# Mirza Hasanuzzaman Editor

# The Plant Family Brassicaceae

Biology and Physiological Responses to Environmental Stresses



The Plant Family Brassicaceae

Mirza Hasanuzzaman Editor

# The Plant Family Brassicaceae

Biology and Physiological Responses to Environmental Stresses



*Editor* Mirza Hasanuzzaman Department of Agronomy Sher-e-Bangla Agricultural University Dhaka, Bangladesh

ISBN 978-981-15-6344-7 ISBN 978-981-15-6345-4 (eBook) https://doi.org/10.1007/978-981-15-6345-4

#### © Springer Nature Singapore Pte Ltd. 2020

This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.

The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

The publisher, the authors and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, expressed or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Singapore Pte Ltd. The registered company address is: 152 Beach Road, #21-01/04 Gateway East, Singapore 189721, Singapore



This book is dedicated to My Sons Mirza Arian Zaman and Mirza Ahyan Zaman

### Preface

Brassicaceae (formerly, Cruciferae) is among the largest angiosperm families belonging to the order Brassicales. It consists of 12–15 tribes with 338–360 genera and about 3709 species distributed all around the globe in all continents, excluding Antarctica. Among the plant families, Brassicaceae has particular agri-horticultural importance, and diverse uses apart from the basic needs. The family consists of various essential genera that have different economic as well as agronomic uses in exploring the world of knowledge using them as model plants. Thus it implies and covers all possible sources by which a plant can be of a bliss/benefit to humankind. The Brassicaceae family comprises many different edible species such as fodder, oilseed, vegetables, and condiments. Rapeseed and mustard are the most crucial oil crops of this family, which is ranked as the third most vital oil source and contains about 14% of the world's edible vegetable oil. Members of this family also uptake heavy metals and serve as hyper-accumulators in soil polluted with heavy metals.

Considering the economic importance and the unique adaptive mechanisms, further research is still needed to understand the response of these plants toward abiotic stresses. This information needs to be translated into improved elite lines that can contribute to achieving food security. The knowledge of the physiological and molecular mechanisms acting on these plants needs to be further extended. In the last decades, a growing body of research has reported an interesting finding on the physiology and stress responses in both Brassicaceae plants. Many research works have also been done to understand their tolerance mechanisms when facing abiotic stresses. Recent advances and developments in molecular and biotechnological tools have contributed to easing and widening this mission. However, most of these results and reports are published sporadically, and there are no comprehensive books dealing with this vital plant family, and their research progresses related to abiotic stress physiology.

The Plant Family Brassicaceae—Biology and Physiological Responses to Environmental Stresses combines a group of twenty-three chapters written by expert researchers that organizes the most recent information with up-to-date citations, which will provide comprehensive literature of recent advances on Brassicaceae plant physiology. This book includes several chapters addressing general and unique aspects and questions of Brassicaceae biology and economic importance, as well as several chapters devoted to the Brassicaceae responses and adaptation to environmental stresses as well as their potential to phytoremediation. This book will be an important source of information both for students and researchers working on biology, physiology, environmental interactions, and biotechnology of Fabaceae and Brassicaceae plants.

I would like to give special thanks to the authors for their outstanding and timely work in producing such excellent chapters. I am highly thankful to Dr. Mei Hann Lee (Senior Editor, Life Science) Springer, Japan, for her prompt responses during the acquisition. I am also grateful to Arulmurugan Venkatasalam, Project Coordinator of this book, and all other editorial staff for their precious help in formatting and incorporating editorial changes in the manuscripts. Special thanks to Dr. Sarvajeet Singh Gill (MD University, India) for his critical review of the initial contents of the book and Dr. Md. Mahabub Alam (Sher-e-Bangla Agricultural University, Bangladesh) for his generous help in formatting the manuscripts. I believe that this book is useful for undergraduate and graduate students, teachers, and researchers, particularly from the field of botany, agriculture, plant physiology, agronomy, environmental sciences, plant breeding, biotechnology, and food sciences.

Dhaka, Bangladesh

Mirza Hasanuzzaman

## Contents

The Plant Family Brassicaceae: Introduction, Biology,And ImportanceAli Raza, Muhammad Bilal Hafeez, Noreen Zahra, Kanval Shaukat,Shaheena Umbreen, Javaria Tabassum, Sidra Charagh,Rao Sohail Ahmad Khan, and Mirza Hasanuzzaman	1
Agricultural, Economic and Societal Importance of Brassicaceae Plants	45
Arabidopsis thaliana: Model Plant for the Study of Abiotic Stress Responses. Ali Raza, Sidra Charagh, Nida Sadaqat, and Wanmei Jin	129
Newly Revealed Promising Gene Pools of Neglected BrassicaSpecies to Improve Stress-Tolerant CropsMohammad Mafakheri and Mojtaba Kordrostami	181
Enhancement of Abiotic Stress Tolerance in <i>Camelina sativa</i> : Conventional Breeding and Biotechnology Larysa V. Nishchenko and Mirza Hasanuzzaman	195
Brassicaceae Plants Response and Tolerance to Salinity Subhankar Mondal and Koushik Chakraborty	203
Brassicaceae Plants Response and Tolerance to Drought Stress: Physiological and Molecular Interventions	229
<b>Rapeseed: Biology and Physiological Responses to Drought Stress</b> Mojtaba Kordrostami and Mohammad Mafakheri	263

<b>Responses and Tolerance of Brassicas to High Temperature</b> Pushp Sharma	277
Brassicaceae Plants Response and Tolerance to Waterlogging and Flood	311
Brassicaceae Plants Response and Tolerance to Nutrient Deficiencies K. S. Karthika, Prabha Susan Philip, and S. Neenu	337
Brassicaceae Plants Response and Tolerance to Metal/Metalloid Toxicity Shyamashree Roy and Sanchita Mondal	363
Toxic Metals/Metalloids Accumulation, Tolerance, and Homeostasisin Brassica Oilseed SpeciesMuhammad Mudassir Nazir, Zaid Ulhassan, Muhammad Zeeshan,Sharafat Ali, and Muhammad Bilal Gill	379
Phytoremediation of Toxic Metals/Metalloids and Pollutants by Brassicaceae Plants	409
Molecular and Biotechnological Interventions for Improving Brassicaceae Crops for Abiotic Stress Tolerance Pankaj Kumar and Dinesh Kumar Srivastava	437
<b>Biotechnological Approach for Enhancing Capability of</b> <i>Brassica</i> <i>oleracea</i> var. italica Against Stresses Under Changing Climate Mohammad Mafakheri and Mojtaba Kordrostami	451
Genome Editing for the Improvement of Brassicaceae for Abiotic Stress Tolerance	473
Bioinformatics Studies on the Identification of New Players and Candidate Genes to Improve Brassica Response to Abiotic Stress	483
Use of Biostimulants for Improving Abiotic Stress Tolerance in Brassicaceae Plants M. H. M. Borhannuddin Bhuyan, Sayed Mohammad Mohsin, Jubayer Al Mahmud, and Mirza Hasanuzzaman	497

