

Mirza Hasanuzzaman
Susana Araújo
Sarvajeet Singh Gill *Editors*

The Plant Family Fabaceae

Biology and Physiological Responses
to Environmental Stresses

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Sarvajeet Singh Gill
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Editors

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

Susana Araújo
Instituto de Tecnologia Química e Biológica
António Xavier
Universidade Nova de Lisboa
Oeiras, Portugal

Sarvajeet Singh Gill
Centre for Biotechnology
Maharshi Dayanand University
Rohtak, Haryana, India

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Preface

The Food and Agriculture Organization of United Nations projects that global population will increase 10.8 billion by 2080, representing an increase by 47% in the future.¹ In such context, worldwide agricultural and food production systems are being challenged to provide enough food to meet the growing demands. Nowadays, agriculture has also to address the sustainable use of existing natural resources while tackling the challenges associated with the impact of climate change.

The cultivation of *Fabaceae* plants, commonly known as legumes, emerges as one of the relevant approaches to tackle these challenges. This plant family with 800 genera and 20,000 species,² being the second most economically important family of plants after *Poaceae*, encloses many benefits for agricultural and food sustainability. Due to their ability to fix atmospheric nitrogen by establishing symbiotic associations with nitrogen-fixing microorganisms, the cultivation of legumes is a sustainable option to reduce the use of fertilizers and production costs, while contributing to improve overall soil conditions. Importantly, several grain legumes are important sources of vegetable protein for humans or important role as forage for animals. Consequently, a growing body of research has been also devoted to study aspects associated with their nutritional quality and health-promoting effects.

Similarly, to other crops, legume physiology and yield are severely affected by non-optimal environmental conditions. Abiotic stresses such as drought, salinity, extreme temperatures, nutrient deficiencies, or toxicities have been reported to cause crucial losses on legume growth and productivity. Although relevant fundamental knowledge underlying the adaptative responses of legumes to abiotic constraints and their genetic basis have been elucidated, more research needs to be done to translate these findings into improved elite lines that can contribute to achieve food security. Recent advances and developments in molecular, biotechnological, and breeding tools have contributed to ease and wider this mission. Still,

¹FAO (2018).

²Lewis et al. (2005).

the ongoing goal is to develop legumes not able to cope with environmental stresses, but still with considerable yield and quality.

The Plant Family Fabaceae—Biology and Physiological Responses to Environmental Stresses combines a group of 20 chapters written by worldwide researchers to provide novel information, regarding the major physiological, metabolic, cellular, and molecular processes, as well as the genetic basis and diversity, associated with abiotic stress responses. This book includes both several chapters addressing general and unique aspects and questions of legume Biology and worldwide impact, and a considerable number of chapters devoted to the effects of environmental stresses have on legume responses. A special focus is provided on running crop breeding and state-of-the-art biotechnological approaches to breed abiotic stress resistance traits into modern crop varieties, highlighting their achievements and still open challenges.

We would like to give special thanks to the authors for their outstanding and timely work in producing such fine chapters. We are highly thankful to Dr. Mei Hann Lee (Senior Editor, Life Science), Springer, Japan, for her prompt responses during the acquisition. We are also thankful to Arulmurugan Venkatasalam, Project Coordinator of this book, and all other editorial staffs for their precious help in formatting and incorporating editorial changes in the manuscripts. Special thanks to Dr. Md. Mahabub Alam, Department of Agronomy, Sher-e-Bangla Agricultural University, Bangladesh, for his generous help in formatting the manuscripts. We believe that this book is useful for undergraduate and graduate students, teachers, and researchers, particularly from the fields of the plant science, botany or agronomy, environmental science, biotechnology, and food science.

Dhaka, Bangladesh
Oeiras, Portugal
Rohtak, India

Mirza Hasanuzzaman
Susana Araújo
Sarvajeet Singh Gill

References

- FAO (2018) The future of food and agriculture—alternative pathways to 2050. Rome, p 224
Lewis G, Schrire B, Mackinder B, Lock M (2005) Legumes of the world. Royal Botanic Gardens, Kew, UK

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Editors and Contributors

About the Editors



Dr. Mirza Hasanuzzaman is Professor of Agronomy at Sher-e-Bangla Agricultural University, Dhaka, Bangladesh. He received his Ph.D. 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. He has been devoting himself in research in the field of crop science, especially focused on Environmental Stress Physiology since 2004. He published over 100 articles in peer-reviewed journals and books. He has edited 12 books and written 35 chapters on important aspects of plant physiology, plant stress responses, and environmental problems in relation to plant species. These books were published by the internationally renowned publishers. He 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 Awards 2017, 2018, and 2019.’ He is 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 Sciences (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.).



Dr. Susana Araújo graduated in Applied Plant Biology (2000) at the Faculdade de Ciências da Universidade de Lisboa, Portugal. In 2007, she obtained her Ph.D. in Biology at the Instituto de Tecnologia Química e Biológica António Xavier da Universidade Nova de Lisboa (ITQB NOVA), Portugal. During her Ph.D. thesis, she developed *Medicago truncatula* lines expressing a stress-related gene and studied their response to water deficit. After a postdoctoral fellowship at ITQB NOVA, she moved to the Tropical Research Institute in Lisbon (2009–2014) to continue her research on legume adaptation to water deficit. In 2015, she moved to the University of Pavia (UNIPV, Italy) as a senior researcher. Under the scope of the PRIMTECH project, she studied the molecular mechanisms behind seed germination and priming. This subject, among others, was further studied after returning to ITQB NOVA as postdoctoral researcher (2016–2018). Presently, she is a researcher at the Plant Cell Biotechnology Laboratory of ITQB NOVA, being an integrated member of the research unit “GREEN-IT—Bioresources for Sustainability.” One of her goals is to develop legumes able to cope and yield within the current climate change scenario. Her main research aims to uncover molecular and physiological mechanisms by which legume plants grow and respond to abiotic stresses. Recently, her research focused on seed biology, with running research on seed development and germination. She has been delivering invited lectures and classes in these topics, while supervising several Ph.D., M.Sc., and B.Sc students. She co-authored 42 manuscripts in peer-reviewed international journals, 11 chapters, edited one book on seed technology, and has contributed with several communications in international meetings. She is a member of the International

Legume Society (ILS) and Portuguese Society of Plant Physiology. Since 2015, she is part of the Editorial Board of *Frontiers in Plant Science*, as Associate Editor of the Plant Breeding section, while being referee for several international scientific journals.



