55]. Both formulations have biological organisms that have been shown to be effective in managing various diseases in several crops [56]. Bioyield contained spores of bacterial strains, which have been found to influence plant growth in tomato, cucumber, tobacco and pepper [57], while Equity has more than 40 beneficial strains of bacilli involved in the production of plant growth regulators and polysaccharides [56]. Colonization of the emerging root by the biocontrol agents might have prevented the *Ralstonia solanacearum* from gaining entry into the host and progressing into the vascular bundle. In the screen house trial, PGPR formulations had significant effect on the wilt incidence, severity and growth of tomato. Bacterial wilt incidence was reduced to 53.3% at 4WAT with application of Equity as compared with 80% in the control. Disease severity reduced from

Treatment	Incidence (%)							
	2003				2004			
	4 WAT	6 WAT	8 WAT	10 WAT	4 WAT	6 WAT	8WAT	10 WAT
By +62	26.5a	26.5a	43.3b	79.0ab	30.5a	39.9b	61.0d	66.3c
By + Ib. l	11.6ab	11.6ab	47.8b	79.4ab	12.3c	21.6c	44.2c	50.0d
Eq + 62	1.0b	1.0b	28.2b	89.0a	20.9abc	35.4b	73.0c	78.2b
Eq + Ib. l	1.0b	10.8ab	29.2b	69.3b	22.7ab	57.8a	81.2b	84.8ab
62	1.0b	10.8ab	45.0b	89.0a	13.4c	35.0b	62.7d	67.8c
Ib.l	21.5a	21.5ab	89.0a	89.0a	26.7a	64.0a	89.4a	89.4a

Means followed by the same letter in the same column do not differ at $P < 0.05$ using DMRT. By-Bioyield; Eq-Equity; Ib-Ibadan local; 62-T/563/JM94/6.

Table 3.

Effect of growth promoting rhizobacter (PGPR) on the incidence of bacterial wilt of tomato.

Treatment	Fruit no/plot	2003		2004	
		Fruit wt/plot	Fruit no/plot	Fruit wt/plot	
By + 62	7.0c	15740	24.0c	472.7c	
By + Ib. l	16.5b	505.3b	53.0a	1659.3a	
Eq + 62	38.0a	1240.1a	8.3d	1160.4d	
Eq + Ib. l	18.5b	598.7b	8.7d	126.4d	
62	20.0b	696.6b	39.0d	1012.3d	
Ib.l	4.0c	147.4c	2.7e	54.5e	

Means followed by the same letter in the same column do not differ at $P < 0.05$ using DMRT.
By-Bioyield; Eq-Equity; Ib-Ibadan local; 62-T/563/JM94/62.

Table 4.
Effect of growth promoting rhizobacter (PGPR) on fruit number and yield of tomato.

3.7 to 2.0 and plant height was also enhanced with Equity and the combination of the two formulations in the screenhouse. Reduction in wilt incidence (46.7%) as compared to 84.9% in the control was achieved on the field in 2004. Field trials showed that PGPR treatments reduced wilt incidence of both tomato cultivars (**Table 3**). Higher yields were recorded on Equity treated cultivar JM94/62 in 2003, while Ibadan local plants treated with Bioyield recorded the highest yield in 2004 (**Table 4**). The combination of the bacilli strains in Equity may account for a lower wilt incidence observed and also positive effect on growth of tomato plants. Additional studies are needed to either identify indigenous PGPR strains for better disease control or incorporate these PGPR into other complimentary plant protection strategies to achieve a sustainable control of wilt in Nigeria.

6. Efforts to improve tomato resilience to *Tuta absoluta* in Nigeria

Following the recent devastating report of *Tuta absoluta* on tomato in Nigeria by Oke et al. [58]; its distribution has been reported in 41 out of the 54 African countries [59] and confirmed by Aigbedion [60] across nine major tomato-producing states in Nigeria. A survey of its natural enemies in Jigawa, Kaduna, Kano and Katsina states identified 10 species of predators belonging to the order Hemiptera and Hymenoptera with *Nesidiocoris tenuis* and *Dicyphus errans* reported as most abundant. Also observed were seven larval hymenoptera parasitoids and egg parasitoids of the genus *Trichogramma* [61, 62]. This information is important in the development of biological control programs and integrated pest management (IPM) strategy for the control of this serious pest.

Chlorantraniliprole and lambda-cyhalothrin were recommended and extensively used for the control of *T. absoluta* all over Nigeria during the early invasion; afterward, control failure was reported with resistance ratio ranging from 4.09 to 16.97 times from seven major tomato-producing areas of Nigeria. Also, lambda-cyhalothrin (resistance ranging from 2.66 to 7.88 times) and deltamethrin (resistance ranging from 2.23 to 6.24 times) were reported [18]. In the greenhouse, the integration of indigenous water + light trap (which trapped mean of 14,164.7 adult *T. absoluta* within 6 weeks), hygiene practices, and six rotational applications of four insecticides: imidacloprid, lambdacyhalothrin, acetamiprid + lambdacyhalothrin and novaluron



Figure 2.
NIHORT IPM: NIHORT-Lyptol; NIHORT-Raktin; NIHORT-Tuta trap tray [18].

S/n	Treatment	Insecticide application time	Mean number of larvae/leaflet	Percentage fruit damage
1	Russell IPM (exotic)	6	1.1 ± 0.5c	18.9c
2	NIHORT IPM (indigenous)	6	1.8 ± 0.3c	24.2c
3	Farmer's practice	19	3.9 ± 0.3b	63.7b
4	Control	0	5.8 ± 0.4a	100a

Table 5.
The efficacy of exotic and indigenous integrated pest management (IPM).

+ bifentrin – proved to be the more effective option in achieving sustainable, effective control of *T. absoluta* [58]. Furthermore, open-field studies conducted in Kano, Kaduna, Katsina, Jigawa and Plateau states of Nigeria revealed that the combination of NIHORT IPM: NIHORT-Lyptol, NIHORT-Raktin and NIHORT-Tuta trap tray (**Figure 2**) compared efficiently with Russell IPM: Recharge, Antario, and Biotrine. Both IPM were more efficient in controlling *T. absoluta* than farmer's practice of 19 applications of pyrethroids, chlorantraniliprole, flubendiamide and spirotetramat (**Table 5**) [6].

Normal fertilization + twice weekly irrigation regimes are critical for tomato growth and the production of flowers which also provides a favorable condition for reproduction of *T. absoluta*. However, proper management and a balanced application of biocontrol will curb its devastation and consequently producing safe tomato fruits [63]. Desneux et al. [64] reported that until further research interventions lower costs associated with biological and biotechnological control techniques and address control failures by chemical pesticides, challenges for global tomato production will remain.

6.1 Improving tomato resilience for tolerance to heat stress

Recent rise in temperature being experienced globally as a result of climate change threatens crop production and productivity. High temperatures negatively affect reproductive organs development of plants, inducing flowers abscission and poor

fruit setting which results in low yield. Optimal temperatures for tomato production range from 21 to 29.5°C (day) and 18.5 to 21°C (night) while day and night temperatures above 29.5 and 21°C, respectively, are detrimental to the optimal growth and reproductive development of tomato [44, 45]. Breeding heat tolerant tomato varieties is critical to meeting the challenges of high temperature resulting from climate change especially in regions where farmers cannot afford to grow tomatoes in temperature-controlled greenhouses. The success of breeding efforts depends on efficient characterization and evaluation of a wide range of germplasm with the aim to identify new sources of heat tolerance that can serve as putative parents for introgressing beneficial alleles to improve cultivated tomato lines. Breeding efforts to develop thermotolerant tomato varieties with desirable fruit yield and quality have commenced in NIHORT.

6.2 Screening of tomato germplasm for sources of heat stress (HS) tolerance

A total of 115 lines were evaluated which included improved lines from the World Vegetable Center (AVRDC), Taiwan, the Tomato Genetics Resource Center (TGRC) of the University of California, Davis, USA and germplasm from genebank of the National Horticultural Research Institute (NIHORT), Ibadan, Nigeria. The lines were screened for their response to long-term mild heat stress in the greenhouse and field of NIHORT from February – April 2023. Plants were nursed in trays and transplanted to the soil in the greenhouse after 4 weeks. Data were recorded on the number of days to the first flower, number of flowers and number of fruits per truss. Data analysis was conducted on 28 lines which survived the screening by flowering and setting fruit. Normality of the collected data were carried out using Shapiro Wilk test for normality before analysis, and appropriate transformation method was used to normalize the variables. Hierarchical clustering was performed in FactoMiner, and dendrogram was drawn in the Factoextra package in R [65].

6.3 Performance of tomato germplasm under heat stress

Many of the tomato plants exhibited severe flower abortion, which negatively affected fruiting of many of the lines because an average temperature of $48.3 \pm 3^\circ\text{C}$ was recorded in the study, which was higher than $30 \pm 3^\circ\text{C}$ [45]. A total of 28 lines however, showed a level of tolerance and were able to set fruits although with limited seed set. Hierarchical clustering grouped the lines into two main clusters (**Figure 3**) with cluster 2 having the largest number of tomato lines in it. Cluster 2 is further divided into three sub-groups (I, II and III). Characteristics of the clusters are shown in **Table 6**. All the lines in cluster 2 were from the World Vegetable Center and were characterized with a high number of flowers. Entries in clusters 1 and 2- IIA and IIB showed no fruit set even though they flowered. This could be as a result of high temperature and that most of the lines possessed exerted stigma. This condition resulted in asynchrony with pollen release and stigma receptivity, and also, the exerted stigma is very sensitive to heat which led to burning at their exposure to high temperature [45, 66]. From this study, only one entry in cluster 2-III was found to set fruit under heat conditions.

Thus, the development of heat tolerance depends on combining different sources of genes for heat tolerance and good fruit quality. Line development can, therefore, be carried out within each cluster to develop heterotic groups. Parents can be selected across clusters to generate parents to develop populations that combine heat tolerance with good fruit quality. For example, PJ76 and PJ 3 belonging to different clusters can

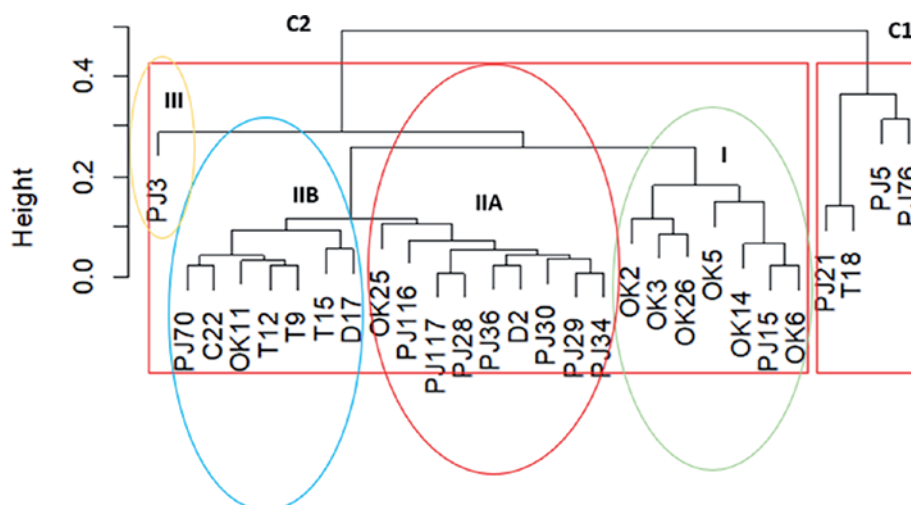


Figure 3.
Dendrogram showing diversity of tomato germplasm for heat tolerance.

Traits	Cluster 2			
	Cluster I	Cluster IIA	IIB	III
Number of days to first flower	46.25 ± 5.75	58.63 ± 1.37	53.57 ± 1.43	46
Number of flowers	33.25 ± 6.75	3.5 ± 3.5	5.86 ± 8.14	11
Number of fruits	—	—	—	2

Table 6.
Heat stress characteristics of clusters in a collection of 28 tomato genotypes.

be used by parents in hybridization to develop progenies with higher heterosis for important agronomic traits such as flower set, fruits per plant and fruit weight under heat conditions.

7. Mutagenic effects of colchicine on the morphology and yield of three Nigerian tomato (*Solanum lycopersicum* L.) accessions

Mutation breeding technology has proved to be one of the effective ways of crop improvement. The use of chemical mutagens like colchicine, has proved to be an efficient and effective tool for the improvement of the quality and yield of imported tomato variety (Roma VF), thus indicating the possibility of isolating beneficial mutants with indigenous genotypes [67]. Colchicine is a powdery mutagenic agent used for inducing polyploidisation and inhibiting mitotic process for crop improvement [68]. In nearly three decades, no new tomato variety has been released in Nigeria [69]. The mutagenic effect of colchicine on the morphology and yield of three tomato accessions NG/MR/May/09/005-SouthWest (SW), NG/SA/07/10/002-NorthEast (NE) and NG/CHU/Jun/0201-SouthEast (SE) was investigated [70]. Seeds were pre-soaked in four different concentrations of colchicine (0.1, 0.3, 0.5, and 1.0 mM) with untreated seeds as control. The experiment was laid out in randomized complete block

design in five replications. The mutants produced were characterized on the basis of morphological traits such as plant height, number of leaves per plant, leaf length, number of branches, number of days to first flowering, fruit weight, germination percentage and number of fruits per plant. The result obtained revealed a significant difference ($P < 0.05$) in some of the morphological traits assessed when compared with the controls, except in the number of branches and plant height where the effect of the mutagen was not significant ($p > 0.05$). Significant reduction in the mean number of days to first flowering was recorded in all the mutants with the value ranging from 65.0 days in 0.5 mM SW accession to 76.2 days in 1.0 mM SE accession when compared to the control (80.20 days). The morphological and yield parameters of the SW and NE accessions of tomato as observed in the study improved with decreasing concentration of colchicine, while that of the SE improved with an increase in the concentration of colchicine. The observed concentration that improved growth and yield parameters in SW and NE tomato accessions was 0.1 mM while 0.5 or 1.0 mM concentrations increased the same parameters in the southeast tomato accessions.

8. In vitro regeneration and genetic transformation of tomato

Plant tissue culture, initially developed to address fundamental questions in plant biology [71, 72], has become a cornerstone for genetic improvement, micropropagation, genetic engineering and biotechnology [73]. This technology encompasses cell, tissue, organ and embryo culture [74] and facilitates plant regeneration through two primary pathways: de novo organogenesis and somatic embryogenesis [75]. Both processes require dedifferentiation or trans-differentiation to achieve totipotency, ultimately altering the developmental fate of progenitor cells [75]. Tomato production in Nigeria faces challenges such as low yields, disease susceptibility and poor seed quality [76]. Tissue culture provides viable solutions, including the development of somaclonal variants, disease-free planting materials through meristem culture and as a precursor for gene transfer [77]. Globally, it has been used for biotic and abiotic stress tolerance [78], production of haploids [79], somatic hybrids and high-yield planting materials [76]. The approach also improves seed quality and availability, enhances crop uniformity and reduces genetic variability [80]. Additionally, transgenic tomatoes developed through tissue culture exhibit increased pest and disease resistance, reducing pesticide use [77].

In Nigeria, micropropagation methods have successfully generated tomato plants. In vitro regeneration protocols for three Nigerian cultivars—Ibadan Local (IbL), Ife, and JM94/46 (JM) were successfully established by [81]—using cotyledons as explants. The cultivars showed variable responses in the two media used. In the protocol consisting of an initial pre-culture medium made up of Murashige and Skoog (MS) with 1.0 mg L^{-1} naphthaleneacetic acid (NAA) and 1.0 mg L^{-1} 6-benzylamino-purine (BAP) and subsequent culture on shoot regeneration medium consisting of MS with 0.1 mg L^{-1} thiamine, 0.5 mg L^{-1} indoleacetic acid (IAA) and 0.5 mg L^{-1} zeatin, the cultivars did not produce any shoots. In a second medium containing MS, 0.1 mg L^{-1} indoleacetic acid (IAA) and 1.0 mg L^{-1} zeatin, shoots were produced in 64–97% of cultured explants. The protocols demonstrated that media composition critically affects regeneration success. The established in-vitro protocols were successfully applied to developing *Agrobacterium*-mediated transformation protocols for cv IBL, Ife and JM with the beta-glucuronidase (GUS) gene (**Figure 4**), demonstrating the amenability of the cultivars to genetic transformation [82].

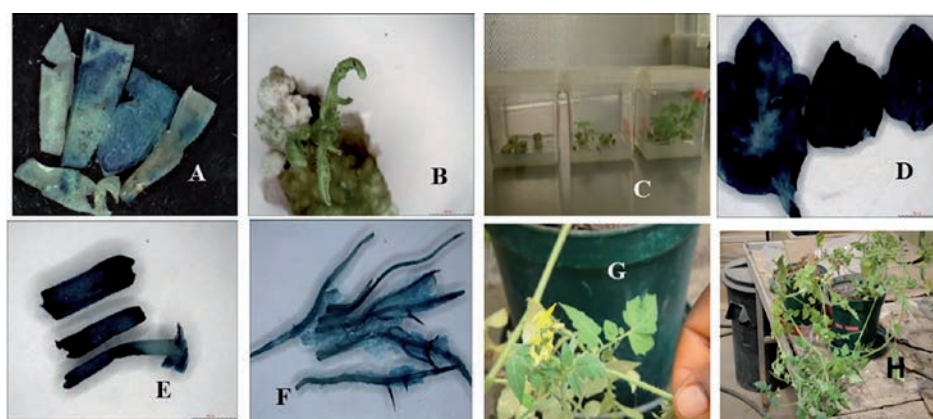


Figure 4.

(A) Positive GUS assay in leaf explant after 4d of co-cultivation. (B) Shoots from transgenic callus (3 wks in XSRM4) – Ife. (C) Seedlings from transgenic plants (6 wks in XSRM4). (D) GUS expression in leaves of independent transgenic plants (jbf). (E) GUS expression in stems – IbL (F) GUS expression in roots – Ife. (G) Flowering transgenic tomato plant. (H) Transgenic tomato plants. Key: b: Ibadan local; j: JM/94/46; f: ife. Ref. [82].

The *in vitro* regeneration of shoots from *S. lycopersicon* cv Beske shoots was reported by Durosomo et al. [83] on MS media supplemented with 2 mg/l Kinetin and 0.1 mg/l NAA with average shoot initiation values of 1.71, 1.57 and 1.57 and average root initiation values of 0.57, 0.00 and 2.85 for cotyledon, hypocotyl and leaf explants, respectively. The *in vitro* regeneration of three newly developed tomato varieties that are resistant to fusarium wilt, namely, Hortitom 1, Hortitom 2 and Hortitom 3 using cotyledon as explants for callus induction, shoot elongation and rooting was reported [84]. An initial germination medium consisting of Murashige and Skoog basal salts supplemented with 30 g L⁻¹ sucrose and no growth hormones was used for initiation of *in vitro* plants. Cotyledon leaves from *in vitro* plants were cultured on MS medium supplemented with 0.5 mg L⁻¹ IAA in combination with different concentrations of Zeatin and Benzylaminopurine (1.0, 2.0 mg L⁻¹ Zeatin; 1.0, 2.0 mg L⁻¹ BAP). Callus induction was significantly influenced by the variety and plant growth regulators (PGRs). The highest callus induction frequency (91.14%) was obtained on MS medium supplemented with 2.0 mg L⁻¹ Zeatin and 0.5 mg L⁻¹ IAA. Highest mean shoot derived from each calli (4.28 ± 0.63) was also observed in medium containing 2.0 mg L⁻¹ Zeatin and 0.5 mg L⁻¹ IAA (**Figure 5**). All the three cultivars studied had maximum callus induction frequency in MS supplemented with 2.0 mg L⁻¹ Zeatin and 0.5 mg L⁻¹ IAA. Murashige and Skoog medium supplemented with 1.0 mg/l IAA was used for root induction. Hortitom 2 and 3 had mean roots per shoot (15 and 14) and mean root length (7.06 and 10.50 cm), respectively. This was higher than the mean number of roots per shoot (12.75) and mean root length (6.25 cm) obtained for Hortitom 1. In similar studies on *in vitro* regeneration studies on local cultivars kerewa, carrot, *Hortitom 1*, *Hortitom 2*, *Hortitom 3* (*Hortitoms* obtained from NIHORT) and commercial cultivars UC82B, roma and sakata, varying degrees of success was achieved by Ajenifujah-Solebo et al. [unpublished data, 2024]. Seeds of six cultivars (*Hortitom 1*, *Hortitom 2*, *Hortitom 3*, *Roma*, *UC82B*, and *Carrot*) were surface-sterilized using 3.5 and 2.5% sodium hypochlorite (NaOCl) for 20 minutes, with 2.5% NaOCl showing more effective sterilization and higher germination rate across cultivars. Germination medium consisted of MS medium supplemented

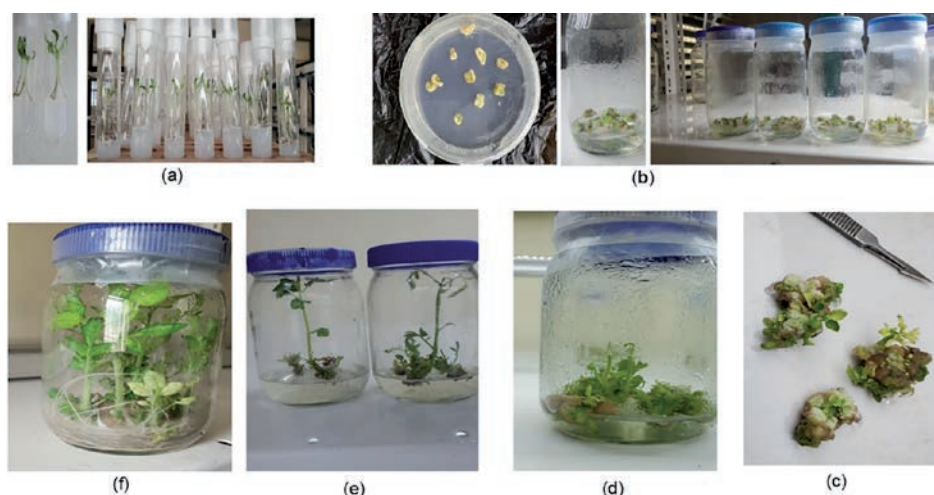


Figure 5.
In vitro regeneration of tomato cultivars Hortitom 1 and Hortitom 2 through indirect organogenesis. (a) *In vitro* germination. (b) Callus induction. (c) Callus regeneration. (d) Multiplication of seedling. (e) Shoot elongation. (f) Root induction.

with 30 g/L sucrose [85]. Cotyledon explants from *in vitro* germinated seedlings were excised into approximately $5 \times 5 \text{ mm}^2$ sizes and cultured on different shoot regeneration media (SRM A, B and C) for shoot or callus induction.

1. SRM A: MS + 0.1 mg/L IAA + 0.5 mg/L Zeatin Modified by Ajenifujah-Solebo et al., [81].
2. SRM B: MS + 0.1 mg/L IAA + 1.0 mg/L Zeatin [81]
3. SRM C: MS + 0.1 mg/L NAA + 2.0 mg/L Kinetin [83].

At 8 weeks after culturing (WAC), responses varied across the three shoot regeneration media (SRMs), showing differences in explant survival, shoot formation and callus induction (**Table 7**). SRM A demonstrated high explant survival rates, with *Hortitom 1* achieving the highest at 95%. Shoot formation ranged from 40% for *Roma* to 70% for *Hortitom 1* and *Hortitom 2*. Callus induction was minimal, with no callus observed in most cultivars. SRM A was the most effective medium for direct shoot regeneration. SRM B exhibited a broader range of explant survival rates, from 40% for *Hortitom 2* to 100% for *Roma*. Shoot formation rates were slightly lower than SRM A, ranging from 40% for *Hortitom 2* and UC to 70% for *Roma*. Callus induction was slightly higher compared to SRM A, with UC recording the highest at 15%, indicating a balance between shoot and callus formation. SRM C was characterized by the highest callus induction rates, with *Carrot* recording up to 75%. Explant survival rates ranged from 30% for *Hortitom 2* and *Hortitom 3* to 100% for *Roma*. However, shoot formation rates were the lowest among the three media, with the highest at only 25% for *Hortitom 1*. This medium was most suitable for callus formation but less effective for direct shoot regeneration. SRM A was, therefore, the most efficient for shoot induction, while SRM C promoted callus formation, with SRM B showing a moderate performance for both parameters.

