Sustainable Agriculture Reviews 58

Asif Iqbal · Mazhar Iqbal ·
Madeeha Alamzeb · Song Meizhen ·
Zhang Xiling · Muhammad Arif ·
Xiongming Du · Eric Lichtfouse *Editors*

Sustainable Agriculture Reviews 58

Phosphorus Use Efficiency for Sustainable Agriculture

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Sustainable agriculture is a rapidly growing field aiming at producing food and energy in a sustainable way for humans and their children. Sustainable agriculture is a discipline that addresses current issues such as climate change, increasing food and fuel prices, poor-nation starvation, rich-nation obesity, water pollution, soil erosion, fertility loss, pest control, and biodiversity depletion.

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Because most actual society issues are now intertwined, global, and fast-developing, sustainable agriculture will bring solutions to build a safer world. This book series gathers review articles that analyze current agricultural issues and knowledge, then propose alternative solutions. It will therefore help all scientists, decision-makers, professors, farmers and politicians who wish to build a safe agriculture, energy and food system for future generations.

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Preface

Food security highly depends on the availability of plant nutrients such as phosphorus, yet rock phosphate reserves are expected to be exhausted in the next 50–100 years. Moreover, about 80% of the phosphorous fertilizers applied to soils become unavailable to plants due to phosphorous fixation in iron and aluminum oxides in acidic soils and with carbonates in alkaline soils. As a consequence, only 10–15% of applied phosphorous is absorbed by crops. Therefore, there is a need for advanced practices for improving phosphorus use efficiency. This book presents recently developed biotechnological tools and management practices that can be used to improve phosphorous use efficiency in agriculture (Fig. 1).

This book, entitled *Phosphorus Use Efficiency for Sustainable Agriculture*, is part of the series Sustainable Agriculture Reviews. The first chapter, by Suh, reviews the principles of permaculture, with focus on general guidelines allowing to invent sustainable agricultural practices in harmony with society. Natural and commercial sources of phosphatic fertilizers are presented in Chap. 2 by Abobatta et al. Chapter 3 by Zain et al. explains that organic phosphorous is an alternative to mineral phosphatic fertilizers. Adaptive responses of crop species against phosphorus deficiency are discussed by Aslam et al. in Chap. 4. Then, Jehangir et al. discuss the use biochar for sustainable phosphorus management in agroecosystems in Chap. 5. Chapter 6 by Farooq reviews efficient phenotyping for assessing genotypic variation in phosphorus use efficiency. Biotechnological tools for improving phosphorus use efficiency are presented in Chap. 7 by Malik et al. Riaz et al. detail the role of arbuscular mycorrhizal fungi in plant phosphorus acquisition in Chap. 8. Chapter 9 by Gabasawa explains that phosphorus cycle enzymes play a key role in alleviating soil phosphorus deficiency. Enhancement of phosphorus nutrition by biological nitrogen fixation in pastures is presented by Bello in Chap. 10.

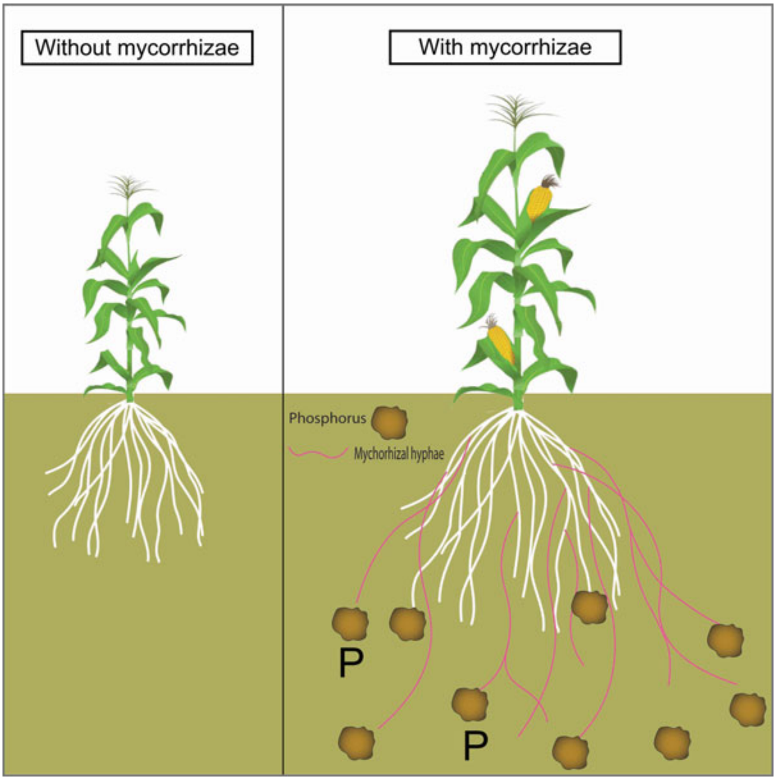

Fig. 1 Plants that have developed symbiotic association with mycorrhizal fungi in the root zone grow better because mycorrhizal fungi produce hyphae. Hyphae are channels that allow to carry nutrients from remote soils areas. (From Chap. 8 by Riaz et al.)

Editors are thankful to all contributors for their contribution in drafting the chapters. The book would not have been accomplished without the assistance of friends and colleagues. Finally, we would like to express our gratitude to Springer Nature's editors for their meticulous work on the publication.

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Contents

1 **Permaculture Principles, Practices, and Environmentalism** 1
Jungho Suh

2 **Sources and Solubilization of Phosphatic Fertilizers** 25
Waleed Fouad Abobatta, Amr Mahmoud Abdel Gawad, Haythum M. Salem, Mohamed A. Abdel-Salam, and Taghred A. Hashim

3 **Organic Phosphorous as an Alternative to Mineral Phosphatic Fertilizers** 49
Muhammad Zain, Muhammad Adeel, Noman Shakoor, Muhammad Arslan Ahmad, Saliha Maqbool, Jiusheng Li, Shafeeq Ur-Rahman, Ming Xu, Asif Iqbal, Waqar Afzal Malik, and Aiwang Duan

4 **Adaptive Responses of Crop Species Against Phosphorus Deficiency** 69
Mehtab Muhammad Aslam, Aisha Lawan Idris, Eyalira Jacob Okal, and Muhammad Waseem

5 **Biochar for Sustainable Phosphorus Management in Agroecosystems** 93
Komel Jehangir, Muhammad Riaz, Rashid Mahmood, and Muhammad Arif

6 **Phenotyping for Assessing Genotypic Variation in Phosphorus Use Efficiency** 115
Amjad Farooq, Waqas Shafqat Chattha, Muhammad Tehseen Azhar, Azeem Iqbal Khan, and Amir Shakeel

7 Advanced Biotechnological Tools for Improving Phosphorus Use Efficiency 137
Hafiza Aasia Malik, Atta Ur Rahman, Fazal Akbar, Nisar Ahmad, Syed Shujait Ali, Muhammad Suleman, Shahid Ali, Zahid Hussain, Nasib Zaman, Akhtar Rasool, Muzafar Shah, Muhammad Israr, and Asif Iqbal

8 Role of Arbuscular Mycorrhizal Fungi in Plant Phosphorus Acquisition for Sustainable Agriculture 155
Muhammad Riaz, Muhammad Tehseen Azhar, Muhammad Kamran, Omar Aziz, and Xiurong Wang

9 Phosphorus Cycle Enzymes to Remedy Soil Phosphorus Deficiency 177
Alhassan Idris Gabasawa

10 Phosphorus Nutrition Enhancement of Biological Nitrogen Fixation in Pastures 207
Suleiman Kehinde Bello, Taofeek Olatunbosun Muraina, Saheed Olaide Jimoh, Ibraheem Olamide Olasupo, and Samaila Usman

Index 231

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Chapter 1
Permaculture Principles, Practices, and Environmentalism

Jungho Suh

Abstract Permaculture emerged in the late 1970s as an alternative-agriculture movement in Australia. Permaculture is a practical philosophy of how to work with nature rather than against it. The underlying ethical principles of permaculture, which are Earth care, people care and fair share, recognise the interdependence between agriculture and the rest of the world and between humans and non-humans. Permaculture is not just about growing food in a sustainable manner. Permaculture is a system integrating the diverse functions of otherwise separate elements of the human settlements including nutrients, species, farms, villages, industries, and sectors. This chapter explores permacultural practices with real-world examples. Permaculture ethics can be practiced at varying spatial scales. At the farming household level, polyculture, crop rotations, and crop-livestock integration can be implemented to maintain soil fertility in a closed nutrient cycle. At the household level, low-impact and energy-efficient housing is carried out. At the community level, permaculture has been the philosophical and design foundation of co-housing or ecovillage movements. At the business level, permaculture offers the business ethics of no waste of resources and corporate social responsibility. Permaculture philosophy can be a guideline underlying a bioregional planning, which denies human dominance over nature. This chapter also brings attention to the problem associated with the dichotomous division of ecocentrism and technocentrism. As represented in the Earth care ethical principle, permaculture is concerned for global resource scarcities and environmental pollution. Thus, permaculture is often understood to take the highly ecocentric environmental view. On the other hand, permaculture advocates for technological development that enables the use of renewable energy sources. Thus, it is inappropriate to place permaculture environmentalism on a linear spectrum of environmentalism where ecocentrism and technocentrism are polarised.

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1.1 Introduction

Permaculture emerged in the late 1970s as an alternative-agriculture movement. It primarily punctuates the renewing of soil fertility in a closed nutrient cycle. Mollison and Holmgren (1978, p. 1) defined permaculture as 'an integrated, evolving design system of perennial or self-perpetuating plant and animal species useful to humans'. Mollison (1988), Mollison and Slay (1991), and Holmgren (2002) expanded the conceptual boundary of permaculture into a design system for creating sustainable relationships between farms, housing, and infrastructure including water and energy systems. Thus, permaculture is not just about organic gardening or farming but more importantly about the organismic design of integrating the diverse functions of otherwise separate elements of nutrients, species, farms, villages, industries, and sectors (Smith 2011b; Ferguson and Lovell 2014).

Owing to the multi-facets and broad scope of permaculture, the thematic focus of scholarly publications on permaculture varies from soil regeneration (Rhodes 2012) and agroecology (Ferguson and Lovell 2014), to energy-efficient building design (Seyfang 2010), ecovillages (Litfin 2014), and grassroots social initiatives (Ferguson and Lovell 2015; Ulbrich and Pahl-Wostl 2019). Permaculture has provoked scholarly discourses on the relation of humans to non-humans, one of the main themes of environmental philosophy. Thus, it was timely that Roux-Rosier et al. (2018) saw permaculture as a set of practices, life philosophy, and social movement with the predominant ethos being agro-ecologic, holistic-mythical, and eco-political, respectively. Further to the wide scope of coverage, permaculture has been a theme that threads together the key concepts in geography, including space, place, change, and scale. Permaculture ethics can be practiced at the farm, the household, the community, the industry, and the bioregional levels.

This chapter undertakes a comprehensive and critical review of the extant permaculture literature. The chapter first outlines permaculture ethics and design principles from the texts written by the permaculture founders. Next, the chapter provides an overview of the real-world applications of permaculture ethics and design principles, as a living and evolving body of knowledge, ideas, and practice employed by the permaculture practitioner community over the past several decades, in food production, village-making, and social initiatives. This is followed by a discussion of the holistic environmentalism embedded in permaculture philosophy and applications. The chapter then brings attention to the limitations of the conventional matrix approach that assigns scores to economic, environmental, and social indicators to measure sustainability.

1.2 Permaculture Ethics and Design Principles

The ethical principles of permaculture are a window through which one can grasp what permaculture is about. The ethical principles of permaculture refer to broad, generic, and underlying moral axioms (Mollison 1988; Mollison and Slay 1991; Holmgren 2002): namely, Earth care; people care; and return of surplus to people and the Earth. The ethic *Earth care* means caring for the natural environment including all the diverse life forms that inhabit the planet, regardless of their usefulness to humans. The *people care* ethic is derived from the *Earth care* ethic, as manifested in Mollison and Slay (1991, p. 3): 'Care for the Earth also implies care for people so that our basic needs for food, shelter, education, satisfying employment, and convivial human contact is taken care of.' The ethic *return of surplus to people and the Earth* is often referred to as *fair share* ethic in short in the permaculture literature. The *fair share* ethic underscores that agriculture encompasses a range of important social functions beyond food production. Thus, two threads of meaning can be discerned from the *fair share* principle (Holmgren 2002). First, all reasonable efforts are to be made to maintain or enhance the biological capacity of the soil, for example, by recycling organic matter into natural fertilizers and by avoiding the use of agrochemicals. Second, the surplus of permaculturally grown food is distributed to the community and the region through any given distribution system. It is not only surplus food that is to be returned to the Earth and people. It can be the surplus of any resources that can be shared with fellow humans (Mollison and Slay 1991).

Holmgren (2002) broke down the permaculture concept into a dozen permaculture design principles as presented in Table 1.1. It is not coincidental that the first permaculture design principle listed is *observe and interact*, which is also a very

Table 1.1 Permaculture design principles (Holmgren 2002)

Observe and interact
Catch and store energy
Obtain a yield
Apply self-regulation and accept feedback
Use and value renewable resources and services
Produce no waste
Design from patterns to details
Integrate rather than segregate
Use small and slow solutions
Use and value diversity
Use edges and value the marginal
Creatively use and respond to change

Note that the permaculture design principles are not just guidelines for agricultural practices, but manifest how humans can interact with the environment. The sequence of the principles does not indicate the order of importance. Rather, these principles are correlated to one another *feng-shui* idiom (Suh 2014). The *feng-shui* theory sees the Earth as a living organism (Matthews 2019). It follows that human settlements, including the agricultural cultivation of land, should be designed such that the right elements are placed in the right places (Mollison and Slay 1991).

The *apply self-regulation and accept feedback* principle warns that the occurrence of negative environmental externalities should be prevented by self-regulation. This principle is associated with the concept of *karma* in Buddhism, the law of cause and effect that everything is interconnected with everything else in the ever-changing world. It should be noted that interconnectedness is the very first law of Commoner's (1971) four ecology laws and Hardin's (1993) three human ecology laws. Commoner's four ecology laws are *everything is connected to everything else*; *everything must go somewhere*; *nature knows best*; and *there is no such thing as a free lunch*. Hardin's three ecology laws are *we can never do merely one thing*; *there is no away to throw to*; and *the IPAT equation* (Environmental Impact = Population × Affluence × Technology).

Beyond the *apply self-regulation and accept feedback* principle, permaculture pursues creating mutually beneficial linkages and relationships between elements: that is, permaculture seeks to *integrate rather than segregate* diverse elements into a system so that each element in the system can perform many functions and each of the functions can be supported by many elements (Mollison and Slay 1991). The *use and value diversity* principle recapitulates the importance of crop-livestock farming systems. Polyculture is an application example of the *use and value diversity* principle. Monoculture not only decreases insurance for yield but also is a major source of crop vulnerability to a variety of pests and diseases that entails the widespread use of toxic chemicals to control them (Mollison 1988; Holmgren 2002).

The *use small solutions* principle debunks the myth of 'economies of scale' that large-scale production through specialisation and mechanisation always leads to more physical output per unit of physical inputs. Traditional mixed farming systems may be in favour of small-scale farming. However, small-scale mixed farms can be more productive than large-scale monoculture farms when total output is used to measure productivity (Rosset 1999). Permaculture prefers to set a limit to the food production scale to the point beyond which the accompanying slow solution principle cannot be carried out. The *use slow solutions* principle is to ensure keeping farm production perennial by maintaining soil fertility without agrochemicals. This principle preaches the importance of a closed nutrient cycle, in which nutrients are regenerated within a farm and no off-farm energy sources are imported.

The *design from pattern to details* principle dictates that detailed information on the patterns of energy flows of the surrounding environment should be sought. This principle posits that permaculturists are supposed to work with the natural surroundings by adapting the technical practices of permaculture. In other words, the methods that execute the design principles of permaculture can vary depending on local circumstances including soil types, climates, and hydrological and topographical features (Mollison and Holmgren 1978; Holmgren 2002).

1.3 Permaculture Practices Applied in Varying Spatial Scales

Permaculture ethics and principles align with a wide range of sustainable living practices in the realms of organic farming, low-impact housing, ecological communities, and grassroots social movements. Some practices have been initiated by permaculturists, and some others have been guided by the permaculture founders themselves. Table 1.2 collates permaculture ethics and applications carried out at varying spatial scales.