Dr. Sarvajeet Singh Gill has completed his Ph.D. at the age of 28 from AMU, Aligarh, and postdoctoral studies from International Centre for Genetic Engineering and Biotechnology (ICGEB). He is working as Assistant Professor of agriculture biotechnology at Centre for Biotechnology, Maharshi Dayanand University. He in collaboration with Dr. Narendra Tuteja (postdoctoral guide) conferred the novel function of DNA helicase (PDH45) in stress tolerance. He has published >100 papers in the journals of international repute, edited >28 books, and has been serving as an editorial board member in the journals of international repute. He has been conferred with 2017 Research Excellence and Citation Award from Clarivate Analytics (Web of Science).

Contributors

Gulraiz Ahmad State Key Laboratory of Grassland Agro-ecosystem, College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou, Gansu, China

Muhammad Ahmad Department of Agronomy, University of Agriculture, Faisalabad, Pakistan

Faical Akaichi Land Economy, Environment and Society, Scotland's Rural College (SRUC), Edinburgh, UK

Afsana Hoque Akhi Molecular Breeding Lab, Plant Breeding Division, Bangladesh Agricultural Research Institute, Gazipur, Bangladesh

Sadia Sabrina Alam Molecular Breeding Lab, Plant Breeding Division, Bangladesh Agricultural Research Institute, Gazipur, Bangladesh

Subham Anurag Department of Environmental Sciences, Central University of Jharkhand, Brambe, Ranchi, Jharkhand, India

Susana Araújo Instituto de Tecnologia Química e Biológica António Xavier, Universidade Nova de Lisboa (ITQB NOVA), Oeiras, Portugal

Bálint Balázs Environmental Social Science Research Group (ESSRG), Budapest, Hungary

Alma Balestrazzi Department of Biology and Biotechnology, “Lazzaro Spallanzani”-University of Pavia, Pavia, Italy

Saon Banerjee AICRP on Agrometeorology, Bidhan Chandra Krishi Viswavidyalaya, Kalyani, West Bengal, India

Christine Oré Barrios Land Economy, Environment and Society, Scotland’s Rural College (SRUC), Edinburgh, UK

Rajan Bhatt Regional Research Station, Kapurthala, India;
Punjab Agricultural University, Ludhiana, Punjab, India

Tasnim Farha Bhuiyan Department of Agricultural Botany, Sher-e-Bangla Agricultural University, Dhaka, Bangladesh

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

Tiziana Centofanti Environmental Social Science Research Group (ESSRG), Budapest, Hungary

Caspar C. C. Chater Departamento de Biología Molecular de Plantas, Instituto de Biología, Universidad Nacional Autónoma de México, Cuernavaca, Mexico;
Department of Molecular Biology and Biotechnology, University of Sheffield, Sheffield, UK

Sandeep Chatterjee Department of Environmental Sciences, Central University of Jharkhand, Brambe, Ranchi, Jharkhand, India

Arzu Çiğ Department of Horticulture, Siirt University, Siirt, Turkey

Fatih Çiğ Department of Field Crops, Faculty of Agriculture, Siirt University, Siirt, Turkey

Alejandra A. Covarrubias Departamento de Biología Molecular de Plantas, Instituto de Biología, Universidad Nacional Autónoma de México, Cuernavaca, Mexico

Shainandni Dogra Punjab Biotechnology Incubator, Mohali, India

Rafael D. C. Duarte CBQF—Centro de Biotecnologia E Química Fina—Laboratório Associado, Universidade Católica Portuguesa, Escola Superior de Biotecnologia, Porto, Portugal

Anamika Dubey Metagenomics and Secretomics Research Lab., Department of Botany, Dr. Harisingh Gour University (A Central University), Sagar, MP, India

Ana Sofia Duque Instituto de Tecnologia Química e Biológica António Xavier (ITQB NOVA), Green-it Unit, Oeiras, Portugal

Ayman EL Sabagh Department of Agronomy, Faculty of Agriculture, Kafrelsheikh University, Kafr El-Shaikh, Egypt;
Department of Field Crops, Faculty of Agriculture, Siirt University, Siirt, Turkey

Murat Erman Department of Field Crops, Faculty of Agriculture, Siirt University, Siirt, Turkey

Shah Fahad Department of Agriculture, University of Swabi, Khyber Pakhtunkhwa, Pakistan

Muhammad Farooq Department of Crop Sciences, College of Agricultural and Marine Sciences, Sultan Qaboos University, Muscat, Oman;
Department of Agronomy, University of Agriculture, Faisalabad, Pakistan;
The UWA Institute of Agriculture and School of Agriculture, & Environment, the University of Western Australia, Perth, WA, Australia

Maham Fatima Department of Environmental Sciences, COMSATS University Islamabad, Vehari Campus, Pakistan

Helena Ferreira Universidade Católica Portuguesa, Escola Superior de Biotecnologia, CBQF - Centro de Biotecnologia e Química Fina—Laboratório Associado, Porto, Portugal

Dibakar Ghosh ICAR-Directorate of Weed Research, Jabalpur, Madhya Pradesh, India

Ana Gomes Universidade Católica Portuguesa, Escola Superior de Biotecnologia, CBQF - Centro de Biotecnologia e Química Fina—Laboratório Associado, Porto, Portugal

Gurinderjit Singh Goraya Himachal Pradesh Forest Department, Former PCCF & HoFF, Himachal Pradesh, Talland, Shimla, HP, India

Sabine Gruber University of Hohenheim, Institute of Crop Production (340a), Stuttgart, Germany

Michael A. Grusak USDA-ARS Edward T. Schafer Agricultural Research Center, Fargo, ND, USA

Carla Gualtieri Department of Biology and Biotechnology, “Lazzaro Spallanzani”-University of Pavia, Pavia, Italy

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

Abdul Hannan Seed Technology Division, Bangladesh Agricultural Research Institute, Rajshahi, Bangladesh

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

Akbar Hossain Bangladesh Wheat and Maize Research Institute (BWMRI), Dinajpur, Bangladesh