Variety	Hormone combination	Percentage calli	Average shoot regeneration per calli
Hortitom 1	2 mg/l zeatin+0.5 mg/l IAA	91.14	4.28 ± 0.63
	1 mg/l zeatin+0.5 mg/l IAA	71.32	2.25 ± 0.45
	2 mg/l BAP + 0.5 mg/l IAA	82.12	2.25 ± 0.76
	1 mg/l BAP + 0.5 mg/l IAA	28.54	1.25 ± 0.45
Hortitom 2	2 mg/l zeatin+0.5 mg/l IAA	94.28	5.13 ± 0.7
	1 mg/l zeatin+0.5 mg/l IAA	85.04	3.05 ± 0.4
	2 mg/l BAP + 0.5 mg/l IAA	88.53	2.44 ± 0.8
	1 mg/l BAP + 0.5 mg/l IAA	35.50	1.70 ± 0.5
Hortitom 3	2 mg/l zeatin+0.5 mg/l IAA	87.43	4.03 ± 0.65
	1 mg/l zeatin+0.5 mg/l IAA	81.75	2.30 ± 0.35
	2 mg/l BAP + 0.5 mg/l IAA	76.31	2.09 ± 0.78
	1 mg/l BAP + 0.5 mg/l IAA	22.64	1.18 ± 0.41

Table 7.
In vitro response of tomato varieties to callus induction.

These studies are essential and contribute to the knowledge base on the amenability of the cultivars to *in vitro* regeneration and genetic manipulation for subsequent incorporation into tomato improvement breeding programmes in Nigeria. Despite its benefits, tissue culture adoption in Nigeria faces challenges, including high equipment costs [76], limited skilled personnel [77], inadequate infrastructure [80] and low awareness among farmers [76]. Overcoming these barriers is crucial to leveraging tissue culture's potential for improving tomato production and addressing food security challenges in the country.

9. Research and innovation landscape

The science, technology, and innovation policy of the Federal Ministry of Innovation, Science and Technology (FMIST) provides for innovative approaches to biotechnology research for agricultural productivity. On the strength of the above, it is imperative to foster, facilitate or enhance the adoption, application, and diffusion of biotechnology and genomics in agriculture with all its benefits, towards attaining food security in Nigeria. The National Biotechnology Development Agency (NABDA) is the focal institution with the mandate for research, promotion, coordination and deployment of modern biotechnology [86]. Established in 2001, the Agency supports sustainable development across the sectors of agriculture, health, industry, and the environment promoting biotechnology innovation and commercialization of biotechnology products for economic growth. It fosters sustainable utilization of biological resources, genetic resources conservation at the National Centre for Genetic Resources and Biotechnology (NACGRAB) and advocacy and establishes mechanisms for collaborative activities at national and international levels. Through partnerships with organizations like the African Union Development Agency, NABDA is advancing genome editing technology for agricultural research and academic programs. With due accreditation by the National Biosafety Management Agency (NBMA) to engage in modern biotechnology research, its collaboration with the National Horticultural

Research Institute (NIHORT) is focused on improving Nigerian tomato varieties with enhanced shelf life and resistance to bacterial wilt, leverages on biotechnology for sustainable development.

NIHORT has the national mandate to conduct research into genetic improvement, production, processing, storage, utilization and marketing of tropical fruits, vegetables, spices and ornamental plants of both nutritional and economic importance. NIHORT was established in 1975 by the Food and Agricultural Organization (FAO) as an agricultural research station and metamorphosed into a full-fledged horticultural research institute under the Federal Ministry of Agriculture and Food security with ARCN as the regulatory agency. NIHORT has since been engaged in basic and applied botanical, horticultural and biotechnological research, providing Science and Technology services in various sectors, spanning from plant resource identification, documentation, and conservation to bioprospecting through development of new biotech, microbial and agri-horticultural technologies, products and services for industrial use and societal benefits. NIHORT has a unique blend of expertise in classical and advanced plant breeding and biotechnology supported with state-of-art laboratories and infrastructures. NIHORT is one of the NBMA-accredited laboratories to carry out genome editing research in Nigeria. The institute has achieved several significant milestones in technology development in the domains of development of new crop varieties that are climate resilient, herbal health products, cosmeceuticals, microbial technologies and floral crafts in recent years. NIHORT has recently embarked on the use of genome editing to support conventional breeding efforts and to enhance horticulture crops production. Breeding and the rapidly growing field of genome editing will significantly boost the quantity and quality of horticulture crops.

Various tertiary academic institutions also contribute to tomato improvement research in the country.

10. Regulatory landscape

Transgenic crops provide complementary solutions to the limitations of traditional breeding. The crops are however subjected to strict regulations regarding their use, import, and export due to various socio-economic considerations. Ultimately, the potential for positive impact by transgenic foods in global food security is dependent on how the public and governing bodies view the technologies [87]. Currently, there are numerous concerns on the use of transgenic crops, both supporting and opposing. The availability of transgene-free, genome editing tools using site-directed nucleases (SDN) has opened a new vista in the field of agriculture. The multifaceted impact of gene-editing tools includes its benefits for human health (e.g., therapeutics, regenerative medicine), and opportunities to improve production qualities and disease resistance of crops and livestock.

The Nigerian regulatory landscape is robust with the necessary procedures and guidance instituted by the competent national authority, the National Biosafety Management Agency (NBMA). The NBMA was established in Nigeria in 2015 to provide regulatory guidance, and an institutional and administrative mechanism for safety measures in the application of modern biotechnology in Nigeria to prevent any adverse effect on human, animals, plants and environment and for related matters to ensure the safe and responsible application of modern biotechnology [88]. The Act was reviewed to make regulatory provisions for the application of gene drive, genome editing and synthetic biology research [89] in

the development of products and services for socio-economic development of the country. The amendment empowers the Agency in the strict regulation and monitoring of activities to prevent or mitigate any adverse effects associated with using genome editing technology on humans, animals, plants and the environment. The Agency, through the NBMA Act, has developed risk management plans and procedures through all stages of employing genome editing technology – from containment activities in the development of products, confined trials, to commercial release; including public awareness and socio-economic considerations. The regulatory provisions require institutions to obtain accreditation and facility certification to enable them to engage in modern biotechnology research and also submit an application on the specific projects being undertaken in the facilities. With the established procedures by the NBMA for the regulation of modern biotechnology and gene editing research, the country is positioned to make revolutionary strides.

11. Training and capacity building

Efforts to build biotechnology capacity in Nigeria have been bolstered through various initiatives involving local and international partnerships. Continuous capacity development in advanced biotechnology techniques is vital for fostering agricultural innovation and achieving global competitiveness. A strategic approach is needed to address knowledge and skills gaps across various stakeholders' groups including undergraduates, postgraduates and research professionals. This entails a phased plan with short term (workshop, seminars and webinars); medium term (short courses, hands on training) and long term (doctoral and postdoctoral fellowships) initiatives. These programs aim to enhance the skills and expertise of students and research scientists in their various institutions. Some of these include the following:

NABDA-ICGEB Collaborations: Nigeria's membership of the International Centre for Genetic Engineering and Biotechnology (ICGEB) provides access to cutting-edge research facilities and fellowships for Nigerian scientists, with NABDA as Liaison and affiliated Centre. These programs include PhD and postdoctoral opportunities, research grants and technology transfer initiatives to foster innovation and collaboration.

African Plant Breeding Academy (AfPBA): Since its establishment in 2011, AfPBA has trained over 161 African plant breeders representing 11 countries, including Nigerians, in advanced plant breeding techniques. Its specialized CRISPR course, coordinated by AOCC/UC Davis and other global partners, focuses on genome editing applications in crop improvement. Participants gain practical experience, including plasmid design and mutation validation, with an emphasis on developing gene-editing proposals for application in their home institutions.

AUDA-NEPAD Genome Editing Advocacy: Launched in Nigeria in 2022, this initiative promotes genome editing applications through stakeholder engagement, policy advocacy and the establishment of collaborative platforms. Study tours, capacity-building projects and a Community of Practice database support research and development across participating African countries.

H3ABioinformatics Network (H3ABioNet): As part of the H3Africa initiative, NABDA serves as a node for H3ABioNet in Nigeria, offering computational infrastructure, training and resources in bioinformatics. This program has significantly advanced genomic research, supporting African scientists in data analysis and capacity building.

Nigeria tertiary institutions: Offer graduate and post graduate programs in biotechnology-related disciplines. The innovative Core Curriculum Minimum Academic Standards (CCMAS) instituted by the National Universities Commission (NUC) provide a framework for standardizing and structuring university programs in Nigeria, blending theoretical knowledge with practical skills, and encourages the inclusion of emerging technologies, such as biotechnology in the curricula to ensure graduates are globally relevant.

These collective efforts, among several others, are shaping a robust biotechnology landscape in Nigeria, enhancing research capacity, promoting innovation, and addressing critical agricultural challenges.

12. Tomato CRISPR-Cas9 genome editing research in Nigeria

Agriculture remains a critical sector for economic development and food security in Nigeria. For tomato improvement, NABDA and NIHORT are championing biotechnology solutions, including CRISPR-Cas9 to address agricultural challenges and specifically to improve the tomato crop. Both institutions are building capacities and developing pipelines for genome editing research. The objective is to apply CRISPR-Cas9 genome editing to produce tomatoes with enhanced disease resistance and prolonged shelf-life without foreign genetic material. Nigeria has developed guidelines for gene editing, and crops produced by genome editing that do not contain any foreign DNA are regulated as those produced by conventional breeding or by natural mutation.

Genome editing offers the ability to make precise and targeted changes in the DNA of a cell or an organism using specific enzymes. The DNA of an organism can be altered and result in modifying traits similar to natural mutation. Several tools including meganucleases, zinc finger nucleases (ZFNs), TAL effector proteins (TALENs) and RNA-guided nucleases (RGENs) or CRISPR (clustered regularly interspaced short palindromic repeats)/Cas9 have been developed to target genome editing in plants and other organisms [90]. With genome editing, the DNA can be altered without the integration of any foreign gene into the genome; hence, the product is regulated as conventional. Using this method, several species of crops with interesting characteristics have been produced [91]. Among the genome editing techniques, CRISPR-Cas9 stands out as the most frequently used because of its efficiency, stability, ease of design, speed, cost-effectiveness, precision and ability to edit several genes at once. CRISPR-Cas9 genome editing has emerged as a transformative tool in global agriculture, enabling precise modifications of plant genomes to improve yield, pest resistance, modify some physiologic processes such as ripening and climate adaptability. CRISPR-Cas relies on creating double-stranded breaks (DSBs) at particular sites and activating DNA repair pathways via either non-homologous end joining (NHEJ) or homology-directed repair (HDR). The NHEJ pathway is a mechanism that is prone to errors, causing random insertions, deletions and substitutions (indels) at the cut sites, resulting in frameshift mutations and specific gene knockouts. On the other hand, the HDR process employs a similar DNA repair template to facilitate accurate genomic alterations, including gene knock-in, gene replacement and the insertion of foreign genes or DNA sequences. Based on the repair process, three kinds of editing results can be obtained: site directed nuclease 1 (SDN1), SDN2 and SDN3. SDN1 occurs when NHEJ induces random modifications in the gene, leading to changes in gene function or resulting in gene silencing or knockout. SDN2 utilizes a repair

template that aligns with the DSB, leading to specific indels or nucleotide replacement via HDR. SDN3 employs a more extended repair template compared to homologous sequences to fix the DSB, facilitating the precise insertion of foreign genes [90].

Multiple steps are involved in the gene-editing procedure using the CRISPR-Cas9 technique including designing of gRNAs, the introduction of CRISPR reagents into plant systems, transformation, and analysis of edits in the transformed lines. First, the reference genome for the crop to be edited is located; whole genome sequences for solanaceous crops (tomato, potato, pepper and eggplant) are available at: <https://solgenomics.net/>. Gene(s) of interest are identified, sequenced and ensured their proper alignment with the target genome. Next, the gRNAs are designed using several software such as CRISPR-P V2.0 [91, 92]. Then, a search for CRISPR vectors in plasmid repositories is done to assemble the gRNAs and CRISPR/Cas9 cassette [93]. The transformation vectors are introduced into the plant using either *Agrobacterium*-mediated transformation or biolistics.

12.1 Extending tomato shelf-life

The fragility and short shelf span of tomatoes facilitate wastage across the tomato value-chain in Nigeria. Inadequate logistics and storage facilities have further increased the wastage, resulting in considerable post-harvest losses of between 45 and 70% recorded for tomato in Nigeria [94]. These losses have resulted in increased levels of importation; in 2023, Nigeria's tomato imports increased significantly, with a 105% rise from the previous year [4] reduction in farmers' gross profit margin from ~80 to ~17% [95], thus discouraging local processing. In recent years, many processors have exited the market, primarily due to unavailability of fresh tomatoes [10]. In 2023, Nigeria imported tomato puree and paste from China 4105.3 tons, with Singapore and Italy supplying 208.9 tons and 162.6 tons, respectively [4]. Local cultivars of tomatoes in Nigeria have largely remained undeveloped despite available and documented technologies for improvement.

Fruit softening is a key component of the irreversible ripening process, contributing to the palatability necessary for frugivore-mediated seed dispersal. Maintaining firmness and shelf life in fruit has often involved in slowing down the rate of ripening, early harvesting and controlling atmospheres to limit respiration and ethylene synthesis, but these can reduce quality [96]. Understanding the genetic basis of fruit softening and ripening is central to improving shelf life and quality. Ripening-related textural changes are linked to cell wall metabolism, with key modifications including the breakdown of pectin and hemicelluloses, leading to reduced cell adhesion and cell wall swelling [97, 98]. Research aimed at extending the shelf-life of tomatoes using CRISPR-Cas9 technology to edit fruit ripening-related genes and associated cell wall-modulating proteins is ongoing at NABDA. The GRAS proteins, derived from three members of plant-specific family of putative transcription factors GAI (gibberellic acid insensitive), RGA (repressor of GAI), and SCR (scarecrow) [99], play a critical role in fruit development and growth. The expression of the *fruit shelf-life regulator* (*SIFSR*), identified as a novel GRAS gene, specifically increased during fruit ripening, but was significantly decreased in the tomato mutant *ripening inhibitor* (*rin*). The expression of multiple cell wall modification-related genes, PG (polygalacturonase), TBG (tomato β -galactosidase), CEL (cellulase), and XYL (β -D-xylosidase) reduced in *SIFSR*-RNAi tomato fruits, significantly enhancing fruit shelf-life [100]. Conversely, overexpression of *SIFSR* in mutant *rin* gave rise to upregulated expression of the same genes significantly shortening the fruit shelf-life (**Figure 6**).

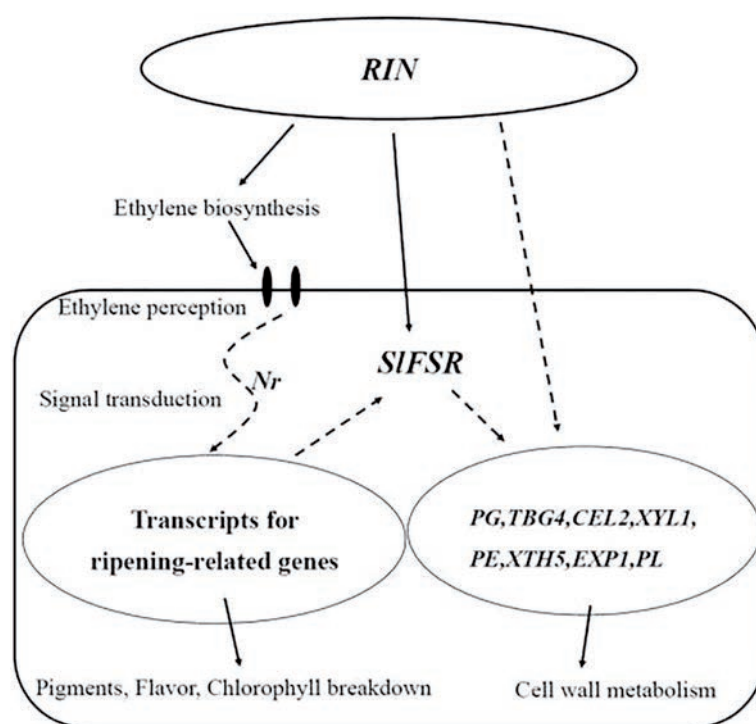


Figure 6.
 Proposed model of *SIFSR* gene function in tomato fruit shelf-life regulation [101].

Also, the tomato fruit ripening-specific *lateral organ boundaries* (LOB) TF, *SILOB1*, up-regulates a suite of cell wall-associated genes during late maturation and ripening of locule and pericarp tissues. *SILOB1* repression in transgenic fruit impedes softening, while overexpression throughout the plant under the direction of the 35 s promoter confers precocious induction of cell wall gene expression and premature softening. Finding alternative ways to extend tomato fruit shelf-life without reducing the quality is critical to ensure the accessibility and likeability of this commodity worldwide. Improving fruit firmness in tomato fresh-market varieties directly impacts their shelf-life potential. The on-going research is exploring single and simultaneous knock-out of *SIFSR* and *SILOB1* identified to regulate a suite of cell wall degrading enzymes to confer longer shelf-life characteristics to local tomato cultivars in Nigeria.

12.2 Developing tomato with bacterial wilt resistance

Management of bacterial wilt (BW) with pesticides is not a viable option because the pathogen survives in the soil for many years and has a wide host range [102]. Host resistance is the single most effective management strategy associated with BW, and planting resistant cultivars is the cheapest, simplest and most environmentally friendly approach to limit losses [36]. Many candidate genes conferring tolerance to biotic and abiotic stresses have been successfully manipulated by gene modification and editing techniques such as RNA interference, insertional mutagenesis and clustered regularly interspaced short palindromic repeat (CRISPR) associated protein 9 (Cas9) [103]. Hence, with the advent of CRISPR/Cas9 genome editing, fast and efficient breeding has become possible in tomato breeding.

Negative regulators of plant disease resistance, which may be considered host susceptibility (S) genes, represent good targets for genome editing. Susceptibility genes are utilized by the pathogen during colonization and infection. They are vital in meeting the pathogen's metabolic or structural requirements, contributing to sustenance and pathogen proliferation [100]. A characteristic of S genes is their conservation between species. In contrast to dominant resistance genes, loss of function of S genes can potentially lead to recessive inherited, broad-spectrum, and durable resistance [104]. It has been reported that the loss of function of S genes – Walls Are Thin 1 (WAT1) and Downy Mildew Resistance 6 (DMR6) – in tomato leads to high tolerance to genetically distinct strains of a broad spectrum of bacteria including the bacterial pathogen *Clavibacter michiganensis* (Cm) [105]. The function of WAT1 and DMR6 as S genes is possibly conserved across plant species and its loss of function can provide broad-spectrum resistance to vascular pathogens (**Figure 7**).

CRISPR/Cas9 has emerged as one of the most promising techniques for knocking out disease susceptibility genes in a variety of plants to increase tolerance/resistance to various diseases. This research leverages on using CRISPR/Cas9 technology to precisely edit key S genes such as Walls Are Thin 1 (WAT1) and Downy Mildew Resistance 6 (DMR6).

The following gene sequences SolWAT1 Gene ID – Solyc01g100890. 4.1 and SolDMR6 Gene ID – and Solyc03g080190.3 were downloaded from Sol genomics. Primers were designed, and the corresponding gene sequences were amplified

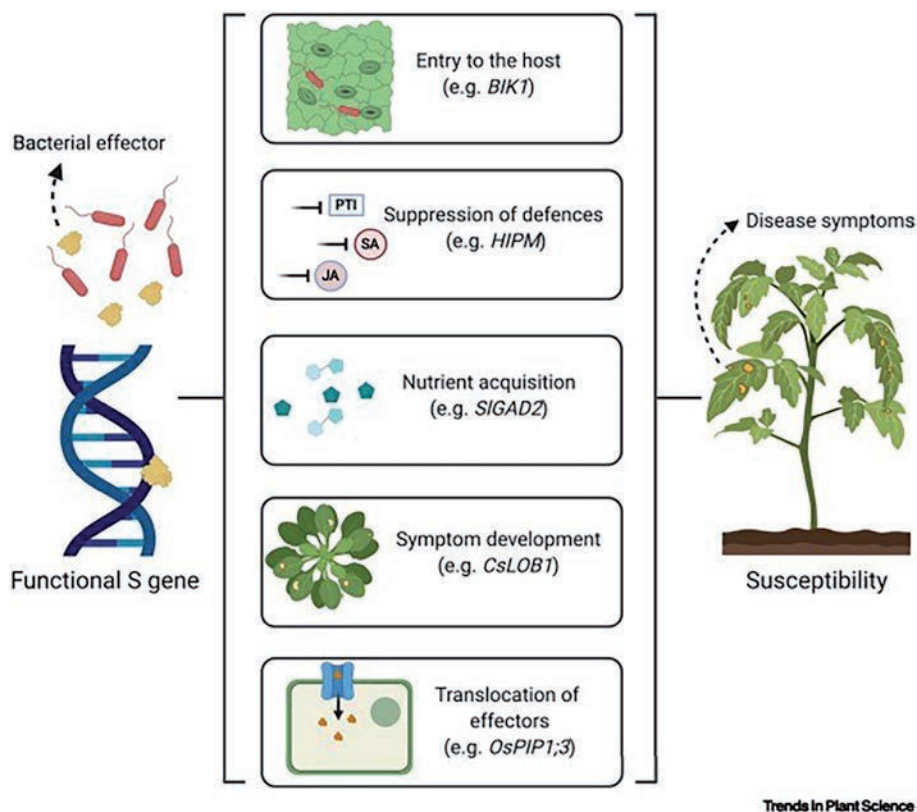


Figure 7.
Manipulation of plant susceptibility (S) genes by bacterial pathogens [106].

from the farmers preferred Nigerian tomato cultivars and sequenced. The sequences were aligned, and gRNAs were designed in the conserved regions and synthesized as oligos. The CRISPR-Cas9 construct is currently being generated and will be delivered to tomato cells by *Agrobacterium*-mediated genetic transformation. Plantlets will be generated, characterized by sequencing to check the type of edits. Edited events will be screened in the greenhouse for resistance to bacterial wilt. Events showing resistance will be backcrossed to produce foreign DNA-free plants. Thereafter, the foreign DNA-free events will be subjected to multi-location field trials. Promising lines will be selected and multiplied for distribution to farmers.

13. Recommendations

To advance tomato improvement in Nigeria, efforts should focus on optimizing and standardizing tissue culture protocols tailored to local cultivars. Available and referenced protocols, which demonstrated high shoot induction efficiency, should be refined further to enhance regeneration across various cultivars. Integrating gene editing techniques, such as CRISPR-Cas9, into established protocols will enable the development of pest-resistant, drought-tolerant, and high-yielding varieties. Infrastructure development is critical and may require the upgrade of existing facilities into regional plant biotechnology laboratories to support commercial applications and integrating it into national breeding programs, as well as fostering collaboration.

The ongoing CRISPR-Cas9 research to address challenges such as bacterial wilt resistance and extending shelf life should be supported with well-equipped laboratories and trained personnel. Strengthening collaborations among research institutions, biotechnology companies, international research bodies and farmers will accelerate the domestication and adoption of these technologies, thus facilitating knowledge exchange on advanced genome editing tools and technologies. Furthermore, the centralisation and proper management of existing repositories for genetic resources and protocols will enhance the efficiency and scalability in research and application.

Awareness campaigns and farmer engagement programs will be essential to promote the benefits of tissue-culture-derived plants, the safety and benefits of genome-edited crops, alongside policy interventions to increase funding, provide subsidies for equipment and incentivize private sector participation. Additionally, the existing gene-editing guidelines should be periodically reviewed to incorporate global advancements, ensuring advances in research and commercialization of genome-edited crops. These measures, combined with enhanced policy support and investment in infrastructure, will enhance the efforts aimed at improving tomato production in Nigeria.

14. Future directions

The integration of tissue culture with genetic engineering, marker-assisted selection and OMICS tools with conventional breeding techniques will revolutionize tomato improvement in Nigeria. Emphasis should be placed on breeding resilient varieties to meet the challenges of climate change for food security and sustainable

agriculture. Future directions should explore the simultaneous improvement of multiple traits in tomatoes, such as drought tolerance, pest resistance and improved nutritional content, leveraging the versatility of CRISPR-Cas9. Expanding research to include indigenous tomato varieties will also ensure that solutions are tailored to local needs and environmental conditions. Multi-location field trials and farmer-led participatory assessments will be critical for identifying and deploying high-performing, disease-resistant and shelf-stable tomato lines, contributing significantly to food security and agricultural sustainability in Nigeria.