The permaculture design principles presented in Table 1.1 are never meant to apply to agricultural society only. Agriculture is considered both an industry of food production and a cause of environmental concerns. Thus, permaculture postulates that there is no environmental, economic, and social sustainability without sustainable agriculture. Permaculture design principles can be embodied in all levels of human-environment interfaces. For example, the ‘closed nutrient cycle’ principle in permaculture can be translated into ‘circular economy’ or ‘regenerative economy’ beyond the agricultural industry. The *fair share* ethic underscores ‘sharing economy’ or ‘localised economy’ (Krueger et al. 2017).

Permaculture advocates for transitioning to a regenerative economy where material and energy resources are recycled, and a circular society where wealth, technology, and knowledge are also circulated in a sustainable loop (Friant et al. 2020). The *use small and slow solution* principle stands behind a localised economy. Schumacher (1973) equated a Buddhist economy with a localised economy whereby goods and services are produced from local resources to meet local needs. Norberg-Hodge (1991) pointed out that it is absurd that consuming food grown in the other side of the globe induces more products and jobs because of more transportation, more use of fossil fuels, more chemical additives and preservatives while it increases pollution and erases local culture. In this context, Norberg-Hodge (2019) put forward that decentralised economies relying on local food and energy are a pathway to making the world sustainable and to fixing the problems caused by the inhumane global economic system.

Table 1.2 The scale of permaculture practices

Scale	Key ethic	Application
Farming or gardening	Earth care	Zoning; mixed farming; crop rotation; growing native plant species; circular economy
Housing	Earth care	Microclimate insulation; *feng-shui*
Community	Earth care; people care; fair share	Community cohesion
Industry, society, and region	Earth care; people care; fair share	Bioregionalism; localised economy; grassroots social initiatives; sharing economy; corporate social responsibility

The permaculture design and ethical principles can be implemented in alternative economies including a circular economy, and a sharing economy a localised economy in varying spatial scales from the farming level to the regional planning level

1.3.1 Food Production in Harmony with Nature

Many authors including Francis et al. (2003), Ferguson and Lovell (2014), Hathaway (2016), and Krebs and Bach (2018) see permaculture as an agroecology movement alternative to industrial agriculture. Agroecology maintains that a farm is much greater than the mere sum of its individual crops and livestock (Pfeiffer 1938; Gliessman 2007; Altieri et al. 2012). Like agroecology, permaculture places emphasis on polyculture, crop rotations, crop–livestock integration, and the regenerative food production system (Pretty 2008; Francis and Porter 2011). While these permaculture farming practices are applicable in some climatic zones, there may be severe limits on their applications in other areas such as in the prairies of North America or the semi-arid plains of Australia (Tisdell 2005). Thus, agricultural practices of permaculture need to be adapted to local climatic conditions (Mollison and Holmgren 1978; Mollison and Slay 1991; Holmgren 2002).

According to permaculture design principles, the area immediately adjacent to the residential house is the most suitable to be a kitchen garden. Plant and animal species that require care and observation are located in the next zone of the vicinity. Main crops and meat animals can be grown in the outer zone. Permaculture design principles recommend that the farther outer zone or the area not suitable for crop production can be reserved for timber production, forage or wildlife.

Integrated rice-duck farming is a typical application of the *integrate rather than segregate* permaculture principle at the farm level. Ducklings feed on rice insects. Duck paddling helps control the germination of weeds. Poultry manure contains a high level of mineral nutrients including phosphorus, which is essential for the growth of plants, and therefore can be recycled into phosphorus fertilizers (Mollison and Slay 1991; Mollison 1996; Furuno 2001; Cordell and White 2013). Due to its labour-intensiveness, however, integrated rice-duck farming is no longer widely practised in Asia as it used to be (Suh 2015). Instead, seasonal differentiation of rice and duck growing is practised, in which an army of ducks are used to sweep rice paddy before ploughing to feed on rice residuals, and snail eggs that would devastate rice plants.

Permaculture is not just a testimony to an ecologically sustainable and economically feasible farming system but has been adopted as a basis of food production around the world. Real-world examples include the Food Forest (15 ha) in South Australia, Ananda Suruci (4.8 ha) in Taiwan, and Solitude Farm (2.4 ha) at Auroville in India. Although these farms are managed for commercial purposes, they have brought about a variety of social benefits. They welcome volunteer workers called ‘willing workers on organic farms’, run permaculture design certificate courses on a regular basis, and also organise open day events. Interacting with volunteer workers, permaculture design certificate students, and agri-tourists, they have inspired future permaculturists.

Remarkably, a group of permaculturists from Australia helped Cuba produce food organically in the 1990s in the face of the shortages of fossil fuels and agrochemicals which could not be imported due to the collapse of formerly the Union of Soviet Socialist Republics (Gamble 2011; Cockrall-King 2012). The

Fig. 1.1 Organopónico Vivero Alamar, a cooperative urban organic farm of 11 hectares located in a residential suburb in Havana, Cuba. The soil in the raised garden beds is prepared from earthworm bins in the open air and under shade. The vegetables and fruits produced at the cooperative organic farm are supplied to the regional hospitals and schools and also sold at the gate of the farm

permaculturists trained local smallholder farmers with permaculture farming techniques. As a result, there emerged *organopónicos*, Cuban-style raised beds of enriched soils (Levins 2005). An *organopónico* can be operated at the household level or institutionalised into a cooperative organic farm as illustrated in Fig. 1.1 (Viljoen and Howe 2005; Newton 2020).

Various types of small-scale urban agriculture have mushroomed, ranging from public community gardens, private residential gardens, vertical gardens, and rooftop gardens (Tornaghi 2013). Food scraps are returned to the soil and used as a natural fertilize to grow food in a vegetable garden. Many community gardens in cities and suburban areas are consciously managed in accordance with permaculture ethics and principles (Holland 2004; Korsunsky 2019). Some studies (e.g. Brombin 2015; Suh 2018) found that gardening plots in suburban areas, regardless of their scale and types, played a role of 'contact zone' where social capital such as social cooperation and cohesion can be generated.

1.3.2 *Low-Impact Housing*

Permaculture is a design system for sustainable and low-impact housing (Seyfang 2010). Low-impact housing is considered an urban activity, reflecting the reality that most people live in cities (Whitefield 2004). Low-impact housing equates to using natural, recyclable, and local building materials, minimising energy needs, and generating energy from renewable energy sources (Pickerill 2013). Building with natural and locally available materials (e.g. mudbricks) is taken for granted in the permaculture building design.

Passive solar design in which houses largely heat and cool themselves can significantly reduce the need for the use of electricity for cooling and heating. Unfortunately, passive solar design may not be applicable in many suburban streets because residential buildings are to be designed and constructed along the grid-shaped streets regardless of solar orientation. Tree planting based on microclimate and pattern analysis is an alternative passive solar design under this circumstance. For example, a grapevine arbour growing on the north side of a house can contribute to reducing household demand for extra cooling or heating because the plant provides shade in summer but not in winter in the southern hemisphere (Holmgren 2018).

Just as it is ideal to have a reserved zone for forestry or pasture at the farming level, it is a norm in urban planning to secure green open space for multiple purposes. For example, green open space in urban areas can have an effect on mitigating urban heat waves. Sun and Chen (2017) found that increasing the volume of green space would be an effective measure to regulate microclimate and alleviate urban heat in the vicinity. Similarly, Grilo et al. (2020) echoed that an increase in green space or green density would be able to significantly mitigate the urban heat island phenomenon. These research findings indicate that the removal of green infrastructure resulting in high-density housing settlements can in turn intensify urban heat waves. It is implied that the ‘compact-city’ planning in favour of urban infill to control urban sprawl should take into account its negative impacts on the urban dwellers.

Low impact development is an innovative or rather radical housing development movement pioneered in rural Britain in the 1990s (Pickerill and Maxey 2009). Low impact development adopts permaculture approaches to housing, food production, and everyday life. Pickerill and Maxey (2009) noted that the low-impact development vision could be extended to urban locations. Indeed, permaculture emphasis on energy saving has been reflected in building codes and standards being implemented in the global North. For instance, the United Kingdom Code for Sustainable Homes was introduced with a focus on energy saving and carbon dioxide emissions (Pilkington et al. 2011). Likewise, all newly built residential homes and extensions in Australia are required to meet energy efficiency building codes by combining the measures to reduce heating and cooling loads with adequate ventilation air movement, and the use of renewable energy sources (Barnett 2018). In response to this urban policy trend and the growing public demand for eco-homes, many private homebuilders have adopted permaculture principles in their building design and construction process. Permaculture has also been the practical foundation of retrofitting pre-existing buildings into more energy-efficient and sustainable settlements, with solar panels and water tanks put in place.

Interestingly, Pilkington et al. (2011) made a comparison between a sample of dwellers in contemporary eco-homes and a sample of permaculturists living in a range of conventional house types. This research found that the average ecological footprint per person amongst the permaculturists was significantly lower than that of the residents at eco-home dwellings. This research concluded that the permacultural consciousness and behaviour were more conducive to reducing domestic energy demand rather than just living in a residential house that meets the energy-efficient building requirements. In a similar token, Litfin (2014) posited that 'consciousness', which refers to the awareness of one's inner being in unity with humanity as a whole and nature, is a driving force in moving towards a sustainable world.

1.3.3 Permaculture Implementation at the Community Level

Permaculture-based ecological food production and energy-efficient housing have been implemented collectively. For example, many co-housing communities were designed and have been managed according to permaculture principles. Co-housing amounts to sharing common spaces across independent housing units, reducing the space needed by each of the member households, and eventually lowering the ecological footprint per person. The concept of co-housing evolved into developing affordable co-housing communities in the global North (Chatterton 2013; Temesgen 2020). Co-housing leads not only to sharing communal space but to proactively invigorating the traditional sense of community life via regular functional meetings, community gardening, and communal meals (McCamant and Durrett 2011).

Ecological village-making movements have emerged since the 1960s in response to rapid urbanisation, and the erosion of traditional rurality, and community cohesion. The ecovillage movement gained momentum in 1995 when the Global Ecovillage Network was launched (Litfin 2014). The members of an ecovillage live in the same place, sharing and pursuing ecological values and lifestyles. They strive to create a sustainable society, demonstrate sustainable community development, and diffuse their experiences and knowledge (LeVasseur 2013).

Due to the rise in land price and a lack of availability of land for establishing new intentional ecovillages, the transformation of existing villages into ecovillages has been triggered (Dawson 2013; Baker 2013). Like intentional communities, transition communities are rooted in permaculture principles applied to the level of community. Transition communities endeavour to move away from the reliance on fossil fuels in the face of the limited stock of non-renewable energy sources and global warming caused by burning them. Intentional communities and transition communities alike have been widespread globally.

Some communities such as Findhorn Foundation (Fig. 1.2) were initially more motivated by spirituality than ecological tenets, and some others such as Totnes are driven by low-impact and energy-efficient housing and lifestyle (Boudinot and LeVasseur 2016). Whatever their primary purpose and focus were, however, spirituality and ecology movements converged in the 1990s. As a matter of fact, nature can be seen as a living system as well as a spiritual being and these two perspectives do not conflict with each other (Litfin 2014). Spiritual search for the inner identity of human beings recognises their connectedness to all other creatures and entails deep

Fig. 1.2 A co-housing cluster within Findhorn Foundation, Scotland, with solar panels on the roofs. The residents share communal spaces including a laundry, a kitchen for communal eating, and a bike shed

empathy with all living beings. It is no wonder that spiritual philosophy was infused into permaculture and ecovillage movements, which committed to working with nature rather than against it (Gibsone and Bang 2015).

The ecovillage pioneers around the world, including Auroville in India, Findhorn in Scotland, Crystal Waters in Queensland, and Lebensgarten in Germany, have become popular tourist destinations. Auroville alone had attracted about a hundred thousand of tourists per year before the pandemic times. Ecovillages have induced diverse types of tourism including spiritual tourism, agritourism, cultural tourism, volunteer tourism, and educational tourism. Permaculture actions towards sustainable lifestyle are considered a new normal, thanks to the growing number of people who are directly or indirectly engaged in the ecovillage movement (Shirani et al. 2015).

Permaculture hatched a new form of an intentional community called connected backyard gardening in the 2000s in South Australia (Holmgren 2018). In a connected backyard gardening scheme (Fig. 1.3), the backyard space of neighbouring houses is connected through mutually accessible gates so that the individual households can benefit from the sharing of resources such as labour, knowledge, skills, shed, gardening tools, and time. Connected backyard gardening is different from co-housing where more than one household shares a legally designated common area. A connected backyard gardening scheme does not involve communal ownership or a community title. Connected backyard gardeners intend to not only promote a sharing economy but also develop social links with neighbours and make a community of place (Suh et al. 2022).

Fig. 1.3 Joe's Connected Backyard Garden located in a northern suburb of Adelaide, South Australia. Several privately-owned plots of backyard are mutually accessible through gates as the one shown in the photo. Not only are gardening tools and equipment shared, but also human resources are in the connected backyard gardening scheme

1.3.4 Permaculture Beyond a Geographically Confined Community

Permaculture has bred a myriad of grassroots initiatives and innovations worldwide (Ulbrich and Pahl-Wostl 2019). First, permaculture has raised social consciousness, spawning green technologies and an eco-friendly lifestyle (Vitari and David 2017). Rob Hopkins in Totnes, England, who was one of the leading figures in the transition town network movement, also taught permaculture design certificate courses at Schumacher College (Smith 2011a). He explicitly accredited the transition town movement to permaculture philosophy and principles (Aiken 2017; Henfrey 2018). Second, permaculture *per se* as a set of innovative knowledge has become a commodity and created new business opportunities. Genus et al. (2021) brought attention to the phenomenon that permaculture inspired renewable-energy businesses, permaculture gardening, energy-efficient building design, and permaculture education programs. Many pioneering ecovillages have offered various commercial permaculture workshops and courses on a regular basis (Veteto and Lockyer 2008; Henfrey and Ford 2018; Magnusson 2018; Brombin 2019). Third, permaculture boosts a new age economy as opposed to the growth-oriented market economy, scaling up the diffusion of permaculture practices to borderless communities beyond the traditional geography concepts of space and place (Aiken 2012). Some intentional communities such as Ecovillage at Ithaca have partnered with local governments and institutions to spread the ecological living practices beyond the physical boundaries of ecovillages (Boyer 2015).

The profit-maximisation goal of private businesses should be subject to environmental impacts as private businesses are part of society, economy, and ecology. Therefore, a corporation is responsible for social integrity and environmental sustainability. Permaculture provides the underlying philosophy of the corporate social responsibility concept, which can be played out into green investment (Kopnina 2017). A partnership between government and private enterprises can effectively promote innovative green technology and a green economy with government funding. An example of this is Toyota's hybrid car manufacturing. Toyota helped populate the environmental philosophy that the development of the right technologies is a gateway to solving environmental pollution and that corporations have the responsibility to produce goods and services with eco-friendly technology (de Burgh-Woodman and King (2013).

Permaculture resonates with bioregionalism. Like permaculture, bioregionalism conveys the view that the doctrine of human dominance over nature is to blame for most contemporary global and local environmental problems (Parsons 2013). Bioregionalism also shares the same view with eco-localism (Curtis 2003), which proclaims that 'we are what we eat'. Like bioregionalism, permaculture considers that housing and food production should accord with the local climate, landform, and energy flow (Holmgren 2002). Both permaculture and bioregionalism concur that the benefits of localisation should not be overshadowed by those of globalisation.

In the global South, permaculture is widely understood as equivalent to indigenous understanding and knowledge of the human-nature relationship (Veteto and Lockyer 2008). In Cuba, permaculture has played a key role in laying the philosophical foundation of the green social movement and breaking down the predominant social mindset that pursues individual wealth and ignores environmental costs (Caraway 2018). The permaculture movement in Cuba is deeply engaged in reconnecting human beings to one another as well as the environment, assuring social collaboration rather than competition. Similarly, small-scale farmers in El Salvador have played a pioneering role in spreading traditional sustainable agriculture in the situation where large-scale industrialised agriculture has contaminated water and soil nationwide (Millner 2016). Permaculture is also seen as the foundation of the pro-poor social movement in India (Fadaee 2019).