Pete Iannetta Ecological Sciences, James Hutton Institute, Dundee, Scotland, UK

Muhammad Ikram Department of Agronomy, Faculty of Agricultural Sciences and Technology, Bahauddin Zakariya University, Multan, Pakistan

Shahid Iqbal Department of Agronomy, Muhammad Nawaz Shareef University of Agriculture, Multan, Pakistan

M Sohidul Islam Department of Agronomy, Hajee Mohammad Danesh Science and Technology University, Dinajpur, Bangladesh

Tofazzal Islam Institute of Biotechnology and Genetic Engineering (IBGE), Bangabandhu Sheikh Mujibur Rahman Agricultural University, Gazipur, Bangladesh

Euan K. James Ecological Sciences, James Hutton Institute, Dundee, Scotland, UK

Vaneet Jishtu Himalayan Forest Research Institute, Shimla, HP, India

Anestis Karkanis Department of Agriculture Crop Production and Rural Environment, University of Thessaly, Volos, Greece

Alison Karley Ecological Sciences, James Hutton Institute, Dundee, Scotland, UK

Mohammad Latif Khan Metagenomics and Secretomics Research Lab., Department of Botany, Dr. Harisingh Gour University (A Central University), Sagar, MP, India

Ashwani Kumar Metagenomics and Secretomics Research Lab., Department of Botany, Dr. Harisingh Gour University (A Central University), Sagar, MP, India

Susana T. Leitão Instituto de Tecnologia Química e Biológica António Xavier, Universidade Nova de Lisboa (ITQB NOVA), Oeiras, Portugal

Anca Macovei Department of Biology and Biotechnology, “Lazzaro Spallanzani”-University of Pavia, Pavia, Italy

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

Marta Maluk Ecological Sciences, James Hutton Institute, Dundee, Scotland, UK

Muhammed Khairujjaman Mazumder Plant Stress and Metabolomics Laboratory, CIL, Assam University, Silchar, Assam, India

Ram Swaroop Meena Department of Agronomy, Institute of Agricultural Sciences, BHU, Varanasi, Uttar Pradesh, India

Md. Motiar Rohman Molecular Breeding Lab, Plant Breeding Division, Bangladesh Agricultural Research Institute, Gazipur, Bangladesh

Debojyoti Moulick Plant Stress and Metabolomics Laboratory, CIL, Assam University, Silchar, Assam, India

Muhammad Mubeen Department of Environmental Sciences, COMSATS University Islamabad, Vehari Campus, Pakistan

Akash Nag Department of Environmental Sciences, Central University of Jharkhand, Brambe, Ranchi, Jharkhand, India

Kamrun Nahar Department of Agricultural Botany, Sher-e-Bangla Agricultural University, Dhaka, Bangladesh

Poornima K. Narayana Indian Institute of Pulses Research, Kanpur, India; Department of Plant and Soil Sciences and Gund Institute for the Environment, University of Vermont, Burlington, VT, USA

Wajid Nasim Department of Agronomy, University College of Agriculture and Environmental Sciences, The Islamia University of Bahawalpur (IUB), Bahawalpur, Pakistan

Georgia Ntatsi Laboratory of Vegetable Production Athens, Department of Crop Science, Agricultural University of Athens, Athens, Greece

Andrea Pagano Department of Biology and Biotechnology, “Lazzaro Spallanzani”-University of Pavia, Pavia, Italy

Shyam Narain Pandey Department of Botany, University of Lucknow, Lucknow, India

Kishore C. S. Panigrahi School of Biological Sciences, National Institute of Science Education and Research, Jatni, Bhubaneswar, Odisha, India

Khursheda Parvin Laboratory of Plant Stress Responses, Department of Applied Biological Sciences, Faculty of Agriculture, Kagawa University, Kita-Gun, Kagawa, Japan;
Department of Horticulture, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka, Bangladesh

Elisabete Pinto Universidade Católica Portuguesa, Escola Superior de Biotecnologia, CBQF - Centro de Biotecnologia e Química Fina—Laboratório Associado, Porto, Portugal

Jorge A. Pinto Paiva Instituto de Biologia Experimental e Tecnológica (IBET), Oeiras, Portugal;
Instituto de Tecnologia Química e Biológica António Xavier (ITQB NOVA), Green-it Unit, Oeiras, Portugal;
Institute of Plant Genetic Polish Academy of Science, Poznań, Poland

Jose A. Polania Departamento de Biología Molecular de Plantas, Instituto de Biotecnología, Universidad Nacional Autónoma de México, Cuernavaca, Mexico

Richa Rai Department of Botany, Rameshwar College, Babasaheb Bhimrao Ambedkar Bihar University, Muzaffarpur, Bihar, India

Idupulapati M. Rao International Center for Tropical Agriculture (CIAT), Cali, Colombia;
Agricultural Research Service, Department of Agriculture, Plant Polymer Research Unit, National Center for Agricultural Utilization Research, Peoria, IL, USA

Disna Ratnasekera Department of Agricultural Biology, Faculty of Agriculture, University of Ruhuna, Matara, Sri Lanka

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

Md. Rezwana Molla Plant Genetic Resources Centre, Bangladesh Agricultural Research Institute, Gazipur, Bangladesh

Diego Rubiales Institute for Sustainable Agriculture, CSIC, Córdoba, Spain

Bedabrata Saha School of Biological Sciences, National Institute of Science Education and Research, Jatni, Bhubaneswar, Odisha, India

Purabi Saikia Department of Environmental Sciences, Central University of Jharkhand, Brambe, Ranchi, Jharkhand, India

Suman Samanta AICRP on Agrometeorology, Bidhan Chandra Krishi Viswavidyalaya, Kalyani, West Bengal, India

Carla S. Santos CBQF—Centro de Biotecnologia e Química Fina—Laboratório Associado, Universidade Católica Portuguesa, Escola Superior de Biotecnologia, Porto, Portugal

Subhas Chandra Santra Department of Environmental Science, University of Kalyani, Kalyani, West Bengal, India

Dimitrios Savvas Laboratory of Vegetable Production Athens, Department of Crop Science, Agricultural University of Athens, Athens, Greece

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

Shailesh Shrestha Land Economy, Environment and Society, Scotland's Rural College (SRUC), Edinburgh, UK