Author details

Shakirat O. Ajenifujah-Solebo^{1*†}, Pamela E. Akin-Idowu^{2†}, Ayodeji O. Aduloju², Victoria O. Adediji¹, Esther T. Akinyode³, Dorcas O. Ibitoye², Olawale Arogundade², Abiola O. Oke², Esther A. Adesegun², Valentine O. Ntui⁴, Olalekan A. Akinbo⁵, Charles O. Adetunji⁶, Yetunde O. Falana¹, Roseline I. Joseph¹ and Firdaus Bello⁷

1 Genetics, Genomics and Bioinformatics Department, National Biotechnology Development Agency, Abuja, Nigeria

2 National Horticultural Research Institute, Jericho GRA, Idi-Ishin, Ibadan, Nigeria

3 Faculty of Agriculture, Ajayi Crowther University, Oyo, Nigeria

4 African Genome Centre, University Mohammed VI Polytechnic, Ben Guerir, Morocco

5 Bureau of the Chief Executive Officer, African Union Development Agency NEPAD, Midrand, South Africa

6 Applied Microbiology, Biotechnology and Nanotechnology Laboratory, Department of Microbiology, Edo University Uzairue, Edo State, Auchi, Nigeria

7 Crop Protection, Faculty of Agriculture, University of Abuja, Abuja, Nigeria

*Address all correspondence to: adetoyin73@yahoo.com

†Co-first authors

IntechOpen

© 2025 The Author(s). Licensee IntechOpen. This chapter is distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. 

References

- [1] FAOSTAT. Crops production quantity. 2022. Available from: <http://www.fao.org/faostat/en/#data/QC> [Accessed: December 23, 2024]
- [2] Ibrahim MA, Yerima AK, Badamasi S. A review of the problems of tomato value chain in Nigeria: Remedial option. *International Journal of Agriculture, Forestry and Fisheries*. 2020;8(3):90-95
- [3] Babadara J. Bending the curve of tomato loss can help Nigerian farmers reduce poverty. 2023. Available from: <https://cals.cornell.edu/news/2023/06/bending-curve-tomato-loss-can-help-nigerian-farmers-reduce-poverty>
- [4] Indexbox. Nigeria-Tomato purée and paste: Market analysis, forecast, size, trends and insights. 2025. Available from: https://www.indexbox.io/search/tomato-puree-price-nigeria/?utm_source=chatgpt.com [Accessed: January 01, 2025]
- [5] Food and Agriculture Organization (FAO). *Tomato Production in Nigeria: Challenges and Opportunities*. FAO; 2020
- [6] FAO. *The State of Food and Agriculture. Moving forward on food loss and waste reduction*. Rome; 2019. Licence: CC BY-NC-SA 3.0 IGO
- [7] World Bank. *Gender and Agriculture: Empowering Women in the Nigerian Tomato Value Chain*. World Bank Publications; 2021
- [8] Ogbonna PE, Akinbile LA, Ayinde IA. Analysis of tomato production in Nigeria. *Agricultural Sciences*. 2018;9(3):123-130
- [9] Adegbite E, Adu-Dapaah H, Osei MK, Adjebeng-Danquah J, Nketia SO, Antwi-Boasiako A, et al. Perspective chapter: Accelerating demand-led tomato breeding for emerging markets in Africa. In: *Tomato-from Cultivation to Processing Technology*. London, UK: IntechOpen; 2022
- [10] PricewaterhouseCoopers Nigeria Limited. *X-Raying the Nigerian Tomato Industry Focus on Reducing Tomato Wastage*. Nigeria; 2018. Available from: <https://www.pwc.com/ng/en/assets/pdf/nigeria-tomato-industry.pdf> [Accessed: January 05, 2025]
- [11] Mohammed US, Umaru I, Zango IT. Assessment of tomato production in northern Nigeria. *Journal of Agricultural Extension*. 2020;24(2):132-140
- [12] Olaniyan AM, Ojo MA, Akande EA, Adeleke AO. Post-harvest losses in tomato production: Causes and control strategies. *Journal of Postharvest Technology*. 2019;7(3):10-18
- [13] Technoserve. How is climate change affecting post-harvest loss in Nigeria?. December 2024. Available from: <https://www.technoserve.org/blog/how-is-climate-change-affecting-post-harvest-loss-in-nigeria/> [Accessed: September 2020]
- [14] Food and Agriculture Organization (FAO). *Hand in Hand Investment Forum: Nigeria Investment Plans and Opportunities*. 2024. Available from: <https://www.fao.org/hand-in-hand/hih-IF-2024/nigeria/en> [Accessed: August 04, 2024]
- [15] National Biosafety Management Act. 2015. Available from <https://nbma.gov.ng/nbma-act/> [Accessed: January 01, 2025]
- [16] Umeh VC, Kuku FO, Nwanguma EO, Adebayo OS, Manga AA. A survey

of insect pests and farmers' practices in the cropping of tomato in Nigeria. *Tropicultura*. 2002;**20**:181-186

[17] Mailafiya DM, Degri MM, Maina YT, Gadzama UN, Galadima IB. Preliminary studies on insect pest incidence on tomato in Bama, Borno State, Nigeria. *International Letters of Natural Sciences*. 2014;**5**:45-54

[18] Oke OA, Oladigbolu AA, Hamisu HS. Evaluation of resistance and toxicity of different insecticides on *Tuta absoluta* Meyrick populations in major tomato growing states of Nigeria. In: Niassy S et al., editors. *Sustainable Management of Invasive Pests in Africa, Sustainability in Plant and Crop Protection*. Vol. 14. Chapter 4. 2020. pp. 45-56. DOI: 10.1007/978-3-030-41083-4_4

[19] Harvey JA, Tougeron K, Gols R, Heinen R, Abarca M, Abram PK, et al. Scientists' warning on climate change and insects. *Ecological Monographs*. 2023;**93**:e1553

[20] Nie PC, Yang RL, Zhou JJ, Dewar Y, Shang SQ. Elucidating the effect of temperature stress on the protein content, total antioxidant capacity, and antioxidant enzyme activities in *Tetranychus urticae* (Acari: Tetranychidae). *Insects*. 2023;**14**:429

[21] da Silva Krechemer F, Foerster LA. *Tuta absoluta* (Lepidoptera: Gelechiidae): Thermal requirements and effect of temperature on development, survival, reproduction and longevity. *European Journal of Entomology*. 2015;**112**(4):658-663. DOI: 10.14411/eje.2015.103

[22] Zhou J, Luo W, Song S, Wang Z, Zhu X, Gao S, et al. The impact of high-temperature stress on the growth and development of *Tuta absoluta* (Meyrick). *Insects*. 2024;**15**:423. insects15060423

[23] Biju VC, Fokkens L, Houterman PM, Rep M, Cornelissen BIC. Multiple evolutionary trajectories have led to the emergence of races in *Fusarium oxysporum* f.sp. lycopersici. *Applied and Environmental Microbiology*. 2017;**83**:e02548

[24] Blancard D. *Color Atlas of Tomato Disease: Observation, Identification and Control*. London: Wolfe Publishing Limited; 1994. p. 212

[25] McGovern RJ. Management of tomato disease caused by *Fusarium oxysporum*. *Crop Protection*. 2015;**73**:78-92. DOI: 10.1016/j.cropro.2015.02.021

[26] Fegan M, Prior P. In: Allen C, Prior P, Hayward AC, editors. "How Complex Is the *Ralstonia solanacearum* Species Complex?" in *Bacterial Wilt Disease and the Ralstonia solanacearum Species Complex*. Saint Paul, MN: APS Press; 2005. pp. 449-461

[27] Hikichi Y, Mori Y, Ishikawa S, Hayashi K, Ohnishi K, Kiba A, et al. Regulation involved in colonization of intercellular spaces of host plants in *Ralstonia solanacearum*. *Frontiers in Plant Science*. 2017;**8**:96-97

[28] Genin S. Molecular traits controlling host range and adaptation to plants in *Ralstonia solanacearum*. *The New Phytologist*. 2010;**187**:920-928. DOI: 10.1111/j.1469-8137.2010.03397.x

[29] Elphinstone J. The current bacterial wilt situation: Global overview. In: Allen C, Prior P, Hayward AC, editors. *Bacterial Wilt Diseases and the Ralstonia solanacearum Species Complex*. St. Paul, MN: American Phytopathological Society; 2005. pp. 9-28

[30] Mansfield J, Genin S, Magori S, Citovsky V, Sriariyanum M, Ronald P, et al. Top 10 plant pathogenic bacteria

- in molecular plant pathology. *Molecular Plant Pathology*. 2012;**13**:614-629.
 DOI: 10.1111/j.1364-3703.2012.00804.x
- [31] Scott JW, Wang JF, Hanson PM. Breeding tomato for resistance to bacterial wilt, a global view. *Acta Horticulturae*. 2005;**695**:161-117
- [32] Gupta SK, Sharma M, Mukherjee S. Buckeye rot of tomato in India: Present status, challenges and future research perspectives. *Plant Disease*. 2022;**106**(1):1085-1095
- [33] Sood D, Sharma A, Sharma M. Prevalence and epidemiology of bacterial wilt of tomato. *International Journal of Economic Plants*. 2022;**9**(4):328-333
- [34] Wenneker M, Verdel M, Groeneveld R, Kempenaar C, van Beuningen A, Janse J. *Ralstonia* (pseudomonas) solanacearum race 3 (bio- var 2) in surface water and natural weed hosts: First report on stinging nettle (*Urticadioica*). *European Journal of Plant Pathology*. 1999;**105**:307-315.
 DOI: 10.1023/A:100879 5417575
- [35] Saddler GS. Management of bacterial wilt disease. In: Allen C, Prior P, Hayward AC, editors. *Bacterial Wilt Disease and the *Ralstonia solanacearum* Species Complex*. Saint Paul, MN: APS Press; 2005. pp. 121-132
- [36] Hanson PM et al. Conventional and molecular marker-assisted selection for pyramiding of genes for multiple disease resistance in tomato. *Scientia Horticulturae*. 2016;**201**:346-354.
 DOI: 10.1016/j.scienta.2016.02.020
- [37] Ong SN, Taheri S, Othman RY, Teo TH. Viral disease of tomato crops (*Solanum lycopersicum* L.): An overview. *Journal of Plant Disease and Protection*. 2020;**127**:725-739. DOI: 10.1007/s41348-020-00330-0
- [38] Rivarez MPS, Vucurovic A, Mehle N, Ravnikaar M, Kutnjak D. Global advances in tomato Virome research: Current status and the impact of high-throughput sequencing. *Frontier of Microbiology*. 2021;**12**:671925. DOI: 10.3389/fmicb.2021.671925
- [39] Abraham P, Banwo OO, Kashina BD, Alegbejo MD. Status of tomato viruses in Nigeria. *Fuduma Journal of Science*. 2023;**3**:482-494
- [40] Arogundade O. Characterization of *Begomoviruses* and satellite molecules associated with leaf curl disease of selected vegetables. In: Laboratory Report in Fulfilment of the TWAS-DBT Postdoctoral Fellowship at the Molecular Virology Laboratory of the School of Life Sciences. New Delhi, India: Jawaharlal Nehru University; 2023
- [41] Arogundade O, Ajose T, Osijo I, Onyeausi H, Matthew JH. Aliyu T. Management of Viruses and Viral Diseases of Pepper (*Capsicum* spp.) in Africa [Internet]. *Capsicum*. IntechOpen; 2020. DOI: 10.5772/intechopen.92266
- [42] Zhou R, Yu X, Ottosen CO, Rosenqvist E, Zhao L, Wang Y, et al. Drought stress had a predominant effect over heat stress on three tomato cultivars subjected to combined stress. *BMC Plant Biology*. 2017;**17**:24. DOI: 10.1186/s12870-017-0974-x
- [43] Ahuja I, de Vos RC, Bones AM, Hall RD. Plant molecular stress responses face climate change. *Trends in Plant Science*. 2010;**15**:664-674
- [44] Silva RS, Kumar L, Shabani F, Picanço MC. Assessing the impact of global warming on worldwide open field tomato cultivation through CSIRO-Mk3.0 global climate model. *The Journal of Agricultural Science*. 2017;**155**:407-420.
 DOI: 10.1017/S0021859616000654

- [45] Ayenan MAT, Danquah A, Hanson P, Asante IK, Danquah EY. Identification of new sources of heat tolerance in cultivated and wild tomatoes. *Euphytica*. 2021;**217**:1-16. DOI: 10.1007/s10681-021-02772-5
- [46] Abera G, Ibrahim AM, Forsido SF, Kuyu CG. Assessment on post-harvest losses of tomato (*Lycopersicon esculentum* Mill.) in selected districts of East Shewa zone of Ethiopia using a commodity system analysis methodology. *Heliyon*. 2020;**6**(4):1-13. DOI: 10.1016/j.heliyon.2020.e03749
- [47] Kiaya V. Post-harvest losses and strategies to reduce them. *The Journal of Agricultural Science*. 2014;**149**(3-4):49-57. Available from: <http://www.journals.cambridge.org/abstract>
- [48] Pavan MP, Gangaprasad S, Dushyanthakumar BM, Nagrajappa A. Identification of promising germplasm lines for fruit biochemical, morpho-physiological and yield traits governing shelf life in tomato (*Solanum lycopersicum* L.). *Journal of Pharmacognosy and Phytochemistry*. 2018;**7**(4):2078-2083
- [49] Osei MK, Danquah A, Blay ET, Danquah E, Adu-Dapaah H. An overview of tomato fruit-ripening mutants and their use in increasing shelf life of tomato fruits. *African Journal of Agricultural Research*. 2017;**12**(51):3520-3528. DOI: 10.5897/AJAR2017.12756
- [50] Meli VS, Ghosh S, Prabha TN, Chakraborty N, Chakraborty S, Datta A. Enhancement of fruit shelf life by suppressing N-glycan processing enzymes. *Proceedings of the National Academy of Sciences*. 2010;**107**:2413-2418
- [51] Uluisik S, Chapman NH, Smith R, Poole M, Adams G, Gillis RB, et al. Genetic improvement of tomato by targeted control of fruit softening. *Nature Biotechnology*. 2016;**34**:950-952
- [52] Wang D, Seymour GB. Molecular and biochemical basis of softening in tomato. *Molecular Horticulture*. 2022;**2**:5. DOI: 10.1186/s43897-022-00026-
- [53] Rodríguez GR, Pratta GR, Liberatti DR, Zorzoli R, Picardi LA. Inheritance of shelf life and other quality traits of tomato fruit estimated from F1's, F2's and backcross generations derived from standard cultivar, nor homozygote and wild cherry tomato. *Euphytica*. 2010;**176**:137-147
- [54] Bartoszewski G, Niedziela A, Szwacka M, Niemirowicz-Szczytt K. Modification of tomato taste intragenic plants carrying a thaumathin gene from *Thaumatococcus daniellii* Benth. *Plant Breeding*. 2003;**122**:347-351
- [55] Adebayo OS, Adesegun EA, Kloepper JW, Fadamiro HY. Efficacy of plant growth promoting Rhizobacteria for the control of bacterial wilt of tomato in Southwestern Nigeria. In: Wesonga J, Kahane R, editors. *Proceedings of First All African Horticultural Congress*. Belgium: Acta Hort; 2011. p. 911. ISHS 2011
- [56] Anith KN, Momol MT, Kloepper JW, Marois JJ, Jones JB. Efficacy of plant growth promoting bacterial, acbenzolar-s-methyl and soil amendment for integrated management of bacterial wilt of tomato. *Plant Disease*. 2004;**88**:669-673
- [57] Raupach GS, Kloepper JW. Biocontrol of cucumber diseases in the field by plant growth promoting rhizobacter with and without methyl bromide fumigation. *Plant Disease*. 2000;**84**:1073-1075
- [58] Oke OA, Kolawole RO, Akinsola OA, Olajide-Taiwo LO, Oladigbolu AA, Ajayi EO. The first effort at adopting integrated pest management IPM to contain the infestation of the Tuta

- absoluta in Nigeria. In: Niassy S et al., editors. Sustainable Management of Invasive Pests In Africa, Sustainability in Plant and Crop Protection. Vol. 14. Chapter 5. 2020b. pp. 57-64. DOI: 10.1007/978-3-030-41083-4_5
- [59] Mansour R, Brévault T, Chailleux A, Cherif A, Grissa-Lebdi K, Haddi K, et al. Occurrence, biology, natural enemies and management of *Tuta absoluta* in Africa. *Entomologia Generalis*. 2018;**38**(2):83-112. DOI: 10.1127/entomologia/2018/0749
- [60] Aigbedion-Atalor PO, Oke OA, Oladigbolu AA, Layade AA, Igbinosa IB, Mohamed SA. *Tuta absoluta* (Lepidoptera: Gelechiidae) invasion in Nigeria: First report of its distribution. *Journal of Plant Diseases and Protection*. 2019;**126**:603-606. DOI: 10.1007/s41348-019-00255-3
- [61] Oke OA, Kolawole RO, Ogunremi OA, Akinsola OA, Awe SA, Oladigbolu AA. First report of *Apanteles* spp. (Hymenoptera: Braconidae) from *Tuta absoluta* (Lepidoptera: Gelechiidae) infesting tomato in Nigeria. *Agricultural Society of Nigeria (ASN)*. In: Proceeding of the 57th Annual Conference, 23 – 27 Oct. 2023, Fulafia Nasarawa State. Ibadan, Nigeria; 2023a. pp. 714-717
- [62] Oke OA, Oladigbolu AA, Akinyemi AO, Aigbedion-Atalor P, editors. First report of the occurrence and abundance of natural enemies of the South American tomato pinworm *Tuta absoluta* (meyrick) in Nigeria. In: *Agricultural Society of Nigeria (ASN)*, Proceeding of the 57th Annual Conference, 23 – 27 Oct. 2023, Fulafia Nasarawa State. *Nigerian Agricultural Journal*. Ibadan, Nigeria; 2023. pp. 725-731
- [63] Oke OA, Oladigbolu AA, Aigbedion-Atalor P, Akinyemi AO. Influence of fertigation on *Tuta absoluta* infestation and tomato yield on the field. In: Proceeding of the 57th Annual Conference, 23 – 27 Oct. 2023, Fulafia Nasarawa State. *Agricultural Society of Nigeria (ASN)*, Ibadan, Nigeria; 2023b. pp. 718-724
- [64] Desneux N, Han P, Mansour R, Arnó J, Brévault T, Campos MR, et al. Integrated pest management of *Tuta absoluta*: Practical implementations across different regions around the world. *Journal of Pest Science*. 2021;**95**:17-39. DOI: 10.1007/s10340-021-01442-8
- [65] R Core Team. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing; 2019. Available from: <https://www.R-project.org/>
- [66] Levy A, Rabinowitch HD, Kedar N. Morphological and physiological characters affecting flower drop and fruit set of tomatoes at high temperatures. *Euphytica*. 1978;**27**:211-218. DOI: 10.1007/BF00039137
- [67] Adelanwa MA, Habeeb ML, Adelanwa EB. Morphological Studies of the Effect of Colchicine and Paradichlorobenzene on Tomato (*Lycopersicon esculentum*). Department of Biological Sciences: Ahmadu Bello University, Zaria; 2011
- [68] Mensah JK, Obadoni BO, Akomeah PA, Ikhajiagbe B, Ajibolu J. The effects of sodium azide and colchicine treatments on morphological and yield traits of sesame seed (*Sesame indicum* L.). *African Journal of Biotechnology*. 2007;**6**:534-538
- [69] Nwosu DJ, Onakoya OA, Okere AU, Babatunde AO, Popoola AF. Genetic variability and correlations in rainfed

- tomato (*Solanum* spp.) accessions in Ibadan, Nigeria. Greener Journal of Agricultural Sciences. 2014;**4**(5):211-219. DOI: 10.15580/GJAS.2014.5.031014141
- [70] Udofia EG, Falusi OA, Abubakar A, Daudu OAY, Ajenifujah-Solebo SOA, Titus SD. Mutagenic effects of colchicine on the morphology and yield of three tomato (*Solanum lycopersicum* L.) accessions. Journal of Agricultural and Food Sciences. 2022;**20**(2):119-132. DOI: 10.4314/jafs.v20i2.8
- [71] Zhang X, Henriques R, Lin SS, Niu QW, Chua NH. Agrobacterium-mediated transformation of *Arabidopsis thaliana* using the floral dip method. Nature Protocols. 2006;**1**:641-646. DOI: 10.1038/nprot.2006.97
- [72] Loberant B, Altman A. Micropropagation of plants. In: Flickinger MC, editor. Encyclopedia of Industrial Biotechnology: Bioprocess, Bioseparation, and Cell Technology. Hoboken, NJ: John Wiley & Sons, Inc.; 2010. pp. 1-17. DOI: 10.1007/s11120-017-0473-9
- [73] Chokheli VA, Dmitriev PA, Rajput VD, Bakulin SD, Azarov AS, Varduni TV, et al. Recent development in micropropagation techniques for rare plant species. Plants. 2020;**9**:1733. DOI: 10.3390/plants912 1733
- [74] Sarasan V, Kite GC, Sileshi GW, Stevenson PC. Applications of phytochemical and in vitro techniques for reducing over-harvesting of medicinal and pesticidal plants and generating income for the rural poor. Plant Cell Reports. 2011;**30**:1163-1172
- [75] Bull T, Michelmores R. Molecular determinants of in vitro plant regeneration: Prospects for enhanced manipulation of lettuce (*Lactuca sativa* L.). Frontiers in Plant Science. 2022;**13**:888425. DOI: 10.3389/fpls.2022.888425
- [76] Adegbola AJ, Ojo DK, Adeniji OA. Tissue culture techniques for the improvement of tomato (*Solanum lycopersicum*) in Nigeria. Journal of Agricultural Science and Technology. 2011;**11**(3):257-266
- [77] Bhojwani SS, Razdan MK. Plant Tissue Culture: Theory and Practice. The Netherlands: Elsevier; 2014
- [78] Rahman MM, Kaul K. Differentiation of sodium chloride tolerant cell lines of tomato (*L. esculentum* Mill.) cv. Jet Star. Journal of Plant Physiology. 1989;**133**:710-712
- [79] Shtereva LA, Zagorska NA, Dimitrov BD, Kruleva MM, Oanh HK. Induced androgenesis in tomato (*Lycopersicon esculentum* Mill.). II. Factors affecting the induction of androgenesis. Plant Cell Reports. 1998;**18**:312-317
- [80] George EF, Hall MA, De Klerk GJ. Plant Propagation by Tissue Culture. Dordrecht: Springer; 2008
- [81] Ajenifujah-Solebo SOA, Isu NA, Olorode O, Ingelbrecht I, Abiade OO. Tissue culture regeneration of three Nigerian cultivars of tomatoes. African Journal of Plant Science. 2012;**6**(14):370-375
- [82] Ajenifujah-Solebo SOA, Ingelbrecht I, Isu NA, Olorode O. Reproducible agrobacterium-mediated transformation of Nigerian cultivars of tomato (*Solanum lycopersicum* L.). American journal of. Experimental Agriculture. 2014;**4**(7):797-808
- [83] Durosomo HA, Popoola AR, Afolabi CG, Idehen EO. Germination and in vitro regeneration response of local Nigerian tomato cultivar using different explant sources. Nigerian Journal of

Biotechnology. 2014;28:35-42. ISSN: 0189 17131

[84] Adeogun TT, Salawu PO, Katibi SO, Chukwu KE, Aduloju AO, Olagunju YO, et al. In-vitro regeneration of tomato through indirect organogenesis for genetic transformation. 2024. In: Proceedings of 42nd Annual Conference of the Horticultural Society of Nigeria, (NJHS). Nigerian Journal of Horticultural Science, Ibadan Nigeria. 2024. pp. 458-462. ISSN: 2814-0508

[85] Cortina C, Culiáñez-Macià FA. Tomato transformation and transgenic plant production. Plant Cell, Tissue and Organ Culture. 2004;76:269-275. DOI: 10.1023/B:TICU.0000009249.14051.77

[86] The National Biotechnology Research Development Agency establishment act. 2022. Available from: <https://nbrda.gov.ng/wp-content/uploads/2022/04/National-Biotechnology-Development-Agency-Est-Act-2022.pdf> [Accessed: December 20, 2024]

[87] Voytas DF, Gao C. Precision genome engineering and agriculture: Opportunities and regulatory challenges. PLoS Biology. 2014;12:e1001877. DOI: 10.1371/journal.pbio.1001877

[88] National Biosafety Management Agency Act. 2015. Available from <https://nbma.gov.ng/nbma-act/> [Accessed: December 20, 2024]

[89] National Biosafety Management Agency. Guideline on Gene Editing. Abuja, Nigeria; 2020. Available from <https://nbma.gov.ng/wp-content/uploads/2022/03/national-gene-editing-guideline.pdf> [Accessed: January 05, 2025]

[90] Tripathi NJ, Ntui VO, Tripathi L. Precision genetics tools for genetic

improvement of banana. The Plant Genome. 2024;17(2):e20416. DOI: 10.1002/tpg2.20416