The *fair share* principle of permaculture inspires that innovative sharing economies are conducive to improving environmental quality and enhancing social

Fig. 1.4 A Grow Free cart placed near the gate of a residential suburban house in Adelaide, South Australia. Seeds, seedlings, fruits, vegetables or even books are put on the shelves for free. The grassroots initiative has spread into other states in Australia, contributing to the growth in urban agriculture and sharing economy

cohesion and economic well-being (Krueger et al. 2017). There are two types of sharing economy: Namely, for-profit sharing and not-for-profit sharing (Lai et al. 2020). Examples of for-profit sharing include Airbnb and Uber. Examples of not-for-profit sharing include bicycle repair training workshops, community gardening, food swapping, street libraries, and the Grow Free network. Grow Free is a community food exchange network organised in Australia to freely give away locally grown organic produce, whereby locals can take what they need from a cart and leave what they can on the cart which is managed by a Grow Free network participant household (Fig. 1.4). Many Grow Free cart stewards communicate with the public via the Grow Free Facebook (https://www.facebook.com/groups/growfree/) so that whoever subscribes the Facebook can be informed of whatever posted about Grow Free sharing or events.

The ‘sharing economy’ should not be confused with the ‘commons economy’ (Belk 2010; Schor and Attwood-Charles 2017; Miller 2020). The word ‘commons’ refers to ‘open access’ resources to which everyone has free access, but no party can claim an exclusive access right. The sharing economy deals with resources for which an individual, a group of individuals, or a state has exclusive ownership. Moreover, sharing requires more mutual caring and generates a higher level of social cohesion than exchanging does (Belk 2010).

1.4 Permaculture Environmentalism

Permaculture has provided the practical as well as philosophical foundation of ecological farming, low-impact housing, and small-scale grassroots collective actions towards a green economy. A wide range of real-world examples of permaculture practices rejects that permaculture principles are applicable only to address small-scale farming and therefore way too tiny to deal with massive global environmental problems. With an emphasis on less domestic demand for energy from non-renewable sources, permaculture is concerned for global resource scarcities and environmental pollution. Permaculture also advocates for technological development that enables the use of renewable energy sources. In this context, permaculture denies the dichotomous worldview that separates ecocentrism and technocentrism.

Figure 1.5 delineates a continuum between two poles of environmentalism labelled deep ecology and cornucopian views. While the basic ideas of the taxonomy in the original references remain intact, it is notable that the second column heading 'environmental stewardship' (Paterson 2003) replaces 'self-reliance and soft technology' in O'Riordan (1981). The cornucopian view (Simon 1980, 1981) holds that increasing economic affluence is the driving force for technological advancement. Environmental managerialism (Bryant and Wilson 1998) is a label for a moderately technocentric environmental view that appropriate policy measures can remedy market failure caused by the presence of externalities, non-excludability, or prisoner's dilemmas (Redclift 1993).

Ecocentrism refutes the perception that human beings are the owners or managers of the natural environment. From the ecocentric perspective, Daly (1993) argued that

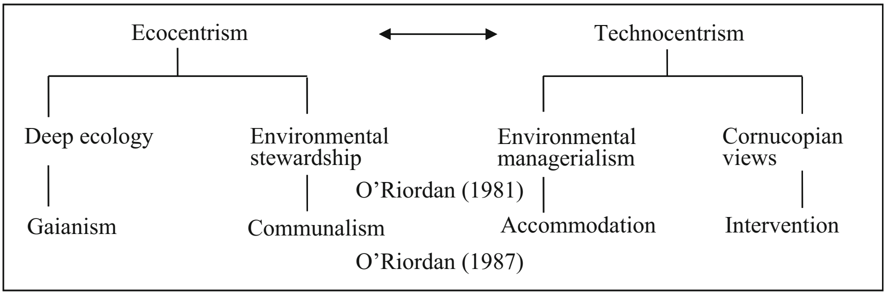


Fig. 1.5 A spectrum of environmentalism (adapted from O'Riordan 1981, 1987). The economic, environmental, and social dimensions of sustainability are all unavoidably interconnected from the permaculture perspective. It is not possible to place permacultural environmentalism on a linear spectrum of environmentalism where ecocentrism and technocentrism are polarised as in the diagram

sustainable economic growth is an oxymoron, and human beings should be saved from the dangerous path of materialistic economic growth. Deep ecology recognises that all non-human creatures have their own right to exist independently of their use value to human species and contends that human beings have no right to degrade their natural habitats (Naess 1984; Kopnina 2013; Imran et al. 2014).

Environmental stewards are not optimistic about the effects of technological development or environmental policy instruments on the conservation of the natural environment and therefore hold the view that there should be a fundamental change in the materialistic human lifestyles. The environmental stewardship perspective is shallow compared with the deep ecology perspective, but is radical when compared with environmental managerialism. Thus, one can place environmental stewardship between deep ecology and environmental managerialism as shown in Fig. 1.5 (Pepper 1984, 1996).

Although the spectrum of environmentalism is not to be interpreted as black and white, the illustration gives an impression that the two umbrella environmental views are contested in every aspect. The dichotomy or linear continuum is problematic because it reduces sustainability to a matter of balancing between human well-being and environmental protection. Worse still, the label 'technocentrism' is often considered to be synonymous with 'anthropocentrism', as opposed to 'ecocentrism'. Anthropocentrism takes a view that nature is valued for the benefits it has for human beings. Anthropocentric environmentalism seeks to use natural resources to maximise human benefits because humans are regarded as the dominant force in nature (Keiter 1994).

Owing to the *Earth care* ethic, permaculture is often understood as a form of highly ecocentric environmentalism (Akhtar et al. 2015; Boudinot and LeVasseur 2016). On the other hand, the ethic *people care* contains anthropocentric concerns. In the permaculture context, however, the *Earth care* and the *people care* principles are complementary to each other. Permaculture takes care for the planet Earth, which is the basis of every life. Moreover, the homocentric position of permaculture should be distinguished from that of individualistic utilitarianism in that permaculture gives priority to social equity and cohesion.

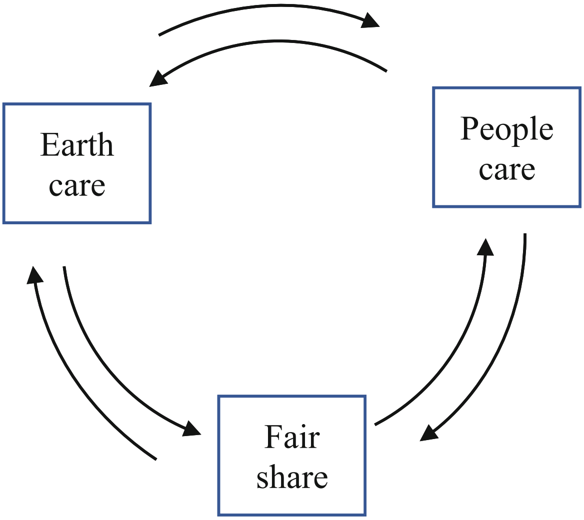
The *fair share* permaculture ethic manifests that community cohesion is integral to sustainable development. This ethical principle is reflected in its advocacy of communalism. Communalism upholds the communal property regime with faith in the inherent character of humans to cooperate and their ability to realise what they can achieve through cooperation (O'Riordan 1987). As in a traditional agricultural society, sustainable agriculture requires cooperation amongst farming households. Thus, permaculture stresses that sustainable agriculture and sustainable society are interdependent.

The ethics and principles of permaculture highlight the limitations of focusing on a single dimension or component of sustainability. The holistic approach of permaculture to sustainability is likened to systems ecology (Mollison and Holmgren 1978; Holmgren 2002; Ferguson and Lovell 2014), which posits that it is impossible for humans to control the natural environmental system, and states they can only live in harmony with it (Odum 1971, 1983). Odum (1971) brought attention to how much the industrialised system, reliant on fossil fuel energies, has departed from the agrarian system where nutrients are metabolically recycled through human–nature interactions. Taking a holistic worldview, permaculture accentuates the interconnectivity between social, environmental, and economic dimensions of sustainability.

The bottom line is that the permaculture principles recognise the interdependence between agriculture and other industries and between humans and the rest of the world. Anthropocentrism takes the view that humans can make rational use of natural environments to meet their needs and to enhance their quality of life. By contrast, ecocentrism makes a strong appeal to the importance of non-market values of ecosystems for human well-being and asserts that human beings should not degrade the Earth's ecosystems and deplete natural resources. Permaculture calls for a paradigm shift to holism from dualism that splits humanity and nature (Ferguson and Lovell 2014). On one hand, permaculture maintains that human beings are part of nature and can never be free of it. On the other hand, permaculture does not deny the uniqueness of humanity and the intellectual power of human beings.

Figure 1.6 illustrates that permaculture philosophy does not differentiate between nature and humans as the latter is a component of the former. The permaculture principles reflect one of Commoner's (1971) four human ecology laws that everything is connected to everything else. The *Earth care* ethic reflects the *people care* ethic, and is reflected in the *people care* ethic. Further, the *fair share* ethic does not detract from the *Earth care* or *people care* ethic. The interconnectedness of permaculture ethics resembles the metaphor of Indra's Net, which is often cited to symbolise the interpenetrating relationship between every existence in the world. The concept of Indra's Net that underlies Vedic cosmology has become the central teaching of Buddhism that everything becomes simultaneously a cause and an effect (Cook 2010; Daniels 2019). In Indra's Net, the whole cosmos is reflected in every

Fig. 1.6 The interconnectedness of the permaculture ethics. Permaculture ethical principles deny the dichotomous worldview that separates human beings and nature. Each of the three permaculture ethical principles feeds into and stems from the others



part of it, and every part is present in the entire cosmos (Thiele 2011; Lim 2019). Thiele (2011) introduced permaculture as an example of sustainability philosophy that is in line with Indra's Net perspective. In Thiele's interpretation, permaculture is equal to polyculture where all elements of a farm interact with one another. Plants can be resources for animal species, animal manure becomes the source of natural fertilizers for plant species.

1.5 Conclusions

The world cannot continue to produce food with the productivist mindset that focuses only on the maximisation of financial profits. Permaculture sees conventional agriculture as a major source of global land degradation, which leads to the destruction of the traditional human-nature relationship. Provided that the non-market positive ecological benefits from permaculture practices are combined with the saved external costs of agrochemicals, permaculture can trample on profit-oriented industrial agriculture. Thus, it is evident to permaculturists that society should introduce and implement post-productivist policy approaches to agriculture and human settlements. Permaculture identifies that capital-intensive agriculture and disintegrative rural communities are a twin problem. In other words, capital-intensive agriculture led to adopting conventional agriculture, which accelerated the erosion of the traditional sense of community.

From the permaculture perspective, agroecology, low-impact housing practices, and building sustainable communities are not separate domains of sustainable development. Likewise, *Earth care*, *people care*, and *fair share* are not separate ethics. Agroecological farming is highly valued because ecologically healthy food production is connected to the health of humans. In this context, permaculture postulates that a sustainable community cannot be established without sustainable agriculture.

There exists a spectrum of human attitudes towards the environment, including cornucopian views, environmental managerialism, environmental stewardship, and deep ecology. Permaculture sees the world as a continuum of organisms interlinked to one another. This chapter maintains that it is inappropriate to position permacultural environmentalism on a linear spectrum of environmentalism presented in Fig. 1.5, which is often mistakenly interpreted as an ideological black-and-white division. Permaculture denies the anthropocentric view that economic prosperity is the key to achieving environmental and ecological sustainability. Neither does permaculture support the ecocentric proposition that economic prosperity cannot go hand in hand with ecological sustainability and therefore should be compromised to achieve the latter. Taking a holistic view of sustainability, permaculture is oriented towards the integration of the multi-dimensions of the sustainability concept.

Permacultural environmentalism is not mere rhetoric but offers a solution to human-induced global environmental and ecological problems. Permaculture ethics and principles have boosted a new age of the economic system that incorporates a circular economy, a sharing economy, and a localised economy. The *Earth care* permaculture ethic calls for recycling and reusing the otherwise would-be wastes, which leads to less production and consumption of goods and services that require the exploitation of non-renewable resources. The *people care* ethic advocates for a localised economy in that the permaculture ethic is primarily concerned about the economic sustainability of a local community. The *fair share* ethic is embodied in various grassroots community-building initiatives such as community gardening and co-housing. The *fair share* ethic triggers innovative institutional reforms, for example, small-scale development and localised and cooperative, as opposed to a competitive growth-oriented, market economy, as a pathway to building a sustainable world.

Permaculture philosophy and principles inspired the establishment and evolution of many ecovillages, which in turn have been a driver of permaculture education through permaculture workshops and courses. Ecovillages have played a part in indirect permaculture education as a number of people have visited ecovillages to observe and learn what ecological living should look like. The new age economy that features the ecovillage movement transcends physically confined community regimes, via online or offline social networks of interested parties. The Grow Free network in Australia is a typical example of creating a sharing economy across borderless communities. Moreover, permaculture ethics have served vital social and spiritual functions in developing countries including Cuba, El Salvador, and India.

After all, an alternative evaluation framework needs to be developed that echoes Hardin's (1993) systems ecology that one action cannot do merely one thing. This means that any action brings multiple effects and that one should not treat a sustainability action as if it is an independent variable. Despite persistent assertions and voices to the contrary, the dichotomous analysis of sustainability is still prevalent in a vast body of sustainability literature. Consequently, policy-makers or city planners are not properly informed of the dynamics and connectedness of all elements of sustainability.

Permaculture is a design system with a focus on (re)building sustainable human settlements in harmony with nature. Permaculture calls for internalising the external costs of agrochemicals and for considering non-market positive ecological benefits from permacultural food production based on permaculture principles. Agriculture is multi-functional within an economic-social-ecological system. Consequently, permaculture concerns are extended to wider communities above and beyond agroecological food production, encompassing low-impact housing and sustainable community rebuilding.

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Chapter 2
Sources and Solubilization of Phosphatic Fertilizers

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Haythum M. Salem, Mohamed A. Abdel-Salam, and Taghred A. Hashim**

Abstract Phosphorus is a major plant nutrient, yet phosphrus deficiency often limits plant growth and yield. There are four forms of phosphorus in the soil such as organic ohosphorus, soluble mineral ions of $H_2PO_4^{-}$ and HPO_4^{2-}, soluble or adsorbed ions, and primary minerals. Phosphorus availability is controlled by climate, soil texture, and cultivation. The quantity of soluble mineral phosphorus in soil is usually low, and even when P fertilizers are added, phosphorus has a tendency to become less soluble. There are three main kinds of phosphorus fertilizers: biological, organic and chemical fertilizers. Phosphorus may also added in nanoparticles. Rock phosphate is a natural and cheap, and suits acid soils. In alkaline conditions, phosphorus is commonly unsoluble, unless amendments such as sulfur, organic matter, or phosphorus solubilizing bacteria are added to improve phosphorus bioavailability. Overall, agricultural management practices are important for increasing phosphorus availability for crops.

Keywords Phosphorus fertilizers · Rock phosphate · Phosphorus deficiency · Phosphorus availability · Phosphorus-solubilizing bacteria

Abbreviations

ADP	adenosine di-phosphate
ATP	adenosine triphosphate
DNA	deoxyribonucleic acid
RNA	ribonucleic acid
Ca	calcium

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Mg	magnesium
Fe	iron
Al	aluminum
C/P	carbon/phosphorus
USA	United State of America
RP	rock phosphate
EPSs	exopolysaccharides
DCPD	di-calcium phosphate di-hydrate
DCP	di-calcium phosphate

2.1 Introduction

Nutrients may be classified on basis of their biochemical and physiological function (Marschner 2012). Phosphorus belongs to the category of essential nutrients (Anwar et al. 2017), which are responsible for the storage, and exchange of energy (Amanullah et al. 2016a, b). Phosphorus is an irreplaceable plant nutrient that performs a definite physiological role in plants (Taiz and Zeiger 2003; Johnston and Dawson 2005; Ndakidemi and Dakora 2007). Phosphorus absence inhibits plants growth (Epstein 2000) because of phosphorus participation as the main component of energy compounds of adenosine diphosphate (ADP) and adenosine triphosphate (ATP) (Marschner 2012; Taiz and Zeiger 2003; Jones Jr 2012) which are responsible for controlling plant processes such as respiration and photosynthesis (George et al. 2011; Karamesouti and Gasparatos 2017). Phosphorus promotes healthy root and shoot growth, improves seed development, plant quality, and crop productivity. Adequate phosphorus increases plant water use efficiency, improves nitrogen and other nutrients efficiency, raises plant disease resistance and plant tolerance to abiotic stresses (Amanullah et al. 2019; Brett 2017).