Luiza Toma Land Economy, Environment and Society, Scotland's Rural College (SRUC), Edinburgh, UK

Ehsan Valiollahi Instituto de Biologia Experimental e Tecnológica (IBET), Oeiras, Portugal;
Instituto de Tecnologia Química e Biológica António Xavier (ITQB NOVA), Green-it Unit, Oeiras, Portugal

Albert Vandenberg Department of Plant Sciences, University of Saskatchewan, Saskatoon, Canada

Marta W. Vasconcelos CBQF—Centro de Biotecnologia e Química Fina—Laboratório Associado, Universidade Católica Portuguesa, Escola Superior de Biotecnologia, Porto, Portugal

Maria Carlota Vaz Patto Instituto de Tecnologia Química e Biológica António Xavier, Universidade Nova de Lisboa (ITQB NOVA), Oeiras, Portugal

Eric J. B. von Wettberg Department of Plant and Soil Sciences and Gund Institute for the Environment, University of Vermont, Burlington, VT, USA;
Mathematical Biology Laboratory, Peter the Great St. Petersburg Polytechnic University, St. Petersburg, Russia

Allah Wasaya College of Agriculture, BZU, Layyah, Pakistan

Michael Williams Department of Botany, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland

Tauqeer Ahmad Yasir College of Agriculture, BZU, Layyah, Pakistan

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

General Aspects

The Biology of Legumes and Their Agronomic, Economic, and Social Impact



Marta W. Vasconcelos, Michael A. Grusak, Elisabete Pinto, Ana Gomes, Helena Ferreira, Bálint Balázs, Tiziana Centofanti, Georgia Ntasi, Dimitrios Savvas, Anestis Karkanis, Michael Williams, Albert Vandenberg, Luiza Toma, Shailesh Shrestha, Faical Akaichi, Christine Oré Barrios, Sabine Gruber, Euan K. James, Marta Maluk, Alison Karley, and Pete Iannetta

Abstract Intensive agriculture and meat-based westernized diets have brought a heavy environmental burden to the planet. Legumes, or pulses, are members of the large Fabaceae (*Leguminosae*) family, which comprise about 5% of all plant species. They are ancient crops whose popularity both for farmers and consumers has gone

M. W. Vasconcelos (✉) · E. Pinto · A. Gomes · H. Ferreira
Universidade Católica Portuguesa, Escola Superior de Biotecnologia, CBQF - Centro de Biotecnologia e Química Fina—Laboratório Associado, Rua Diogo Botelho 1327, 4169-005 Porto, Portugal
e-mail: mvasconcelos@porto.ucp.pt

M. A. Grusak
USDA-ARS Edward T. Schafer Agricultural Research Center, 1616 Albrecht Blvd. North, Fargo, ND 58102-2765, USA

B. Balázs · T. Centofanti
Environmental Social Science Research Group (ESSRG), Budapest, Hungary

G. Ntasi · D. Savvas
Laboratory of Vegetable Production Athens, Department of Crop Science, Agricultural University of Athens, Athens, Greece

A. Karkanis
Department of Agriculture Crop Production and Rural Environment, University of Thessaly, Volos, Greece

M. Williams
Department of Botany, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland

A. Vandenberg
Department of Plant Sciences, University of Saskatchewan, Saskatoon, Canada

L. Toma · S. Shrestha · F. Akaichi · C. O. Barrios
Land Economy, Environment and Society, Scotland's Rural College (SRUC), West Mains Road, Edinburgh EH9 3FH, UK

S. Gruber
University of Hohenheim, Institute of Crop Production (340a), 70599 Stuttgart, Germany

E. K. James · M. Maluk · A. Karley · P. Iannetta
Ecological Sciences, James Hutton Institute, Dundee, Scotland, UK

through several stages of acceptance, and in recent years, legumes have regained their luster. This is due to a global understanding that: (1) farming systems need to promote biodiversity, (2) biological nitrogen fixation is an important tool to reduce the application of external chemical inputs, namely in the form of nitrogen fertilizers, and that (3) plant-based foods have fewer adverse environmental effects per unit weight, per serving, per unit of energy, or per protein weight than do animal source foods, across various environmental indicators. Legumes play a key role in answering these three global challenges and are pivotal actors in the diversification and sustainable intensification of agriculture, particularly in light of new and urgent challenges such as climate change. In this chapter, we showcase the importance of legumes as contemporary agents of change, whose impacts start in the field, but then branch out into competitive global economies, modernized societies, and ultimately, improved food security and human health.

Keywords Biodiversity · Biological nitrogen fixation · Nutrition and health · Pulses · Sustainability

1 Introduction

The word legume comes from the Latin word *legumen* which can be translated to “seeds harvested in pods.” In many parts of the world, such as in Canada, Bangladesh, or India, the world pulse is used when referring to legume grains, especially those with a low content in fat. Legumes or pulses have accompanied farmers since the Neolithic revolution, the very onset of farming practices of mankind. Pea (*Pisum sativum*), lentil (*Lens culinaris*), chickpea (*Cicer arietinum*), and bitter vetch (*Vicia ervilia*) belong to the “Big Eight,” that package of “founder crops” which have been domesticated in the Fertile Crescent during the 10th and 9th millennia BCE (Asouti and Fuller 2013). Legumes were domesticated alongside grasses as early as 10,000 years ago (Hancock 2012). Among the earliest legume crops were chickpea, garden pea, and lentil (Sprent 2009; Hancock 2012; Smýkal et al. 2015). The domestication of other important legumes followed later on in different regions of the world, for example, soybean in east Asia (Sedivy et al. 2017), Azuki bean (*Vigna angularis*) in west Asia (Lee 2012), or common bean (*Phaseolus vulgaris*) in Mesoamerica (Lopez et al. 2013). The cultivation of soybean [*Glycine max* (L.) Merrill] dates from China in around 2500 BCE, being now spread throughout the world mostly due to its elevated protein content of the seeds that can reach almost 40%. Despite its particular worldwide importance, soybean is heavily reliant on inoculation to bring it into profitable use in non-native countries like Brazil (Alves et al. 2003).

It is thought that the introduction of legumes into cropping systems in Europe (before the tenth century) enabled an improvement in soil quality and provided nourishment to populations, relieving famine and improving overall population growth.