## **Editors and Contributors**

#### About the Editor



Dr. Mirza Hasanuzzaman is a Professor of Agronomy at Sher-e-Bangla Agricultural University, Dhaka, Bangladesh. He received his PhD on 'Plant Stress Physiology and Antioxidant Metabolism' from the United Graduate School of Agricultural Sciences, Ehime University, Japan, with Japanese Government (MEXT) Scholarship. Later, he completed his postdoctoral research in Center of Molecular Biosciences (COMB), University of the Ryukyus, Okinawa, Japan, with 'Japan Society for the Promotion of Science (JSPS)' postdoctoral fellowship. Subsequently, he joined as Adjunct Senior Researcher at the University of Tasmania with Australian Government's Endeavour Research Fellowship. Professor Hasanuzzaman has been devoting himself to research in the field of Crop Science, especially focused on Environmental Stress Physiology since 2004. Professor Hasanuzzaman published over 100 articles in peer-reviewed journals and books. He has edited 15 books and written 35 book chapters on important aspects of plant physiology, plant stress responses, and environmental problems in relation to plant species. These books were published by internationally renowned publishers. Professor Hasanuzzaman is a research supervisor of undergraduate and graduate students and supervised 20 MS students so far. He is Editor and Reviewer of more than 50 peer-reviewed international journals, and recipient of 'Publons Global Peer Review Award 2017, 2018, and 2019', Professor Hasanuzzaman is an active member of about 40 professional societies and acting as Publication Secretary of Bangladesh Society of Agronomy. He has been honored by different authorities due to his outstanding performance in different fields like research and education. He received the World Academy of Science (TWAS) Young Scientist Award 2014. He attended and presented 25 papers and posters in national and international conferences in different countries (USA, UK, Germany, Australia, Japan, Austria, Sweden, Russia, etc.).

#### Contributors

Sharafat Ali Institute of Crop Science and Zhejiang Key Laboratory of Crop Germplasm, Zhejiang University, Hangzhou, China

Mohammad Israil Ansari Department of Botany, University of Lucknow, Lucknow, India

M. H. M. Borhannuddin Bhuyan Citrus Research Station, Bangladesh Agricultural Research Institute, Jaintapur, Sylhet, Bangladesh

Koushik Chakraborty Division of Crop Physiology & Biochemistry, ICAR National Rice Research Institute, Cuttack, India

**Sidra Charagh** Centre of Agricultural Biochemistry and Biotechnology (CABB), University of Agriculture, Faisalabad, Pakistan

Heba T. Ebeed Botany and Microbiology Department, Faculty of Science, Damietta University, Damietta, Egypt

**Muhammad Bilal Gill** International Centre for Environmental Membrane Biology, Foshan University, Foshan, China;

Tasmanian Institute of Agriculture, College of Science and Engineering, University of Tasmania, Hobart, TAS, Australia

Muhammad Bilal Hafeez College of Agronomy, Northwest A&F University, Yangling, China

**Mirza Hasanuzzaman** Department of Agronomy, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka, Bangladesh

Nusrat Jabeen Biosaline Laboratory, Department of Botany, University of Karachi, Karachi, Pakistan

Syed Uzma Jalil Amity Institute of Biotechnology, Amity University Uttar Pradesh, Lucknow, India

**Rida Javed** Centre of Agricultural Biochemistry and Biotechnology (CABB), University of Agriculture, Faisalabad, Pakistan

**Wanmei Jin** Key Laboratory of Biology and Genetic Improvement of Horticultural Crops (North China), Beijing Academy of Forestry and Pomology Sciences, Beijing, China

**K. S. Karthika** ICAR-National Bureau of Soil Survey and Land Use Planning, Regional Centre, Bangalore, India

**Rao Sohail Ahmad Khan** Centre of Agricultural Biochemistry and Biotechnology (CABB), University of Agriculture, Faisalabad, Pakistan

Mojtaba Kordrostami Nuclear Agriculture Research School, Nuclear Science and Technology Research Institute (NSTRI), Karaj, Iran

**Pankaj Kumar** Science and Engineering Research Board, Department of Science & Technology, Government of India, New Delhi, India; CSIR-IHBT, Palampur, India

**Mohammad Mafakheri** Department of Horticultural Sciences, Faculty of Agricultural Sciences, University of Guilan, Rasht, Iran

Jubayer Al Mahmud Department of Agroforestry and Environmental Science, Sher-e-Bangla Agricultural University, Sher-e-Bangla Nagar, Dhaka, Bangladesh

**Sayed Mohammad Mohsin** Laboratory of Plant Stress Responses, Department of Applied Biological Sciences, Faculty of Agriculture, Kagawa University, Miki-Cho, Kita-Gun, Kagawa, Japan;

Department of Plant Pathology, Sher-e-Bangla Agricultural University, Sher-e-Bangla Nagar, Dhaka, Bangladesh

Sanchita Mondal Department of Agronomy, Bidhan Chandra Krishi Viswavidyalaya, Mohanpur, Nadia, West Bengal, India;

Division of Crop Physiology & Biochemistry, ICAR National Rice Research Institute, Cuttack, India

Subhankar Mondal Division of Crop Physiology & Biochemistry, ICAR National Rice Research Institute, Cuttack, India

Muhammad Mudassir Nazir Institute of Crop Science and Zhejiang Key Laboratory of Crop Germplasm, Zhejiang University, Hangzhou, China