[91] Lei Y, Li L, Hai-Yang L, Sen L, Feng X, Ling-Ling C. CRISPR-P: A web tool for synthetic single-guide RNA design of CRISPR-system in plants. Molecular Plant. 2014;7(9):1494-1496. DOI: 10.1093/mp/ssu044

[92] Benchling quick and easy CRISPR designs. Available from: <https://benchling.com/crispr> [Accessed: October 2, 2020]

[93] Addgene CRISPR plasmids: Plants. Available from: <http://www.addgene.org/crispr/plant/> [Accessed: October 2, 2020]

[94] Sahel Research. The Tomato Value Chain in Nigeria. Nigeria; 2017. Available from: https://www.google.com/url?q=http://sahelcp.com/wp-content/uploads/2017/07/Sahel-Newsletter-Volume15_Tomato.pdf&sa=D&source=hangouts&ust=1535552701149000&usg=AFQjCNGKYgek8lH9vTXmHmHALL8b-3N-_g [Accessed: August 28, 2018]

[95] Ojikutu A. Post-harvest losses and welfare of tomato farmers in Ogbomoshos, Osun state, Nigeria. Journal of Stored Products and Postharvest Research. 2014;5:8-13. DOI: 10.5897/JSPPR2014.0160

[96] Shi Y, Vrebalov J, Zheng H, Xu Y, Yin X, Liu W, et al. A tomato LATERAL ORGAN BOUNDARIES transcription factor, SILOB1, predominantly regulates cell wall and softening components of ripening. Proceedings of the National Academy of Sciences of the United States of America. 2021;118(33):1-8. DOI: 10.1073/pnas.2102486118

[97] Wang D, Yeats TH, Uluisik S, Rose JKC, Seymour GB. Fruit softening: Revisiting the role of pectin. Trends in Plant Science. 2018;23:302-310

- [98] Greg T, Xueren Y, Aidi Z, MiaoMiao W, Qinggang Z, Xiaofen L, et al. Ethylene and fruit softening. *Food Quality and Safety*. 2017;**2017**(1):253-267
- [99] Pysh LD, Wysocka-Diller JW, Camilleri C, Bouchez D, Benfey PN. The GRAS gene family in Arabidopsis: Sequence characterization and basic expression analysis of the SCARECROW-LIKE genes. *The Plant Journal*. 1999;**18**:111-119
- [100] Van Schie CCN, Takken FLW. Susceptibility genes 101: How to be a good host. *Annual Review of Phytopathology*. 2014;**52**:551-581. DOI: 10.1146/annurev-phyto102313-045854
- [101] Zhang L, Zhu M, Ren L, Li A, Chen G, Hu Z. The SLFSR gene controls fruit shelf-life in tomatoes. *Journal of Experimental Botany*. 2018;**69**(12):2897-2909. DOI: 10.1093/jxb/ery116
- [102] Imada K, Sakai S, Kajihara H, Tanaka S, Ito S. Magnesium oxide nanoparticles induce systemic resistance in tomatoes against bacterial wilt disease. *Plant Pathology*. 2016;**65**:551-556. DOI: 10.1111/ppa.12443
- [103] Tiwari JK, Singh AK, Behera TK. CRISPR/Cas genome editing in tomato improvement: Advances and applications. *Frontiers in Plant Science*. 2023;**14**:1-14. DOI: 10.3389/fpls.2023.1121209
- [104] Berg JA, Appiano M, Bijsterbosch G, Visser RGF, Schouten HJ, Bai Y. Functional characterization of cucumber (*Cucumis sativus* L.) clades V MLO genes. *BMC Plant Biology*. 2017;**17**(1):1-15. DOI: 10.1186/s12870-017-1029-z
- [105] Thomazella DPT, Seong K, Mackelprang R, Dahlbeck D, Geng Y, Gill US, et al. Loss of function of a DMR6 ortholog in tomato confers broad-spectrum disease resistance. *Proceedings of the National Academy of Sciences of the United States of America*. 2021;**118**(27):e2026152118. DOI: 10.1073/pnas.2026152118
- [106] Eleni K, Jan M, Van der Richard GFV, Yuling B. Susceptibility reversed: Modified plant susceptibility genes for resistance to bacteria. *Trends in Plant Science*. 2022;**27**(1):69-79

Variation in Agromorphological Traits and Phenolic Compounds, Vitamin C Contents, and Antioxidant Activity in the Fruits of Mexican Tomato Landraces

Araceli Minerva Vera-Guzmán, Mónica Lilian Pérez-Ochoa, José Cruz Carrillo-Rodríguez and José Luis Chávez-Servia

Abstract

Exploration of the genetic potential of Mexican tomato landraces has followed a variety of routes, such as the characterization of agromorphological traits and fruit composition within the extensive genetic diversity preserved on farms by traditional farmers. In this context, the objective of this study was to evaluate the agromorphological variation and fruit composition of tomato landraces from southern Mexico via three reference experiments under greenhouse conditions with 95, 17, and 27 population samples, representing an active collection of tomato landraces. First, agromorphological characterization (95 samples) was conducted, and later, fruit composition, that is, the contents of lycopene, total phenolic compounds, total flavonoids, and vitamin C, were analyzed via spectrophotometry, where antioxidant activity was determined via DPPH and FRAP methods. In the first experiment, six groups of phenotypic diversity were recorded on the basis of agromorphological traits. In the second experiment, fruit composition was influenced by the crop cycle and interactions among populations and crop cycles. The third experiment allowed us to elucidate the high variability among the evaluated populations, some of which presented higher values than those determined for the control variety Floradade. All the populations characterized and evaluated came from farmers' plots, where their own genetic material was selected every crop cycle without the intervention of plant breeders.

Keywords: flavonoids, fruit quality, lycopene, on-farm conservation, phenotypic diversity

1. Introduction

The evolution of cultivated species or plant genetic resources takes different evolutionary routes depending on the genetic background of domestication and

diversification; these backgrounds respond to strategies of adaptation to anthropogenic and agroecological pressures in ecogeographic contexts, where distinctive or differential characteristics continue to develop and the *in situ*/on-farm evolutionary dynamics continue and are revalued and preserved by growers, conservators, and consumers as part of the biological evolution of the cultivated species [1].

Local varieties of tomato or tomato landraces have specific characteristics and different population genetic structures depending on their phylogenetic origin and the diversification and recombination of the species. For example, the theories of origin of the cultivated tomato suggest that the central region of Mexico and the coastal areas of Ecuador and Peru are probable regions where domestication took place [2], and the probable wild parent forms such as *Solanum lycopersicum* L. var. *cerasiforme* and *S. pimpinellifolium* L. are still preserved *in situ* in these regions, although the intermediate forms prior to the current tomato, *S. lycopersicum* L. var. *lycopersicum*, are unknown [3, 4], implying recombination between wild and cultivated forms. This is not the case in regions that are neither centers of origin nor diversification [5], where some tomato landraces were derived phylogenetically from old improved varieties (heirloom tomatoes) or from varietal introductions over the last few decades of the last century, for example, the diversity of European traditional tomatoes reported by Pons et al. [6].

Tomato landraces are preserved by the individual and/or collective decisions of growers and consumers, who note one or more distinctive morphoagronomic characteristics of the plant and/or fruit quality valued by consumers in terms of flavors, aromas, textures, and special colors in the fruit for fresh consumption or in the preparation of dishes. Landraces are the result of adaptations to specific agroecological conditions that are typically low in inputs, present high heterogeneity, respond to local tastes (sensory properties) or taste needs, are important components of agrobiodiversity, provide ecosystem services, and require different contingent valuations, which are applied to commercial varieties [7–9].

Adaptations to particular edaphoclimatic conditions, biotic pressures, agronomic selection, the appearance of mutations (e.g., multiple flowers fused to generate multilocular fruits), the development of different gastronomic cultures related to the use of fresh semi-green, ripe, and dry varieties, types of fruits of short or long shelf lives, and, over time, regional culinary traditions (e.g., Europe, the Mediterranean region, Central Asia, and North, Central, and South America, among others) that together have led to all the tomato landrace diversity documented to date [6, 10–17].

Mexican tomato landraces in the hands of small producers have developed desirable agronomic traits for breeding programs, for example, resistance to the bacterium *Candidatus Liberibacter solanacearum* [18], resistance to soil pathogens enabling use as a rootstock for commercial varieties [19], tolerance to stress in saline soils [13], and high genetic diversity in terms of traits of agronomic interest and fruit quality [20, 21]. The selection of fruits for characters important to culinary use, which has been carried out by traditional farmers in the different indigenous communities of Mexico, has yielded particular properties of flavors to recreate traditional Mexican gastronomy, for example, various types of “moles,” sauces, soups, salads, and accompaniment of various meats [22–24]. In this work, a description of the variability and phenotypic diversity based on plant, physiological, and fruit characteristics is presented, complemented with a laboratory evaluation of the content of soluble solids, pH, titratable acidity, reducing sugars, lycopene, vitamin C, and antioxidant activity of 95 populations of tomato landraces native to Southeast Mexico cultivated by farmers from different indigenous groups or native peoples (**Figure 1**).



Figure 1.
 Documentation of diversity and collecting of samples of tomato landraces from indigenous communities in Oaxaca, Mexico.

2. Phenotypic, genetic, and biocultural diversity of tomato landraces

The greatest diversity of Mexican tomatoes is conserved *in situ*/on-farm, forming a portion of the agrobiodiversity of traditional agricultural production systems and between communities and families of indigenous communities, constituting part of their biocultural heritage [25]. The producers of traditional varieties of tomato are usually over 50 years old and have little schooling, but they have been sowing the same varieties from seed for more than 10 years that they grow repeatedly in small plots of 10–40 rows of up to 100 m in length using manual cultivation practices and/or with a yoke. The fruits selected for seeds must satisfy the characteristics of color, size, and flattened-multilocular shapes, which are peculiar to local or regional varieties (**Figure 1**) and differ substantially from commercial saladette, ball, or processing tomatoes. Production is essentially destined for self-consumption, sales between neighbors, and local and regional markets and is rarely marketed in formal shopping centers. However, these types of small to large or very large fruits are appreciated in Mexican gastronomy [24, 26, 27].

forms are consistent with the Chilean Limachino tomato preserved by small producers, which also has a shorter shelf life [15]. Additionally, in both countries, it is usually cut and consumed as ripe and fresh fruit.

On the basis of the characterization data described above and standardized by variable and population, a hierarchical grouping cluster analysis was performed by Ward's method, where six phenotypic diversity groups were classified according to the variation in plant, physiological, and fruit characteristics (**Figure 3**). In the reproductive phases from flowering to fruit ripening, the phenotypic groups differ in flowering and fruiting or fruit settling, and the populations show indeterminate growth and differ in weight, dimensions, and number of fruits per cluster, with variations of 6–12 locules per fruit. Villena et al. [30] noted that different farmers can plant different populations of the same recognized local variety (landrace), and their specific differences are due to the mass or individual selection made by each producer. There may even be agromorphological differences between populations and high variability within populations, but together, they help preserve the local variety *in situ*.

Traditional tomato producers from the same or different communities obtain seeds by exchanging seeds or fruits or by acquiring fruits from local markets where local varieties are sold. This process invariably generates different flows of germ-plasms and genes in different directions that also carry susceptibility to diseases or pests [15, 23, 30]. However, with more distant cultivating communities or with reduced seed exchange, the genetic flow decreases, and diverse phenotypic–genetic groups are formed. Among the tomato populations from south-southeastern Mexico, six significantly different phenotypic groups were distinguished in terms of reproductive phenology, plant height, fruit dimensions and weight, fruit yield per plant, number of fruits per cluster, and number of locules in the fruit (**Table 1**).

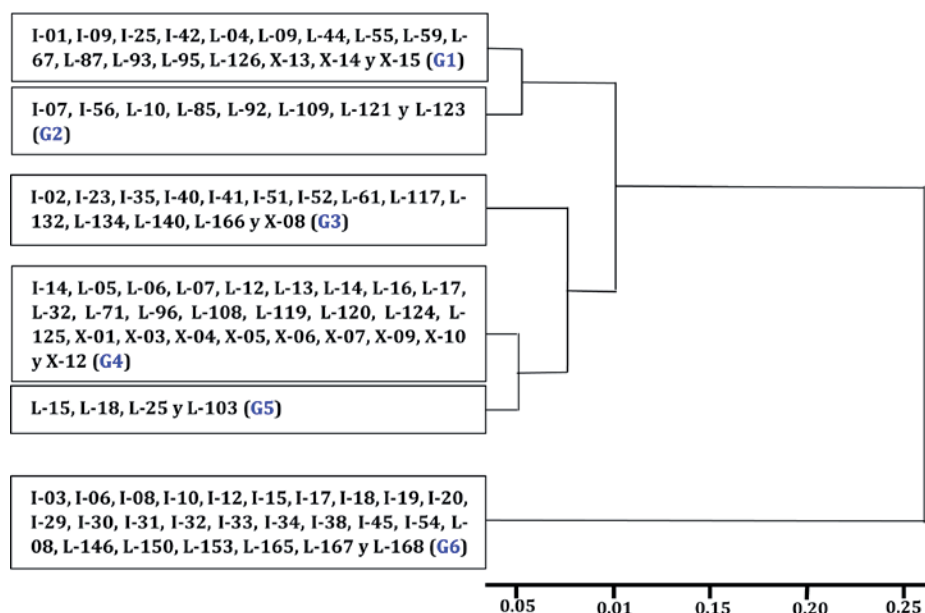


Figure 3.
Phenotypic dendrogram of 95 populations from Mexican tomato landraces using r^2 semipartial distances and Ward's clustering method.

Descriptor	F values	Groups of phenotypic diversity in the landraces					
		1	2	3	4	5	6
Days to flowering ¹	37.1**	36.0 a ²	33.1 b	31.7 b	31.7 b	<u>22.2 c</u>	31.4 b
Days to fruiting ¹	14.9**	48.6 a	45.9 ab	45.0 b	43.9 b	<u>38.2 c</u>	44.0 b
Days to maturing ¹	9.5**	110.5 a	110.1 a	<u>98.1 b</u>	107.6 a	107.2 a	105.3 a
Plant height at 90 dat ¹ (m)	12.9**	<u>1.95 b</u>	2.16 a	2.15 a	2.18 a	2.08 a	2.08 a
Number of fruits per cluster	1874**	2.1 d	<u>1.2 e</u>	4.6 a	2.6 c	1.8 d	3.8 b
Fruit yield/plant (kg)	598.7**	0.561 c	0.593 c	1.263 b	0.562 c	<u>0.410 d</u>	1.766 a
Fruit weight (g)	2874**	<u>51.4 c</u>	101.7 a	62.9 b	<u>44.1 c</u>	<u>43.3 c</u>	97.7 a
Fruit length (mm)	190.4**	40.9 b	41.6 b	42.4 b	<u>35.3 c</u>	41.1 b	51.2 a
Fruit width (mm)	140.3**	<u>48.1 e</u>	64.0 b	53.3 cd	<u>50.3 de</u>	56.3 c	71.7 a
Number of locules	105.0**	<u>5.7 c</u>	10.1 b	<u>7.6 c</u>	<u>7.3 c</u>	<u>8.2 c</u>	11.3 a

¹Days after transplant (dat);

²in rows, means of groups followed by same letter indicate no significant differences (Tukey's test, $p < 0.05$); The highest values are in **bold**, and the lowest values are underlined.

Table 1.

Significance of the F values of the analyses of variance and mean comparisons between phenotypic diversity groups of the dendrogram in **Figure 3**.

The variation and differences between the phenotypic diversity groups described here are similar to those described in different countries. For example, among 24 Greek tomato landraces, the variation in the polar and equatorial diameters of the fruit ranged from 45.7 to 65.5 mm and 4.6 to 76.1 mm, respectively, with four to eight locules per fruit and yields of 0.485–2.471 g per plant [14]. Among traditional local Romanian tomato populations, the fresh weight of the fruit ranged from 68.0 to 131.0 g [16]. This finding indicates that each region of traditional tomato cultivation follows its own evolutionary dynamics under domestication and anthropic pressures and responds to local consumer demands. However, local initiatives to undertake conservative genetic improvement programs that strengthen *in situ* conservation and improve cultivation using local criteria are incipient.

3. Fruit composition of traditional tomato varieties from South-Southeastern Mexico

Tomatoes (*Solanum lycopersicum* L.), native to Mexico, are consumed fresh or in foods prepared according to traditional cuisine practices. Native tomatoes are a source of phytochemical compounds that influence the flavor of the fruit and its nutritional and nutraceutical properties [31]. The composition of tomato fruits varies according to their genotype, origin, management conditions, environmental factors, etc. [8, 32]. Tomato landraces are distributed mainly in the south-southeastern region of Mexico and can be found in various shapes, colors (pink, orange, red), and flavors [24]. Although native tomato is highly accepted by consumers locally and regionally, little is known about their phytochemical composition in terms of population, origin, and crop cycle. In this sense, the variation in the composition of 17 populations of tomato landraces originating from Oaxaca, Mexico, was evaluated via cultivation in a greenhouse for two cultivation cycles under a randomized block design with four repetitions.

The parameters evaluated in the composition experiment were soluble solids ($^{\circ}$ Brix), pH, titratable acidity, and reducing sugars according to AOAC [33] methods and lycopene and vitamin C contents determined via spectrophotometric means [34, 35]. Significant differences were found in the results ($p \leq 0.01$) for soluble solids ($^{\circ}$ Brix) in the pulp and juice, lycopene contents (fresh and dry weight basis), and reducing sugars due to the effects of the crop cycle, population, and cycle–population interaction; for pH and titratable acidity, differences were only observed between populations and the cycle–population interaction; and for vitamin C, differences were only observed between crop cycles ($p \leq 0.01$) and populations ($p \leq 0.05$) (Table 2). In terms of the magnitude of the variance, the crop cycle had a greater effect on the phytochemical compounds than did the population (genotype) and the cycle–population interaction (C $\times$ P). These findings indicate that environmental factors during the crop cycle influence the accumulation of metabolites in tomato fruits.

In the comparison of crop cycle averages (Table 3), the values of $^{\circ}$ Brix (pulp and juice), reducing sugars, and vitamin C were greater in cycle 1 (summer); in contrast, the lycopene content (fresh weight, FW, and dry weight, DW) was greater in cycle 2 (fall), whereas pH and titratable acidity were not significantly different. These findings indicate that the environmental conditions of each cycle affect the accumulation of these metabolites and that the increase in vitamin C content is not necessarily related to increases in lycopene content. These results are in contrast to the results for commercial varieties, where a direct relationship between lycopene and vitamin C has been observed previously and where both compounds are related to temperature [36, 37]. The results presented here for the fruit composition between populations indicate that there are no specific patterns; for example, the L-019 population presented a relatively high $^{\circ}$ Brix and lycopene content (FW and DW) but had relatively low vitamin C content; L-109 excelled in $^{\circ}$ Brix, pH, reducing sugars, and vitamin C; L-09, in $^{\circ}$ Brix and titratable acidity; and L-059, L-061, and L-096 presented high values for vitamin C. The variation in the composition between populations suggests that, among native kidney tomatoes, there are phenotypes with different origins or that producers and conservators have maintained them accordingly isolated and that they have significantly differentiated from the best-known traditional varieties [38, 39].

Variables	Source of variation					CV (%)
	Cycle (C)	Population (P)	C $\times$ P	Rep./C	Error	
$^{\circ}$ Brix pulp	11.03**	1.69**	0.89**	0.03 ^{ns}	0.101	7.3
$^{\circ}$ Brix juice	3.27**	2.00**	1.28**	0.01 ^{ns}	0.099	7.3
pH	0.023 ^{ns}	0.070**	0.027*	0.007 ^{ns}	0.011	2.4
Lycopene fresh weight	14.00*	61.45**	24.54**	1.12 ^{ns}	2.63	11.2
Lycopene dry weight	87033.3**	314679**	6415.2**	1819.5 ^{ns}	1494	11.5
Titratable acidity	<0.001 ^{ns}	0.089**	0.011**	<0.001 ^{ns}	0.002	10.8
Reducing sugars	10.82**	0.84**	0.71**	0.03**	0.07	13.6
Vitamin C	1.36**	0.84*	0.41 ^{ns}	0.01 ^{ns}	0.188	16.5

^{ns}Not significant ($p > 0.05$); * significant at $p \leq 0.05$; ** significant at $p \leq 0.01$; CV = coefficient of variation.

Table 2.
 Significance of the square means of the analysis of variance in the phytochemical evaluation of 17 populations and genotypes of tomato landraces cultivated under greenhouse conditions for two crop cycles.

Cycle/pop.	°Brix		pH	Lycopene ²		Titratable acidity ²	Reducing sugars ²	Vitamin C ²
	Pulp	Juice		FW	DW			
Comparisons between crop cycles								
Cycle 1	5.16 a ¹	4.79 a	4.34 a	14.19 b	273.5 b	0.34 a	2.88 a	9.81 a
Cycle 2	4.17 b	4.18 b	4.22 a	14.52 a	348.0 a	0.40 a	1.75 b	6.75 b
Comparison between populations/genotypes								
L-010	4.47 a-c1	4.34 a-d	4.20 c-e	12.89 dg	332.6 b-f	0.36 c-g	2.11 a-c	7.35 a-e
L-016	4.29 a-d	4.12 b-e	4.25 bc	15.65 bc	358.7 b-d	0.41 c	1.67 d-g	5.70 b-f
L-019	4.59 ab	4.82 a	4.20 c-e	21.62 a	461.9 a	0.39 cd	1.95 c-f	<u>4.28</u> <u>f</u>
L-025	4.64 ab	4.62 a	4.13 c-e	11.44 fg	<u>257.8</u> g	0.50 b	2.03 b-d	5.38 d-f
L-040	3.92 d-f	3.66 e-g	4.27 bc	15.17 b-e	377.1 bc	0.32 e-g	1.62 e-g	7.60 a-e
L-043	4.35 a-d	4.41 a-d	4.15 c-e	17.11 b	386.8 b	0.41 c	1.89 c-f	4.87 ef
L-05	4.51 a-c	4.47 a-d	4.21 b-e	13.30 c-g	299.8 d-g	0.53 b	1.56 f-h	5.54 c-f
L-059	4.08 c-e	4.07 c-e	4.18 c-e	11.72 fg	296.6 e-g	0.38 c-e	1.86 c-g	9.06 a
L-061	4.20 a-d	3.99 d-f	4.29 a-c	13.94 c-f	337.8 b-e	0.35 c-g	1.82 c-g	9.32 a

Cycle/pop.	°Brix		pH	Lycopene ²		Titratable acidity ²	Reducing sugars ²	Vitamin C ²
	Pulp	Juice		FW	DW			
L-067	4.74 a	4.62 a	4.23 b-d	13.00 d-g	281.5 e-g	0.32 e-g	2.44 ab	8.45 a-c
L-087	3.57 fg	<u>3.40</u> g	4.23 b-d	11.66 fg	337.5 b-e	0.33 d-g	1.48 gh	<u>3.95</u> f
L-09	4.65 ab	4.78 a	<u>4.07</u> e	15.40 b-d	325.5 c-f	0.61 a	1.79 c-g	5.70 b-f
L-091	4.69 ab	4.55 ab	4.24 b-d	12.89 e-g	275.4 fg	0.60 a	1.98 c-e	6.05 b-f
L-095	3.79 e-g	4.07 c-e	4.26 bc	<u>11.40</u> g	280.2 e-g	0.32 e-g	1.72 c-g	8.00 a-d
L-096	<u>3.41</u> g	3.58 fg	4.09 de	16.62 b	454.6 a	0.37 c-f	<u>1.20</u> h	9.04 a
L-109	4.76 a	4.63 a	4.44 a	15.31 b-e	326.3 c-f	0.31 fg	2.48 a	9.21 a
L-110	4.64 ab	4.48 a-c	4.36 ab	15.38 be	321.6 c-f	<u>0.30</u> g	2.51 a	8.46 ab

¹Within the columns, the means between cycles and populations followed by the same letter (below) are not significantly different (Tukey's test $p \leq 0.05$);

²lycopene in FW and DW, fresh and dry weight, respectively, vitamin C in mg 100 g⁻¹, and titratable acidity in % citric acid.

The highest values are **bold**, and the lowest values are underlined.

Table 3.

Average soluble solid content, pH, lycopene content, titratable acidity, reducing sugar content, and vitamin C as a function of the crop cycle and population/genotype of tomato landraces cultivated under greenhouse conditions.