More than 820 million people have insufficient food and many more consume low-quality diets that cause micronutrient deficiencies. This has contributed to a substantial rise in the incidence of diet-related noncommunicable diseases. All legumes offer a high level of protein in above- and belowground biomass, particularly in grains, in comparison to other crops such as cereals. They are self-supporters of nitrogen fertilization through atmospheric nitrogen fixation in root nodules in symbiosis with soil bacteria from the families *Rhizobium*, *Bradyrhizobium*, and others. The genetic regulation of these processes has been intensively investigated and various forward- and reverse-genetic approaches have identified nearly 200 genes required for symbiotic nitrogen fixation in legumes (Roy et al. 2019).

In times with low availability of meat, pulses—legumes with predominant grain usage—provided a valuable source of proteins for the human diet. The biblical tale of Esau who sold his birthright to his younger brother Jacob for the price of a lentil stew illustrates the estimation of the pulses in early societies. In the past, meat was often unavailable to common people, i.e., for the majority of ancient societies. Pulses, therefore, were a sufficient alternative to meat for a healthy and whole food diet. The traditional Milpa cropping system, a combination of maize, beans, and squash, is a good example for the integration of legumes in sustainable cropping systems and in the whole food human diet (Altieri et al. 2011). It integrates physiological and morphological benefits of crops, including pulses, at the field, and offers a balanced food composition for human consumption with beans as the main provider of protein. The Milpa system originated from Mesoamerica and has spread to many tropical and subtropical regions across the world because of its benefits. Meanwhile, it can be considered a model for innovative cropping systems today and in the future.

In the middle of the twentieth century, pulses disappeared more and more from the menu in the industrial countries and as well from cropping systems at the same time. Pulses were considered to be an old-fashioned food, with nonnutritive compounds such as lectins, alkaloids, saponins, or phytates (Muzquiz et al. 2012), with lengthy time-consuming preparation methods and some causing intestinal irritations. Finally, meat was available to all social classes. There are additionally some agricultural challenges of legume growing: they have lower yields and lower economic value in comparison to cereals. For example, a farmer in temperate Europe (France, Germany, Poland) can achieve a yield of 4.8–7.6 t ha⁻¹ winter wheat and only 2.7–3.5 t ha⁻¹ dry pea (FAO Stat 2019).

Recently, there seems to be a return to the value of pulses. Concerns about ecological impacts of meat production, ethical concerns in terms of animal welfare, and considerations for human health (Chai et al. 2019; Hagmann et al. 2019) have promoted an interest in a more sustainable plant-based food production, with legumes as a substantial contributor. In times of public discussions about the loss of biodiversity, sustainable agriculture, and climate change, a renaissance of legumes in agricultural systems seems a reasonable and promising way to design the future of our planet.

2 The Biology of Legumes

2.1 Taxonomy and Morphology

The Earth currently has almost 400,000 species of plants. About 5% of plant species are members of the large plant family Fabaceae (*Leguminosae*) which produce their protein-rich seeds within simple dehiscent dry fruits botanically known as legumes (commonly known as pods). The Fabaceae family includes 770 genera and nearly 20,000 worldwide distributed species (LPWG 2017). The Fabaceae evolved to have root systems that enable symbiotic relationships with various species of soil bacteria that are capable of fixing atmospheric nitrogen, thereby providing a basic biological source of nitrogenous compounds such as proteins and their biochemical derivatives. Legume species are very diverse and are adapted to almost all terrestrial ecosystems in the form of trees, shrubs, vines, and annual herbs. Legume flowers characteristically have five petals that have evolved to a wide range of characteristic sizes, shapes, and colors. Legume species can be self-pollinating, cross-pollinating or both. The traditional classification of *Fabaceae* into the three subfamilies, *Caesalpinioideae*, *Mimosoideae*, and *Papilionoideae*, has been revised by The Legume Phylogeny Working Group (LPWG 2017) and Sprent et al. (2017). A new subfamily classification presented by LPWG (2017) divides the Leguminosae into six subfamilies: *Detarioideae* (84 genera; ca. 760 species; Pantropical), *Cercidoideae* (12 genera; ca. 335 species; Pantropical, *Cercis* warm temperate), *Duparquetioideae* (1 genus; 1 species; West and West-central Africa), *Dialioideae* (17 genera; ca. 85 species; Pantropical), *Caesalpinioideae* (148 genera; ca. 4400 species; Pantropical, some temperate), and *Papilionoideae* (503 genera; ca 14,000 species; cosmopolitan). The previous subfamily *Mimosoideae* has been incorporated into the *Caesalpinioideae* as the mimosoid clade. Species from *the Detarioideae*, *Cercidoideae*, *Duparquetioideae*, and *Dialioideae* are all non-nodulators. Nodulation has been confirmed in only eight genera in the *Caesalpinioideae* sensu stricto subfamily. Most, but not all mimosoids and papilionoids can nodulate (Sprent et al. 2017).

The *Caesalpinioideae* subfamily is highly variable, mostly trees and shrubs with zygomorphic asymmetrical flowers. The mimosoid clade are adapted to tropical and subtropical climates and exist mostly in the form of trees and shrubs. Their flowers are symmetric with valvate petals and have large numbers of prominent stamens. The *Papilionoideae* is the largest, most widely adapted and diverse legume subfamily. Their floral morphology (standard, wings, and keel petals) is demonstrated by that of the widely known species (bean, pea, and soybean) that have edible pods and seeds used in food systems as vegetables and dry seeds. The members of this ecologically diverse group include trees, shrubs, and herbs.

2.2 Nodulation

Legumes form symbiotic relationships with nitrogen-fixing bacteria (rhizobia), most of which belong to the genera *Rhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Ensifer* (Sinorhizobium), and *Azorhizobium* in the Alphaproteobacteria (Denison and Okano 2003; Tampakaki et al. 2017a, b; Ferguson et al. 2019) and in the genera *Paraburkholderia*, *Cupriavidus*, and *Trinickia* in the Betaproteobacteria (Gyaneshwar et al. 2011; Estrada-de los Santos et al. 2018). The infection of roots by rhizobia results in the formation on roots (and occasionally stems) of unique organs called nodules (Ferguson et al. 2013) in which the biological nitrogen fixation process takes place (Ferguson et al. 2019). In this process, the bacterial enzyme nitrogenase catalyzes the reduction of atmospheric N₂ to ammonia (Howard and Rees 1996), which is a plant-available N form.