Phosphorus participates in the synthesis of phospholipids, proteins as well as DNA and RNA nucleic acids (Taiz and Zeiger 2003; Jones Jr 2012). Phosphorus enhances plant growth, maturity, fruiting, and seed formation (Ndakidemi and Dakora 2007; Singh et al. 2011; Zafar et al. 2011; Hussain et al. 2012; Ndor et al. 2012; Latati et al. 2015; Karamesouti and Gasparatos 2017; Rahman et al. 2008; Rotaru 2010; Hussain 2017; Fouda 2017). Phosphorus increases the size and number of nodules, and the activity of the nitrogenase enzyme (Al-Niemi et al. 1998). Phosphorus is critical in photosynthesis and N-fixation (Broughton et al. 2003; Brear et al. 2013; Nyoki and Ndakidemi 2013; Latati et al. 2014) and promotes root growth, length, and density (Lopez-Bucio et al. 2003; Desnos 2008) that increase the availability of nutrients for plants (Shen et al. 2011.

Some inoculants of bacteria specializer in dissolving insoluble phosphate can be used as biofertilizers and marketed under commercial names. Microphos is a commercial fertilizer preparation, which contains viable microbial inoculants possessing phosphorus solubilizing activity (Zaidi et al. 2009). Phosphate solubilizing microorganisms are used as biofertilizers by selecting those which show solubilization of insoluble phosphorus. After selecting the most powerful isolate, it is subjected to identification and tested for phosphorus plant nutrition (Bashan et al. 2013). The ability to solubilize phosphorus is not necessarily correlated with the ability to promote plant growth (Collavino et al. 2010). From the standpoint of plant nutrition, plants mainly absorb phosphorus as orthophosphate ions ($H_2PO_4^-$ and HPO_4^{2-}). Soluble organic phosphorus compounds are also present in soils but usually in small contents.

2.2 Phosphorus Forms

There are three types of phosphorus containing substances:

1. Humus (organic matter).
2. Phosphorus bound with Ca, Mg, Fe, and Al (inorganic compounds).
3. Phosphorus compounds are connected with cells of living matter (organic and inorganic). Some soil microbes have a role in conversions of organic and inorganic phosphorus forms through several mechanisms of solubilization and mineralization (Khan et al. 2009) into plant-available forms.

The labile or the unstable phosphorus may be considered available fraction which could be utilized by plants, that fraction contains the rapidly mineralizable organic phosphorus, soluble mineral phosphorus, and sorbed phosphorus with low energy, however, the non-labile or stable fraction which comprises of the organic phosphorus that is resistant to degradation, comparatively insoluble mineral phosphorus and the high-energy sorbed phosphorus (Sanchez 2006). Plants absorb soluble phosphorus from the soil solution and that has resulted in replenishment from the labile fraction, which is correspondingly replenished by the non-labile fraction (Sanchez 2006; Ryan et al. 2013) and that is called phosphorus buffering capacity.

Phosphorus of organic residues of plants and animals and microbial cells are sources of organic phosphorus that represent 30–70% of total phosphorus in arable soils (Li et al. 2014), a wide diversity of microorganisms are able to degrade organic matter releasing mineral phosphorus which becomes available for plant uptake (Sanchez 2006). Nucleic acids and phospholipids decompose easily giving inositol phosphate that is a curial component of humus (Haneklaus and Schnug 2016). Mineralization is governed by many factors such as moisture content, tillage, management, temperature, pH, and redox potential (Karamesouti and Gasparatos 2017). Released phosphorus is associated with phosphorus content in organic matter as well as the microbial requirements of phosphorus (Marschner 2012). Mineralization and immobilization of phosphorus depend on the carbon-phosphorus ratio in the residues. Microorganisms affect phosphorus availability and are responsible for organic matter decomposition, hence increasing the release of phosphate ions and organic acids improves the solubility of phosphate compounds (Ryan et al. 2013.

It provides exchangeable sites for holding phosphate ions (Johnston and Dawson 2005). Root exudates contain organic acids such as oxalic, citric, and galacturonic acids which are capable of boosting the release of phosphate ions and increasing its phosphorus availability (Haneklaus and Schnug 2016; Oburger et al. 2013).

2.3 Phosphorus Shortage

Phosphorus content in soil is affected by many factors including origin of the soil (parent material), climate, soil texture (Nearing et al. 2005; Karamesouti and Gasparatos 2017), and cultivated crops (Salem et al. 2014). Phosphorus depletion in soils is attributed to the limited content of the element in the mineral of parent material in addition to its tendency to form less soluble compounds (Smith et al. 2011). Soluble phosphorus is susceptible to loss by leaching (Ryan et al. 2013). There may be cases of phosphorus toxicity to plant (Haneklaus and Schnug 2016). Diagnosis of phosphorus toxicity in relation to plant growth is reflected in chlorosis and necrosis (Silber et al. 2002).

Mineralization of organic matter, weathering, and dissolution of primary and secondary minerals and phosphorus fertilizers are the sources of soluble phosphorus in soil (Sanchez 2006). Unfortunately, the available ions of phosphorus–soluble phosphorus–converted to less available forms because of adsorption, sorption, and rainfall responses which are correlated with the predominance of cations such as calcium, iron, and aluminum ions in addition to the pH value (Delgado and Scalenghe 2008; Schnug and Haneklaus 2015; Karamesouti and Gasparatos 2017).

Under acidic conditions, soluble phosphorus precipitation through reacting with the amorphous and hydrous oxides of iron and aluminum (Gasparatos et al. 2006; McLaughlin et al. 2011; Shen et al. 2011). Either soluble in soil solution or the adsorbed Fe/Al oxides which constitute an active coating on the surface of soil colloids and clay mineral surfaces (Gérard 2016) producing various crystals of minerals such as gibbsite, goethite, hematite, and ferrihydrite (Gasparatos et al. 2006).

Likewise, in the presence of calcium carbonates either neutral or calcareous soils, calcium cations dominate the phosphorus availability and forming a low soluble compounds of calcium phosphate (Iqbal et al. 2017; Bastounopoulou et al. 2011) monocalcium phosphate, dicalcium phosphate dihydrate, and hydroxyapatite or fluorapatite (Ryan et al. 2013). Under calcareous soil conditions, phosphorous is captured because of its reaction with calcium carbonate (Iqbal et al. 2019), which reduces soluble calcium phosphate (Osemwotai et al. 2005; Shen et al. 2011). Adsorbed and precipitated phosphate are inversely proportional to the size of calcium carbonate particles due to increasing of the specific surface area (Milića et al. 2019; Von Wandruszka 2006).

Clay minerals retain phosphate ions tightly (Devau et al. 2010), and the phosphate ions react with the clay silicate minerals through the substitution reactions between hydroxyl and phosphate ions particularly in 1:1 clay minerals as kaolinite.

Soil water is one of the factors, which affect P diffusion through the soil, the optimum water tension is 33 kPa (0.33 bar) that supplies the maximum availability of phosphorus. Increasing soil temperature is associated with increased kinetic reaction consequently a quick equilibration among phosphorus pools (soluble, labile, and non-labile), resulting in accelerated replenishment of soluble P (Sanchez 2006).

2.4 Solubilization of Rock Phosphate

Rock phosphate is used as a natural fertilizer. However, the slow release of soluble phosphorus from it supplies adequate requirements to complete the growth cycle (Hellal et al. 2019). Some Egypt Governorates such as Qena, Deshna, cretaceous rock phosphate are applied by farmers as phosphorus fertilizer that they get from adjacent hills. Therefore, it is well known that:

(a) Cultivated soils in Egypt have slightly alkaline with pH range of 7.8–8.2, and so, they are not suitable to use rock phosphate, which requires acidic pH.
(b) Application of mineral fertilizers has many adverse environmental effects on cultivated soils. Industrial fertilizer's application leads to many chemical and mineralogical changes, which will disturb this ecological equilibrium (Elmaadawy et al. 2015).

Globally rock phosphate is represented as a naturally occurring geological material that contains one or more phosphate minerals suitable for commercial use. It is well known that about 75% of the world's phosphate resources are from sedimentary, marine rock phosphate deposits, 15–20% from igneous and weathered deposits, and only 1–2% from biogenic resources. Due to weathering, there are five main types of phosphate sources in the world that include marine phosphate deposits, igneous phosphate deposits, metamorphic deposits, biogenic deposits, and phosphate deposits.

Types of phosphate minerals in the mineral environment include:

(1) Fluorapatite ($Ca_{10}(PO_4)_6F_2$), in igneous and metamorphic environments, as in carbonatites and mica pyroxenites.
(2) Hydroxyapatite ($Ca_{10}(PO_4)_6(OH)_2$), in igneous and metamorphic environments and biogenic deposits, e.g., in bone deposits.
(3) Carbonate-hydroxy-apatites ($Ca_{10}(PO_4,CO_3)_6(OH)_2$), on islands and in caves, as part of birds and bat excrements, guano.
(4) Francolite ($Ca_{10}NaMg(PO_4)_6(CO_3)F_2$), carbonate-substituted apatite present in marine environments, and a much smaller extent in weathering environments for instance over carbonatites (Van Straaten 2002).

About 80–90% of the worldwide phosphorus total demand was directed to agriculture and food production fields (Reyes and Allsopp 2012). Where phosphorus deficiency leads to a reduction of crop yield. Mined rock phosphate is extensively used in agriculture. Global production percentage was higher in China (39%), the USA (16%), Morocco and Western Sahara (15%), and Russia (6%). Jordan, Egypt, and Tunisia produce 3% of the global production (Marjolein et al. 2012).

The world's annual phosphate production in 2012 was about 217 million tons, and the global reserves were about 67 billion tons (Elmaadawy et al. 2015). The present phosphate reserves may cover the world's requirements of phosphates for more than 100 years with respect to the increase in world population. Egypt has about 4% of the world's phosphate reserves (2.78 billion tons) and produces about 3% of the world's phosphate production (about 6 million tons per year).

The localities of rock phosphate in Egypt are:

(1) Along the Red Sea Coast from Safaga to Quseir land stretch.
(2) The Nile Valley between Idfu and Qena and particularly near Sebaiya and El Mahammid, at Gabel Abu Had and WadiQena which have more economic deposits,
(3) Western Desert at Abu Tartur plateau between the Kharga and Dakhla oases.

The rock phosphate of these regions are associated with iron or sulphides. The phosphorite spreading from Bahariya Oasis to Sinai has no economic potential (Salib 2006).

The organic acids simultaneously solubilized the rock phosphate (Vassileva et al. 2000). Biologically phosphorous solubilization depends on two main factors:

(a) Mode of biocatalyst applications (free or encapsulated cells).
(b) The initial concentration of rock phosphate in the cultivated medium.

Furthermore, there are two main routes used for the solubilization of rock phosphate as follow:

1. Partial acidulation.
2. Complete acidulation, which is performed by organic or mineral acids.

In the partial dissolution route, one-third of the phosphate material is acidulated by acids to produce soluble mono-calcium phosphate, which is known in the fertilizer industry as superphosphate, which is important for increasing the available phosphorus from rock phosphate and improving crop yield from the phosphorus-deficient soil.

Khalil (2013(reported that, application of rock phosphate and different soil amendments as sulphur or phosphate dissolving bacteria inoculation individually or together had a significant effect on broad bean yield and its quality, increased nitrogen, phosphorus, and potassium contents in straw and seeds of broad bean. The highest nutrient contents were found when the plants are fertilized with a mixture of RP and different soil amendments.

Badr and Taalab (2005) studied the release of phosphorus from RP through composting using organic materials and its effect on corn growth and they found that the concentration of total phosphorus was significantly enhanced in the final product as organic materials decreased during composting compared to control where no phosphorus was added. Where phosphorus from rock phosphate was solubilized and transformed into available forms during composting.

Husnain et al. (2014) found that ogun rock phosphate had a similar effect as nitrogen, phosphorous, and potassium 20-10-10 when applied with organic manures and urea for plant production. Whereas, reactive rock phosphate improved soil fertility and maize crop productivity. In addition, Moroccan rock phosphate contained the highest citric acid extractable phosphate as compared to other rock phosphate tested and was the most effective in increasing maize production. Filamentous fungi such as *Aspergillus* and *Penicillium* species are widely used as producers of organic acids, applied directly into the soil to solubilize the rock phosphate. Inoculation of phosphate-solubilizing fungi and mycorrhizal fungi improves the physicochemical, biochemical, and biological properties of rock phosphate-amended soil (Kumari and Phogat 2008; Santi et al. 2000).

In this respect, rock phosphate dissolution by microorganisms directly affects the fertility of soils. Hellal et al. (2013) produced compost from rice straw enriched with rock phosphate and inoculated with *Aspergillus niger, Trichoderma viride*, and or farmyard manure. The resulting composts were evaluated as organic phosphate fertilizers for maize plants in pot experiments. The results showed that a higher amount of soluble phosphorus was attained from composts inoculated with *Aspergillus niger* plus *Trichoderma viride* with or without farmyard manure. Produced composted rice straw was much better than the superphosphate in sustaining maize with available phosphorous (Reyes et al. 2006).

Zhong and Huang (2005) reported that bacteria, fungi, and yeast can play important roles in phosphorus solubilization. Where phosphate-dissolving microbes can enhance the solubilization of phosphors to a varying extent. In addition, acids, acid phosphates, and alkaline phosphates have synergic effects on phosphate dissolution.

Mycorrhizal enzyme activities increase in soils enriched with microorganisms. In addition, soil microorganisms, so-called mycorrhiza helper bacteria are known to stimulate mycelia growth of mycorrhizal fungi that can affect the arbuscular mycorhiza formation and function (Alguacil et al. 2008; El Tarabily et al. 2008).

AbdelHakam (2011) concluded that rock phosphate from red sea sediments could be used with compost of plant residues or chicken manure mixed with certain microorganisms as a phosphorus fertilizer to improve the phosphorus status and rare earth elements in the clay soil and consequently the phosphorus availability and uptake by wheat plants. Rasha (2014) confirmed that rock phosphate inoculated with bacteria and mycorrhizae proved the appropriate technology to use rock phosphate and organic waste for continuous crop production as well as supporting a healthier environment.

2.5 Availability of Phosphorus and Implications on Agriculture Systems

The appropriate rates of phosphorus application increase fertilizer use efficiency (Karamesouti and Gasparatos 2017). The soil content of phosphorus did not change where phosphorus was applied at rates equivalent to plant uptake (Haneklaus and Schnug 2016). Rowe et al. (2016) concluded that elevating the efficiency of phosphorus fertilization depends on applying adequate phosphorus rates, whereby plants are able to utilize them. Applying slow-release fertilizers is an effective choice particularly in acid soils (Karamesouti and Gasparatos2017).

Using polymer-coated fertilizers, inoculation of microorganisms, liquid foliar sprays mitigate phosphorus fixation and microbial immobilization (Withers et al. 2014).

The proper time of phosphorus application is important in increasing the efficacy of phosphorus fertilization (Officer et al. 2009) Applying phosphate fertilizers pre-cultivation is not expected to achieve the desired outcome under the humidity conditions hence the phosphate ions will be lost through fixation (Pagani et al. 2013). Phosphate fertilization should be done during the early growth of plants during root propagation (Karamesouti and Gasparatos 2017; Schroder et al. 2011). This encourages photosynthesis and plant growth (Pagani et al. 2013).

Management practices are important in elevating fertilizer phosphorus use efficiency. Meanwhile, phosphorus fertilization should be scheduled during plant growth particularly the initial period of growth during root propagation (Abobatta 2018; Schroder et al. 2011) that encourage photosynthesis thus reflecting on yield and yield components (Pagani et al. 2013). In addition, applying the phosphate fertilizer around the root zone increases its uptake by plants (Karamesouti and Gasparatos 2017). Surface and subsurface placement of phosphorus and injection of liquid phosphorus within the rhizosphere zone increase plant absorption particularly in calcareous high pH soils or soils of high iron and aluminum oxides (Pagani et al. 2013). The broadcast application does not provide the optimum distribution of phosphorus fertilizers (Schroder et al. 2011).