S. Neenu ICAR-Central Plantation Crops Research Institute, Kasaragod, Kerala, India

Larysa V. Nishchenko Institute of Food Biotechnology and Genomics, National Academy of Sciences of Ukraine, Kiev, Ukraine

**Prabha Susan Philip** ICAR-National Bureau of Soil Survey and Land Use Planning, Regional Centre, Delhi, India

Mrinalini Prasad Faculty of Science, Department of Botany, Dayalbagh Educational Institute (Deemed University), Dayalbagh, Agra-5, India

**Rajiv Ranjan** Faculty of Science, Department of Botany, Dayalbagh Educational Institute (Deemed University), Dayalbagh, Agra-5, India

**Ali Raza** Oil Crops Research Institute, Chinese Academy of Agricultural Sciences (CAAS), Wuhan, China

Ali Razzaq Centre of Agricultural Biochemistry and Biotechnology (CABB), University of Agriculture, Faisalabad, Pakistan

Shyamashree Roy Regional Research Station, Old Alluvial Zone, Uttar Banga Krishi Viswavidyalaya, Majhian, Dakshin Dinajpur, West Bengal, India

Nida Sadaqat Institute of Molecular Biology and Biotechnology (IMBB), University of Lahore, Lahore, Pakistan

**Pushp Sharma** Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana, India

Kanval Shaukat Department of Botany, University of Balochistan, Quetta, Pakistan

**Dinesh Kumar Srivastava** Department of Biotechnology, Dr. Y. S. Parmar University of Horticulture and Forestry, Solan, Himachal Pradesh, India

Neerja Srivastava Department of Biochemistry, IBSBT, CSJM University, Kanpur, UP, India

**Javaria Tabassum** China National Rice Research Institute, Chinese Academy of Agricultural Science (CAAS), Hangzhou, Zhejiang, China

Zaid Ulhassan Institute of Crop Science and Zhejiang Key Laboratory of Crop Germplasm, Zhejiang University, Hangzhou, China

**Shaheena Umbreen** Department of Botany, University of Agriculture, Faisalabad, Pakistan

Noreen Zahra Department of Botany, University of Agriculture, Faisalabad, Pakistan

**Muhammad Zeeshan** Institute of Crop Science and Zhejiang Key Laboratory of Crop Germplasm, Zhejiang University, Hangzhou, China

## The Plant Family Brassicaceae: Introduction, Biology, And Importance



Ali Raza, Muhammad Bilal Hafeez, Noreen Zahra, Kanval Shaukat, Shaheena Umbreen, Javaria Tabassum, Sidra Charagh, Rao Sohail Ahmad Khan, and Mirza Hasanuzzaman

**Abstract** The model plant family Brassicaceae, also known as Cruciferae, is among the largest angiospermic family belonging to the order Brassicales. The family consists of annuals, biennials as well as herbaceous perennials. The Brassicaceae family comprises many different edible species such as fodder, oilseed, vegetables, and condiments. This family is crucial for vitamins A, B1–2, B6, C, E, K, and minerals such as magnesium, iron, and calcium. Members of the family Brassicaceae produce secondary metabolites that are not only family-specific but also species- and genus-specific. The family consists of various important genera that have diverse economic as well as agronomic use in exploring the world of knowledge using them as model plants. This family has precisely documented advances in the understanding of phylogeny, polyploidy, and genomics in the members of the Brassicaceae family in a very brief and concise review. There are numerous plants having great economic and agronomic importance in family Brassicaceae to scientific

A. Raza (🖂)

Oil Crops Research Institute, Chinese Academy of Agricultural Sciences (CAAS), Wuhan 430062, China e-mail: alirazamughal143@gmail.com

M. B. Hafeez College of Agronomy, Northwest A&F University, Yangling 712100, China

N. Zahra · S. Umbreen Department of Botany, University of Agriculture, Faisalabad 38040, Pakistan

K. Shaukat Department of Botany, University of Balochistan, Quetta, Pakistan

J. Tabassum China National Rice Research Institute, Chinese Academy of Agricultural Science (CAAS), Hangzhou, Zhejiang, China

S. Charagh · R. S. A. Khan Centre of Agricultural Biochemistry and Biotechnology (CABB), University of Agriculture, Faisalabad 38040, Pakistan

M. Hasanuzzaman Department of Agronomy, Faculty of Agriculture, Sher-e Bangla Agricultural University, Dhaka 1207, Bangladesh

© Springer Nature Singapore Pte Ltd. 2020 M. Hasanuzzaman (ed.), *The Plant Family Brassicaceae*, https://doi.org/10.1007/978-981-15-6345-4\_1 and medicinal significance. Moreover, various species of Brassicaceae are explored for their pharmacological potential.

**Keywords** *Arabidopsis* · *Brassicas* · Brassicaceae Evolution · Genome duplication · Polyploidy

#### 1 Introduction, Biology, and Economic Importance of Brassicaceae Family

#### 1.1 Introduction

Family Brassicaceae (Cruciferae) is among the largest angiospermic families belonging to the order Brassicales. It consists of 12–15 tribes with 338–360 genera and about 3709 species distributed all around the globe in all continents excluding Antarctica (Al-Shehbaz 1973; Al-Shehbaz and Warwick 2006; Appel and Al-Shehbaz 2003). Besides different geographical distribution of the family from the northern to the southern hemisphere, its distribution has been reported to be limited on mountainous and alpine regions in the tropics. However, *Arabis alpina* has demonstrated its occurrence in both hemispheres from mountains to alpines and Arctic habitats (Koch and Kiefer 2006). According to Price et al. (1994), Central Asia, Mediterranean, and Southwestern regions are enormously dominated by the plants of family Brassicaceae. *Draba* is the largest genera of the family with about 365 species followed by *Erysimum, Lepidium, Cardamine,* and *Alyssum* with 225, 230, 200, and 195 species, respectively (Anjum et al. 2012).