The nodulation process in many, but not all, legumes follows root infection by efficient compatible rhizobia strains. The root infection causes the curling of the root hairs that entrap the rhizobia and then, after the formation of infection threads through these structures, the bacteria enter the root cells (Peleg-Grossman et al. 2007; Fournier et al. 2015). According to Oldroyd and Downie (2008), the induction of cortical cell divisions is necessary for the nodule's morphogenesis. The bacteria within the nodule cells are a differentiated symbiotic form of rhizobia called bacteroids. Each bacteroid is surrounded by the symbiosome (or peribacteroid) membrane (Denison and Okano 2003; Peleg-Grossman et al. 2007). In the initiation of the rhizobia-legume symbiosis, several compounds (e.g., Nod factors and flavonoids) are implicated. Nod factors are lipochitoooligosaccharides secreted by rhizobia that are involved in the initiation of cell divisions in the cortex, which leads to root hair curling and the formation of infection threads (Ibáñez and Fabra 2011; Murray 2011). Flavonoids produced by legume roots activate NodD proteins and consequently the expression of the Nod genes that are implicated in the synthesis of Nod factors (del Cerro et al. 2017).

Taken together, this chemical cross-talk between the rhizobia and the host legume allows the latter to impose a degree of stringency on which bacteria can enter and form a symbiotic nodule, but as it is based on nod genes rather than *nif* genes, it cannot guarantee that the symbiosis will be effective, and hence compatible, but “cheating” rhizobia are considered to be a significant problem for nodulated legumes (Sprent et al. 2017).

Oxygen plays a significant role in nitrogen fixation because an adequate supply of oxygen in the nodules is needed by bacteroids for respiration (Denison and Okano 2003). See review by Minchin et al. (2008). It is also important to point out that the nitrogen fixation process is characterized by high energy (ATP) demands (Rutten and Poole 2019), because the reduction of 1 molecule of N₂ to ammonia utilizes at least 16 molecules of ATP (Maier 2004). These energy requirements are covered by the respiration of bacteroids (Miller et al. 1988), but sufficient transport of carbohydrates to the roots is needed to maintain sufficiently high respiration rates. Nevertheless, excessive oxygen concentrations can inactivate the nitrogenase (Denison and Okano 2003), and thus the protein leghaemoglobin (Lb) is also an important component

of the nodules, as it acts as an oxygen carrier that facilitates a controlled flux of oxygen to the nitrogen-fixing bacteroids (Denison and Okano 2003). Furthermore, Lb protects nitrogenase from being inactivated by free oxygen, while the Lb-bound oxygen is accessible to bacteroids (Abdelmajid et al. 2008; Rutten and Poole 2019). The internal red-pink color of the nodules is due to the presence of leghaemoglobin (Rejili et al. 2012). Abdelmajid et al. (2008) linked higher nitrogen fixation capacity with a higher accumulation of leghaemoglobin in the nodules.

3 Agronomic Impact

3.1 Nitrogen Supply via Biological Nitrogen Fixation (BNF)

Over the past decades, the excessive application of inorganic nitrogen fertilizers has resulted in groundwater contamination with nitrates (Lv et al. 2019). Groundwater pollution via leaching of these pollutants (NO_3^-) is one of the most serious environmental problems and is positively related to high nitrogen fertilization rates (Vinod et al. 2015; Zheng et al. 2019). Thus, to reduce the groundwater pollution with nitrates, it is important to reduce the excess application of inorganic fertilizers in agricultural fields and/or to apply organic nitrogen sources such as compost or manure. The use of legumes as green manures or the inclusion of legumes in crop rotation systems is alternative to inorganic nitrogen fertilizers that can contribute to higher crop yields and improved soil quality (Castro et al. 2017; Ntatsi et al. 2018).

Biological N fixation by legumes (e.g., faba bean, lentil, pea, chickpea, alfalfa, red clover etc.) ranges from 21 to 389 kg ha⁻¹ (Table 1) (Cazzato et al. 2012; Nimmo et al. 2013; Büchi et al. 2015; Hossain et al. 2016; Snapp et al. 2017; Akter et al. 2018; da Silva Júnior et al. 2018; Dhamala et al. 2018; Ntatsi et al. 2018; Pampana et al. 2018; Ntatsi et al. 2019).

The N₂-fixation capacity of legumes (e.g., the proportion of N derived from the atmosphere [%Ndfa] and biomass productivity) is mainly dependent on plant species, genotypes, symbiotic bacteria (e.g., *Rhizobium* spp.) strains, and environmental conditions (Büchi et al. 2015; Hossain et al. 2016; Akter et al. 2018; Ntatsi et al. 2018; Benjelloun et al. 2019; Ntatsi et al. 2019).

Despite the fact that legumes contribute to nitrogen enrichment of soil BNF, it is worth mentioning that their over-frequent use of these plant species can also lead to nitrate leaching (De Notaris et al. 2018; Hansen et al. 2019). Thus, it is important to optimize the use of legumes (e.g., appropriate crop rotation sequences, mixtures of legumes, and nonlegumes) in order to reduce the risk of nitrate leaching (Hansen et al. 2019; Rakotovololona et al. 2019).