2.6 Rock Phosphate as a Natural Fertilizer

Rock phosphate sources are natural minerals that require minimum metallurgical processing. As natural compounds, they can be used in organic agriculture. It is suitable for direct application and can be more efficient than water-soluble phosphate fertilizers in terms of phosphorus recovery by plants under such conditions. In addition, natural or indigenous rock phosphate is usually cheap. Due to their extremely variable and complex chemical composition, rock phosphate is a source of several nutrients other than phosphorus. Although these advantages, it has some limitations as observed by Zapata and Roy (2004).

Sedimentary rock phosphate show a very complex structure, have extremely variable chemical constituents and may contain elements such as heavy metals and even radionuclides. The long-term dissolution kinetics of rock phosphate determined with formic acid and citric acid showed slow reaction initially (0–20 min) because of the presence of free calcium carbonate (Abdollatif et al. 2009).

Soil properties and plant characters affected the dissolution rate of rock phosphate. Whereas, chemical composition and particle size of rock phosphate control their reactivity. Sedimentary rock phosphate is generally most reactive and suitable for direct application. Calcium carbonate can reduce the rate of rock phosphate dissolution in some soils. The rate of rock phosphate application needs to be based on the soil phosphorus status as indicated by soil test (Perrott and Wise 2000).

Phosphorous solubilization efficiency of all the sources of the rock phosphate samples is applied to the sand and calcareous soils attained; generally, its highest values in the second week thereafter tended to decrease with time up to the sixth week (AbdelHakam 2011).

2.7 Processing Affect Phosphorus Availability for Plants

There are various processing that affects phosphorus availability for different plants. Figure 2.1 explains some processing that enhances phosphorus availability for a plant like phosphate mineralization, weathering, desorption, and dissolution (Amanullah et al. 2021). While there are other processes that affect negatively phosphorus available for different crops include immobilization, adsorption, precipitation, and runoff & erosion.

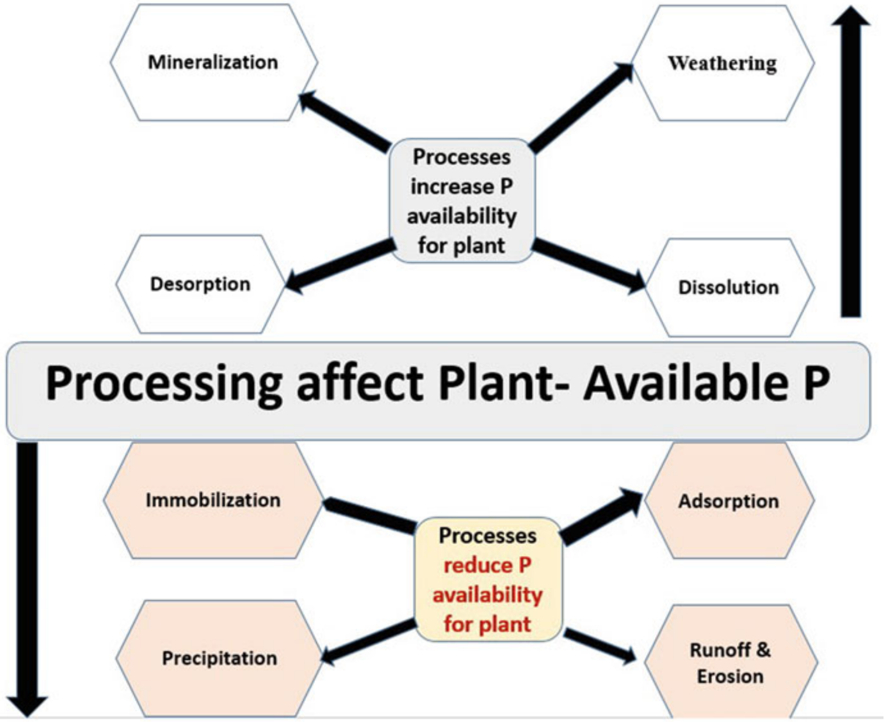

Fig. 2.1 Factors that influence phosphorus absorption

2.7.1 Phosphate Mineralization

Mineralization is a process through which organic phosphorus in soil is converted into inorganic phosphorus with the help of soil microbes. Immobilization is the reverse of mineralization. During immobilization, inorganic phosphorus forms are converted back to organic forms and are absorbed into the living cells of soil microbes. Immobilization naturally happens when crop residues are incorporated into the soil. As crop residues decompose, more phosphorus becomes available in the soil solution through mineralization. Mineralization and immobilization processes are biological processes, they are highly influenced by soil moisture, temperature, pH, organic carbon to organic phosphorus ratio of crop residues, microbial population, etc. (Spohn and Kuzyakov 2013).

2.7.2 Adsorption and Desorption

Adsorption is fast and reversible in nature, a process in which phosphorus present in soil solution is attached/bound to the surface of soil particles. The phosphorus binding takes place on clay surfaces or the iron (Fe) and aluminum (Al) oxides and hydroxides present in the soil.

Soils with higher iron and aluminum oxides concentrations have a greater ability to adsorb phosphorus than soils with relatively low iron and aluminum oxides. Also, soil clay content favors phosphorus adsorption. Soils with greater clay content have higher adsorption capacity than coarse-textured sandy soils (Sun et al. 2020; Khan et al. 2017).

2.7.3 Weathering, Precipitation, and Dissolution

Weathering is a process in which minerals break down over time and release phosphorus in the soil solution for plant uptake. Apatite is a primary mineral, very stable and resistant to weathering. Therefore, phosphorus is released very slowly compared to secondary phosphorus minerals such as calcium, iron, or aluminum phosphates.

Precipitation is a process by which metal ions such as Al_3^+ and Fe_3^+ (these ions are dominant in acidic soils) and Ca_2^+ (dominant in calcareous soils) react with soil phosphate ions to form minerals such as Al^-, Fe^-, or Ca^-phosphates. Precipitation is a slow process and involves a permanent change into metal phosphates. These metal phosphates can release phosphorus in soil solution upon dissolution, but the release rate is very slow.

A dissolution is a form of weathering when the phosphate minerals dissolve and release phosphate back into the soil solution (Compton et al. 2000).

Phosphorus is lost from the soil in different ways like:

(a) Crop/plant uptake.
(b) Runoff and erosion.
(c) Leaching.

Surface runoff is the main path for phosphorus loss (dissolved and eroded soil particles) from the soil surface. Leaching is the loss of soluble phosphorus (minimal compared to surface runoff) from sub-surface soil as water penetrates vertically down the soil profile (Withers et al. 2001).

2.8 Factors Influence Availability of Phosphorus

There are different elements that affect phosphorus availability in soil solution include:

(a) **Organic stock**

Organic matter mineralization leads to the release of available forms of phosphorus for the plant into soils. Where organic molecules will compete with phosphate adsorbed to soil surfaces and will reduce phosphorus retention.

(b) **Clay content**

The higher clay content of the soil has a high phosphorus withholding capacity because clay particles have a very large surface area per unit volume that easily adsorb phosphorus.

(c) **Soil mineralogy**

Phosphorus adsorption capacity is affected by the mineral composition of the soil. For example, soils with a high content of Al^{3+} and Fe^{3+}also tend to have the greatest phosphorus adsorption capacity.

(d) **Soil pH**

Maximum phosphorus availability detected pH between 6 and 7. At lower pH, acidic soils have larger amounts of Al^{3+} and Fe^{3+} bonded strongly with phosphate. Whereas, higher pH alkaline soils phosphate tends to precipitate with calcium.

(e) **Other factors**

Phosphorus mineralization from organic matter decomposition is affected by temperature, moisture, and soil aeration. For example, in warm, humid climates organic matter decomposes faster compared to cool dry climates.

2.9 Biodiversity of Phosphate Dissolving Microorganisms

Soil microorganisms have the ability to convert unavailable organic phosphorus compounds into available simple inorganic forms. Several bacterial and fungal species can increase phosphorus availability in soil and are used as biofertilizers and known as phosphate solubilizing microorganisms (Table 2.1). The bacterial species phosphate solubilizing bacteria or phosphate dissolving bacteria, while the fungal ones are phosphate-solubilizing fungi. Phosphorus solubilizing bacteria in soil constitute 1 to 50% and fungi solubilizing ones constitute 0.1–0.5% of total soil microorganisms (Wakelin et al. 2004). *Aspergillus* and *Penicillium* fungi are predominant phosphate solubilizing microorganisms and can be isolated from the rhizosphere and non-rhizosphere (Zaidi et al. 2009).

The potential phosphate solubilizing activity for various microorganisms such as bacillus, pseudomonas, actinomycetes, and mycorrhizae was characterized. Also, rhodococcus, arthrobacter, serratia, chryseobacterium, gordonia, phyllobacterium, delftia sp. (Chen et al. 2006), *Azotobacter* (Kumar et al. 2001), *Enterobacter*, *Pantoea*, and *Klebsiella* (Chung et al. 2005), *Vibrio proteolyticus*, *Xanthobacter agilis* (Vazquez et al. 2000) are known as phosphate solubilizers. Moreover, symbiotic nitrogen-fixing rhizobia such as *Rhizobium leguminosarum* (Abril et al. 2007) also showed phosphorus solubilizing activity (Zaidi et al. 2009). Several phosphate-solubilizing bacteria have also been isolated from stressed environments for example *Kushneria sinocarni* (halophilic bacteria) isolated from the sediment on the eastern coast of China, which may be useful in salt-affected agricultural soils (Zhu et al. 2011).

Fungi with phosphate dissolving activity represent 0.1–0.5% of total fungal counts**.** They are characterized by retaining their activity upon repeated sub-culturing under laboratory conditions compared to phosphorus solubilizing bacteria**.** In addition, soil fungi are able to cross long distances more easily than bacteria and hence, may be more important to phosphorus solubilization in soils

Table 2.1 Phosphate dissolving microorganisms

Type	Species
Mycorrhizae	Vascular Arbuscular Mycorrhizae (Glomus sp.)
Actinomycetes	Streptomyces
Fungi	*Trichoderma viridae, Aspergillus awamori, A. niger, A. tereus, A. flavus, A. nidulans, A. foetidus, A. wentii. Fusarium oxysporum, Chaetomium globosum*
Bacteria	*Azospirillum brasilense*, *Bacillus* sp., *Bacillus circulans, B.cereus, B. megaterium,B. polymyxa, B. subtilis, Bradyrhizobium* sp., *Brevibacterium* sp., *Pseudomonas* sp., *P putida, P. fluorescens, Thiobacillus ferroxidans, T. thioxidans, Rhizobium meliloti, Xanthomonas* sp.
Cyanobacteria	*Anabena sp., Calothrix braunii, Nostoc sp., Scytonema sp.,*

[a]Modified from Sharma et al. (2013)

(Kucey 1983). In general, phosphorus solubilizing fungi are known to produce more acids than bacteria with superior phosphorus solubilizing activity (Venkateswarlu et al. 1984).

Aspergillus, Penicillium, and *Trichoderma* are the most representative filamentous fungi that solubilize phosphate (Fenice et al. 2000; Khan and Khan 2002; Altomare et al. 1999). Regarding yeasts, Gizaw et al. (2017) reported that *Phichia norvegensis, Cryptococcus albidus var aerius, Candida etchellsii, Cryptococcus albidus var albidus, Rhodotrula aurantiacaA, Rhodotorula aurantiaca B, Cryptococcus luteolus, Cryptococcus albidus var diffluens, Cryptococcus terreus A*. recorded phosphate solubilizing activity. Their phosphate-solubilizing index (PSI) ranges 1.72–3.35 after 15 days of incubation. *Phichia norvegensis and Cryptococcus albidus var aerius* were superior in phosphate solubilization 3.35 and 3.2 PSI respectively. Therefore, these species can be the candidate and exploited after further evaluation as biofertilizers for teff productivity.

Phosphate-solubilizing fungi are expected to be present widespread, many are usually detected in agricultural soils such as *Penicillium sp.,* and *Aspergillus sp*. they known to increase plant growth by 5–20% after inoculation (Sharma et al. 2013).

Actinomycetes are a group of soil microorganisms characterized by their ability to survive in extreme environments (e.g. drought) and also possess other potential benefits such as phosphate solubilization, antibiotic and phytohormone-like compounds productions that benefit plant growth, there are about 20% of actinomycetes have phosphate solubilizing activity, such as *Streptomyces* and *Micromonospora* (Hamdali et al. 2008a, b).

In addition, under alkaline soil conditions arbuscular mycorrhizal fungi have an important role in improving the growth and productivity of citrus orchards (Abobatta 2019a). Furthermore, Widada et al. (2007) reported that using a combination of arbuscular mycorrhizal fungi and rhizobacteria has positive effects on plant growth in acid soil.

Sims and Pierzynski (2005) studied the mechanism of phosphorus solubilization by phosphate solubilizing microorganisms and they recognized the main methods of the soil phosphorus cycle that affect soil solution phosphorus concentrations as follow:

(1) dissolution– precipitation (mineral equilibria).
(2) sorption– desorption (interactions between phosphorus in solution and soil solid surfaces).
(3) mineralization–immobilization (biologically mediated conversions of P between inorganic and organic forms).

Phosphate solubilizing bacteria increases the prospects of using phosphatic rocks in crop production. Where its efficiency increased through co-inoculation with other beneficial bacteria and mycorrhiza as biofertilizers to improve plant growth and increase crop productivity. There are several mechanisms for microbial phosphate solubilization including; production of organic acid and phosphatase enzyme, biological phosphorus mineralization, stimulating phosphorus solubilizing inoculants that may contribute significantly to plant phosphorus uptake (Khan et al. 2009). Soil microorganisms have a significant role in the soil phosphorus cycle (i.e. dissolution–precipitation, sorption–desorption, and mineralization– immobilization). Therefore, phosphate solubilizing microorganisms represent a source of phosphorus to plants upon its release from dead cells. As a result, changes in environmental conditions such as drought, freezing, and thawing, can result in a sudden increasing available phosphorus in the solution due to an unusually high proportion of microbial cell lysis (Butterly et al. 2009).

Inorganic phosphorus solubilization occurs mainly by organic acid production as a product of the microbial metabolism that leads to lowering the pH. Enhancing chelation of the cations bound to phosphorus, competing with phosphorus for adsorption sites on the soil, by forming soluble complexes with metal ions associated with insoluble phosphorus (Ca, Al, Fe) and thus phosphorus is released (Trolove et al. 2003; Maliha et al. 2004; Zaidi et al. 2009). Detection of organic acids produced by phosphorus solubilizing microorganisms by high-performance liquid chromatography and enzymatic methods (Whitelaw 2000). Yi et al. (2008) studied the role of polysaccharides in the microbial mediated solubilization of phosphorus**,** exopolysaccharides (EPSs) are polymers consisting mainly of carbohydrates excreted by some bacteria and fungi onto the outside of their cell walls (Sutherland 2001). Soil microorganisms can solubilize and mineralize phosphorus from inorganic and organic pools of total soil phosphorus. The use of phosphate-solubilizing microorganisms for better crop productivity besides sustaining soil health.

2.10 Manufacture of P Fertilizers

Plant growth requires an adequate concentration of phosphorus which is replenished by phosphorus fertilization (Haneklaus and Schnug 2016; Karamesouti and Gasparatos 2017). Promoting phosphorus sustainability and increasing its fertilizer use efficiency requires consideration of the appropriate dose, the proper time, and the application method (McLaughlin et al. 2011; Pagani et al. 2013; Schroder et al. 2011; Withers et al. 2014). Source of phosphorus fertilizers include three bio-fertilizers, organic fertilizers, and chemical fertilizers. Bio-fertilizers are microorganisms, which increase phosphorus. Mycorrhiza is a fungus that can be in symbiotic association with a green plant (Karamesouti and Gasparatos 2017). It plays an important role in increasing plant growth and producing high biomass, encouraging mineral nutrition, particularly phosphorus (Sharma et al. 2008). Phosphorus-solubilizing bacteria, which include *Proteobacteria, Bacillus, Ramlibacter*, and *Lysobacter* increase phosphorus availability by secreting acids, which solubilizes insoluble phosphorus (Zhang et al. 2021).