The composition of the 17 native tomato populations varied in terms of their °Brix value in the pulp, from 3.41 to 4.76; °Brix value in the juice, from 3.40 to 4.82; pH, from 4.07 to 4.44; lycopene content (FW), from 11.40 to 21.62 mg 100 g⁻¹; lycopene content (DW), from 257.8 to 461.9 mg 100 g⁻¹; titratable acidity, from 0.30 to 0.61%; reducing sugar content, from 1.20 to 2.51%; and vitamin C, from 3.95 to 9.32 mg 100 g⁻¹.

In terms of the crop cycle–genotype/population interaction, there were no significant differences in vitamin C content; that is, the environmental conditions did not affect vitamin C biosynthesis or lead to differences between populations (**Table 4**). For the other compounds, significant differences were observed in the

Pop./Cycle	°Brix		pH	Lycopene ²		Titratable acidity ²	Reducing sugars ²	Vitamin C ²
	Pulp	Juice		FW	DW			
L-010/2	4.47 d-g ¹	4.34 d-h	4.20 c-f	12.89 e-g	332.6 c-f	0.36 e-j	2.11 de	7.35 a
L-016/2	4.29 d-h	4.12 f-i	4.25 b-f	15.65 b-e	358.7 b-e	0.41 c-g	1.67 e-h	5.71 a
L-019/2	4.59 c-f	4.82 b-d	4.20 c-f	21.62 a	461.9 a	0.40 d-h	1.95 d-g	4.28 a
L-025/2	4.64 b-e	4.61 b-f	4.13 d-f	11.44 f-i	257.8 f-h	0.50 bc	2.03 d-f	5.38 a
L-040/1	3.87 g-j	<u>3.23</u> k	4.31 a-d	9.52 h-i	242.5 g-i	<u>0.27</u> k	1.70 d-h	—
L-040/2	3.94 f-j	3.80 h-k	4.26 b-f	17.05 bc	421.9 ab	0.35 f-k	1.59 e-h	7.60 a
L-043/1	4.63 b-e	4.17 e-i	4.15 d-f	14.48 c-g	311.7 d-g	0.46 b-d	2.25 cd	3.36 a
L-043/2	4.26 d-h	4.49 c-g	4.15 d-f	17.99 b	411.9 a-c	0.39 d-i	1.77 d-g	5.38 a
L-05/2	4.51 d-g	4.47 c-g	4.21 c-f	13.30 d-g	299.8 d-h	0.53 ab	1.56 f-h	5.54 a
L-059/1	5.43 a	4.50 c-g	<u>4.07</u> f	11.25 g-i	228.0 h-i	0.43 c-f	3.21 ab	10.03 a
L-059/2	3.63 h-j	3.92 g-j	4.22 c-f	11.87 f-i	319.5 d-g	0.37 e-j	1.41 gh	8.73 a
L-061/1	5.20 a-c	4.23 d-h	4.27 b-f	12.87 e-h	272.8 f-h	0.44 c-e	2.72 bc	10.09 a
L-061/2	3.87 g-j	3.91 g-j	4.30 a-e	14.30 c-g	359.5 b-e	0.33 g-k	1.52 f-h	9.07 a
L-067/1	5.57 a	5.70 a	4.10 ef	<u>9.49</u> i	<u>173.3</u> i	0.35 f-k	3.39 a	9.86 a
L-067/2	4.47 d-g	4.25 d-h	4.28 b-f	14.17 c-g	317.6 d-g	0.32 h-k	2.12 de	8.00 a
L-087/2	3.57 ij	3.40 jkl	4.23 c-f	11.66 f-i	337.5 c-f	0.34 f-k	1.48 f-h	3.95 a
L-09/2	4.65 b-e	4.78 b-e	4.07 f	15.40 be	325.9 df	0.61 a	1.79 dg	5.71 a
L-091/2	4.69 b-d	4.55 c-g	4.24 b-f	12.89 e-h	275.4 f-h	0.60 a	1.98 d-f	6.05 a

Pop./Cycle	°Brix		pH	Lycopene ²		Titratable acidity ²	Reducing sugars ²	Vitamin C ²
	Pulp	Juice		FW	DW			
L-095/2	3.79 h-j	4.07 f-i	4.26 b-f	11.40 f-i	280.2 e-h	0.32 h-k	1.72 d-h	8.00 a
L-096/2	<u>3.41</u> j	3.58 i-k	4.09 ef	16.62 b-d	454.6 a	0.37 e-j	<u>1.20</u> h	9.05 a
L-109/1	5.43 a	5.23 ab	4.51 a	16.80 bc	317.2 d-g	0.29 j-k	3.12 ab	10.58 a
L-109/2	4.09 d-i	4.03 f-j	4.36 a-c	13.81 c-g	335.3 c-f	0.34 f-k	1.84 d-g	7.84 a
L-110/1	5.26 ab	5.04 bc	4.45 ab	16.03 b-e	276.3 f-h	0.30 i-k	3.03 ab	11.01 a
L-110/2	4.02 e-j	3.92 g-j	4.28 b-f	14.72 b-f	367.0 b-d	0.30 i-k	1.98 d-f	5.92 a

¹In the columns, means followed by the same letter (below) are not significantly different (Tukey's test $p \leq 0.05$);
²lycopene in FW and DW, fresh and dry weight, respectively, vitamin C in $\text{mg } 100 \text{ g}^{-1}$, titratable acidity in % citric acid.
The highest values are **bold**, and the lowest values are underlined.

Table 4.

Interaction of crop cycle and genotype/population in terms of soluble solid content, pH, lycopene content, titratable acidity, reducing sugar content, and vitamin C content in the fruits of tomato landraces grown under greenhouse conditions.

crop cycle–population interactions. For example, populations L-040, L-043, L-059, L-061, L-067, L-109, and L-110 presented relatively high lycopene contents in cycle 2, and L-059, L-067, and L-110 presented relatively high contents of soluble solids and reducing sugars in cycle 1. The interaction results revealed that the accumulation of some metabolites in tomato fruits depends on the environmental conditions of cultivation and the response of the population (genotype) to these changes.

Native or local populations or genotypes (landraces) are characterized by high phenotypic heterogeneity between and within genotypes. Cebolla-Cornejo et al. [40] highlighted the importance of evaluating the environmental effects and interactions between populations and the environment to estimate intrapopulation variation. For example, Divéky-Ertsey et al. [41] evaluated the effects of genotype and genotype $\times$ environment interactions on the phytochemical composition of Hungarian tomato landraces grown in open fields and microtunnels for two consecutive years and determined that variations in microclimatic conditions in different years had greater effects. The location and production system of the quality and bioactive parameters, such as soluble solids, acidity, lycopene, phenolic compounds, and antioxidant activity, depend on the evaluated genotype.

In a second evaluation of the content of phenolic compounds, lycopene, vitamin C, and antioxidant activity in 27 populations of tomato landraces from Oaxaca, Mexico, they were also planted and cultivated in greenhouses but in a single evaluation cycle. The determination of total polyphenols, total flavonoids, and antioxidant activity (2,2-diphenyl-1-picrylhydrazyl (DPPH) and fluorescence recovery after photobleaching (FRAP) methods) was performed using UV–visible spectrophotometric techniques described by Benzie and Strain [42], Lin and Tang [43], and Singleton and Rossi [44]. The traditional tomato populations were significantly different ($p \leq 0.01$) in terms of °Brix value, pH, vitamin C content, lycopene content, total polyphenol content, flavonoid content, and antioxidant activity (DPPH and FRAP) on a wet basis (**Table 5**). Different outstanding populations of one or more compounds were

Pop. ID	°Brix	pH	Vit. C ²	Lycopene ²	Polyphenols ³	Flavonoids ⁴	Antioxidant act ⁵	
							DPPH	FRAP
Sq. Means	8.25**	0.127**	0.527**	1.96**	0.008**	0.017**	0.098**	0.136**
I-08	6.47 a-e ¹	3.97 c-g	6.11 b-g	15.86 a-d	0.223 a-e	0.051 a-c	0.918 a-d	0.841 a-f
I-31	7.37 a-c	3.88 fg	8.24 b-g	14.44 a-f	0.198 c-e	0.047 a-c	0.897 a-d	0.746 a-f
I-35	6.32 a-e	3.86 g	8.49 a-g	14.52 a-f	0.234 a-e	0.040 bc	1.012 a-c	1.048 ab
I-38	5.55 c-e	3.97 c-g	9.23 a-g	9.10 fg	0.224 a-e	0.031 c	0.803 cd	0.493 f
I-42	6.22 b-e	3.99 c-g	3.46 fg	11.56 d-g	0.199 c-e	0.029 c	0.871 a-d	0.818 a-f
I-51	5.13 de	3.99 c-g	9.76 a-f	9.40 e-g	0.192 c-e	0.016 c	0.914 a-d	0.799 a-f
X-01	6.28 b-e	4.30 a	12.43 ab	17.85 a-c	0.225 a-e	0.029 c	0.800 cd	0.727 a-f
X-02	6.04 c-e	4.27 a	7.66 b-g	14.60 a-f	0.213 b-e	0.051 a-c	0.843 b-d	0.586 c-f
X-03	4.91 e	4.24 ab	4.63 c-g	14.01 b-f	0.209 b-e	0.025 c	0.801 cd	0.496 f
X-04	6.73 a-e	4.11 bc	12.37 ab	12.70 c-g	0.240 a-e	0.037 bc	0.814 cd	0.603 b-f
X-05	7.27 a-c	4.08 cd	11.03 a-d	19.06 ab	0.246 a-d	0.048 a-c	0.973 a-d	0.968 a-e
X-06	6.07 c-e	4.09 cd	11.69 a-c	17.31 a-c	0.215 b-e	0.038 bc	0.803 cd	0.541 d-f
X-07	8.12 ab	4.04 c-e	15.53 a	16.33 a-d	0.269 ab	0.093 a	1.069 ab	1.052 ab
X-08	5.49 c-e	4.02 c-f	6.02 b-g	16.39 a-d	0.211 b-e	0.027 c	0.791 cd	0.634 a-f
X-09	5.05 de	4.06 c-e	9.54 a-g	12.43 c-g	0.185 de	0.021 c	0.806 cd	0.536 ef
X-10	6.27 b-e	4.07 c-e	6.80 b-g	14.78 a-e	0.228 a-e	0.029 c	0.776 d	0.707 a-f
X-12	7.00 a-d	4.02 c-f	6.70 b-g	19.62 a	0.200 c-e	0.047 a-c	0.770 d	0.683 a-f
X-13	6.77 a-e	4.04 c-e	4.46 d-g	16.21 a-d	0.177 e	0.042 bc	0.756 d	0.556 d-f
X-14	6.42 a-e	4.08 cd	9.69 a-g	15.95 a-d	0.206 b-e	0.027 c	0.829 cd	0.764 a-f
X-15	8.32 a	4.04 c-e	10.83 a-e	17.45 a-c	0.280 a	0.079 ab	1.089 a	1.096 a
COMP5	6.40 a-e	3.95 d-g	3.77 e-g	13.23 c-g	0.207 b-e	0.026 c	0.868 a-d	0.745 a-f
HCS-106A	5.73 c-e	3.92 e-g	3.75 e-g	13.13 c-g	0.203 c-e	0.039 bc	0.917 a-d	1.002 ad

Pop. ID	°Brix	pH	Vit. C ²	Lycopene ²	Polyphenols ³	Flavonoids ⁴	Antioxidant act ⁵	
							DPPH	FRAP
HCS-24	6.02 c-e	3.99 c-g	<u>2.51</u> g	12.48 c-g	0.239 a-e	0.037 bc	0.977 a-d	0.871 a-f
HCS-37	6.38 a-e	4.00 c-g	4.41 d-g	13.21 c-g	0.254 a-c	0.052 a-c	0.852 b-d	0.812 a-f
HCS-38	6.90 a-e	4.08 c d	3.65 e-g	12.82 c-g	0.193 c-e	<u>0.026</u> c	0.855 c-d	0.744 a-f
HCS-39	6.37 a-e	4.02 c-f	12.55 ab	15.57 a-d	0.222 a-e	<u>0.020</u> c	0.969 a-d	1.022 a-c
Floradade	5.59 c-e	4.05 c-e	6.46 b-g	<u>7.75</u> g	0.186 de	<u>0.022</u> c	0.900 a-d	0.658 a-f

¹In the columns, means followed by the same letter (low) are not significantly different (Tukey's test $p \leq 0.05$);
²lycopene and vitamin C in mg 100 g⁻¹ fresh weight (fw);
³polyphenols in mg equivalents of gallic acid g⁻¹ fw;
⁴flavonoids in mg equivalents of quercetin g⁻¹ fw;
⁵FRAP and DPPH in μmol equivalents of Trolox g⁻¹ fw.
The highest values are **bold**, and the lowest values are underlined.

Table 5.
Phytochemical composition and antioxidant activity in the fruits of 27 populations of tomato landraces grown under greenhouse conditions.

identified; for example, the X-15 population excelled in °Brix, total polyphenols, and antioxidant activity (DPPH and FRAP); X-01 and X-02, in pH; X-07, in vitamin C and flavonoids; and X-12, in lycopene (Table 5). The values of these populations exceeded those of the commercial variety Floradade, which was used as a control, indicating that the native tomato populations are sources of phytochemical compounds of nutritional and nutraceutical interest for food and health purposes.

The following average value ranges were observed between populations for the phytochemical compounds: soluble solids, 4.91–8.32°Brix; pH, 3.86–4.30; vitamin C, 2.51–15.53 mg 100⁻¹ g; lycopene, 9.10–19.62 mg 100⁻¹ g; polyphenols, 0.177–0.280 mg 100⁻¹ g; flavonoids, 0.016–0.093 mg 100⁻¹ g; antioxidant activity determined via the DPPH method, 0.756–1.089 μg of Trolox 100⁻¹ g; and antioxidant activity determined via FRAP, 0.496–1.096 μg of Trolox 100⁻¹ g. The values of these components were very similar to or greater than those reported in other kidney tomato populations of the Sierra Sur, Istmo, Sierra Norte, and Central Valleys of the State of Oaxaca, Mexico [45]. For example, the X-15, X-12, and X-07 populations in this study presented higher contents of soluble solids, lycopene, and vitamin C on a fresh basis, respectively, than the tomato populations mentioned previously. Bioactive compounds are highly influenced by the environment, management conditions, genotype or variety, and interactions between them [46, 47]; however, in such studies, populations of landraces with high variability in fruit or plant traits, even within the same population, are more or less constant in composition. Medina-Dzul et al. [48] also reported high variation between populations of native tomatoes in southern Mexico in terms of lycopene, total phenols, and flavonoids, which they attributed essentially to environmental effects rather than to the genotype.

Growing traditional tomatoes helps preserve the flavors of interest to their growers and has recently been revalued, as the characteristic flavors, aromas, textures, and colors of traditional tomatoes are associated with a wide range of antioxidant compounds (phenolic compounds, lycopene, and vitamin C), which help in the

prevention of cardiovascular and chronic degenerative diseases [49]. The frequent consumption of these native tomatoes among the rural Mexican population has a strong impact on human health, and among these communities, there are families who continue to preserve traditional diets and are recognized as the longest-living in the community. Together, traditional tomato plants have local and regional value, and their loss of diversity is due to sociocultural factors such as the food transition and more urban ways of life.

4. Remarks

First, one of the main contributions of Mexican tomato farmers and conservators under domestication and the continued cultivation under their production principles is the contribution to on-farm/*in situ* agrobiodiversity, which exceeds the amount of diversity preserved *ex situ* or in gene banks. This diversity of tomatoes is closely linked to Mexican gastronomic diversity, recognized by the FAO/UNESCO as an intangible heritage of humanity. The decades-long absence of formal institutional tomato genetic improvement programs in Mexico has allowed the almost natural or regional resurgence of tomatoes for traditional uses; however, this does not indicate that transnational seed companies dominate the market, with the planting of varieties mainly for export purposes to the United States or Canada, and the south-southeastern region of Mexico, where subsistence farmers predominate, is thus not of interest to transnational seed companies. In summary, tomato exporters to the United States are mainly located in the central-northern region of Mexico, and those from the central-south-southeastern region produce for the national, regional, or local markets; however, in this region, the greatest diversity of tomatoes is preserved because wild forms occur close to the cultivation plots, even when their presence is only observed during the season or after the rainy season.

In the ecogeographic context of the origin of the diversity described for the populations evaluated for characterization and preliminary agromorphological evaluation, different differential traits of their close parents can be distinguished. For example, at least six groups are phenotypically distinguished as having a similar fruit shape (shoulder blade) but differ in fruit size and number of locules, for example, large fruits 5.1 and 7.2 cm in length and diameter compared with small fruits 3.5 and 5.6 cm in length. This is an obvious way to recognize the variability in fruit sizes in the field, but it also influences reproductive physiology and plant characteristics.

In terms of fruit composition, the experiments performed in this study helped characterize the wide variability in pH, soluble solids (°Brix), titratable acidity, reducing sugars, lycopene, polyphenols, flavonoids, vitamin C, and antioxidant activity among populations of local tomato varieties or farmers' varieties. In these traditional agrosystems, the conscious and unconscious introduction of wild forms and the subsequent selection of farmers in their cultivation plots promote different degrees of recombination [27]. The frequency of recombination also influences the composition of the fruit between populations, as the composition of the fruit is influenced by the effects of the crop cycle or crop conditions and genotypic/population–environment interactions; however, these populations consistently have a short shelf life. Based on the studies carried out, a genetic improvement program with local objectives and purposes has been initiated.

Acknowledgements

We greatly appreciate all the Mexican farmers who have allowed us to visit their tomato plots, take samples of plants or fruits, and exchange ideas with the purpose of improving their cultivation. We also thank the National Polytechnic Institute for support with field trips through the SIP-20240902 and SIP-20240822 projects.

Conflict of interest

The authors declare that they have no conflicts of interest.

Author details

Araceli Minerva Vera-Guzmán¹, Mónica Lilian Pérez-Ochoa¹,
José Cruz Carrillo-Rodríguez² and José Luis Chávez-Servia^{1*}

1 CIIDIR-Oaxaca, Instituto Politécnico Nacional, Oaxaca, Mexico

2 Instituto Tecnológico del Valle de Oaxaca, Tecnológico Nacional de México, Oaxaca, Mexico

*Address all correspondence to: jchavezs@ipn.mx

IntechOpen

© 2025 The Author(s). Licensee IntechOpen. This chapter is distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. 

References

- [1] Meyer RS, Purugganan MD. Evolution of crop species: Genetics of domestication and diversification. *Nature*. 2013;**14**:840-852. DOI: 10.1038/nrg3605
- [2] Peralta IE, Spooner DM. History, origin and early cultivation of tomato (*Solanaceae*). In: Razdan MK, Mattoo AK, editors. *Genetic Improvement of Solanaceous Crops*. Vol. 2, Tomato. Enfield, New Hampshire, USA: Science Publishers; 2007. pp. 1-24
- [3] Blanca J, Cañizares J, Cordero L, Pascual L, Diez MJ, Nuez F. Variation revealed by SNP genotyping and morphology provides insight into the origin of the tomato. *PLoS One*. 2012;**7**(10):e48198. DOI: 10.1371/journal.pone.0004198
- [4] Razifard H, Ramos A, Della-Valle AL, Bodary C, Goetz E, Manser EJ, et al. Genomic evidence for complex domestication history of the cultivated tomato in Latin America. *Molecular Biology and Evolution*. 2020;**37**(4):1118-1132. DOI: 10.1093/molbev/msz297
- [5] San-San-Yi JSA, Fujimura T, Yamanaka S, Watanabe J, Watanabe KN. Potential loss of unique genetic diversity in tomato landraces by genetic colonization of modern cultivars at a non-center of origin. *Plant Breeding*. 2008;**127**:189-196. DOI: 10.1111/j.1439-0523.2007.01446.x
- [6] Pons C, Casals J, Palombieri S, Fontanet L, Riccini A, Rambia JL, et al. Atlas of phenotypic, genotypic and geographical diversity present in the European traditional tomato. *Horticulture Research*. 2022;**9**:uhac112. DOI: 10.1093/hr/uhac112
- [7] Rocchi L, Paolotti L, Cortina C, Boggia A. Conservation of landrace: The key role of the value for agrobiodiversity conservation. An application on ancient tomatoes varieties. *Agriculture and Agricultural Science Procedia*. 2016;**8**:307-316. DOI: 10.1016/j.aaspro.2016.02.025
- [8] Lázaro A. Tomato landraces: An analysis of diversity and preferences. *Plant Genetic Resources*. 2018;**14**(4):315-324. DOI: 10.1017/S1479262117000353
- [9] Cammareri M, Sinesio F, Paparao M, Pons C, Romero-del Castillo R, Saggia-Civitelli E, et al. Local agro-environmental conditions impact fruit quality sensory properties and consumer acceptance of long shelf-life tomatoes. *Agronomy*. 2023;**13**:1265. DOI: 10.3390/agronomy13051265
- [10] Martínez-Vázquez EA, Hernández-Bautista A, Lobato-Ortiz R, García-Zavala JJ, Reyes-López D. Exploring the breeding potential of Mexican tomato landraces. *Scientia Horticulturae*. 2017;**220**:317-325. DOI: 10.1016/j.scienta.2017.03.031
- [11] Massaretto IL, Albaladejo I, Purgatto E, Flores FB, Plascencia F, Egea-Fernández JM, et al. Recovering tomato landraces simultaneously improve fruit yield and nutritional quality against salt stress. *Frontiers in Plant Science*. 2018;**9**:1778. DOI: 10.3389/fpls.2018.01778
- [12] Boziné-Pullai K, Csambalik L, Drexler D, Reiter D, Tóth F, Bogdányi FT, et al. Tomato landraces are competitive with commercial varieties in terms of tolerance to plant pathogens—A case study of Hungarian gene bank accessions on organic farms. *Diversity*. 2021;**13**:195. DOI: 10.3390/d13050195

- [13] Ladewig P, Trejo-Téllez LI, Servín-Juárez R, Contreras-Oliva G-MFC. Growth, yield and fruit quality of Mexican tomato landraces in response to salt stress. *Noulae Botanicae Horti Agrobotanici Cluj-Napoca*. 2021;**49**(1):12005. DOI: 10.15835/nbha49112005
- [14] Tagiakas RI, Avdikos ID, Goula A, Koutis K, Nianiou-Obeidat I, Mavromatis AG. Characterization and evaluation of Greek tomato landraces for productivity and fruit quality traits related to sustainable low-input farming systems. *Frontiers in Plant Science*. 2022;**13**:994530. DOI: 10.3389/fpls.2022.994530
- [15] Donoso A, Carrasco B, Araya C, Salazar E. Genetic diversity and distinctiveness of Chilean Limachino tomato (*Solanum lycopersicum* L.) reveal an *in situ* conservation during the 20th century. *Frontiers in Conservation Science*. 2023;**4**:1156786. DOI: 10.3389/fcsc.2023.1156786
- [16] Maxin A, Albu VC, Vodnar DC, Mihaiescu T, Mang SM, Camele I, et al. Assessment of tomato (*Solanum lycopersicum*) landraces for their agronomic, biochemical characteristics and resistance to *Phytophthora infestans*. *Agronomy*. 2023;**12**:21. DOI: 10.3390/agronomy13010021
- [17] Posadinu CM, Rodríguez M, Conte P, Piga A, Attene G. Fruit quality and shelf-life of Sardinian tomato (*Solanum lycopersicum* L.) landraces. *PLoS One*. 2023;**18**(12):e0290166. DOI: 10.1371/journal.pone.0290166
- [18] Garzón-Tiznado JA, Melgoza-Villagómez CM, López-Orona CA, Castro-Espinoza L, Velarde-Félix S, Figueroa-Pérez MG, et al. Resistance to *Candidatus Liberibacter solanacearum* haplotype B in tomato landraces from Mexico. *Journal of Phytopathology*. 2020;**168**:632-640. DOI: 10.1111/jph.12943
- [19] Velasco-Alvarado MJ, Lobato-Ortiz R, García-Zavala JJ, Castro-Brindis R, Cruz-Izquierdo S, Corona-Torres T, et al. Mexican native tomatoes as rootstocks to increase fruit yield. *Chilean Journal of Agricultural Research*. 2017;**77**(3):187-193. DOI: 10.4067/S0718-58392017000300187
- [20] Marín-Montes IM, Rodríguez-Pérez JE, Sahagún-Castellanos J, Hernández-Ibáñez L, Velasco-García AM. Morphological and molecular variation in 55 native tomato collections from Mexico. *Revisita Chapingo Serie Horticultura*. 2016;**22**(2):117-131. DOI: 10.5154/r.rchsh.20216.03.008
- [21] Marín-Montes IM, Lobato-Ortiz R, Carrillo-Castañeda G, Rodríguez-Pérez JE, García-Zavala JJ, Velasco-García AM. Alellic richness of native tomato populations (*Solanum lycopersicum* L.) for plant breeding. *Agrociencia-Mexico*. 2019;**53**:355-370
- [22] Chávez-Servia JL, Carrillo-Rodríguez JL, Vera-Guzmán AM, Rodríguez-Guzmán E, Lobato-Ortiz R. Utilización actual y potencial del jitomate silvestre mexicano. Oaxaca, México: Subsistema Nacional de Recursos Fitogenéticos para la Alimentación y la Agricultura (SINAREFI), Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación, CIIDIR-Unidad Oaxaca del Instituto Politécnico Nacional e Instituto Tecnológico del Valle de Oaxaca; 2011. 72 p
- [23] Moreno-Ramírez YR, Hernández-Bautista A, Ramírez-Vallejo P, Castillo-González F, Rocandio-Rodríguez M, Vanoye-Eligio V, et al. Social and environmental factors in the diversity of tomato landraces from

the south-central region of Mexico. *Ciencia Rural*. 2019;**49**(5):e20180514. DOI: 10.1590/0103-8478cr20180514