The vast literature has been reported regarding the taxonomic and systematic essay of Brassicaceae plants. von Hayek (1911) was the pioneer to publish about the family; later, various other taxonomists contributed to the ocean of family Brassicaceae. Vaughan and MacLeod (1976) were amid the writers who successfully published a book entitled "The Biology and Chemistry of the Cruciferae" discussing and compiling the vast knowledge of family Brassicaceae. The family is well identified and differentiated from other families by its distinctive flower architecture. Numbers of taxonomists/researchers like (Al-Shehbaz 1984; von Hayek 1911; Schulz 1936) have made an effort to give a natural system of classification to divide the family into different tribes. von Hayek (1911) and Schulz (1936) have divided the family into 10 and 19 tribes, respectively, based on fruit shape, an arrangement of the seed, and embryo. However, Janchen (1942) divided Brassicaceae into 15 tribes. Schranz et al. (2005) precisely documented advances in the understanding of phylogeny, polyploidy, and genomics in the members of the Brassicaceae family in a very brief and concise review.

The plants which revolutionized modern biology are *Arabidopsis* and *Brassica*. Therefore, it is considered that there would be no life for model plants, or we would lack many more crop plants without this particular Brassicaceae family (Franzke et al. 2011). Besides being as a model plant to explore the genomic and molecular

arrays, various species of Brassicaceae are used to explore the flowering time and floral architecture (C. *bursa-pastoris*), fruit and flower morphology (*Iberis* spp.), seed physiology, and morphology of fruit, (*Lepidium* spp.) adaptive modification of waterusage gradient (*Cardamine hirsute*), trace metal tolerance and hyper-accumulation (*Arabidopsis lyrata* and *A. suecica*), salt stress (*Eutrema-Thellungiella* spp.) and contact between plant and pathogen (*Arabis alpine*), etc. (Franzke et al. 2011). There are numerous plants having great economic and agronomic importance in family Brassicaceae (Bailey et al. 2007) to scientific (Hall et al. 2002a; Koch and Mummenhoff 2006) and medicinal significance. Moreover, various species of Brassicaceae are explored for their pharmacological potential.

#### 1.2 Biology of Family Brassicaceae

The family consists of annuals, biennials as well as herbaceous perennials. Mostly the plants are herbs with the least percentage (5%) of typically woody like Faresetia somalensis, Heliophila scandens, Cramboxylon spp., Zilla spinosa, Vella spp., Parolinia spp., etc. (Franzke et al. 2011). The main root system of Brassicaceae plants is tap root which sometimes may be swollen (when it is the storage organ of the plant) or may be conical shaped, e.g., radish and napiform in a turnip. Leaves of the Brassicaceae show alternate arrangements rarely opposite. In shrubby species of Mediterranean, the leaves are arranged in a terminal rosette. Leaves are exstipulate and often pinnately incised. However, the pungent smell from the crushed leaves of Brassicaceae plants is among the distinctive characteristic attributes of the family. Moreover, leaves are usually covered with hair-like structures called trichomes. The flower morphology is strictly uniform in all members of the family Brassicaceae (exceptions in color do exist). Hence, the family name Cruciferae comes from the appearance of the flora with 4 petals arranged in the form of a cross, usually, hermaphrodite and actinomorphic, rarely zygomorphic. Other floral characters of the family are as follows: (1) sepals—four—arranged in 2 whorls; (2) stamens—six—with the exception in Lepidium spp. Having 2-4 and Megacarpaea polyandra with 8-24 stamens; (3) ovary—superior; (4) nectary—varies from species to species, both in position and dominant nectar compound (Davis et al. 1998); (5) arrangements of flowers—bracteates racemose—frequently corymb-like at apex; (6) pollination-entomogamy; (7) fruit-vary but typically dehiscent bivalve capsule (silique)—maybe indehiscent or achene, rarely nutlet, schizocarp, or drupe; (8) seed size-vary from minute (Mancoa mexicana) to large (Megacarpaea gigantea) seeds (Al-Shehbaz 1984, 1986); (9)—mode of propagation—mostly by seeds—very few species show vegetative propagation, e.g., A. rusticana (horseradish) and Neobeckia lacustris (American watercress).

Mode of photosynthesis in Brassicaceae is typically C3 in the majority of the members (Uprety et al. 1995); however, some spp. of the genus *Moricandia* like *M. arvensis, M. sinaica, M. suffruticosa, M. spinosa, and M. nitens* are C3–C4 intermediates (Apel et al. 1997; Razmjoo et al. 1996; Rylott et al. 1998).

Members of the family Brassicaceae produce secondary metabolites that are not only family-specific but also species- and genus-specific. Secondary metabolites play an essential role in the defense of plants against pathogens, herbivory, and weed eradication (Angelini et al. 1998; Bednarek 2012; Clauss et al. 2006). Secondary metabolites produced by the Brassicaceae include glucosinolates, oils, and seed fatty acids. Fahey et al. (2001) reported that greater than 96 glucosinolates are present in family Brassicaceae, of which many are specific to genera and spp.

#### 1.3 Economic Importance of Family Brassicaceae

The family is enormously blessed with plants that have a wide range of economic importance from food to fodder, medicines to use, as research model plants, to high yielding crops to ornamental plants. Thus it implies and covers all possible sources that a plant can be of a bliss/benefit to humankind. The Brassicaceae family comprises many different edible species such as fodder, oilseed, vegetables, and condiments. This family is crucial for vitamins, A, B1–2, B6, C, E, K, and minerals such as magnesium, iron, and calcium (Wink and Van Wyk 2008). The most common vegetable crops are kohlrabi, broccoli, cabbage, turnip, and cauliflower enriched with dietary fibers (Shankar et al. 2019; Table 1). The family also has ornamental value, and various species are cultivated for its aesthetic value like *Iberis, Lobularia, Cheiranthus, Erysimum, Hesperis*, etc. It has many plants that are used as dyes, including *Isatis tinctoria*, which is a medicinal plant and also being used as a dye for color indigo (Hamburger 2002). *Amoracia rusticana, Cheiranthes cheiri*, kale and collards, *Matthiola incana, Raphanus raphanistrum* (Austin 2003), and *Lepidium ruderale* (Buchanan 1995) are also used for various dyes.

Furthermore, members of this family also uptake the heavy metals and serve as hyper-accumulators in soil polluted with heavy metals. Some species can hyper-accumulate cadmium, zinc, and nickel. About 25% of the Brassicaceae members are known to be hyper-accumulators. *Brassica juncea* and *Brassica oleracea* can aggregate and tolerate heavy metals (Devi 2017). Moreover, some members can uptake excess nitrates (Kingsbury 1964). *Erysmium cheiri* seeds are enriched with cardiac glycosides (Wink and Van Wyk 2008). Additionally, Canola and *Brassica napus* are the most important oil crops of this family (Alagoz and Toorchi 2018). After soybean and palm oil, Brassica seed oil is ranked as the third most crucial oil source (Friedt et al. 2018; Raza et al. 2019a) and contains about 14% of the world's edible vegetable oil (Shankar et al. 2019).