Table 1 Biological nitrogen fixation (BNF) capacity (kg ha^{-1}) of commonly cultivated legumes

Common name	Scientific name	BNF (kg ha^{-1})	Cultivation area	References
Faba bean	<i>Vicia faba</i> L.	118.6–311	Greece, Italy	Ntatsi et al. (2018), Pampana et al. (2018)
Pea	<i>Pisum sativum</i> L.	36.6–125.3	Canada, Greece	Hossain et al. (2016), Ntatsi et al. (2019)
Common vetch	<i>Vicia sativa</i> L.	107–131	Switzerland	Büchi et al. (2015)
Grass pea	<i>Lathyrus sativus</i> L.	101–149	Switzerland	Büchi et al. (2015)
White lupin	<i>Lupinus albus</i> L.	53.1–64.1	Italy	Cazzato et al. (2012)
Chickpea	<i>Cicer arietinum</i> L.	21.0–103.6	Canada	Hossain et al. (2016)
Lentil	<i>Lens culinaris</i> Med.	23.0–86.8	Switzerland, Canada	Büchi et al. (2015), Hossain et al. (2016)
Common bean	<i>Phaseolus vulgaris</i> L.	16.3–71.9	Canada	Akter et al. (2018)
Cowpea	<i>Vigna unguiculata</i> (L.) Walp.	36–75	Brazil	da Silva Júnior et al. (2018)
Soybean	<i>Glycine max</i> (L.) Merr.	90–95	USA	Snapp et al. (2017)
Alfalfa	<i>Medicago sativa</i> L.	103–209	Canada, China	Nimmo et al. (2013)
Egyptian clover	<i>Trifolium alexandrinum</i> L.	35–59	Switzerland	Büchi et al. (2015)
Red clover	<i>Trifolium pretense</i> L.	35.4–389	Denmark, USA	Snapp et al. (2017), Dhamala et al. (2018)

3.2 Pre-crop Benefits Through a Combination of Residual Nitrogen and Break-Crop Effects

Legume cropping, including rotation, intercropping, green manure, and legume-enriched pastures, shows significant advantages over nonlegume systems in terms of fertilizer use and hence emissions of the greenhouse gases CO_2 and N_2O (Jensen and Hauggaard-Nielsen 2003). Grain and forage legumes, by virtue of their symbiosis with N_2 -fixing bacteria, can reduce the need for N fertilizer application. If legume cropping becomes more widely adopted, this could reduce the demand for manufactured fertilizer (Jensen et al. 2012). In terms of soil N inputs from BNF,

an approximate value of 9 kg N mineralized per ton of stubble may be possible for grain legume crops, with higher transfer values being recorded for forage legume systems—15 to 20 kg N per tonne (Peoples et al. 2004, 2009, 2017). Typical rates of BNF for grain and forage legumes are between 100 and 200 kg shoot N ha⁻¹ per year or growing season (Peoples et al. 2019).

Reduced fertilizer usage associated with legume cropping is only suitable after the successful establishment of the root-nodule symbiosis, adequate levels of BNF, and appropriate crop management practices to maintain N₂ fixation. This may involve inoculation of plants with appropriate strains of rhizobia to improve nitrogen fixation, carrying a cost in terms of energy and GHG emissions, and careful monitoring of soil N. Liming of soils is important too in maintaining N₂ fixation, N₂ fixation having the potential to acidify unbuffered soils and hence inhibit nitrogenase activity. This acidifying activity has the potential also to mineralize inorganic phosphate and reduce the requirement for P fertilizer addition (Williams et al. 2017).

Skowronska and Filipek (2014), in their review of life cycle analysis studies on fertilizer manufacture, provide illustrative data on the extent of GHG savings possible through reduced fertilizer production. Depending on the type of N fertilizer, the combined GHG cost of production, packaging, and delivery ranges from 1.9 to 6.3 kg CO₂e (carbon dioxide equivalent) kg⁻¹ fertilizer. The GHG cost for P fertilizer is considerably less, 0.6–1.66 kg CO₂e kg⁻¹ fertilizer, with manufacture of calcium carbonate for soil amendment accounting for 0.15 kg CO₂e kg⁻¹ (Skowronska and Filipek (2014).

Calculation of the reduction in field GHG emissions possible with legume cropping is problematic given the wide variance in data available due to differing crops, soils, climate, management, and most significantly the type of measurement and the time course of measurements employed. Using values averaged across 67–71 site-years of data, Peoples et al. (2019) report an overall reduction in N₂O emissions for legume crops compared with N fertilized crops and pastures of approximately 59%, assuming N₂O emissions of 0.47 t CO₂e ha⁻¹ for legume crops and 1.16 t CO₂e ha⁻¹ for N fertilized crops and pastures.

3.3 Increased Crop Diversification and Biodiversity

Modern intensive agricultural systems are relatively simplified, focussing on a small number of crop species, often in monocultures, and reliant on mineral fertilizers and chemical crop protection to maximize their productivity. Heterogeneous crop systems, however, can show improved production efficiency, yield stability, and resilience to environmental stresses. Legume crops have great potential for optimizing these benefits, whether by increasing the diversity of crops within the crop rotation sequence or as components of crop species mixtures. The positive contribution of legumes to diversification arises directly from legume-specific traits and indirectly from their reduced reliance on agronomic inputs. This is underpinned primarily by the ability of legumes to fix atmospheric nitrogen into nitrogen-rich organic

compounds—as well as their capacity to capitalize on generating a symbiotic- or facilitative-microbiome in the rhizosphere (Chen et al. 2019).

Nonlegume crops show up to 30% greater biomass production in a legume-supported rotation: the benefit of BNF is estimated to be maximal when grain and forage legume crops are present in half of the years of the crop sequence (Iannetta et al. 2016). Despite this, grain legume production in Europe is falling (Magrini et al. 2016) and is characterized by only a few legume crop species, which has constrained progress in legume crop improvement. There are ample opportunities to diversify the range of legume crops and take advantage of adaptive traits in of orphan legume species to improve, for example, their resilience to biotic and abiotic stresses (Cullis and Kunert 2017). By enhancing soil nutrient supply and function, legumes can promote nutrient acquisition by nonleguminous plants growing in a species mixture. Legume crops exhibit multiple traits that complement or facilitate the growth of nonlegume species, leading to more efficient use of resources. This allows greater productivity and profitability per unit land area to be achieved with intercropping compared with monocultures (Martin-Guay et al. 2018). Floral resource provision in legume-supported mixtures, along with increased canopy and root system heterogeneity, and reduced reliance on agronomic inputs, can promote the abundance and activity of beneficial organisms, which facilitate ecosystem services such as pollination, nutrient cycling, and suppression of pests, diseases, and weeds (Everwand et al. 2017).

4 Economic Impact

Understanding the economics of legume systems requires an analysis of the factors influencing the equilibrium between supply (farmers) and demand (consumers) and the interlinkages along the supply chain, while assessing the impact of any shocks to the system on other aspects such as trade and environment. As is the case of any other agricultural industry, but even more so due to their benefits to the public good (European Parliament 2013), changes to the equilibrium between the supply and demand of legumes translates into wider long-term effects, and as such, an analysis of legume production (e.g., assessment of farm profitability) is incomplete and potentially incorrect if not coordinated with an analysis of demand, and of the corresponding ripples on trade, environment, and health.