[24] Carrillo-Rodríguez JC, Sosa-Hernández N, Vera-Guzmán AM, Chávez-Servia. Diversidad biocultural de tomate nativo en Oaxaca, México. Desde el Herbario CICY. 2023;**15**:18-23

[25] Boege-Schmidt E. El Patrimonio Biocultural de los Pueblos Indígenas de México: Hacia la Conservación *in situ* de la Biodiversidad y Agrobiodiversidad en los Territorios Indígenas. 2nd ed. México, D.F: Instituto Nacional de Antropología e Historia y Comisión Nacional para el Desarrollo de los Pueblos Indígenas; 2010. 342 p

[26] Estrada-Castellanos JB, Carrillo-Rodríguez JC, Jerez-Salas M, Chavez-Servia JL, Perales-Segovia C. Small farmer practices for production improvement of the kidney-type tomato landraces: A case study in Oaxaca. *African Journal of Agricultural Research*. 2011;**6**(13):3176-3182

[27] Ríos-Osorio O, Chávez-Servia JL, Carrillo-Rodríguez JC. Traditional production and diversity of native tomato (*Solanum lycopersicum* L.): A study case in Tehuantepec-Juchitan, Mexico. *Agricultura, Sociedad y Desarrollo*. 2014;**11**(1):35-51

[28] International Plant Genetic Resources Institute (IPGRI). Descriptors for Tomato (*Lycopersicon* spp.). Rome, Italy: International Plant Genetic Resources Institute; 1996. 46 p

[29] Muños S, Ranc N, Botton E, Bérard A, Rolland S, Duffé P, et al. Increase in tomato locule number is controlled by two single-nucleotide polymorphisms located near WUSCHEL. *Plant Physiology*. 2011;**156**(4):2244-2254. DOI: 10.1104/pp.111.173997

[30] Villena J, Moreno C, Roselló S, Cebolla-Cornejo J, Moreno MM. Dissecting a vegetable landrace: Components of variation in Spanish 'Moruno' tomatoes as a case studio. *Scientia Horticulturae*. 2023;**318**:112128. DOI: 10.1016/j.scienta.2023.112128

[31] Felföldi Z, Ranga F, Roman IA, Sestras AF, Vodnar DC, Prohens J, et al. Analysis of physico-chemical and organoleptic fruit parameters relevant for tomato quality. *Agronomy*. 2022;**12**(5):1232. DOI: 10.3390/agronomy12051232

[32] Pérez-Díaz F, Arévalo-Galarza M, Pérez-Flores LJ, Lobato-Ortiz R, Ramírez-Guzmán ME. Crecimiento y características postcosecha de frutos de genotipos nativos de tomate (*Solanum lycopersicum* L.). *Revista Fitotecnia Mexicana*. 2020;**43**(1):89-99

[33] AOAC. Official Methods of Analysis. 15th ed. Vol. 2. Washington D.C USA: Association of Official Analytical Chemists inch. 400 – 2200 Wilson Boalevard, Arlington Virginia USA; 1990. pp. 910-928

[34] Davis AR, Fish WW, Perkins-Veazie P. A rapid spectrophotometric method for analyzing lycopene content in tomato and tomato products. *Postharvest Biology and Technology*. 2003;**28**(3):425-430. DOI: 10.1016/S0925-5214(02)00203-X

[35] Dürüst N, Sümengen D, Dürüst Y. Ascorbic acid and element contents of foods of Trabzon (Turkey). *Journal of Agricultural and Food Chemistry*. 1997;**45**(6):2085-2087. DOI: 10.1021/jf9606159

[36] Brandt S, Pék Z, Barna É, Lugasi A, Helyes L. Lycopene content and colour of ripening tomatoes as affected by

environmental conditions. Journal of the Science of Food and Agriculture. 2006;**86**(4):568-572. DOI: 10.1002/jsfa.2390

[37] Roselló S, Adalid AM, Cebolla-Cornejo J, Nuez F. Evaluation of the genotype, environment and their interaction on carotenoid and ascorbic acid accumulation in tomato germplasm. Journal of the Science of Food and Agriculture. 2011;**91**(6):1014-1021. DOI: 10.1002/jsfa.4276

[38] Gaspar-Peralta P, Carrillo-Rodríguez JC, Chávez-Servia JL, Vera-Guzmán AM, Pérez-León I. Variación de caracteres agronómicos y licopeno en líneas avanzadas de tomate (*Lycopersicon esculentum* L.). Phytón, Revista Internacional de Botánica Experimental. 2012;**81**:15-22

[39] Méndez-Infante I, Vera-Guzmán AM, Chávez-Servia JL, Carrillo-Rodríguez JC. Quality of fruits in Mexican tomato (*Lycopersicon esculentum* Mill.) landraces. Vitae-Foods: Science, Engineering and Technology. 2011, 2011;**18**(1):26-32. DOI: 10.17533/udea.vitae.6170

[40] Cebolla-Cornejo J, Roselló S, Nuez F. Phenotypic and genetic diversity of Spanish tomato landraces. Scientia Horticulturae. 2013;**2013**(162):150-164. DOI: 10.1016/j.scienta.2013.07.044

[41] Divéky-Ertsey A, Ladányi M, Biró B, Máté M, Drexler D, Tóth F, et al. Tomato landraces may benefit from protected production—Evaluation on phytochemicals. Horticulturae. 2022;**8**:937. DOI: 10.3390/horticulturae8100937

[42] Benzie IFF, Strain JJ. Ferric reducing/antioxidant power assay: Direct measure of total antioxidant activity of biological fluids and modified version for simultaneous measurement of total

antioxidant power and ascorbic acid concentration. Methods in Enzymology. 1999;**299**:15-27. DOI: 10.1016/S0076-6879(99)99005-5

[43] Lin JY, Tang CY. Determination of total phenolic and flavonoid contents in selected fruits and vegetables, as well as their stimulatory effects on mouse splenocyte proliferation. Food Chemistry. 2007;**101**(1):140-147. DOI: 10.1016/j.foodchem.2006.01.014

[44] Singleton VL, Rossi JA. Colorimetry of total phenolics with phosphomolybdic-phosphotungstic acid reagents. American Journal of Enology and Viticulture. 1965;**16**(3):144-158. DOI: 10.5344/ajev.1965.16.3.144

[45] Vera-Guzmán AM, Chávez-Servia JL, Carrillo-Rodríguez JC. Variación en calidad de frutos de poblaciones de tomate (*Solanum lycopersicum* L.) tipo riñón. Journal of the Interamerican Society for Tropical Horticulture. 2011;**55**:82-85

[46] Chávez-Servia JL, Vera-Guzmán AM, Carrillo-Rodríguez JC, Pachecho-Triste IA, Crisanto-Juárez AU. Variación morfológica y de licopeno en frutos de tomate semidomesticado y cultivado en Oaxaca, México. Journal Interamerican Society of Tropical Horticulture. 2011;**54**:151-153

[47] Crisanto-Juárez AU, Vera-Guzmán AM, Chávez-Servia JL, Carrillo-Rodríguez JC. Calidad de frutos de tomates silvestres (*Lycopersicon esculentum* var. *cerasiforme* Dunal) de Oaxaca, México. Revista Fitotecnia Mexicana. 2010;**33**(SPE4):7-13

[48] Medina-Dzul K, Latournerie-Moreno L, Ruíz-Sánchez E, Díaz-Mayo J, Ortiz-Salazar G. Bioactive compounds in 28 native tomato accessions from southeast Mexico. Journal of Applied

Botany and Food Quality. 2024;**97**:45-53.
DOI: 10.5073/JABFQ.2024.097.006

[49] Khan UM, Sevindik M, Zarrabi A, Nami M, Ozdemir B, Kaplan DN, et al. Lycopene: Food sources, biological activities, and human health benefits. *Oxidative Medicine and Cellular Longevity*. 2021;**2021**(1):2713511. DOI: 10.1155/2021/2713511

The Experience in Planting *Solanum lycopersicum*: Organic Cultivation in East Siberia, Transgenesis and the Connection with Plasticity of Tomato Genome Expression

*Natalya Igorevna Rekoslavskaya, Rurik Salyaev,
Tatyana Kopytina, Irina Sotnikova and Irina Mokschonova*

Abstract

The technology for large-scale production of vine-ripening tomatoes is well developed for greenhouses and even for open ground in the Irkutsk region. The climate of Eastern Siberia is characterized by early frosts until about mid or late May in spring and from mid-August in autumn. Therefore, until the 1960s, growing tomatoes in Siberia was a difficult task both on farms in villages and in industrial agriculture, since the old style glass-covered greenhouses were not reliable and did not provide protection against low outside temperatures. It was only when long tunnel-type greenhouses with electrical heating covered with polymer film were used to cover greenhouses where large-scale tomato growing became successful. Tomato is widely used for scientific research purposes, especially for microcloning, micropropagation, and genetic transformation *in vitro* experiments, and for studying leaf-stem morphogenesis and embryogenesis. When conducting these experimental studies, different mediums using phytohormones and micronutrients were proven to be quite useful. Tomato plants were used for developing “edible” vaccines against HIV-1, HBV and HPV. The plasticity of tomato and its high survival rate under various abiotic stresses are due to the presence of a huge endogenous pool of the precursor of auxin biosynthesis.

Keywords: tomato propagation, green houses, *in vitro* cultivation, “edible” vaccines against HIV, HBV, HPV, N-malonyl-D-tryptophan

1. Introduction

1.1 Organic cultivation of tomato in Irkutsk region of East Siberia

Tomato is a heat-loving plant introduced from Central and South America and was used as an ornamental plant. In the nineteenth century, tomato came to Europe to be

grown as a cultivated plant in garden, including Russia. To date, tomato cultivation has reached approximately 60% of all areas used for growing vegetables, including greenhouses.

The annual need for tomatoes for humans is 25–30 kg per year, since tomato is a rich source of vitamins, antioxidants and beneficial alkaloids, such as tomatine, esculesin, lycopene, which have high medicinal use.

The climate of Eastern Siberia is characterized by early frosts until about mid or late May in spring and from mid-August in autumn. Until the 1960s, tomatoes were not grown in open ground in vegetable farms and industrial production. Only with the use of polymer films for covering tomatoes in film tunnel greenhouses has the cultivation of tomatoes become a highly profitable and highly agro-economic production (**Figure 1**).



Figure 1.

Tunnel greenhouse with film coating on a wire frame for growing tomatoes from April to October.



Figure 2.

High-tech production of tomato fruits in a tunnel greenhouse at the field site of SIPPB SB RAS. Photo made by V. A. Korotkoruchko.



Figure 3.
The cover of the book of the author Yuri Fedorovich Palkin: “Tomato in open ground and greenhouses in garden plots of the Irkutsk region”. Publishing Haus “Oblmashinform”. Irkutsk, 2004 (in Russian) [1].

Heated film greenhouses made it possible to grow tomatoes from April to November, which turned out to be economically advantageous for obtaining mass harvests of up to 70 tons of tomato fruits per hectare (**Figure 2**).

The use of new promising agricultural technologies made it possible to bring tomato production to a level that fully satisfies the demand of the population.

Since 1970, the head of the Laboratory of Plant Productivity Physiology, SIPPB SB RAS, Doctor of Agricultural Sciences, Professor Yuri Fedorovich Palkin and his team, have developed innovative technologies for obtaining high and early yields of tomato fruits in film greenhouses for usage among the local population of Irkutsk and the surrounding region (**Figure 3**).

Currently, a powerful infrastructure has been created in the Irkutsk region—electrical, water supply networks, roads on a vast territory of 40 thousand hectares to obtain high and early yields of tomato fruits ripened on plants, regardless of natural conditions.

The purpose of the chapter was to demonstrate the wide possibilities of experimental work with tomatoes, using their high qualities of stability, plasticity, survival under unfavorable conditions and in harsh conditions of transgenesis.

2. Cultivation of tomato *in vitro*

2.1 Materials and methods

2.1.1 Composition of tissue culture media and mixtures of vitamins and microelements used

Seeds of *Solanum lycopersicum* Mill. var. Ventura were sterilized in a 2% sodium hypochlorite solution for 15 minutes and then washed with 3 portions of sterile distilled water for 5–10 minutes each wash.

Sterilized seeds were laid out on $\frac{1}{2}$ MS agar media in Phytakon or Magenta vessels and placed under low light in a plant room. After 12–14 days (but no later), the seedlings were divided into cotyledons and hypocotyls, which were laid out without additional sterilization on appropriate media containing sucrose, macroelements according to Murashige and Skoog, vitamins, growth regulators and phytohormones. To avoid the release of endosymbionts from explants into agar medium, 10 mg/l AgNO_3 and 8 mg/l KJ were added to the MS medium.

The work used phytohormones, at concentrations: 0.1–5 mg/l indolylbutyric acid (IBA), 1–2 mg/l 2,4-dichlorophenoxyacetic acid (2,4-D), 1–5 mg/l benzylaminopurine (BAP), 1 mg/l gibberellin (GA) and 25 mg/l epibrassinolide (Bras).

2.1.1.1 Compositions of the media

Murashige and Skoog (MS) medium (basic salt) [2], g/l:

- $\text{KNO}_3 = 1.9$
- $\text{NH}_4\text{NO}_3 = 1.65$
- $\text{MgSO}_4 \cdot 7 \text{H}_2\text{O} = 0.37$
- $\text{CaCl}_2 \cdot 2\text{H}_2\text{O} = 0.44$
- $\text{KH}_2\text{PO}_4 = 0.17$
- $\text{MnSO}_4 \cdot 4\text{H}_2\text{O} = 0.0223$

Heller's medium (ammonium-free) [3], g/l

- $\text{CaCl}_2 = 0.057$
- $\text{KCl} = 0.75$
- $\text{MgSO}_4 = 0.122$
- $\text{NaNO}_3 = 0.6$
- $\text{NaH}_2\text{PO}_4 = 0.11$

McCown's medium (reducing) [4], g/l

- $\text{CaCl}_2 = 0.073$
- $\text{Ca}(\text{NO}_3)_2 = 0.6$
- $\text{KH}_2\text{PO}_4 = 0.17$
- $\text{K}_2\text{SO}_4 = 0.99$

- $\text{MgSO}_4 = 0.181$

- $\text{NH}_4\text{NO}_3 = 0.4$

Microelements according to Murashige and Skoog [2], mg/l:

- $\text{H}_3\text{BO}_3 = 6.2$

- $\text{MnSO}_4 \cdot 4\text{H}_2\text{O} = 22.3$

- $\text{ZnSO}_4 \cdot 4\text{H}_2\text{O} = 8.6$

- $\text{CuSO}_4 \cdot 5\text{H}_2\text{O} = 0.025$

- $\text{CoCl}_2 \cdot 6\text{H}_2\text{O} = 0.025$

- $\text{Na}_2\text{MoO}_4 \cdot 2\text{H}_2\text{O} = 0.25$

Fe-chelate solution, g/l:

- $\text{FeSO}_4 \cdot 7\text{H}_2\text{O} = 27.8$

- $\text{Na EDTA} \cdot 2\text{H}_2\text{O} = 37.3$

Vitamins according to Murashige and Scoog [2], mg/l:

- Meso-inositol = 100

- Thiamine = 10.0

- Nicotinic acid = 0.5

- Pyridoxine = 0.5

Vitamins according to Kao and Michayluk [5], mg/l

- Nicotinamide = 1

- Ascorbic acid = 1

- Vitamin A = 10

- Vitamin D₃ = 0.5

- Ca-pantothenate = 0.01

- Vitamin B₁₂ = 0.2

- p-Aminobenzoic acid = 0.01

- Biotin = 0.005

- Choline chloride = 0.5
- Riboflavin = 0.1

Antibiotics, mg/l:

- Kanamycin = 25–100
- Cefotaxime = 50–100
- AgNO₃ = 10
- KJ = 8

3. Results

3.1 The searches for zones of 12-day-old tomato seedlings sensitive to the action of phytohormones

In order to induce dedifferentiation in the cotyledons and hypocotyls of tomato seedlings and obtain calli capable of shoot regeneration, it was necessary to take 12-day-old seedlings. At later times, the mitotic index in explants sharply decreased and the ability to induce dedifferentiation and regeneration decreased significantly.

To determine the zones with the highest sensitivity to phytohormones, hypocotyl explants with removed roots and separated cotyledons were laid out on agar MS medium, containing 1 mg/l BAP, 1 mg/l IBA and 25 mg/l Bras, 10 mg/l AgNO₃ and 8 mg/l KJ (**Figure 4**).

As can be seen in **Figure 4(1)**, cotyledons laid flat and explants without roots began to grow on the side or part of their surface that was adjacent to the agar. In explants, the hypocotyl zone under the cotyledons turned out to be the most sensitive to phytohormones. Predominantly, it was due to the growth of this zone that the explant bent by 90° (**Figure 4(2)**). The twice increase in the concentrations of BAP and IBA led to the formation of calluses on the cut end of separated cotyledons (**Figure 4(3)**). The addition of 1 mg/l 2,4-D to the medium resulted in root formation in the cut zones (**Figure 4(4)**). If the BAP concentration was increased to 5 mg/l, then callus formation did not occur, but direct organogenesis began in the cut zone (**Figure 4(5)**). In hypocotyl segments, direct organogenesis began in the cut zone of basal part (**Figure 4(6)**). An excess of cytokinin is indicated by the blueness of the explants, which arose as a result of a lack of phosphorus in these objects under these conditions (**Figure 4(5)** and **(6)**).

Therefore, the increase in concentrations of BAP was more responsible for the dedifferentiation and callus formation of isolated cotyledons (**Figure 5**).

With a decrease in BAP concentration, leaf-stem organogenesis began on morphogenic calli (**Figure 6**).

When morphogenic calli of tomato cotyledons were transferred to a hormone-free medium, a rapid burst of organogenesis and rhizogenesis began (**Figure 7**).

Figure 8 shows the mass development of explants and regenerants after transfer on hormone-free 1/2 MS medium. For mass production of regenerants, it was necessary to reduce the amount of ammonia nitrogen to prevent the accumulation of toxic ammonia in vessels or use ammonia-free media.

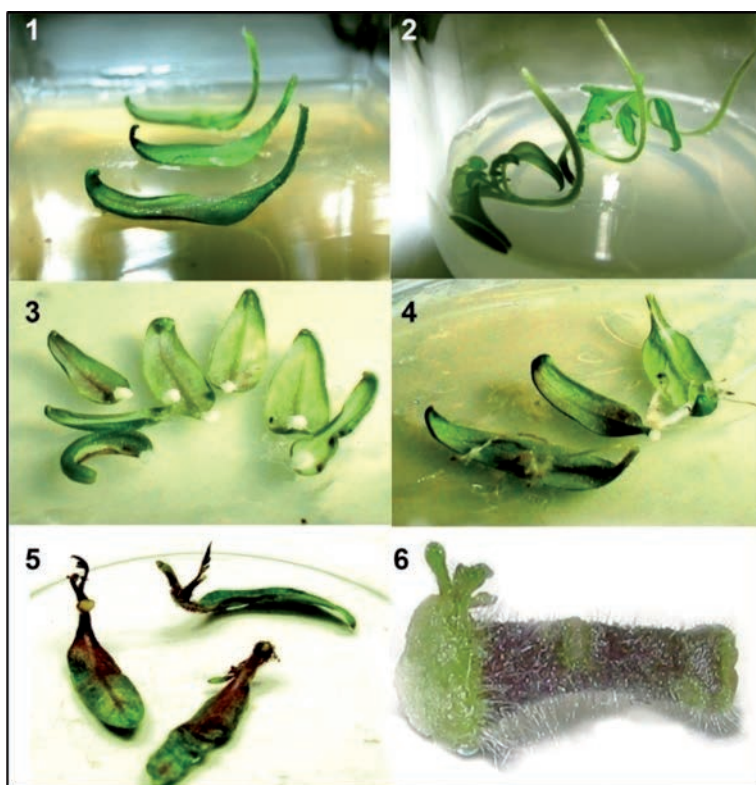


Figure 4.
 The sensitivity response of organogenesis of tomato explants of 12-day-old seedlings to different phytohormones in MS medium + AgNO_3 + KI + Bras. $\text{N}^\circ\text{N}^\circ$ (1,2)—balanced concentration of 1 mg/l BAP and 1 mg/l IBA; (3)—increased BAP to 2 mg/l and IBA to 2 mg/l; (4)—the addition of 1 mg/l 2,4-D; (5, 6)—increased BAP to 5 mg/l.

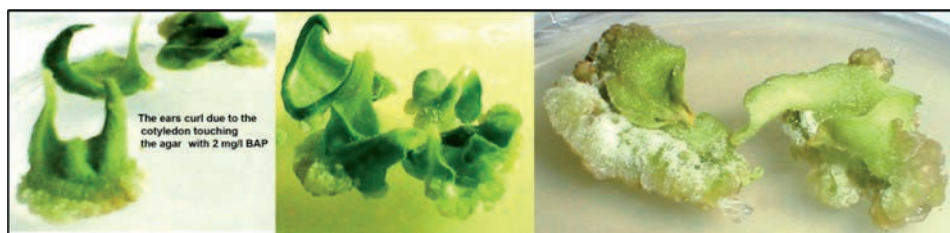


Figure 5.
 The dedifferentiation of cotyledons and calluses formation in the presence of increased level of BAP. MS medium + AgNO_3 + KJ + Bras.

Upper in the center: stock tomato cotyledons callus (2 mg/l IBA + 5 mg/l BAP).

For mass rooting of regenerants, the use of 0.5 mg/l ABA was successful (Figure 9).

During the accommodation of the regenerants to open air, the lid of the Magenta vessels was opened, starting from 5 minutes, gradually increasing the opening intervals during about 2 weeks (Figure 10).

The regenerants, strengthened after accommodation in air in Magenta vessels, took root well after being placed in a greenhouse and gave a good harvest (Figure 11).

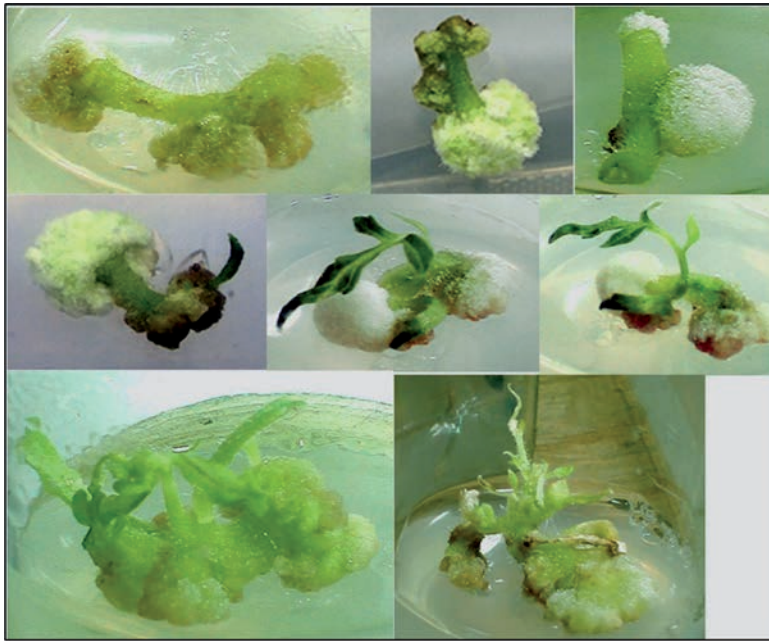


Figure 6.
Beginning of leaf-stem morphogenesis on morphogenic cotyledon calli with a decrease in BAP concentration.



Figure 7.
A burst of leaf-stem organogenesis and rhizogenesis after the transfer of morphogenic calluses on hormone-free MS medium.