Moreover, it also includes some protein and biodiesel crops such as *Brassica* carinata, Crambe abyssinica, Eruca vesicaria, and Camelina sativa (Gugel and Falk 2006; Warwick et al. 2007; Warwick and Gugel 2003). Erysimum spp., Sinapis alba, Armoracia rusticana, and Brassica juncea of Brassicaceae are used as spices (Gugel and Falk 2006; Warwick et al. 2007). According to Agusdinata et al. (2011) and Shonnard et al. (2010), Camelina oil can cut GHG (greenhouse gas emissions) up to 75 percent than that of petroleum-based jet fuel. Arabidopsis and Capsella

Genus, species	Cultivar (group)	Common name	Edible part
B. oleracea	var. capitata	Cabbage (white, red, cone, etc.)	Leaves
	var. acephala	Kale	Leaves
	var. viridis	Collard greens	Leaves
	var. alboglabra	Chinese broccoli, kai-lan	Leaves
	var. gemmifera	Brussels sprouts	Buds
	var. gongylodes	Kohlrabi	Stem
	var. botrytis	Cauliflower	Inflorescence
	var. <i>italic</i>	Broccoli	Inflorescence
	var. botrytis	Romanesco broccoli	Inflorescence
	var. <i>italica</i> $\times$ <i>alboglabra</i>	Broccollini, broccoflower	Inflorescence
B. rapa	ssp. Rapa	Turnip	Root
	ssp. Pekinensis	Chinese cabbage, napa cabbage	Leaves
	ssp. narinosa (or rosularis)	Asian greens	Leaves
	ssp. Chinensis	Bok choy, pak choy	Leaves
	ssp. Pervidis	Komatsuna, Japanese mustard spinach	Leaves
	ssp. Nipposinica	Mizuna	Leaves
	ssp. Parachinensis	Rapini, broccoli rabe	Leaves, stem, flower buds
B. napus	var. napobrassica	Rutabaga (swede)	Root
	var. pabularia	Siberian kale	Leaves
	var. oleifera	Rapeseed	Seeds
B. juncea	var. rugosa (or integrifolia)	Mustard greens	Leaves
		Brown Indian mustard	Seeds
B. nigra		Black mustard	Seeds
B. carinata		Ethiopian mustard	Leaves, seeds
Brassica hirta		White mustard	Seeds
Amoracia rusticana		Horseradish	Root
Barbarea verna		Land cress	Leaves

 Table 1
 A table summarizing some of the most vital members of family Brassicaceae used as vegetables in the human diet
 Adapted from Šamec and Salopek-Sondi (2019)

Genus, species	Cultivar (group)	Common name	Edible part
Eruca vesicaria		Arugula (rocket)	Leaves, stems
Lepidium sativum		Garden cress	Leaves, stems
Nasturtium officinale		Watercress	Leaves, stems
Raphanus		Radish	Root
sativus	var. longipinnatus	Daikon	Root
Wasabia japonica		Wasabi	Root

Table 1 (continued)

are well-known model plants (Soengas Fernández et al. 2011). For bio-fumigation processes, *Brassica* is extensively used as a biocontrol agent (Ahuja et al. 2011).

A wide range of the plant species of the family is blessed to have the medicinal potential, and the local people of the area use it as medicine to treat various diseases (Table 2). Brassicaceae members like cauliflower, Brussels sprout, kale, green mustard, cabbage, and broccoli decrease the risk of several types of cancer (Wang et al. 2004). The anticarcinogenic potential of these vegetables is attributed to glucosinolates, iso-thiocyanate, indole antioxidants, and other phytoalexins (Zukalová and Vasak 2002). An important component of Brassicaceae vegetables known as indole-3-carbinol acts as an anticarcinogenic compound through different hormonal and metabolic changes (Hanf and Gonder 2005), and also reduces the tumor especially in reproductive organs (Staub et al. 2002). The extracts from Brassica species proved helpful to control the hepatoma cells (Steinkellner et al. 2001). Brassica plants contain amino acids such as L-glutamine, L-histidine, L-alanine, L-aspartic acid, L-valine, L-tryptophan, L-threonine, L-phenylalanine, and L-methionine; moreover, different phytochemicals such as indole phytoalexins (N-Methoxyspirobrassinol methyl ether, 1-methoxyspirobrassinol, 1-methoxyspirobrassinin, camalexin, brassilexin, spirobrassinin, brassinin, glucosinolates (neoglucobrassicin, gluconapin, glucobrassicin, gluconasturtiin, glucobrassicanapin, glucoalyssin, glucoraphanin, and glucoiberin), and phenolics (kamepferol, anthocyanins, p-coumaric, quercetin, sinapic acid, ferulic, caffeic, chlorogenic, neochlorogenic, hydroxybenzoic, isoferuloylcholine, and feruloyl) have antioxidant, cardiovascular protective, and anticarcinogenic properties (Jahangir et al. 2009).

#### **2** General Description of the Brassicaceae Family

The family consists of various important genera have diverse economic as well as agronomic use in exploring the world of knowledge using them as model plants.