Chemical fertilization constitutes applying water-soluble or less soluble salts to soil, its efficacy depends on soil reaction (Karamesouti and Gasparatos 2017). Phosphate rock minerals such as apatite have total phosphorus of 70 to 180 g phosphorus kg^{-1} (UNIDO/IFDC 1998). Reserves of rock phosphate in Australia, Brazil, Canada, Egypt, Jordan, Morocco, China, Russia, Senegal, South Africa, Syria, Togo, Tunisia are 82, 260, 5, 100, 1500, 5700, 200, 80, 1500, 100, 60, 100, 1100 million Mg respectively, while other countries have 950 million Mg (Van Kauwenbergh 2010).

In calcareous soils, phosphate ions initially precipitate as di-calcium phosphate di-hydrate (DCPD) which is converted to di-calcium phosphate (DCP); acidic fertilizers play a crucial role in dissolving calcium compounds (Sanchez 2006). rock phosphate is a very effective choice in acidic soils (Johnston and Syers 1998). Low water-solubility orslow-release phosphorus fertilizers reduce phosphate leaching. Some fertilizers are coated with polymers to reduce the direct contact phosphorus fixers.

Other phosphorus chemical fertilizers are wet-process phosphoric acid, normal superphosphate, concentrated super-phosphate including doublesuperphosphate or triple superphosphate all of which provide phosphorus only. Other soluble phosphorus fertilizers which provides other nutrients bedside phosphorus include mono-ammonium phosphate, and di-ammonium phosphate contains nitrogen besides phosphorus (Van Kauwenbergh 2010). There are fertilizers that provide potassium along with phosphorus.

2.10.1 Nano Fertilizers

Nano-fertilization is a promising technique, which provides the fertilizer material in nanoparticles with a size less than 100 nm. This size is of extremely high activity surface (Abobatta 2019b; SSSAJ 2015; Janmohammadi et al. 2016; Naderi and Danesh-Shahraki 2013; Rameshaiah and Jpallavi 2015). Such size renders the fertilizer easily dispersed and diffused in soil with great resistance to fixation (Naderi and Danesh-Shahraki 2013). It provides a slow-release source of fertilizer that supplies plants with nutrients for a prolonged time (Rameshaiah and Jpallavi 2015). Many studies referred to the efficiency of applying nano-hydroxyapatite (HA-NPs) as a promising alternative source of phosphorus (Mikhaka et al. 2016; Doe 2015; Liu and Lal 2014). Nano forms elevate the fertilizer use efficiency of phosphorus, also, the slow release increases the availability of phosphorus (Kottegoda et al. 2011, Montalvo et al. 2015; Taşkın et al. 2018). Besides applying low rates of nano fertilizer instead of the high rates of ordinary fertilizers, decreases the cost of phosphorus fertilization (Taskin et al. 2018).

2.11 Conclusion

Phosphorus is one of the main elements for plant nutrition, therefore, phosphorus deficiency inhibits plant growth. Phosphorus exists in different forms in the soil, such as organic phosphorus, adsorbed phosphorus, soluble phosphorus, and phosphate primary minerals. There are different factors that affect phosphorus availability in soils such as parent material, climate, organic matter, soil texture, and insensitive cultivation. Several microorganisms enhancing phosphate solubilization include bacteria, fungi, actinomycetes, and mycorrhizae.

Phosphorus fertilization provides adequate plant requirements, the phosphorus fertilizers include bio-fertilization, organic fertilization, and chemical fertilization. In addition, rock phosphate is suitable for acidic soils. While, under alkaline soil conditions the application of conditioners such as compost, organic manure, phosphorus soluble microorganisms, and plant waste could increase the efficiency of rock phosphate as phosphatic fertilizer. Furthermore, nano-fertilization is a promising technique for phosphorus fertilization, so, nanoparticles hydroxyapatite is considered a promising alternative source of phosphorus that promotes the growth and productivity of plants.

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Chapter 3
Organic Phosphorous as an Alternative to Mineral Phosphatic Fertilizers

Muhammad Zain, Muhammad Adeel, Noman Shakoor, Muhammad Arslan Ahmad, Saliha Maqbool, Jiusheng Li, Shafeeq Ur-Rahman, Ming Xu, Asif Iqbal, Waqar Afzal Malik, and Aiwang Duan

Abstract Phosphorous is an essential macronutrient required for plant growth. However, phosphorous is deficient in most soils and is moderately available to plants. The use of mineral phosphorous fertilizer has highly contributed in feeding the increasing world population by supporting high crop yield. However, edaphic

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processes cause phosphorous to be immobilized in soil, thus decreasing phosphorous availability for plants uptake. This low phosphorous use efficiency of mineral phosphorous fertilizer and the depletion of phosphate reserves are major issues calling for alternatives such as organic phosphorus. This chapter reviews phosphorous reserves and production in different countries, sources of organic phosphorous, testing techniques of organic phosphorous, and positive effects of organic phosphorous on crop productivity and soil health.

Keywords Organic phosphorous · Mineral phosphorous · Testing techniques · Soil health · Crop productivity

Abbreviations

Mt	Million tons
Pg	Petagrams
lbs	Pound
K	Kelvin
ppt	Parts per trillion
ppb	Parts per billion
ha^{-1}	Per hectare
cm	Centimeter

3.1 Introduction

From bullets to fertilizers, phosphorus has become a key player in human existence (Sharpley et al. 2018). Phosphorous is a vital element for plant development as phosphorous is essential to cellular function (Anwar et al. 2017). Ultimately all living beings intake phosphorous either directly or indirectly via food sources from soil (Bünemann 2015). Phosphorous is an important part of the phospholipids that are made up of cell membranes, genetic code carriers (deoxyribonucleic acid and

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ribonucleic acid), and intracellular energy transfer (adenosine triphosphate) (McLaren et al. 2020). Phosphorus is a key nutrient in food production and is a non-renewable resource (Cordell et al. 2009). There is no alternative available to replace phosphorous, so solutions regarding P deficiency must come from either less consumption of phosphorous, more efficient consumption and reuse, and minimal losses in the chain from mining to the dining table (Sarvajayakesavalu et al. 2018).

Phosphorous is present in both organic and inorganic forms in soil (Amanullah et al. 2016a, b). Inorganic phosphorous include apatite as the most prevalent primary phosphorous mineral; secondary phosphorous mineral comprises amorphous aluminum and various calcium and iron phosphates (Bünemann 2015; McLaren et al. 2020). Organic phosphorus mainly includes orthophosphate esters, including inositol phosphates, orthophosphate diesters, organic polyphosphates, and phosphonates (Pierzynski et al. 2005). Figure 3.2 presents different forms of organic phosphorous and the relative distribution percentage in nature (Table 3.2). Orthophosphate esters (esters of phosphoric acid) are not reactive at neutral pH range in soils, but hydrolyze instantly at higher pH range and in the availability of phosphatase enzymes (Amanullah et al. 2019, 2021). Phosphoric acid is a comparatively strong acid, and pK value is around 2 with an ionizable proton. This is the reason behind the complete ionizing of orthophosphate esters at the pH range of common soils. Organic phosphorus makes covalent bonding and the highest oxidation state is phosphorus (Paraskova 2014).

3.2 Global Inorganic Phosphorous Status and Challenges

Worldwide production of inorganic phosphorous fertilizers will reach a maximum peak in 2033 and 1/3 of that peak will level by the end of this century (Craswella et al. 2010). According to some recent statistics, the utilization of inorganic fertilizers was 197.5 Mt. in the world and China is the world's leading user, consuming 35% of the world's total inorganic fertilizers. In the last few decades, the application of inorganic fertilizer in China increased from 12.69 Mt. to 60.23 Mt. (Cui et al. 2021). However, the efficiency of phosphorous inorganic fertilizers has been decreasing year by year since 1985.

Inorganic phosphorous is continuously depleting and 70% of phosphorous global production is currently created from reserves which will be finished in the next 100 years and continuously increasing demand for inorganic phosphorous will result in a significant global production deficit (Khan et al. 2017). Table 3.1 presents the country-wise data of phosphorous reserves and their production. The demand for rock phosphate – phosphorus pentoxide – will increase from 176 Mt. in 2010 to 262 Mt. by 2050 (Oumnih et al. 2017). The average growth rate is predicted to be 1% per year before leveling off in 2100, then 0% growth rate per year between 2050 and 2100. This scenario will result in a production deficit of over 200 Mt. per year by 2075, which is much greater than the current production rate of phosphorous fertilizer.

Table 3.1 Country-wise data of phosphorous reserves and their production in the world

Country	Mine production (000 Mt)		Reserves (000 Mt)
	2018	2019	
United states	25,800	23,000	1,000,000
Algeria	1200	1200	2,200,000
Australia	2800	2700	1200,000
Brazil	5740	5300	1,700,000
China	120,000	110,000	3,200,000
Egypt	5000	5000	1,300,000
Finland	989	1000	1000,000
India	1600	1600	46,000
Israel	3550	3500	62,000
Jordan	8020	8000	1000,000
Kazakhstan	1300	1300	260,000
Mexico	1540	1500	30,000
Morocco	34,800	36,000	50,000,000
Peru	3900	3700	210,000
Russia	14,000	14,000	600,000
Saudi Arabia	6090	6200	1,400,000
Senegal	1650	1600	50,000
South Africa	2100	1900	1400,000
Syria	100	2000	1,800,000
Togo	800	800	30,000
Tunisia	3340	3000	100,000
Uzbekistan	900	900	100,000
Vietnam	3300	5500	30,000
Other countries	970	1000	770,000
World Total (round)	249,000	240,000	69,000,000

Table 3.2 Sources of organic phosphorous fertilizers in the agriculture system

Organic source	Total phosphorous (%)
Poultry manure	0.5–1.5
Sewage sludge	0.4–2.5
Compost	0.2–0.5
Green manure	0.2–0.5
Wood ash	2–5
Fish meal	5–10
Bone meal	20–30
Rock phosphate	17–26

This scenario demands alternative options of phosphorous sources and more sustainable utilization of phosphorous reserves. Organic phosphorous has recently emerged as the best alternative to minimize inorganic phosphorous consumption. This chapter presents the biological cycling and forms of organic phosphorous, available testing techniques of organic phosphorous, commercially available organic phosphorous fertilizers, and impacts on agricultural crops.

Furthermore, we have presented some solid facts to consider organic phosphorous as an alternative to inorganic phosphorous in the context of delaying peak phosphorous production.

3.3 Phosphorus in the Soil Agriculture System

The phosphorus cycle is slow compared to other nutrients biogeochemical cycles due to P trace amounts available in the atmospheric phase. Phosphorous tends to move from terrestrial soil to surface water and end up in oceans, where phosphorous deposits in a long-term sink (Margenot et al. 2017).

Pools and processes of phosphorous dynamics understanding in the agricultural system can help in sustainable phosphorous management (Fig. 3.1) (Frossard et al. 1995). Soil phosphorous exists in both inorganic and organic forms. In soil systems, phosphorous exists as phosphates. Orthophosphate is the simplest phosphate, has the chemical formula of PO_4^{3-}. Other forms are hydrogen phosphate (HPO_4^{2-}) and H_2PO^{4-} (dihydrogen phosphate). The soil phosphorous can be categorized into three sub-pools. The total global pool size is estimated as 40.6 ± 18 Pg phosphorous in the top half meter comprising of 3.6 ± 3 Pg phosphorous for labile phosphorous, 8.6 ± 6 Pg phosphorous for organic phosphorous, 3.2 ± 2 Pg phosphorous for inorganic phosphorous, and 12.2 ± 8 for occluded phosphorous (Yang et al. 2013). The labile inorganic phosphorous represents the most readily available phosphorous for plants but generally in small amounts. The organic phosphorous contains both the easily mineralized phosphorous and more stable phosphorous (Iqbal et al. 2019a, b). Inorganic phosphorous is held on mineral surfaces in soil by adsorption with a much slower rate of dissolution compared to labile phosphorous. Occluded phosphorous represents the fraction that is not available to plants (Condron et al. 2005; Pierzynski et al. 2005).

Major pools of inorganic phosphorous and non-living organic phosphorous are relatively constant in size. However, the smaller pools like soil solution and microbial biomass contain both forms of phosphorous which can fluctuate in size as presented by the arrows in Fig. 3.1.

3.4 Organic Phosphorus Fertilizer

Scientists have made big progress with help of farmers in understanding phosphorous fate and transport in many environmental sectors but mainly have failed to give new products and/or application techniques that are extensively accepted and that massively improve the plant acquisition productivity (Iqbal et al. 2017). However, under a specific environment, important progressions have been attained. For

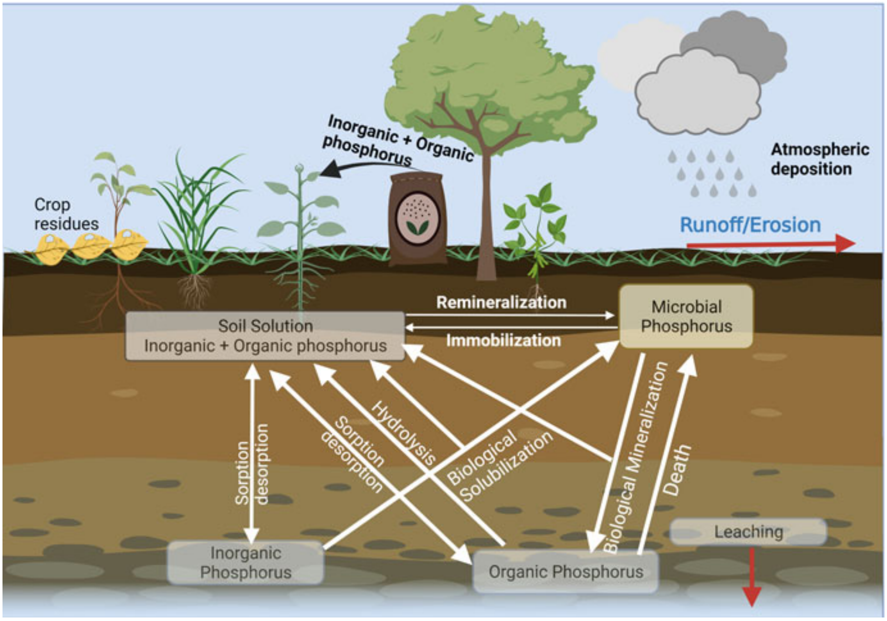

Fig. 3.1 Pools and pathways in phosphorous cycling in agricultural systems

example, usage of liquid phosphates formulation in extremely calcareous soils has reduced the precipitation as meagerly soluble calcium phosphate minerals. But in other attempts like co-application of the humic ingredients, use of nanoparticles, or sorption of the double-layered hydroxides have not given the required results which were necessary to continue the economically increasing crop yields without any other environmental cost (Weeks and Hettiarachchi 2019).

To enrich the soil physicochemical properties and soil health, management applications such as crop residue incorporation, manure application have been adopted (Wang et al. 2015). Sustainable cropping systems may include the combined use of organic fertilizers (crop residues or manure) and inorganic fertilizer efforts to enhance microbial activities and ecosystem functioning in nutrients provisioning to growing plants (Drinkwater and Snapp 2007). For example, dairy manure and inorganic fertilizer used as organic and inorganic soil modifications can restore soil organic carbon and soil health (Mandal et al. 2007; Wang et al. 2008). Phosphorous application through organic amendments substantially improves the soil carbon retention resulting in higher crop harvests, preserving carbon in the surface soil, and rise crop yields (Papadopoulos et al. 2014). Furthermore, soil organic phosphorous amendments could decrease the dependency on inorganic fertilizers (Bhattacharyya et al. 2015). Thus, modifying soil with appropriate organic phosphorous input could be a better strategy to improve soil carbon and soil health through active microbial community structure under low fertility as well as in shallow soils (Yuan et al. 2014). Dry matter and other organic phosphorous inputs provide the essential plant nutrients through improved soil aggregations and aeration, adding organic matter, and maintaining soil pH particularly in acidic soils (Dong et al. 2012; Hirzel and Walter 2008; Yan et al. 1996).

A 2 years field trial showed that inorganic and organic phosphorous inputs considerably influenced the soil's biological and chemical characteristics, the composition of soil microbes, and abundance in silage corn production systems in podzolic soil in boreal climate. The results propose that P1 treatment in which dry matter with higher phosphorus pentoxide, carbon, and nitrogen was used markedly promoted active microbial community arrangement and abundance, soil available phosphorous and acid phosphatase as respective to control, and P2 treatment in which inorganic phosphorous amendment was used. Redundancy analyses also demonstrated a strong association among P1 and P2 treatments, acid phosphatase, soil available phosphorous, total bacterial phospholipids fatty acids, total phospholipids fatty acids, and fungi suggesting that organic phosphorous amendment could be a sustainable management practice and effective strategy for attaining higher forage yield of silage corn in podzolic soils under boreal climate (Ali et al. 2019).