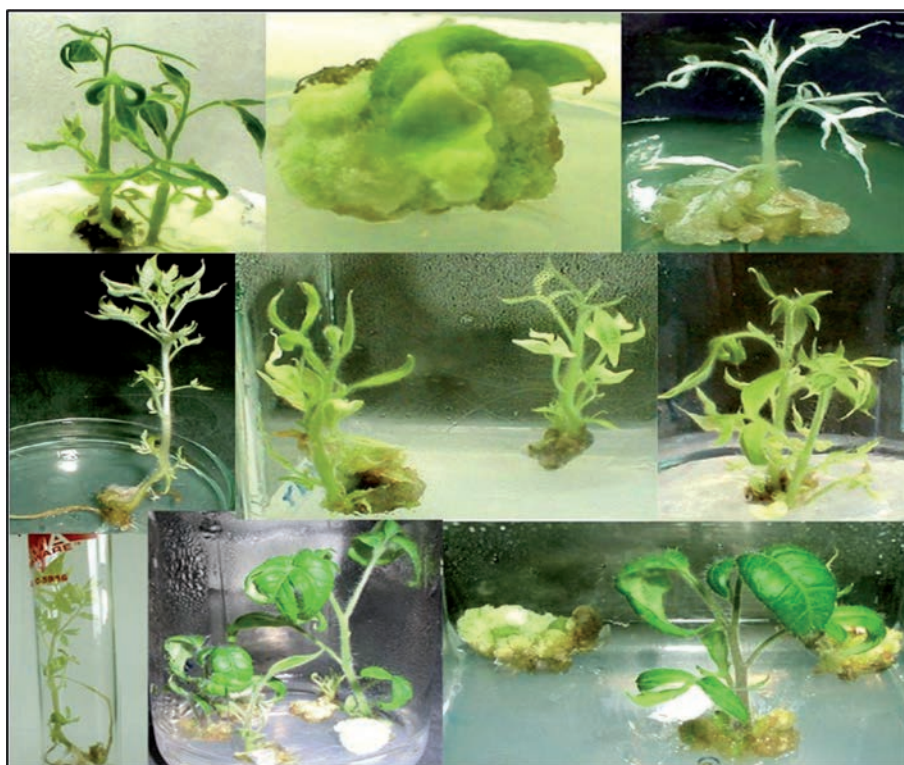


Figure 8.
 Developing of in vitro plantlets from regenerants of tomato cotyledons calluses in 1/2 MS free of phytohormones.

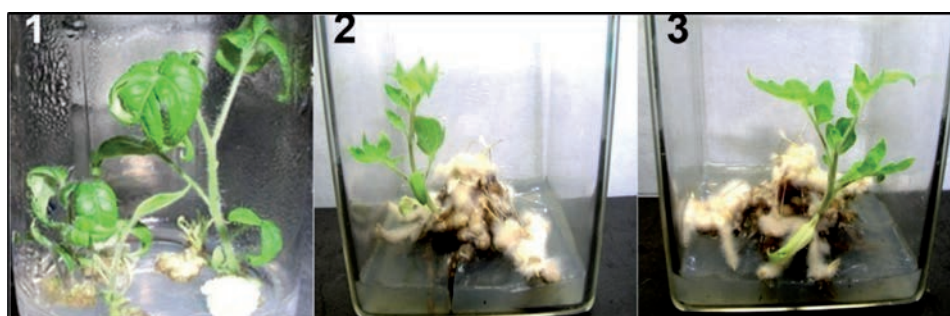


Figure 9.
 Mass rooting of regenerants induced by 0.5 mg/l ABA: №№ (2 and 3). № (1)—control without 0.5 mg/l ABA.

3.2 Development of oral plant “edible” vaccines against dangerous infectious diseases on the basis of tomato fruits

3.2.1 The concept of an “edible” vaccine based on transgenic plants

In 1990, WHO and a group of philanthropic organizations established the Children's Vaccine Initiative with the goal of creating a safe, heat-stable, oral vaccine widely used.



Figure 10.
Rooted plantlet preparation to open air before transfer to open air condition. 1/2 MS without hormones.



Figure 11.
The view of the harvest produced by tomato regenerants var. Ventura in vitro. To the left—in greenhouse, to the right—picked red tomatoes var. Ventura obtained from three tomato plants. The inscription on tomatoes (to the right): The harvest of regenerants R1, R2 and R4.

In 1992, Drs. Ch. Arntzen and H. Mason (USA) introduced the concept creating an “edible” vaccine based on transgenic plants for the production and delivery of antigens.

3.2.2 Advantages of plant transgenic “edible” vaccine

1. Obtaining antigen in large quantities in a relatively pure form; expression in seeds;
2. Cheapness of the “edible” vaccine; delivery in absence of “cold chain”;
3. Oral administration and induction of a mucosal immune response with the production of mucosal antibodies.

3.2.3 Development of binary “edible” vaccine against HIV-1 and HBV

The genetic construct of p35STBI-HBSAg was created in “Vector” (Koltzovo, Novosibirsk region, Russia) by professor S.N.Shchelkunov and his team (**Figures 12 and 13**).

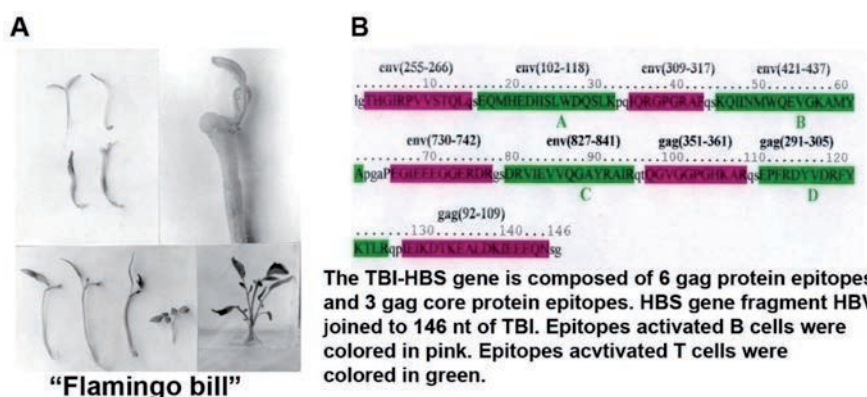


Figure 12. Development of binary “edible” vaccine against HIV-1 and HBV on the basis of transgenic tomato plants. (A)—Method of tomato regenerant obtaining by “flamingo bill” [6], (B)—the sequence of the chimeric gene TBI compiled from nucleotides -encoded B-cell epitopes (pink) and T-cell epitopes (green). The HBS fragment of HBV was joined to C-terminal of TBI.

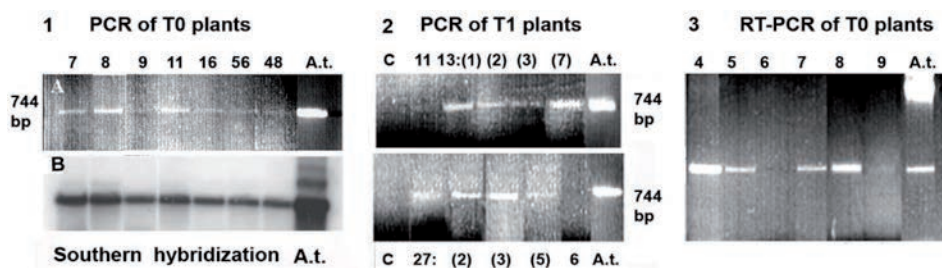


Figure 13. Genetic evidences of insertion and expression of the TBI gene in transgenic tomato plants of To and T1 generations. (1)—PCR (A) and Southern blot hybridization (B) with DNA isolated from To plants; (2)—PCR with DNA isolated from T1 plants; (3)—RT-PCR with RNA isolated from To plants. The numbers indicate the numbering of plants. C—control nontransformed plants.

744 bp—the size of primer to the fragment of TBI. A.t.—vector *Agrobacterium tumefaciens* EHA105 harboring plasmid pBIN p35STBI-HBS (**Figure 14**).

The amount of antigenic protein TBI-HBS synthesized in tomato fruits was in the range of 20–150 ng per 1 g of total soluble protein. As a result, these vaccine transgenic plants produced fruits that developed a high antibody response during oral immunization of mice after feeding freeze-dried fruits transgenic for TBI-HBSAg [7–9].

The work with mice was approved at a meeting of the bioethical council of the Federal State Budgetary Institution of Science and the Siberian Institute of Plant Physiology and Biochemistry of the Siberian Branch of Russian Academy of Sciences (Meeting of the bioethical commission No. 9 of October 30, 2019). When keeping mice, the standard conditions prescribed in GOST 33215–2014 and 33,216–2014 were observed (**Figure 15**).

3.2.4 Development of oral vaccine against HBV

The construct pBINPreS2-S was synthesized by Professor S.N.Shchelkunov and his team (“Vector,” Koltzovo Novosibirsk region, Russia).



Figure 14.
Transgenic tomato plants var. Ventura with the gene TBI-HBS as an “edible” vaccine against HIV-1 and HBV in greenhouse (left) and in the chamber of phytotron (right).

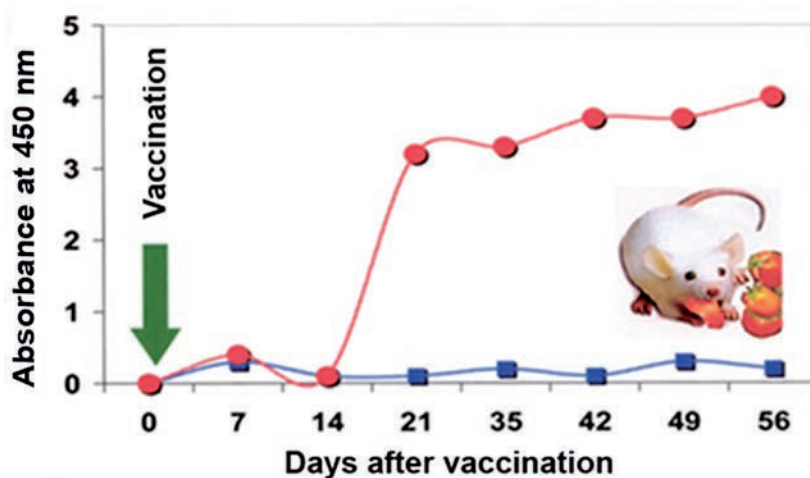


Figure 15.
Induction of antibody synthesis after an oral vaccination of mice. Red line is the level of antibodies to TBI-HBSAg in mice blood serum. Blue line is the level of control ones. Absorbance at A₄₅₀ is extinction at 450 nm.

HBV envelope proteins are encoded by the genes: preS1-S2-S (L), encoding the large domain PreS1-S2-S (L), preS2-S (M), encoding the middle domain PreS2-S (M), and s (S), encoding small domain—the main surface antigen of HBsAg. The addition of PreS2 protein to S (HBsAg) enhances the immune response after vaccination.

In this work, genetic constructs with the p35S-preS2-S genes were used to transform tomato plants.

The direct infection of agrobacteria A.t.EHA105 harboring pBINPreS2-S of morphogenic calluses produced tomato plantlets with impaired morphology (**Figure 16**).

Therefore, it was decided to transform 12 dayold tomato explants of the Ventura variety by direct infection of the *Agrobacterium* construct with pBINPreS2-S by



Figure 16.
 Rooted tomato regnerant with the gene PreS2-S HBV selected on MC with 100 mg/l kanamycin.

injection into the apex of the explant, followed by strict selection on MS medium containing 100 mg/l kanamycin (**Figure 17**). This method was named the transformation of explants *in apex* or *in planta*.

As can be seen in **Figure 18(A)** and **(B)**, tomato regenerants formed a good yield of fruits, which were used to produce tomato vaccine material with PreS2-S for oral vaccination of mice.

DNA isolated from transgenic tomato fruits revealed PCR amplifications in size corresponding to the boundaries of the primers (**Figure 19**). The amount of PreS2-S synthesized in tomato fruits was in the range 20–200 µg per 1 mg of total

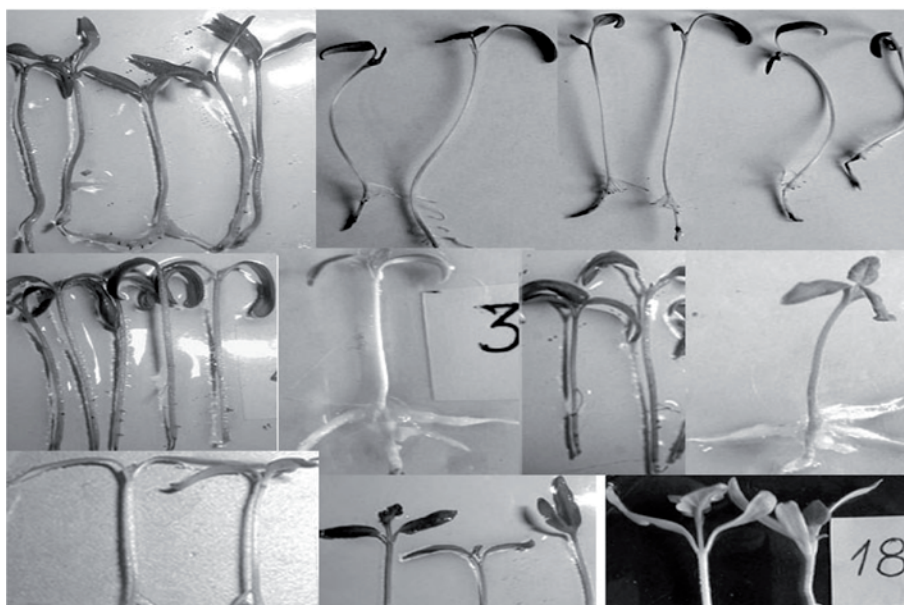


Figure 17.
 Selection of transformed with PreS2-S HBV coat protein regenerants (explants) on the MS medium with 100 mg/l kanamycin.

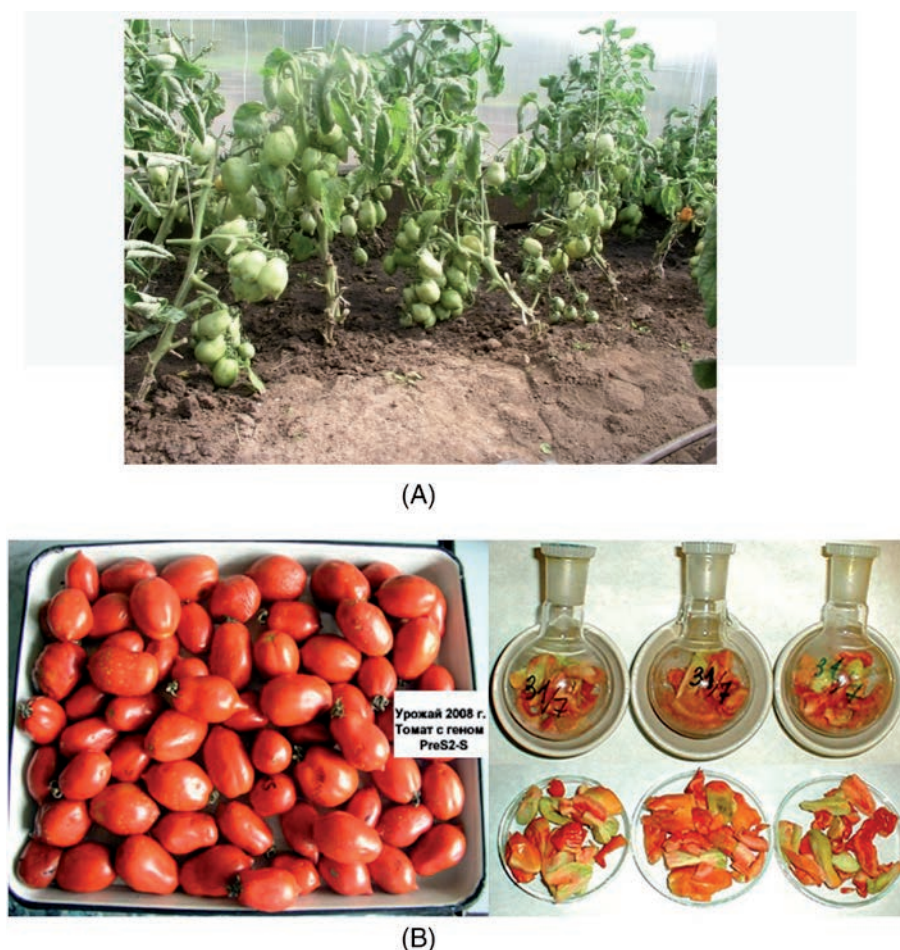


Figure 18.

(A) Transgenic regenerants var. Ventura with fruits expressing PreS2-S HBV growing in green house. (B) Harvest obtained from transgenic tomato plants with the PreS2-S gene (left) and freeze-dried tomato fruit material used for vaccination of mice (right) in order to obtain blood serum against HBV.

soluble protein (TSP). This amount of PreS2-S antigenic protein was sufficient to vaccinate mice (**Figure 20**).

Freeze-dried vaccine material from transgenic tomato fruits was easily eaten by laboratory mice, and oral vaccination occurred. Mice were orally vaccinated twice with the interval of 1 month. Each mouse received approximately 500 µg of PreS2-S as a result of this oral vaccination (**Figure 21**).

3.2.5 Development of the therapeutic oral vaccines against HPV

According to WHO forecast (Global Cancer Observatory), the number of cancer cases by 2045 year will increase by at least 75% or by 1/3 (one third) compared to 2022 year (**Figure 22**). Since there are no particular reasons for such a decrease in immunity: global disasters, sharp environmental deteriorations or a drop in the level, and quality of life of people, there is probably an unaccounted critical factor that quite significantly reduces the anti-cancer innate protection of humanity.

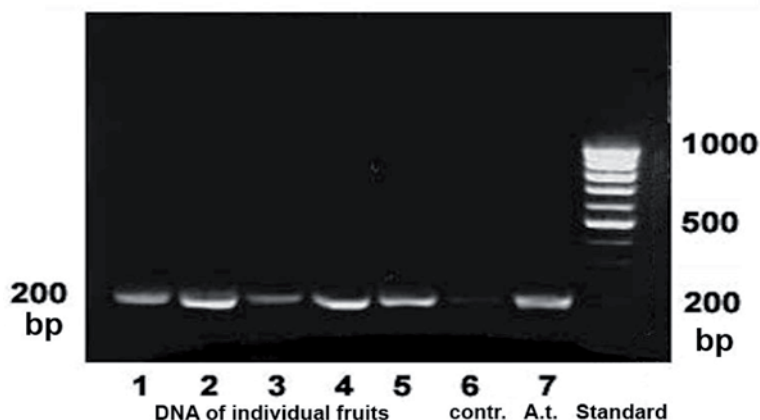


Figure 19.
 PCR with primers to the fragment of 200 bp of *PreS2-S. №Nº* (1,2,3,4,5)—used DNA isolated from individual transgenic fruits. Line (6)—control, H_2O , line (7)—*A. tumefaciens* plasmid DNA *pBINPreS2-S*. Line (8)—standard, DNA ladder 100 bp.



Figure 20.
 White laboratory conventional mice happily ate vaccine material from tomato fruits with transgenic *PreS2-S* and were easily orally vaccinated.

Such a hidden and dangerous agent could be the papillomaviruses, which are practically present in every person in the form of “warts on a leg” and does not seem to pose a visible danger in the future.

Therefore, it was decided to study the possibility of creating an “edible” vaccine based on the fruits of transgenic tomato plants. The advantages of a plant transgenic vaccine are safety, low cost, easy transition to commercialization due to the possibility of mass production of the vaccine, and the absence of the need to maintain a “cold” vaccination chain and infrastructure in case of pandemics and environmental disasters.

To create the preventive edible vaccines and therapeutic vaccines, genetic constructs were created in which the main component was the cucumovirus replicase RdRp, thanks to which it was possible to obtain a high yield of target products up to 25–30% of the total soluble protein and successfully vaccinate laboratory experimental mice (**Figure 23**). Constructs were synthesized in GenScript (USA).

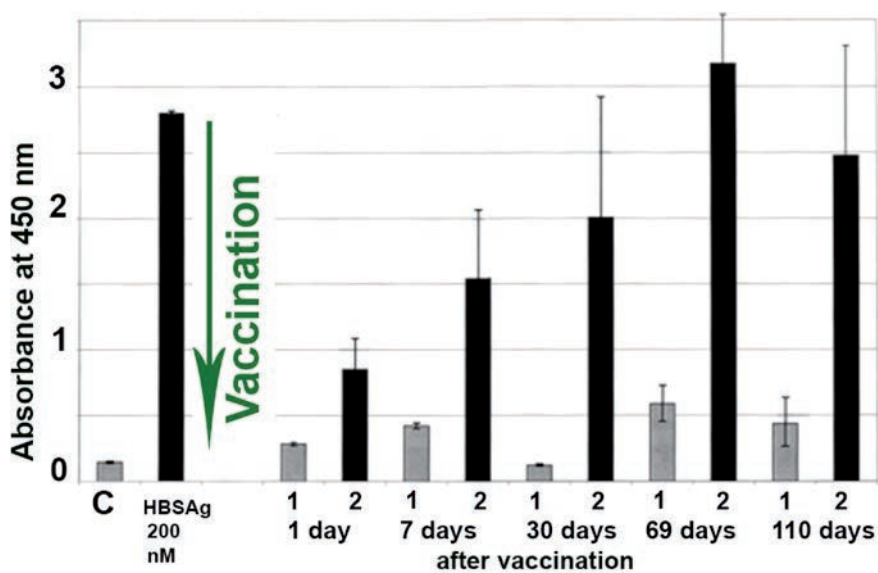


Figure 21.
The dynamics of the content of PreS2-S in blood serum of mice orally vaccinated with tomato vaccine material (2) and in blood serum of nonvaccinated mice (1). C—negative control; 200 nm HBSAg standard in the presence of standard 20 nm IgG to HBSAg.

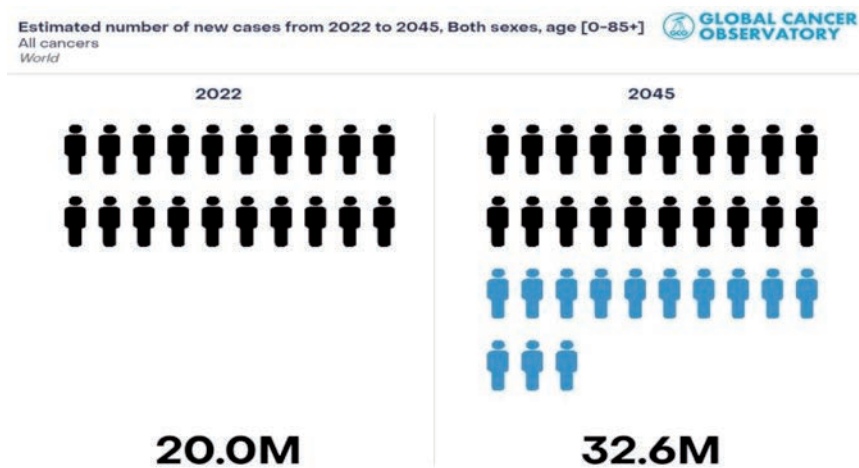


Figure 22.
Cancer development forecast by 2045 year made by Global Cancer Observatory (WHO).

The suspension of *A. tumefaciens* harboring pBINrDRP HPVs was injected into large (>200 g) tomato fruit directing into locules and left for 2–3 weeks in cold chamber (6–8°C). After the transformation *in fruto* was completed, the synthesized target proteins were extracted with buffer and used for analysis.

Quantitative analysis of the synthesized *in fruto* target proteins L1 is presented in Table 1.

Quantitative determination of antigenic proteins was carried out using enzyme-linked immunosorbent assay (ELISA) using the following primary antibodies: HPV16 E2 Antibody (TVG 261, sc-53,336) (Santa Cruz Biotechnology. Inc., USA),

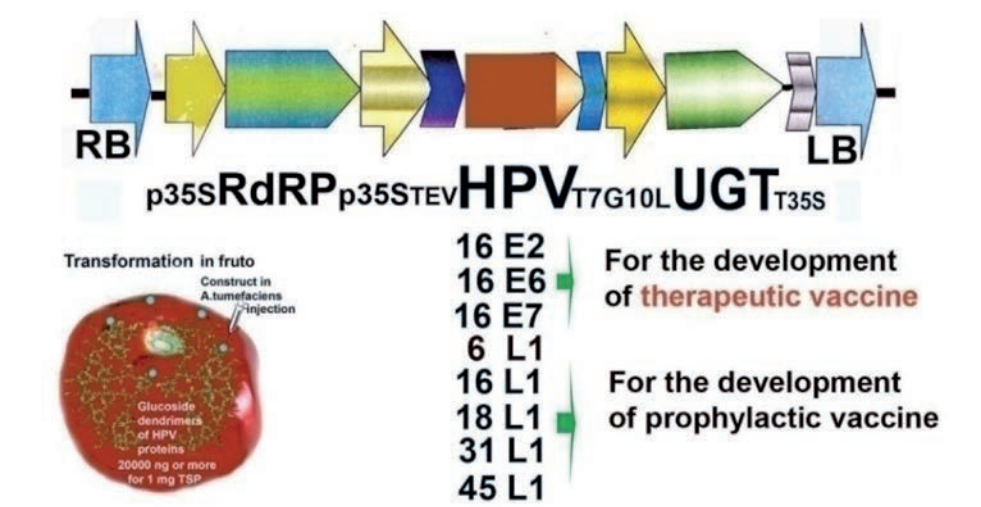


Figure 23.
 Genetic constructs and the bioreactor for the synthesis in fruto of antigenic HPVs proteins created on the basis of tomato transgenic fruits.