S. No	Botanical name	Common name	Part used	Pharmacological activity	References
1	Brassica rupestris L.	Brown mustard	Whole plant	Anticancer and antioxidant activity	Amri (2014)
2	Brassica tournefortii Gouan	Asian mustard	Whole plant	Anticancer and antioxidant activity	Amri (2014)
3	Brassica napus L.	Rapeseed	Whole plant	Anticancer, anti-goat, antioxidant, analgesic, diuretic, and anti-catarrhal activity, anti-scurvy and anti-inflammatory of bladder	Amri (2014); Rahman et al. (2018); Saeidnia and Gohari (2012)
4	Brassica L. var. perviridis	Mustard spinach	Whole plant	Anticancer and antioxidant activity	Amri (2014)
5	Brassica rapa L. var. rapifera	Turnips	Whole plant	Anticancer and antioxidant activity	Amri (2014)
6	Brassica rapa L. var. chinensis	Bok choy	Whole plant	Anticancer and antioxidant activity	Amri (2014)
7	Brassica rapa L. var.pekinensis	Chinese cabbage	Whole plant	Anticancer and antioxidant activity	Amri (2014)
8	Brassica oleracea	Cauliflower	Leaves	Antibacterial activity	Prasad (2014)
9	<i>Brassica</i> <i>carinata</i> A. Braun.	Ethiopian or Abyssinian mustard	Whole plant	Utilized in bio-fumigant, to repress pathogens and soil-borne pests Potential as new edible oil/protein crops	Rahman et al. (2018); Warwick (2011)
10	Malcolmia africana (L.) R.Br.	African mustard	Spices	Antioxidant activity and phenol content	Owis (2015)
11	Brassica oleracea L. var. capitata	Cabbage	Raw and processed cabbage	Antioxidant, anti-inflammatory, and antibacterial properties	Prasad (2014); Rokayya et al. (2013)

 Table 2 The summary of the members of family Brassicaceae used for their pharmacological potential

S. No	Botanical name	Common name	Part used	Pharmacological activity	References
12	Brassica rapa L.	Broccoli raab	Vegetables	Anticancer, diuretic, analgesic, anti-gout potential, aphrodisiac activity, anti-inflammatory and anthelmintic activity Improves insulin resistance in type 2 diabetic patients	Amri (2014); Gul et al. (2013); Ravikumar (2015)
13	Brassica oleracea var. capitata f. rubra	Red cabbage	Leaves	It is competent in stomach diseases, diabetic, anti-cancer activity, antioxidant, hypolipidemic, anti-hyperglycemic, and cardio-protective	Chauhan et al. (2016)
14	Brassica juncea L.	Mustard	Seed Leaves Dried leaf and flower Total plant	Anticancer, anti-diabetic, diuretic, analgesic, emetic activity, and rubefacient Antihyperglycemic, antioxidant, antiatherogenic, antifungal activity, allergenicity and antitumor activity The antiatherogenic effect, antioxidant, and fungicidal activity. Used to treat dengue fever, splenic disorders, and dyspepsia	Amri (2014); Kumar et al. (2011); Rahman et al. (2018)
15	Brassica campestris Linn.	Sarson	Seed oil	Used to remove dandruff from hair, used to make an ointment for curing itching and skin infections, hair tonic and laxative	Bhatnagar et al. (2016)

 Table 2 (continued)

S. No	Botanical name	Common name	Part used	Pharmacological activity	References
16	Raphanus sativus	Radish	Leaves and seeds Underground parts	Antimicrobial activity Treatment of intestinal parasites, asthma and chest pain	Parvaiz et al. (2013); Prasad (2014); Singh and Singh (2013)
17	Lepidium sativum L.	Garden cress	Seeds	Used in treating dysentery and bone fracture, healing in human and migraine; used as a saag and anthelmintic, anti-arthritic activity valuable in the cure of cough asthma, with expectoration, poultices for sprains, leucorrhoea, leprosy, skin infections, diarrhea, dysentery, dyspepsia, lumbago, splenomegaly scurvy, and seminal weakness	Dutta et al. (2014); El Sayed and Aly (2014); Khan et al. (2013); Raval (2016)
18	Nasturtium Officinale R.Br.	Water cress	Vegetative shoot	It has many uses in the form of salad, pot herb, and its saag have been used as appetizers which help as a diuretic, antibiotic, and also relieves from problems of the chest	Khan et al. (2013)

 Table 2 (continued)

Besides, the family is enormously blessed with plants that possess pharmaceutical properties and are used as medicine to treat various diseases. Some of the important genera of the family are briefly discussed as follows.

S. No	Botanical name	Common name	Part used	Pharmacological activity	References
19	Sisymbrium Irio L.	London rocket	Leaves and seeds Whole plant	Antipyretic, anti-vomiting, diarrhea, and cough. A tonic herb with a mustard-like aroma. It has laxative, diuretic, and expectorant effects, and benefits the digestion, internally used for bronchitis, coughs, laryngitis, and bronchial catarrh.	Gulshan et al. (2012); Khan et al. (2013)
20	Brassica nigra L.	Black mustard	Seeds	Anticancer, anti-diabetic, diuretic, activity in cold and influenza, stimulant activity, emetic, antibacterial, anti-catarrhal activity, and laxative. Anti-spasmodic, aphrodisiac activity, appetizing, digestive and aperitif activity Used against alopecia, Anti-dandruff activity, Used in neuralgia Used for common cold and arthritis	Amri (2014); Obi et al. (2009); Rahman et al. (2018); Tomar and Shrivastava (2014)
21	Armoracia rusticana	Horseradish	Roots and leaves	Anti-lipase and antioxidant activity	Calabrone et al. (2015)
22	Calepina irregularis	White ball mustard	Mustard extracts	Analgesic activity	Rahman et al. (2018)
23	Lepidium meyenii	Маса	Leaves	Restores the levels of testosterone in the males Hypoglycaemic and anti-obesity effect	Pachiappan et al. (2017)

 Table 2 (continued)

S. No	Botanical name	Common name	Part used	Pharmacological activity	References
24	Capsella bursa-pastoris Moench	Bambaisa	Whole plant Seeds	Used in fertility regulation Astringent	Sher et al. (2011)
25	Cheirantus cheiri L.	Wallflower	Flower and seed	Diuretic, aphrodisiac, jaundice, tumors	Erum et al. (2017)
26	Aethionema oppositifolium	Opposite-leaf candytuft	Spices	Antioxidant activity	Owis (2015)
27	Cardamine Hirsuta Linn	Hairy bittercress	Whole plant	Used for indigestion	Nag (2013)
28	<i>Rorippa indica</i> (Linn.) Hiern	Indian yellow cress	Whole plant	Used for a toothache, sore throat, rheumatic arthritis, hepatitis, abdominal and blood disorders	Nag (2013)
29	Descurainia sophia (L.) Webb	Skhabootay	Flowers and leaves Seeds	Antiscorbutic. Used as Cardiotonic, demulcent, diuretic, expectorant, febrifuge, and laxative	Haq (2012); Sher et al. (2011)
30	Nasturtium officinale R.Br.	Talmeera	Shoot Leaves	Purgative, emetic Effective in cough	Nag (2013); Shah et al. (2015)
31	Alliaria petiolata (M.Bieb.)	Garlic mustard	Leaves	Antimicrobial activities It acts as an antiseptic to ulcers and also plays a role in wound healing, especially complications caused in bronchi, could also be used disinfectant.	Cipollini and Cipollini (2016); Rahman et al. (2018)
32	Raphanus sativus var. longipinnatus	White radius	Leaves	Antimicrobial activities	Singh et al. (2018)