On average, the phosphorous concentration is 24 lbs. phosphorus pentoxide per ton in beef feedlot manure, and dairy manure has 18 lbs. phosphorus pentoxide per ton. Yet, it is important to test the manure to estimate the exact amount how much phosphorous is present. Dairy manure and composted feedlot are also basic sources of available organic phosphorous. Microbial digestion during the composting process decreases the volume by one-third to one-half, hence enhancing the phosphorous content. Furthermore, composting has the lowest costs per unit of phosphorous for transportation. The level of nutrients differs in compost-based on the source material used to produce the organic phosphorous fertilizer. According to Davis et al. (2002), the mean phosphorous concentration for dairy manure compost in New Mexico, Colorado, and Utah are 22 lbs. phosphorus pentoxide per ton of compost. After the well finished composting it is necessary to note that cured compost should not have a strong ammonia odor and should have smelled "earthy". Additionally, the nutrients in cured compost are stabilized and that provides a low release of available phosphorous to plant.

Phosphorus sources approved for application in organic agriculture systems have various properties that affect phosphorous availability and management. Common phosphorous approved sources include cover crops, rock phosphate, soil organic matter, manure, bone meal, guano, compost, rock phosphate, and mycorrhizal fungi (Fig. 3.2) all of which are commonly used in research. Bone meal and guano are among the less commonly mentioned phosphorous sources but can have a high phosphorous concentration (ranging from 7–12% to 1–9%, respectively) (Nelson and Janke 2007).

3.5 Testing Techniques of Organic Phosphorous

The determination of organic phosphorus is the main challenge from environmental samples due to that still there are no direct quantities determination methods. Mostly organic phosphorus is estimated by indirectly, calculating the difference between

Fig. 3.2 Sources of organic phosphorous in agriculture

inorganic phosphorus and total phosphorus measurement (Turner et al. 2005). As well as, organic phosphorus pools define after a sequential extraction of various bounds inorganic phosphorus compounds is performed (Psenner 1988).

Phosphorus exists in nature in both forms such as organic and inorganic with various states, such as solid particles or in a solution that is associated with soil and sediments or merged into plants constituents. Additionally, organic phosphorus may have a variety of chemical forms e.g. soluble (orthophosphate), condensed organic and inorganic phosphorus, particles forms, for example, minerals and organic/mixed forms in complexes, clays, and hydroxides. Phosphorus can be found in cell/organelles of living organisms such as cell membranes, deoxyribonucleic acid, and proteins as well as in synthetic organic phosphorus compounds i.e. herbicides, insecticides, and plant growth regulators (Condron et al. 2005). Furthermore, those compounds have quite various chemical properties, for example, some are soluble in water, while others are fats-soluble as well as some of these are stables, that enable their storage in soil, other forms are easily available. That is meaning that they may be converted by micro-organisms from complex forms of phosphorus to simple forms (Stewart and Tiessen 1987; Williams et al. 1967). Therefore, it is necessary to have precise methods which can measure the qualitative and quantities of the various types of phosphorus from one another, so that's why their behavior can be studied.

The analytical procedure of organic phosphorus determination includes many various steps such as samples collection, preparation of samples, analysis, processing the data, and explanation of results. Additionally, the sampling procedures and sample preparation are the main part of the analysis of organic phosphorus, since they can give rise to major variability in the results. The first step of testing organic phosphorus is sampling. During the sampling, it is important to write down the sampling location, types, quantity, and number of samples to be collected, and the actual procedure of sampling. Because the sample is representative of specific sites, as well as during the analysis less than 1 g of samples are used. Various kinds of samples are used for the examination of organic phosphorus viz. soil, sediment and compost samples.

Another important way for the preparation of the sample is the extraction procedure in which the compound is isolated from the matrix. The basic objective of this step is to isolate the analyte from complex samples, clean the analyte from interfering compounds and pre-concentrate the analytes to a specific level which can be analyzed by the selective method of analysis (Harris 2010).

Sequential extraction is a basic method used for the measurement of phosphorus in environmental samples applied for various forms of phosphorus and their chemical binding. The samples were exposed to the extractants for enhancing strength, both acidic and basic in all fractionation methods. Some extractants applied in the 1st fractionation method are ammonium fluoride, ammonium chloride, sodium hydroxide, and sulfuric acid.

The fractions of samples could be separated, depending on the solubility of phosphorus, into pools of available phosphorus, aluminum, calcium/iron-bound phosphorus, and depending upon the method, refractory phosphorus, residual phosphorus, and recalcitrant phosphorus. In 1957, Chang and Jackson developed the first comprehensive method (Chang and Jackson 1958), which has been extensively used and modified by others (Fife 1959; Williams et al. 1967). Additionally, to determine different inorganic phosphorus pools, that allow to indirectly estimate organic phosphorus by measuring the variance between inorganic phosphorus before and after digestion of the sodium hydroxide extract. Although, the disadvantage of this procedure was that it might not assess plant available or organic phosphorus, which incidentally was also labile phosphorus fraction.

The current fractionation method, that designed exactly for the measurement of organic phosphorus, was proposed by Bowman and Cole in 1978 (Bowman and Cole 1978). The uniqueness in this procedure was differentiated between labile, moderately available, resistant, and acid non-soluble phosphorus. Hedley et al. (1982) combined the original method (method of Jackson and Chang) with the organic phosphorus method (method of Bowman and Cole) for the identification of ten various phosphorus fractions, which included organic, inorganic, and microbial phosphorus. New extractants are used in order to enhance the extraction efficacy of organic phosphorus such as sodium bicarbonate, hydrogen peroxide, and hydrochloric acid. Sequential fractionation methods are still used today because are well described and easy to perform with basic laboratory equipment.

Nuclear magnetic resonance spectroscopy is an advanced technique in which a variety of samples of organic phosphorus (31 phosphorus) nuclear magnetic resonance are measured (Cade-Menun 2005). In 1980, Newman and Tate first applied this technique to the quantification of P in grassland soils (Newman et al. 1980). This procedure differentiates the groups of phosphorus based on specific frequencies of resonance that are comparative to an applied magnetic field and can distinguish between polyphosphate, pyrophosphate, orthophosphate, monoesters, orthophosphate, phosphonates, and orthophosphate diesters (Reitzel et al. 2006). The benefits of this method can detect and calculate the signals of multiple phosphorus-containing compounds simultaneously and differentiate between compounds with alike structural information. This technique has high detection limits with poor sensitivity. The shortcoming of this technique is the particular extraction method in which solvent extract with higher pH that can alter the structure of chemical compounds and hydrolyze labile one as well as in nuclear magnetic resonance technique has some chemical shift such as the orthophosphate diester region, can overlap and resolve very poor. Moreover, this technique is also time-consuming.

Spectrophotometry is a technique in which chemical concentration is measured by light (Harris 2010). Conventionally phosphorous was measured spectrophotometrically by the molybdenum blue technique proposed by Murphy and Riley (1962). This method is also called molybdate reactive phosphorus. The principle of this method is the available phosphate ($PO_4{}^{3-}$) in the sample react with the molybdate ($MoO^{2-}{}_4$) ions in the acidic condition that makes molybdo phosphoric acid.

The acid is then reduced, either with tin chloride (SnCl) or ascorbic acid ($C_6H_8O_6$), to form a molybdenum blue complex, which can be observed calorimetrically (Jarvie et al. 2002). The colour intensity is directly proportional to the concentration level of phosphate that formed blue complexes, preferably all the free phosphate is available. Nevertheless, the origination of blue complexes is slow or incomplete colour production that leads to underestimation of inorganic phosphorous. The colour development is speed up with the inclusion of antimony (III) as a catalyst. The basic advantage of this method is that it is less expensive, easy to perform, and has good sensitivity and low detection limits. The drawback of this procedure is that subject to intervention from complex matrices, for example, soil. As well as some complexes may be formed with other elements (chromium, arsenic, and silicon) rather than phosphorous such as blue molybdate complex (Blomqvist et al. 1993; Jarvie et al. 2002). When the phosphorous was measured from soil extracts (mineral soil) by this method, there is some risk in results by overestimating in creating false positives from the matrix (Jarvie et al. 2002). Furthermore, this method was planned to estimate the inorganic orthophosphate phosphorous, whereas it has also been shown to possibly comprise loosely bound organic and inorganic phosphorous (Stevens 1979). To solve this difficulty and evade over-elaborating the results, discriminating extraction may be applied as a preceding molybdenum reactive phosphorous quantifications procedure.

Induced coupled plasma is also called the atomic spectroscopy method in which in the presence of high temperature a substance is cracked down into atoms (Harris 2010). Ionize argon gas is used to gain high temperatures (6000–10,000 K). Induced coupled plasma is mostly coupled with mass spectrometry and atomic emission spectroscopy. The basic benefits of induced coupled plasma-mass spectrometry and induced coupled plasma-atomic emission spectroscopy have a capacity to measure multi-elements, as well as detection limit is very low, ppt (parts per trillion) range of mass spectrometry and ppb (parts per billion) range of atomic emission spectroscopy. Although, the disadvantage of induced coupled plasma-mass spectrometry and induced coupled plasma-atomic emission spectroscopy, these both can't distinguish between the elements and whole molecule in various oxidation states. Additionally, still, today induced coupled plasma-atomic emission spectroscopy is commonly used for the determination of inorganic phosphorous, for example, total phosphorus quantification.

Ion-exchange chromatography is an analytical method in which constituents with an observed sample are isolated from one another based on their distribution ratios in both phases i.e. stationary phase and mobile phase (Rieman and Walton 2013). This chromatography technique is useful for the determination of inositol phosphorous (Cooper et al. 2007; Ruiz-Calero and Galceran 2005). In ion-exchange chromatography depend on the interaction between the functional group of the column with phosphate ion.

Mass spectrometry is an important analytical method that is used for the qualitative and quantities of analytes in various kinds of samples (Ardrey 2003; Downard and Morrissey 2007; Ruiz-Calero and Galceran 2005). By using mass spectrometry to analyze any samples that can be ionized. The advantages of mass spectrometry are that analysis requires a small size of the sample with high sensitivity.

3.6 Impact of Organic Phosphorous on Soil

Numerous studies have reported the application of organic material for the improvement of soil characteristics and have found markedly beneficial effects on soil properties under various types of soil (Mondini et al. 2008; Tejada et al. 2006; Zingore et al. 2008; Zhang and Fang, 2007). For instance, Bouajila and Sanaa (2011) conducted an experiment in Tunisia and used different rates (40, 80, and 120 tons ha^{-1}) of farmyard manure and household waste. He found an increase in soil nitrogen content, organic carbon and reported that the soil quality improvement was dose-dependent. He further documented that the water infiltration rate under manure treatment was nearly twice as compared to the control plots. The addition of the organic materials in the soil results in an increase in soil porosity and a decrease in the soil bulk density, hence organic material affected the soil water holding capacity (Bronick and Lal 2005). Guo et al. (2016) used cattle manure compost and found that soil organic matter was increased by 87% at 0–20 cm soil depth. The positive effect of organic matter was reported by Rawls et al. (2003) as the organic matter affects the soil structure composition, water retention, and soil adsorption properties.

Sanchez-Monedero et al. (2004) experimented and compared the green manure-treated soil with untreated soil. They found that green manure-treated soil stored 7–14% more carbon and 22–36% more organic carbon storage than untreated soil and chemical fertilizer-treated soil. Application of organic manure notably enhanced the soil pH than that of control soil (Zhang and Fand, 2007). They further investigated that the soil treated with organic manure had more stable water aggregates, saturated hydraulic conductivity, and low bulk density as opposed to chemical fertilizer treated and untreated soil. Thus, Zhang and Fang (2007) concluded based on their experiment that fertilizer source is an important distinguishing aspect that affects the soil properties.

Condron et al. (2005) reported that in most soils, organic phosphorous is 30–65% of the total phosphorous. However, in a wide range of soils with medium to long term (5–25 years) field trials of different phosphorous inputs, it was found that 5–52% of the total phosphorous was in moderately labile and labile organic phosphorous pools as reported by Negassa and Leinweber (2009). To better utilize the soil organic phosphorous for its maximum agricultural benefit, first, we should understand the processes which are involved in its mobilization and accumulation. Organic phosphorous is mainly comprised of orthophosphate monoesters and diesters, while the polyphosphates and phosphonates may not be in huge quantity (Condron et al. 2005). The phosphate monoesters are classified into two groups; labile monoesters which are breakdown products of deoxyribonucleic acid and ribonucleic acid and consist of nucleotides, inositol phosphates which are storage complex presented in the plant cells. While phosphate diesters originate from the plant detritus and the microbial cells and are consist of nucleic acids in deoxyribonucleic acid and ribonucleic acid form. Polyphosphates and phosphonates originate from the microbial biomass along with the phosphate diester and their presence in soil is an indication of phosphorous cycling by microbes (Turner et al. 2003).

Application of organic manure with nitrogen, phosphorous, and potassium significantly increased the soil organic matter, Olsen phosphorous and soil total phosphorous by 1, 3, and 2 times as compared to the alone nitrogen, phosphorous, and potassium treatment and by 2, 17, and 4 times than that of control treatment respectively as found by Ahmed et al. (2019) in his study at three different sites. Silva et al. (2017) compared the effects of rock phosphates and triple superphosphate on the microbial community in maize crop and found that Massilia and Herbaspirillum, which belongs to Oxalobacteraceae was enriched in rock phosphate amended soil than triple superphosphate treated soil. The second most abundant microbes were Klebsiella and were in rock phosphate amended soil. The Bacillus species and Burkholderia species were also higher in rock phosphate treated soil than that of the triple superphosphate amended soil. Makela et al. (2020) investigated that decrease in rhizosphere and soil pH due to synthetic fertilizer is might be because of the acidic nature of synthetic fertilizer that may contain ammonium ions. However, meat bone meal and digestate contain the organic matter that may buffer soil pH. Mondini et al. (2008) found that soil amendment with meat and bone meal caused a significant increase, about 50% of the added nitrogen in nitrate (NO_3^-) and ammonium (NH_4^+) enhanced the microbial content, biomass, and activity as a function of application rate.

3.7 Impact of Organic Phosphorous on Crops

The effects of organic phosphorous on the crops varied based on the different organic phosphorous sources and their application level. Furlani et al. (1987) conducted an experiment and found that organic sources of phosphorous such as phenyl phosphates, glyceryl, and ethyl ammonium significantly improved the dry matter and phosphorous contents of plants as compared to the inorganic phosphorous sources like ferric, potassium dihydrogen, aluminum phosphates, and calcium. Makela et al. (2020) reported that meat bone meal has higher shoot biomass and phosphorous uptake in spelt wheat as compared to the synthetic phosphorous fertilizer. Ali et al. (2019) reported that the application of dairy manure with phosphorus pentoxide enhanced active microbial community composition, biochemical attributes, and the forage production of silage corn.

Vinci et al. (2018) reported that treatment with fungus inoculation and compost not only increased the plant growth and phosphorous uptake but also improved the expression of metabolites that are related to photosynthetic activity. Interestingly, the combination of inorganic fertilizer with Trichoderma was less effective and depicted a decrease in nitrogen content and plant biomass. Organic fertilizer treatment with a combination of fungi has more beneficial effects on plants than alone organic fertilizer application. El Kinany et al. (2019) conducted an experiment and reported that after 12 months of plant growth which were transplanted into arbuscular mycorrhizae fungus amended compost had more biomass (shoot and root biomass), mineral nutrient contents, and chlorophyll contents than that of the plants which are grown without compost addition.

Taskin et al. (2018) compared the organic phosphorous source (nano-hydroxyapatite) with phosphoric acid in their study and found that nano-hydroxyapatite enhanced the phosphorous contents in lettuce by 13% and shoot biomass of lettuce by 11% than that of the phosphoric acid. Nano-hydroxyapatite was foliar applied on the baobab *(Adansonia digitata*) seedlings and it was noted that phosphorus contents, dry biomass, and leaf chlorophyll contents were increased by 55% and 38%, by 90% and 35%, and by 88% and 19% as compared to the monoammonium phosphate and diammonium phosphate respectively (Soliman et al. 2016).