The economics of legumes in the European Union (EU) shows a production trend closely correlated to the different types of subsidies and payments linked to the Common Agricultural Policy (CAP) reforms, and the global market prices for fertilisers (Fig. 1). Linked to similar factors affecting livestock production, feed demand mirrors production trends for dry pulses (only starting in the 1980s in the case of beans). Imports mirror the demand for processing in the case of soybeans, and mirror the production trends for peas and, respectively, lentils, lupins and other pulses, while showing an opposite trend to the domestic production of beans (following the rise in the 1980s in its use for feed and food).

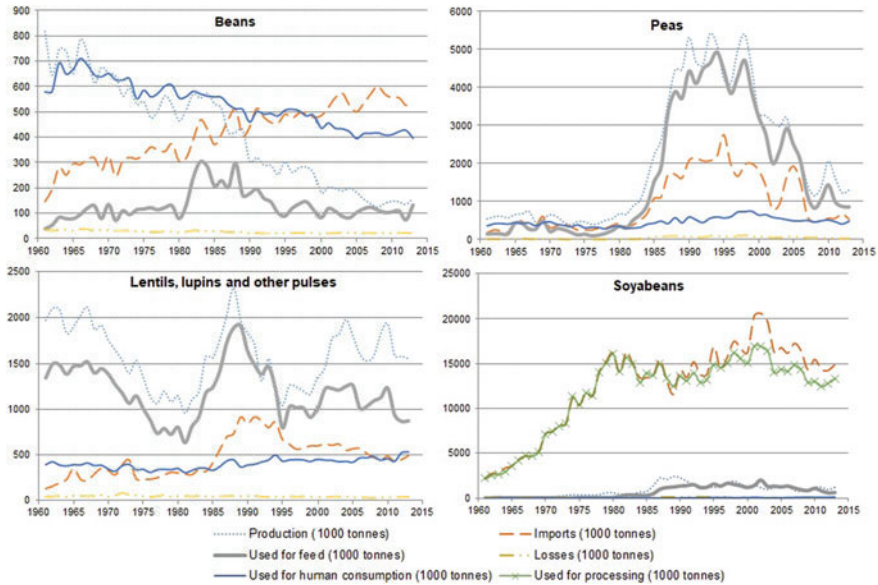


Fig. 1 Legumes production and imports, uses and losses in the European Union. *Source* Own creation based on FAOSTAT data (extracted November 2019)

The cultivation of dry pulses (i.e., grain legumes except soybeans) in EU countries is significantly more frequent in: regions with higher receipt of voluntary coupled CAP support to protein crops; regions with higher shares of organic farming; regions with a more important role of legume consumption in regional diets; regions with relatively deep soils and; regions displaying lower competition for land use with sunflower. Livestock density and share of irrigable agricultural areas are significantly negatively correlated with the share of dry pulses. Up to a certain temperature sum maximum, also higher temperature sums seem to be beneficial for the cultivation of dry pulses. In contrast to dry pulses, regional soybean shares in the arable area are positively correlated with a region's distance to the next main port and with the share of irrigable agricultural area. Agglomeration and spillover effects may matter (i.e., farms located in the neighborhood of dry legume producers are also more likely to commence cultivation of dry legumes; regions with a high share of dry pulses tend to be close to each other), as in the case of dry pulses where a significant spatial lag coefficient was found. Such effects, however, are likely to be effective on a spatial scale smaller than the regional level. Potentially significant causal factors, which have not been tested due to poor data availability, that may be positively linked to legume production include proximity to processing facilities and trading companies and access to extension services and regional networks and training programs (Oré Barrios et al. 2020). Other factors well acknowledged in the literature (European Parliament 2013) with positive causal effects on the cultivation of legumes are market factors, i.e., producer prices for outputs (pulses) and inputs (nitrogen fertilisers).

The economic circumstances of farms cultivating legumes are linked to some of the factors mentioned above, e.g., larger organic farms show higher profitability. There are also indirect economic benefits of legume cultivation such as the lower cost of agricultural inputs (nitrogen and tillage cost saving) and yield effects on other crops (e.g., cereals included in the rotation). While profits and the economic sustainability of the farm are necessary, they may not always be sufficient and farmers' decision-making may be influenced by noneconomic factors, such as their perceptions of how what they create affects other issues beyond the farm gate, such as the environment and human health.

Similarly, consumers' choices may be influenced by environmental and health concerns as opposed to purely economic reasons and assessing the weight of the different attributes of choice would help predict sustainable changes in shopping habits and subsequent consumption patterns. A study on the own-price elasticities of legumes shows that consumer's demand can only change significantly if factors other than price are considered, such as provision of targeted campaigns and better communication of legumes' health and environmental benefits, better availability of healthy convenience foods, access to information on cooking, and easy recipes (Akaichi 2019).

As represented in Fig. 1, while the consumption trend for beans has been in a stable decrease, the consumption of peas, lentils, lupins, and other dry pulses shows a gentle but steady increase, likely correlated to a slow change in consumer diets reflecting a healthier pattern.

While slow, changes in consumption patterns to include more legumes are apparent and need to be translated into production patterns. The current EU demand for legumes is met partly by domestic production, partly by imports (Fig. 1) and equilibrium analysis is necessary to assess the sustainability of the whole sector when faced with shocks such as price fluctuations in the context of higher dependency on imports, or changes in environmental policies leading to stronger incentives to EU producers and thus a larger share of the demand being met by local production.

5 Social Impact

5.1 Nutrition and Food Security

Food insecurity is a reality for millions of people and households, especially in poor and developing countries (FAO 2019). Recent data reveals that over 2 billion people around the world do not have regular access to safe, nutritious and sufficient food, including eight percent of the population in Northern America and Europe (FAO 2019). Indeed, more than 820 million people in the world were still hungry in 2018. Such living conditions increase the risk of malnutrition and ultimately impair the health of populations (FAO 2019). It is recognized that lack of protein-energy intake, as well as micronutrient deficiencies, are major undernutrition triggers, both