 Table 2 (continued)

S. No	Botanical name	Common name	Part used	Pharmacological activity	References
33	Brassica alba Boiss.	White or yellow mustard	Seedling leaves Seeds	It is helpful for blood purification. It has strong sanitizer properties and is utilized to preserve food, used for the cure of cold, cough, and sore throats	Rahman et al. (2018)
34	Sisymbrium officinale L. Scop.	English watercress	Whole plant	It is used to treat sore throat and as an expectorant to cure common asthma and cold	Rahman et al. (2018)
35	Neslia paniculata	Ball mustard	Whole plant	It is a forage crop used as food for cattle, skin disorders.	Rahman et al. (2018)
36	Sisymbrium erysimoides	Smooth mustard	Whole plant	Used to treat bronchitis and has anti-inflammatory activity	Rahman et al. (2018)
37	Sisymbrium orientale	Asian hedge mustard	Whole plant	Used to treat bronchitis	Rahman et al. (2018)
38	Sisymbrium officinale	Hedge mustard	Whole plant	Used to treat bronchitis and snake-bite antidote Anti-asthmatic, anti-spasmodic, and anti- addiction activity	Rahman et al. (2018)
39	Camelina sativa	Camelina	Whole plant	Likely to be used as food, fodder, and biofuel. Also used in paints, cosmetics, and dyes. Likely to be used as edible oil and protein crops	Warwick (2011)
40	Crambe abyssinica	Crambe	Whole plant	Use as erucamide. Likely to be used as edible oil and protein crops	Warwick (2011)

 Table 2 (continued)

S. No	Botanical name	Common name	Part used	Pharmacological activity	References
41	E. vesicaria	Rocket	Seed oil	It is utilized as a lubricator, hair oil, and for massage and relaxation. It used as a blistering agent and pickling. Likely to be used as edible oil and protein crops	Warwick (2011)
42	Aethionema grandiflorum	Persian stonecress	Whole plant	Used to treat meningitis, bacterial infections, and typhoid	Parvaiz et al. (2013)
43	Erysimum kotschyan	Wallflower	Spices	Antioxidant activity	Owis (2015)
44	Sterigmostemum incanum	-	Spices	Antioxidant activity	Owis (2015)
45	Aethionema dumanii	-	Spices	Antioxidant activity	Owis (2015)
46	Brassica hirta	White mustard	Extracts	Anti-microbial activity	Rahman et al. (2018)
47	Eruca sativa	Rocket salad	Leaves and whole plant	It posses astringent properties, digestive, emollient, depurative, laxative, rubefacient, tonic properties, stomachic, anti-inflammatory, antibacterial activity, diuretic. hair tonic, antidandruff, and antioxidant activity antidiabetic activity	Barlas et al. (2011); Koubaa et al. (2015); Salma et al. (2018); Sher et al. (2011)

 Table 2 (continued)

#### 2.1 Arabidopsis

Arabidopsis is one of the most important genera of the family Brassicaceae on the basis of its morphology and molecular phylogeny various aspects of its taxonomical history has been explored and reported (Al-Shehbaz and O'Kane 2002; Al-Shehbaz et al. 1999). Genus Arabidopsis has about 9 species and 8 subspecies (Koch et al. 2008). Arabidopsis has no well-documented economic importance, but its small genome and short life cycle paved the way to better study, understand, and explore the development, physiology, and gene function of plants through genetic approaches, thus making it a highly valuable and cherished model plant.

#### 2.1.1 Arabidopsis thaliana (L.) Heynh

It is the key species of the genus Arabidopsis. It is a small herbaceous annual plant about 10-40 cm in height, cosmopolitan in its distribution being native to Europe and Middle Asian mountain ranges. More than 750 accessions of the species have been collected around the globe. It has a short life cycle of about 5-7 weeks with a flowering period from April to early June and produces about 10,000 seeds/plants. Moreover, the species is self-fertile and self-compatible. It has a small genome that has been completely sequenced (Initiative 2000). Thus, it is the 1st plant and the 3rd multicellular organism after Caenorhabditis elegans (Blaxter 1998), and Drosophila melanogaster (Adams et al. 2000) to have their genome completely sequenced. Through various available mutants, A. thaliana can be transformed through vector Agrobacterium tumefaciens (http://www.geochembio.com/biology/ organisms/arabidopsis/) (Al-Shehbaz and O'Kane 2002; Koornneef et al. 2004). Hence, Arabidopsis thaliana helped to explore every aspect of plant biology and provide insight to increase crop production through various molecular and biotechnological approaches (Buell and Last 2010). Moreover, it that has been explored to understand plant responses under different stress conditions (Dinneny et al. 2008; Kreps et al. 2002; Nakashima et al. 2009; Roosens et al. 2008) and variation in adaptive attributes (Alonso-Blanco and Koornneef 2000; Koornneef et al. 2004; Vaughn et al. 2007; Weigel 2012). Besides other species of Arabidopsis like A. lyrata, A. halleri, A. arenosa, etc. are explored for the variation in complex traits like selfincompatibility, heavy metal tolerance and hybridization-polyploidization (Clauss and Koch 2006; Roosens et al. 2008).

#### 2.1.2 Arabidopsis Halleri

It is previously named as *Cardaminopsis halleri* (L.) Hayek. However, later, on the basis of molecular evidence, it was placed in genus *Arabidopsis*. It is reported to occur on heavy metal contaminated soils and is among the important hyperaccumulators of zinc (Zn) and cadmium (Cd) (Bert et al. 2000; Küpper et al. 2000). Interestingly

it is closely related to *Arabidopsis lyrata*, which is infertile and a non-accumulator of heavy metals (Macnair et al. 1999).

#### 2.1.3 Arabidopsis Suecica

It is an allotetraploid species of genus that is formed by the hybridization of *Arabidopsis thaliana* with *Arabidopsis arenosa* (Koornneef et al. 2004; Pontes et al. 2004).