Type	Content L1, μ/mg TSP	Content L1, μ/g dry weight	Content L1, μ/g fresh weight
HPV6 L1	25.4 ± 0.1	117.4 ± 1.2	4.7 ± 0.1
HPV16 L1	25.4 ± 0.3	117.8 ± 1.6	4.7 ± 0.1
HPV18 L1	26.3 ± 1.0	117.6 ± 0.3	4.7 ± 0.1
HPV31 L1	25.9 ± 0.7	119.5 ± 1.2	4.8 ± 0.1
HPV45 L1	26.7 ± 0.6	119.2 ± 1.1	4.7 ± 0.1
HPV16 E2	25.3 ± 0.5	118.3 ± 1.4	4.7 ± 0.1
HPV16 E6	24.3 ± 0.8	117.6 ± 0.7	4.8 ± 0.2
HPV16 E7	25.1 ± 0.9	118.6 ± 0.6	4.8 ± 0.3

Table 1.
 Main characteristics of the quantitative content of antigenic proteins by type of candidate vaccine against the most types of human papillomavirus HPV16 L1, HPV18 L1, HPV31 L1, and HPV45 L1 synthesized in fruto.

HPV16 E6/18 E6 Antibody (C1P5, sc –460) (Santa Cruz Biotechnology, Inc., USA), Papillomavirus 16 E7 Antibody [SPM405] (GenWay Biotech, Inc., USA).

In general, we can say that the quantity of synthesized antigenic proteins was approximately the same, since their genes were placed in almost identical genetic constructs with the same regulatory genes and compositional elements. The amount of “early” antigenic proteins E2, E6, and E7 was about 20% of the TSP. Therefore, we can assume that the plant expression system we have developed based on transgenic tomato fruits is promising for the synthesis of “early” antigenic proteins of viral origin and suitable for obtaining these proteins in the required quantities for the purpose of their use in the development of oral therapeutic vaccines against cervical cancer.

In fruto-synthesized quantities of target L1 envelope proteins of highly carcinogenic HPV types were used for oral vaccination of mice.

The average age of mice keeping in laboratory conditions is 2 years. Therefore, as can be seen in **Figure 24**, a high level of antibodies against the L1 envelope proteins of highly carcinogenic viruses 16, 18, 31, and 45 types was maintained almost throughout the whole life of orally vaccinated mice.

3.2.6 Immunogenicity and anticancer activity of HPV16 E2 made in tomato viral expression synthesis on the base of tomato fruits

Although for all structural “early” antigenic proteins of papillomaviruses E2, E6, and E7, it is known that they are capable of activating the immune system and T cell immunogenesis, and some studies even show the antitumor effect of HPV E6 and E7. Of greater interest to us was the “early” protein HPV16 E2, which is assessed as a tumor suppressor and a blocker of the expression of oncoproteins E6 and E7.

Moreover, the super tumor suppressor HPV16 E2 instantly destroys the membranes of HeLa cancer cells, and E6 and E7 are capable of only aging HeLa cells, which at the same time lose adhesion and proceed to flotation.

In order to study the antitumor effect of HPV16 E2, an experimental model of primary tumors formation was developed in mice injected with HeLa cancer cells.

After injection of HeLa cancer cells into the right side of mice, only an increase in the size of the testes was observed externally a month later. In some males, the enlargement of the testes reached a fivefold value, especially if there were damage to the back of the male’s body due to fights between males (**Figure 25**).

After oral vaccination of male mice with vaccine material of transgenic tomato fruits containing about 500 µg of the HPV16 E2 protein, a decrease in the size of the testes by almost half was observed the very next day. This rapid response to vaccination can hardly be attributed to the activation of gene expression and subsequent protein synthesis. Most likely, the HPV16 E2 protein includes pre-existing mechanisms for repairing defects in carcinogenesis.

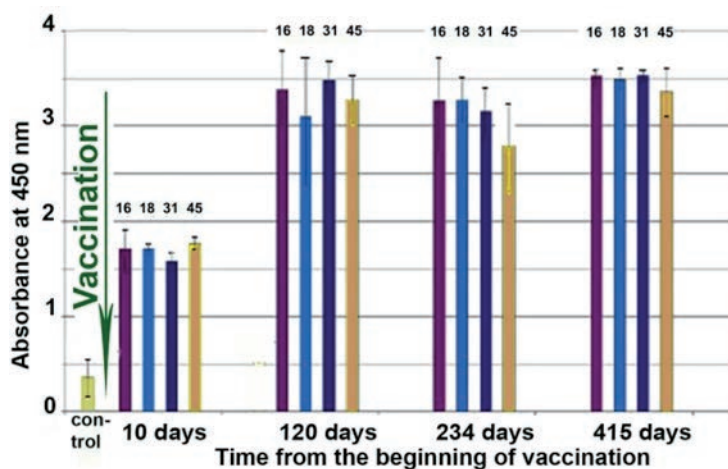


Figure 24.

The dynamics of the antibody immune response in blood serum of oral vaccinated mice after the administration of “edible” vaccines against HPVs of 16, 18, 31 and 45 types. Control—the level of antibodies in the blood serum of nonvaccinated mice.

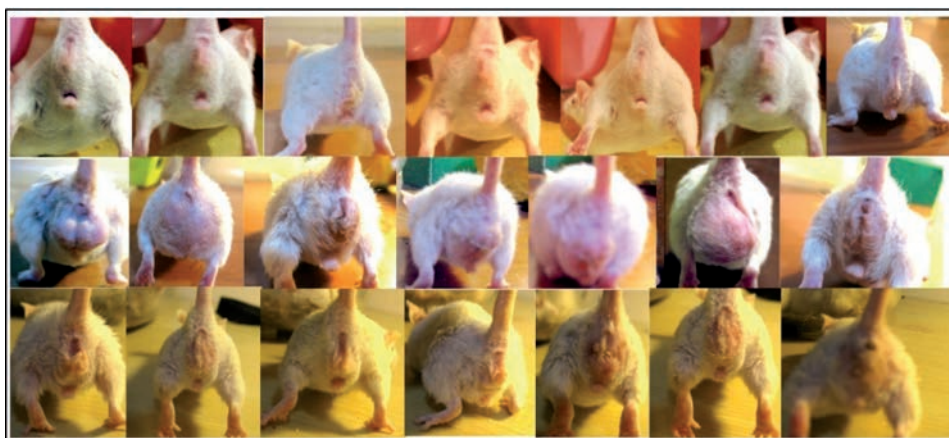


Figure 25.
Genitals and testis of male mice are presented in the picture. Top row—normal healthy male mice. Middle row—after 3 months of the injection of 100 µl of cancer HeLa cells into hips. Bottom row—after 1 month of the oral administration with tomato fruit vaccine materials containing 500 µg of HPV16 E2 to mice from the middle row that were injected with HeLa cells.

On the other side, in spermatozoa in the radial zone of the head there is a receptor for the main envelope protein of papillomaviruses L1 syndecan-1, due to which HeLa cells gather to the receptor zone.

The HeLa genome contains 6 intact HPV18 genomes and up to 50 papillomaviruses' DNA fragments.

After two subsequent oral vaccinations, the size of the testes returned to normal within 2 weeks.

It should also be noted that during infection and subsequent vaccination of males (as well as vaccination of females), no negative phenomena were noted in the behavior of males, even if they ran in a cage, fed and played with swollen testes.

After opening the abdominal cavity of infected mice, significant changes were discovered in the lungs, revealing an increase in their size by 1.8–2 times (**Figure 26**, second row).

As can be seen in **Figure 26**, injection of mice (both males and females) with HeLa cancer cells led to tumor growth of the lungs (**Figure 26**, second row). Vaccination of mice led to normalization of the lungs and a decrease in tumor formation (**Figure 26**, third row). Feeding mice with tomato fruit vaccine material containing the HPV16 E2 gene did not change the appearance of the lungs or cause tumor formation (**Figure 26**, bottom row).

In these experiments, isolation of the lungs was only possible by using tweezers and holding the heart connected to the lungs. Since the lungs have a fragile surface and a sticky coating, it was possible to isolate the lungs intact only by holding them with hearts together with tweezers.

It was found in our studies that injection of HeLa cancer cells led to a decrease in the synthesis of interferon, T cell receptor, CD4/CD8 T lymphocytes, as well as apoptotic enzymes: granzyme B, perforin, and granulysin [10].

Vaccination of mice or treatment of isolated lungs with vaccine material from tomato fruits transgenic for the HPV16 E2 gene dramatically increased the synthesis



Figure 26.

View of lungs isolated together with hearts from control mice (top row), lungs from mice injected with HeLa (second row), lungs from mice first injected and then vaccinated with HPV16 E2 (third row), lungs from mice vaccinated only (bottom row) with HPV16 E2.

of interferon, T cell receptor, and generation of CD4/CD8 T lymphocytes, and also activated the synthesis of apoptotic enzymes: granzyme B, perforin, and granulysin up to 1000–10,000 times [11].

The question arises as to what role HPV16 E2 plays and what happens when HeLa cells, which cause testicular and lung tumors in mice, encounter the HPV16 E2 protein.

It was demonstrated that immediately after adding 30 μ l of the supernatant of the transgenic tomato homogenate with HPV16 E2 (30 μ l of supernatant of centrifuged transgenic tomato homogenate and 20 μ l of 0.4% trypan blue, i.e., death indicator dye) to HeLa cells, staining of the HeLa cells and their flotation occurred due to membrane destruction and disruption of adhesion to the slide of the preparation [12]. This suggested a disruption of the vital functions of HeLa cells and their transition to a latent, surviving state even close to dye.

To understand what was happening in addition to membrane destruction, a fraction of nuclei was isolated from HeLa cells in HEPES buffer (20 mM Hepes, pH 7.4, 10 mM KCl, 2 mM $MgCl_2$, 1 mM EDTA) and Western blot hybridization of HeLa nuclei and HPV16 E2 protein was performed (**Figure 27**).

Infection with papillomaviruses causes DNA damage: unpaired ssDNA and dsDNA, double DNA breaks, base duplexes, and many other errors and abnormalities that activate a variety of DNA repairs. The key protein and repair sensor is the TOPBP1 protein. HPV16 E2 binds to TOPBP1 in the fraction of isolated nuclei of HeLa cancer cells and activates DNA repair (**Figures 27 and 28**) [13–16].

The distinctive ability of tomato plants to create “edible” vaccines is the ability to accept genetic constructs that realize the synthetic capabilities of tomato fruits to produce high quantities of heterologous proteins.

When creating “edible” vaccines, varieties of tomatoes with a high content of raw protein (about 7%), the so-called “ketchup” varieties, such as Ventura, Japanese crab, Altai pink, and other pink-fruited tomatoes, were used.

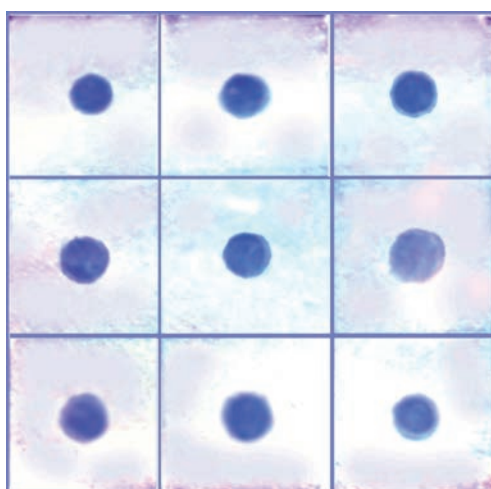


Figure 27.
 Western blot hybridization of the isolated nuclei of HeLa cancer cells with HPV16 E2 (antibody used: HPV15 E2 Antibody, TVG 261, sc-523,338, Santa Cruz Biotechnology, Inc., USA [11]).

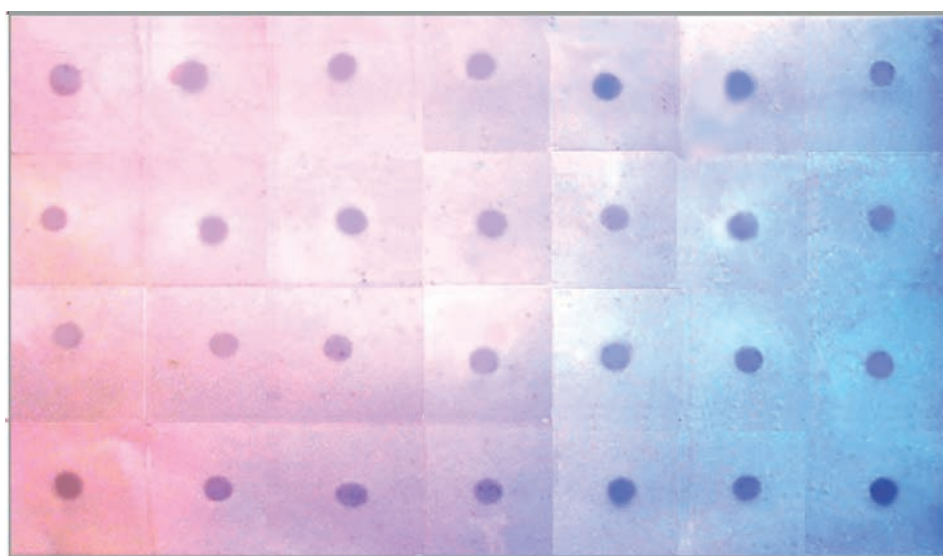


Figure 28.
 Western blot hybridization of isolated nuclei of HeLa cancer cells with an antibody to TOPBP1 (antibody used: PAD801Rao1 polyclonal antibody to TOPBP1 (rat), Cloud - Clone, China).

4. On the racemization of tryptophan, alanine, and other amino acids in connection with the plasticity and adaptability of tomato plants

The tomato is a unique work of nature, which has created a plant capable of withstanding numerous environmental stresses and environmental impacts, while remaining a highly productive and well-growing plant in unfavorable environmental conditions, especially drought and soil salinity, and also characterized by high speciation in form, size, and quality of fruits.

Despite the fact that the pathways of phytohormone biosynthesis have been studied and precursor genes and genes at the final stages of phytohormone biosynthesis have been identified, none of the studies have obtained successful results in stimulating growth, development, and productivity as a result of the insertion of these genes and their subsequent expression.

Apparently, the famous plant physiologist and specialist in hormonal regulation of plants, a Professor at the University of Edinburgh Dr. Anthony Trewavas, was right that “Phytohormones are just metabolic drive belts” (personal communications at the conferences, 70–80 years of the twentieth century).

Growth, development, and productivity are multifactorial processes encoded not just by individual genes, but by entire gene clusters and even contigs, which are a set of gene clusters responsible for the encoding and development of traits and biosynthetic pathways, leading to the stimulation of growth, development, and increased productivity of agricultural plants.

No one has yet been able to co-organize genomic fragments or DNA contigs to create a truly “green revolution” in agriculture.

But in all likelihood, this co-organization exists, and the genes in the contigs are located together, since under certain favorable conditions there are rapid activation of growth and an increase in yield.

We were the first to show that when tomato plants wilt at the stage of 4–5 true leaves with moisture loss up to 50–60%, the synthesis and accumulation of the auxin biosynthesis precursor N-malonyl-D-tryptophan, which represents its reserve form, occurs [17].

Racemization of amino acids is a bypass way of preserving amino acids by converting them into a non-proteinogenic form and eliminating the possibility of being involved in protein biosynthesis.

N-malonyl-D-tryptophan accumulates in very large quantities, approximately in the range of 0.5–1 mg per 1 g fresh weight when developed tomato leaves wilt. In this case, an amount of indolyl acetic acid precursor is synthesized that is 10,000–100,000 times greater than the plant cell’s needs for stimulating cell division. Tomato plants tolerate wilting quite well and, when watering is resumed, they activate growth and development, and bear fruit very successfully.

Direct application of such large quantities of indolyl acetic acid is highly toxic and can lead to plant death. After watering is resumed, the synthesis of N-malonyl-D-tryptophan continues for some time and then it disappears in the tissues of tomato leaves.

A similar pattern of N-malonyl-D-tryptophan accumulation occurs during the ripening of tomato seeds and wheat grains. During germination, N-malonyl-D-tryptophan continues to be synthesized and disappears with the acceleration of growth processes in tomato and wheat seedlings.

It is possible that N-malonyl-D-tryptophan takes part in the co-organization of entire gene clusters, the activation of which leads to enhanced growth and development, as well as productivity.

Auxin effects are known to be concentration dependent. But due to the toxicity of the breakdown products of indolyl acetic acid, this phytohormone cannot be added in large quantities. But the presence of N-malonyl-D-tryptophan, generally non-toxic, in large quantities is not a damaging factor, and the released malonyl radical is involved in the synthesis of malonyl-Co A, an important metabolite of energy metabolism. Since a correlation has been identified between the synthesis and accumulation of N-malonyl-D-tryptophan and the most important growth processes,

such as growth activation in the post-stress period after drought, during seed ripening and germination, it is possible that large amounts of this bound form of auxin precursor could participate in promoting of co-organization of contigs when stimulating plant growth.

Conflict of interest

The authors declare no conflict of interest.

Author details

Natalya Igorevna Rekoslavskaya*, Rurik Salyaev, Tatyana Kopytina, Irina Sotnikova and Irina Mokschoonova
Siberian Institute of Plant Physiology and Biochemistry of the Siberian Branch of Russian Academy of Sciences, Russian Federation

*Address all correspondence to: rekoslavskaya@sifibr.irk.ru

IntechOpen

© 2025 The Author(s). Licensee IntechOpen. This chapter is distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. 

References

- [1] Yu P. Tomato in Open Ground and in Greenhouses on Plot Open Ground of Irkutsk Region. Irkutsk: "Oblmashinform" Publishing; 2004. 50 pages. [in Russian]
- [2] Murashige T, Scoog F. A revised medium for rapid growth and bioassay with tobacco tissue cultures. *Physiologia Plantarum*. 1962;**15**:473-497. DOI: 10.1111/j.1399-3054.1962.tb08052.x
- [3] Heller R. Recherches sur la nutrition minerale des tissus vegetaux cultives *in vitro*. *Annales des Sciences Naturelles. Botanique et Biologie Végétale*. 1953;**14**:1-223
- [4] Lloyd G, McCown B. Commercially-feasible micropropagation of mountain laurel, *Kalmia latifolia*, by use of shoot-tip culture. *Proceedings of the International Plant Propagator's Society*. 1980;**30**:421
- [5] Kao K, Michayluk M. Nutritional requirements for growth of *Vicia hajastana* cells and protoplasts at a very low population density in liquid media. *Planta*. 1975;**126**:105-110
- [6] Pozueta-Romero J, Houlne G, Canas L, Schantz R, Chamarro J. Enhanced regeneration of tomato and pepper seedling explants for agrobacterium-mediated transformation. *Plant Cell, Tissue and Organ Culture*. 2001;**67**:173-180. DOI: 10.1023/A:1011997926381
- [7] Shchelkunov S, Salyaev R, Pozdnyakov S, Rekoslavskaya N, Nesterov A, Ryzhova T, et al. Immunogenicity of a novel, bivalent, plant-based oral vaccine against hepatitis B and human immunodeficiency viruses. *Biotechnology Letters*. 2006;**28**:959-967. DOI: 10.1007/s10529-006-9028-4
- [8] Salyaev R, Rekoslavskaya N, Stolbikov A, Hammond R, Shchelkunov S. Retention of the ability to synthesize HIV-1 and HBV antigens in generations of tomato plants transgenic for TBI-HBS gene. *Doklady. Biochemistry and Biophysics*. 2009;**425**:120-123. DOI: 10.1134/S1607672909020173
- [9] Salyaev R, Rekoslavskaya N, Stolbikov A, Hammond R, Shchelkunov S. Synthesis of hepatitis B virus antigen in tomato plants transgenic for the preS2-S gene. *Doklady. Biochemistry and Biophysics*. 2007;**416**:290-293. DOI: 10.1134/S1607672907050171
- [10] Salyaev R, Rekoslavskaya N, Stolbikov A. The induction of the synthesis of interferon, CD4 and CD8 T lymphocytes in blood and spleen of mice after oral vaccination with the "early" protein HPV16 E2. *Doklady. Biochemistry and Biophysics*. 2019;**488**:316-319. DOI: 10.1134/S1607672919050077
- [11] Salyaev R, Rekoslavskaya N. The effect of "early" proteins E2, E6 and E7 of papillomavirus of high-risk cancerogenous type HPV16 on cancer HeLa cells inducing tumor growths in mice lungs. *Acta Biomedica Scientifica*. 2022;**7**:261-276
- [12] Rekoslavskaya N, Chemezova A, Tchemezov A. Chapter 6. New evidences about unusual behaviour of HeLa cells in stress environment concerning immortality status. In: Baloch Z, editor. *New Finding on Human Papillomavirus*. London, UK, UK: Intechopen Publisher of Open Access books; 2024. pp. 1-21. DOI: 10.5772/intechopen.1004634
- [13] Prabhakar AT, Morgan IM. A new role for human papillomavirus

16 E2: Mitotic activation of the DNA damage response to promote viral genome segregation. *Tumour Virus Research*. 2024;**18**:20029. DOI: 10.1016/j.tvr.2024.200291

[14] Prabhakar AT, James CD, Fontan CT, Otoa R, et al. Human papillomavirus 16 E2 interaction with TOPBP1 is required for E2 and viral genome stability during the viral life cycle. *Journal of Virology*. 2023;**97**:3.1-3.319. DOI: 10.1128/jvi.00063-23

[15] Prabhakar AT, James CD, Das D, Otoa R, et al. CK2 phosphorylation of human papillomavirus 16 E2 on serine 23 promotes interaction with TOPBP1 and is critical for E2 interaction with mitotic chromatin and the viral life cycle. *ASM Journals/mBio*. 2021;**12**(5):e0116321. DOI: 10.1128/mBio.01163-21

[16] Das D, Bristol NL, Pichierri P, Morgan JM. Using a human papillomavirus model to study DNA replication and repair of wild type and damaged DNA template in mammalian cell. *International Journal of Molecular Sciences*. 2020;**21**:7564. DOI: 103390/ijms.21207564

[17] Rekoslavskaya N. N-Malonyl-D-Tryptophan, the Condition of the Formation and Possible Physiological Role. [Doctor Theses]. Moscow: Institute of Plant Physiology; 1991

Edited by Natalya Rekoslavskaya

The book is dedicated to one of the favorite plants, the fruits of which are widely used by people, the tomato, *Solanum lycopersicum* L. Of great interest to readers will be information about the global tomato yield, as well as the methods being developed to control biotic and abiotic stresses (insect pests, bacteria, fungi, and viruses) in order to achieve high yields. The main pests of tomatoes are described in detail. Agromorphological, biotechnological, physical, and pharmaceutical methods for combating pathogens are proposed, along with progressive pathogen clearance techniques to enhance the post-harvest shelf life of tomato fruits for both market and domestic use. Interesting time data on the origin of tomatoes, their transportation routes in the Middle Ages, and people's attitudes towards these fruits are presented. Of great interest are the selection paths that led to modern high-yielding varieties with a high content of sugars, lycopene, vitamins, and other beneficial substances, developed by biologists and nature enthusiasts who have worked on these wonderful fruits. Innovative methods for improving tomato productivity are presented in detail, including biotechnological, genetic, cellular, and in vitro technologies. The book presents colorful images of unique tomato varieties, as well as technologies for obtaining new plants through the cultivation of isolated cells and tissues. The book is of interest to a wide range of readers, including young students, biotechnological specialists, and agricultural workers.

W. James Grichar, Agricultural Sciences Series Editor

Published in London, UK

© 2026 IntechOpen
© Irena Carpaccio / unsplash

IntechOpen

ISSN 3029-052X

ISBN 978-1-83634-695-1