#### 2.2 Brassicas

*Brassica* is the essential genera of the family, consisting of 37 species (Gómez-Campo 1980). Most of the crop plants are included in this genus which has edible buds, flowers, leaves, roots, seeds, and stems. Most of the wild species are used for hybrid seed development. These hybrid seeds and modified species are therefore of prime importance in developing resistant varieties against various pests (OECD 2016; Rakow 2004).

#### 2.2.1 Brassica Oleracea L

*Brassica oleracea* shows a very distinguish phenotype with 9 chromosomes. It is widely distributed in Asia, Turkey, and Southern Greece. It has fleshy leaves. The plant has a woody appearance and is perennial (OECD 2016; Rakow 2004). There are six groups of the *Brassica oleracea*, e.g., var. *acephala*, var. *botrytis*, var. *fruticosa*, var. *gongylodes*, *and* var. *italic*. These are used as vegetables, oil, and as a fodder crop (Rakow 2004).

#### 2.2.2 Brassica Rapa L

*Brassica rapa* possesses 10 chromosomes and sometimes it is called *B. campestris. B. rapa* has been reported to be of Mediterranean origin excluding the coastal areas. These areas are mountainous and have a very cold temperature; therefore, the species show preferred rapid growth to low-temperature conditions. It is spread throughout Germany, Eastern Europe, while introduced in the Western Asian countries. In south Asian countries, such as India, also it is cultivated (OECD 2016). It is cultivated as an oilseed crop in China, Canada, and Finland. Seven different varietal groups of *B. rapa* are now being reported to be separate/independent species which was var. *campestris*, var. *chinensis*, var. *japonica*, var. *narinosa*, var. *parachinensis*, var. *pekinensis*, and var. *rapa*. The need for the separation was due to diversity and variability in the said species due to their isolated evolution. For example, var. *pekinensis* (Chinese cabbage) is adapted to a more relaxed environment and grown as an oilseed crop. The var. *chinensis* and var. *japonica* both are leaf vegetables in China and Japan, respectively. The most primitive leaf vegetable is var. *campestris*. Var. *rapa* has been reported to be cultivated all over the globe and utilized enormously as a fodder crop, var. *narinosa* shows high tolerance and resistance to chilling stress (Rakow 2004).

#### 2.2.3 Brassica Nigra (L.) Koch

*B. nigra* is species with 8 chromosomes. It is a noxious weed found in the Mediterranean region, Ethiopia, and Turkey. The plant tends to have a height of almost 2 m and does not need vernalization treatment for flowering (OECD 2016; Rakow 2004).

#### 2.2.4 Crossed and Cultivated Species

*Brassica carinata, Brassica juncea, and Brassica napus* are the species which are cultivated and formed after interspecific crosses between the wild species of *Brassica* to acquire the desirable character which may enhance its economic value.

#### Brassica Carinata A. Braun

It is the species which comprises 17 chromosomes and is formed by crossing *B. nigra* which is a species of 8 chromosomes with *B. oleracea* with 9 chromosomes (OECD 2016; Rakow 2004). Cultivation of this species is restricted to Ethiopia. *Brassica carinata* is a slow-growing plant which might be an inherited character from *B. oleracea*. Its seeds are rich in oil content (Cardone et al. 2003; Rakow 2004).

#### Brassica Juncea (L.) Czern and Coss

It is derived from an interspecific cross of *Brassica nigra* (n = 9) and *Brassica rapa* (n = 10). Ukraine, India, Italy, and China are the main regions of its diverse population. The difference between Chinese and Indian spp. is made in terms of their seed color as Chinese seeds are yellow while the Indian ones are brown and larger (OECD 2016; Rakow 2004). Mostly it is grown for oilseeds and is commonly called Indian mustard. Other than the oils, their leaf and root (turnip) are also of great economic importance. The species are grown widely in China, but it cannot be considered native to the region because none of its wild relatives exist in the area. In some Western countries such as Canada, *Brassica juncea* is cultivated as an important condiment production crop (Rakow 2004).

#### Brassica Napus L

It is an amphidiploid species and consists of 19 chromosomes, which has been obtained as a result of an interspecific cross between *B. rapa* (n = 9) and *B. oleracea* (n = 9) (Parkin et al. 1995; Rakow 2004). Wild species other than the cultivated forms of *B. napus* could be found on beaches, coastal areas of Britain, Gotland, Netherlands, and Sweden (Rakow 2004). In many countries, *Brassica napus* are the most productive cultivated species grown as oilseeds. The potential of yield is pretty much high as the photosynthetic activity is high concerning per unit of the leaf which is further positive and proportional to several chloroplast present per unit area of a leaf (Liu et al. 2009).

#### 2.3 Etymology

The name Brassicaceae is derived from new Latin from *Brassica* meaning the type genus (Webster 1889) and -aceae, standard name representing family name used in the modern taxonomy system. *Brassica* (genus name) is derived from Classical Latin meaning cabbage and other crucifers. Brassicaceae's old name was Cruciferae referring to "cross-bearing", representing four petals of mustard flowers that resemble the Cross symbol. Cruciferae is among the eight plant families whose names does not derive from any genus nor have the suffix -aceae, but it is an authorized alternative name (ICBN: International Code of Botanical Nomenclature).

# **3** Taxonomy and the Phylogenetic Relationship Between the Brassicaceae Family

#### 3.1 Taxonomy

Family Brassicaceae is among the important angiospermic families with diverse economic and scientific importance, e.g., *Arabidopsis thaliana and Brassica*, etc. It has been delineated into 321 genera, 51 tribes, and 3660 species (Al-Shehbaz 2012; Al-Shehbaz 2014; German and Friesen 2014). It is a remarkable model family to explore the phylogenetic relationship and evolution through the course of time due to its diverse morphological, ecological, and genetic diversity. In its early evolutionary history, Brassicaceae experienced whole-genome duplications (Edger et al. 2015; Kagale et al. 2014), providing excellent opportunities to explore these critical evolutionary processes (Kagale et al. 2014). In short, the Brassicaceae family has many benefits to be a model family for relative and evolutionary studies (Couvreur et al. 2009; Franzke et al. 2011; Mitchell-Olds 2001).