Abdel-Hamid et al. (2003) investigated the relative residues effectiveness of superphosphate and phosphate rock. They reported that superphosphate has greater relative residues effectiveness as compared to phosphate rock. Furthermore, he found that the wheat crop effectively obtained phosphorous from phosphate residues because of its low phosphorous requirement. The relative residues effectiveness values for wheat and sesame plants were 0.11–0.52 and 0.02–0.24 respectively. The relative residues values based on dry matter yield differed from the values based on phosphorous contents. Thus, based on these findings it is recommended that phosphate rock should be mixed with organic manures for application in the soil as slow release. Badr and Taalab (2005) studied the effects of phosphorous release from phosphate rock on the growth of corn and found that total phosphorous concentration was significantly increased in the final product by decreasing organic matter as compared to the control treatment or the treatment with no phosphorous application. It was also observed that phosphate rock phosphorous was transformed and solubilized into available form during the composting.

Akande et al. (2011) experimented on the ogun phosphate rock and organic waste (urea, cow dung, compost, poultry manure) to evaluate its effects on the growth and yield of the two varieties of kenaf. The treatments used were nitrogen, phosphorous, potassium, ogun phosphate rock, and urea, ogun phosphate rock and cow dung, ogun phosphate rock and poultry manure, ogun phosphate rock, and compost, and they were compared with no-fertilizer application treatment. They reported that the application of phosphorous markedly enhanced the kenaf seed yield and plant height. The plants which were treated with nitrogen, phosphorous, potassium were taller than the plants with no fertilizer application. Rochayati et al. (2014) conducted a field experiment and investigated the response of reactive phosphorous rock on maize crop and soil health. It was found that reactive phosphate rock significantly increased maize crop productivity and soil fertility. They further reported that Moroccan phosphate rock has more citric acid than the other tested phosphate rocks and is most suitable for increasing maize productivity.

3.8 Conclusion

An organic production system may improve the soil organic contents, fertilizer uptake by plants, and the cycling of fertilizer. Given the importance of organic phosphorous for plants and soil, we have found that organic phosphorous is more beneficial as compared to mineral phosphorous. Primary organic phosphorous sources are phosphate rock, compost, and manure. Based on our literature review, it was observed that the application of organic phosphorus significantly improved soil health and crop productivity. Phosphate rock is more effective at low pH soil of less than 5.5 and under low calcium concentration. Compost and manure-based phosphorous had more phosphorous availability to plants ranging from the 70–100%. On the other hand, in sense of economic considerations, local availability and the amount of phosphorous required to meet the crop need will play an important role in the final decision of producer to use the organic phosphorous alone or in combination with mineral fertilizers.

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Chapter 4
Adaptive Responses of Crop Species Against Phosphorus Deficiency

Mehtab Muhammad Aslam, Aisha Lawan Idris, Eyalira Jacob Okal, and Muhammad Waseem

Abstract Phosphorus (P) is necessary for plant growth and productivity. P deficiency leads to huge yield losses, and continuous depletion of P in industrial agriculture is becoming a major issue of food security. Moreover, most P is not readily available for plants, thus restricting plant growth. Therefore, P uptake efficiency should be enhanced by identifying key root traits, genes or beneficial microbial associations involved in P uptake. In this chapter we review crops responses to P deficiency, the mechanisms of P acquisition and P homeostasis, response of root exudation to P deficiency, and microbial communities that favor P acquisition. More than 80% of plants establish a symbiotic associations to improve nutrient acquisition ability, ultimately improving plant growth and yield. Plants have evolved an array of strategies to overcome P scarcity-related problems.

Keywords P deficiency · Root exudates · Soil microbes · Plant growth

4.1 Introduction

Phosphorus (P) is one of the key plant macronutrients needed to maintain plant growth and productivity, but its limited availability negatively affects crop yield (Lambers et al. 2008; Khan et al. 2017). Its deficiency not only restricts P uptake and

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remobilization but also limits the uptake of other essential nutrients including magnesium (Mg) and potassium (K) (Loneragan and Webb 1993; Karthika et al. 2018). P stress threatens global food security but also substantially reduces crop yield (Brown et al. 2013). However, the provision of food to the ever-growing population relies on improved crop production. Thus, an appropriate amount of nutrients (P, nitrogen; N, K, sulfur; S) availability is essential to obtain optimal crop yield. To overcome P deficiency related problems and improve crop yield, an excessive amount of P fertilizers are consumed every year (White 2009). High uses of P fertilizer in the agricultural soils led to P saturation and resulted in eutrophication (Amanullah et al. 2016a, b), while low P still restricts crop growth and yield in several regions of the world (Carpenter 2005; MacDonald et al. 2011; Mekonnen and Hoekstra 2018; He et al. 2020). P fertilizers obtained from rock P reserves are the irreversible source of P led to the gradually depletion of P-rock reserves. To fulfill the agricultural P demands and saving P reserves without damaging the environment is became a key challenge of concern (MacDonald et al. 2011; Cordell and White 2015; Pang et al. 2018).

In response to P limitation, plants evolved a series of physiological, morphological, biochemical, and molecular adaptations to enhance their access to P acquisition (Plaxton and Tran 2011). Root exudate modulates soil pH containing P mobilizing compounds, including organic acids, phosphatases, and protons, consequently lead to enhance P availability (Hinsinger et al. 2003; Chen et al. 2006; Mäkelä et al. 2020). Several mechanisms have been adapted to acquire P through colonization of plant roots with soil microbiota. For instance, plants survive in a microbe-rich ecosystem where they communicate with diverse commensal, pathogenic, and beneficial microbes. Mechanisms by which plants respond to beneficial and pathogenic microbes have attracted substantial attention among plant and microbial researchers (Amanullah et al. 2019, 2021). Maize is reported to develop mycorrhiza and increases lateral root growth under P deficiency (Gavito and Miller 1998; Zhu and Lynch 2004). Similarly, buckwheat exhibited the potential ability to extend root structure under low-P (Grant et al. 2001). White lupin is capable of developing cluster roots (Almeida et al. 2020; Aslam et al. 2021a, b), and exudate organic acids to maximize P uptake under P limitation (Watt and Evans 1999; Lambers et al. 2006; Müller et al. 2015). Wheat, maize, and oilseed rape roots have been reported to secrete malic acid under nutrient starvation (Hinsinger 2001). Therefore, increased exudation of P mobilizing components can facilitate P uptake and regarded as an important strategy to improve crop growth performance under low P conditions (Anwar et al. 2017; Iqbal et al. 2017). In this book chapter we elucidated the mechanisms of P acquisition, mobilization, and root exudate mediated P absorption. Moreover, we also discussed the crop adaptation strategies to low P including, morphological, genetic modifications, and plant behavior to subterranean environment.

4.2 Crops Adaptive Responses to Phosphorus Starvation

Crops have evolved a complex array of adaptive strategies to overcome P deficiency problem (Zhang et al. 2014; Kanno et al. 2016). Indeed, roots are critical to uptake water and nutrient from their surrounding soil and exhibit a range of root developmental modification traits to adapt against several abiotic stresses. Plant root adaptive traits play a critical role in maintaining the terrestrial ecosystem and its responses to rapidly fluctuating environments (Iversen et al. 2015). The alteration of root traits is an effective mechanism to improve crop growth with an increased P uptake capability (Niu et al. 2013). More than 80% of plants establish arbuscular mycorrhiza fungi (AMF) association with plant roots to improve the ability of nutrient acquisition. A wide pyramid of research had been reported on genotypic modification of crops sensitive to P deficiency that allow root architecture modifications to stimulate P uptake (Gahoonia et al. 2001; Lynch and Brown 2001; Hermans et al. 2006; Ling et al. 2008).

4.2.1 Modifications of Root Architecture

Root architectural modifications play a vital role in soil exploration at a broader scale and are considered a powerful vehicle to ameliorate P uptake efficiency (Lynch 1995). Roots are the primitive crops organ that acquires nutrients and water, and also perceive stress-related signals from the rhizosphere (Gahoonia and Nielsen 2004). In addition to morphological changes roots also provide more surface area to acquire inorganic P (Pi) from low P soils (Fig. 4.1a). A growing body of evidence indicates that root architectural modifications play a significant role in P uptake mechanisms (Lambers et al. 2006). Crop roots generally respond to P starvation through accumulating a high ratio of carbon in the roots, subsequently improved root growth, root hairs, increased lateral root development, and Pi acquisition (Vance et al. 2003; Li et al. 2007). Root shape and structure describe the range of the components that constitutes root architecture and their subsequent associations (Hodge et al. 2009). Accumulating evidence demonstrated that Arabidopsis and white lupin have been used as model crops to investigate root structural and genetic modifications to Pi deprivation. For instance, white lupin inhibits cluster root formation in P-sufficient solution but induces cluster root formation and increases root elongation with abundant root hairs under P deficient solution, resulting in increased root area (Cheng et al. 2011a, b; Funayama-Noguchi et al. 2015). Similarly, P starvation attenuates primary root length, stimulates lateral root length, and promotes root hair growth in numerous crop species (Linkohr et al. 2002; López-Bucio et al. 2003; Sun et al. 2014) suggesting the significant role of root architectural modifications to acquire more Pi from the soil. An array of studies evidenced that upon Pi starvation root architectural modification concomitant with genotypic adaptation thereby facilitating P uptake ability (Jain et al. 2007; Heuer et al. 2017; Soumya et al. 2021).

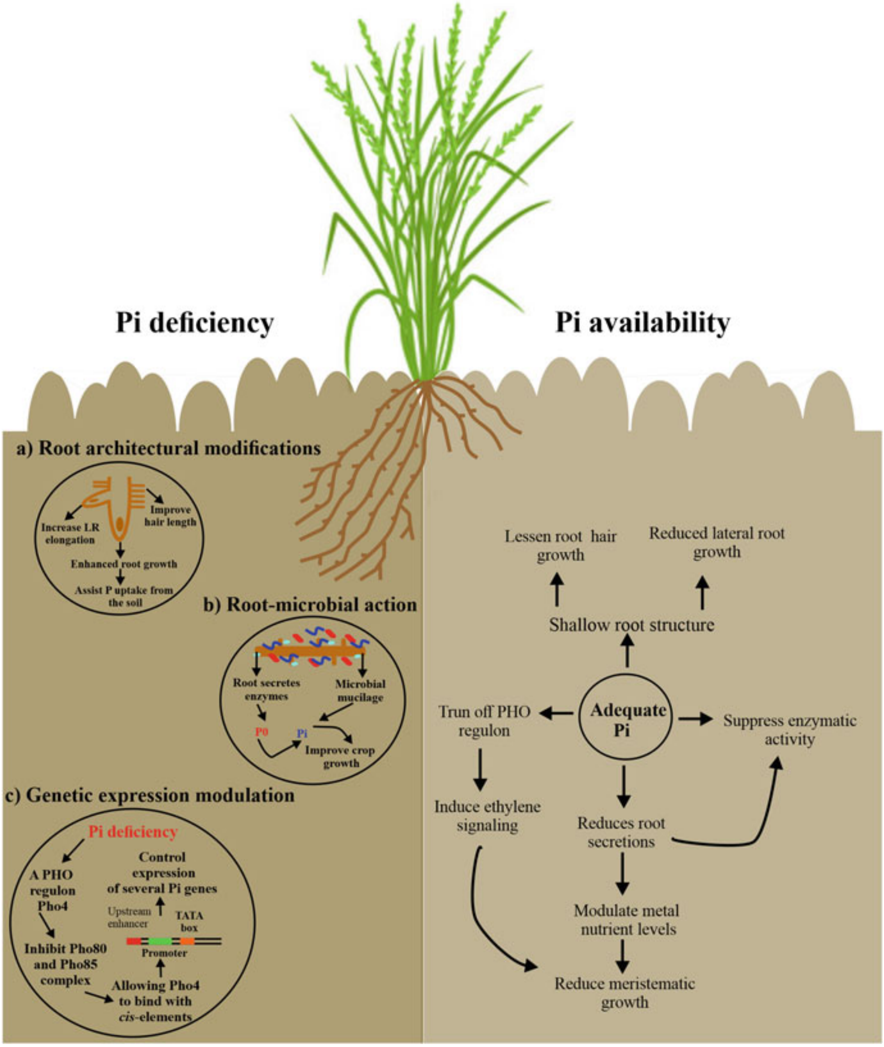

Fig. 4.1 Crop responses to phosphorus deficiency and availability. (**a**) Phosphorus deficiency modulates root architecture through lateral root formation and abundances of root hairs. (**b**) Alternation in root-associated microbiota assist P uptake and improve overall plant growth (**c**) Transcriptional regulation and activation of a certain type of root-associated transporter proteins and complexes also facilitate P uptake (left panel). In the right panel under optimum P in soil, enzymatic activity in root for P and transcriptional regulation of root-associated complexes suppressed causing shallow root architecture and reduced plant growth. Pi (inorganic phosphorus), LR (lateral root), PHO (phosphate), TATA (Goldberg-Hogness box)

4.2.2 Root Associated-Microbial Modulation

Crops harbor a mesmerizing microbial community associated with their roots and exist in the rhizospheric region collectively considered as root microbial association (Pascale et al. 2020). When crops encountered P deficiency they employ a range of strategies to modulate microbial community (Iqbal et al. 2019a, b) including exudation pattern, microbial mucilage, structural modulation, and the coordinated defense responses (Harrison 2012; Castrillo et al. 2017). Therefore, to mitigate P deficiency responses, one of the common strategies is the establishment of crop-root-soil association (Fig. 4.1b) (Fabiańska et al. 2019). Crop root-microbial association is a unique trait to be involved in improving plant growth (Pant et al. 2015). Recently, an increasing number of evidences supported that crop root secretions greatly modulate soil microbial community under nutrient variability (Pant et al. 2015; Hacquard et al. 2016; Zhong et al. 2020). For instance, P availability controls the secretion of strigolactone which overwhelms arbuscular mycorrhiza fungi association, encourages root colonization (Akiyama et al. 2005), and assist in P transportation to the host crop. Similarly, P deficiency triggers the secretion of secondary metabolites having an elite antimicrobial activity like phenylpropanoid, glucosinolates, and flavonoids strengthen the crop's immunity (Pant et al. 2015). Altogether, these interpretations suggest that P deficiency and adaptations of crops to P deficiency responses determine structural modification in the root microbiome.

Soil microbes are known to attribute to several crops growth-related processes such as nitrogen-fixing ability, soil stability, soil exploration, and nutrient accessibility (Meena et al. 2018). Beneficial soil microbes release enzymes into the rhizosphere that mobilize soil nutrients such as acid phosphatases (APases). APases are capable of converting immobile organic P (P0) into Pi to make it readily accessible for a plant to absorb. As a result, microbes can improve nutrient accessibility and ultimately enhance nutrient uptake and improve plant growth (Chen et al. 2017; Meena et al. 2018). The inoculation of plant roots with beneficial microbes has attracted substantial interest in maintaining agricultural sustainability and reduces excessive input of synthetic fertilizers. Hence, exploring the interrelationships between plants, rhizosphere, microbes, and the environment would be of great importance in understanding their contribution and responses to drought tolerance.

Soil microorganisms contribute to many vital functions for plant growth and productivity, including (i) nitrogen fixation, (ii) aggregate stability, and (iii) nutrient accessibility to the plants. Soil microorganisms release enzymes that solubilize nutrients during decomposition and mineralization converting immobile nutrients stored in organic matter into inorganic forms available for plants uptake (Singh et al. 2011). Consequently, soil microorganisms can enhance nutrient availability and therefore increase plant nutrient uptake (Richardson and Simpson 2011a, b). Following this concept, incubating plant roots with beneficial microorganisms has attracted considerable interest in maintaining agricultural sustainability and reducing synthetic fertilizer consumption. To understand plant roots-microbial ecological interaction and to assess the activity and persistence of beneficial microbial inoculants within the rhizosphere. Soil microbes play a critical role in P uptake, laid the basic foundation for generating P efficient crops, sustainable agriculture, and an improved ecosystem. It has been shown that phosphorus deficient favorably modulates the soil microbial composition compared to phosphorus sufficient (Fabiańska et al. 2019), suggesting that the plants rapidly consume Pi. Therefore, it is necessary to identify plant novel traits or specific drought-resistant beneficial bacteria related to phosphate solubilization and drought tolerance.

4.2.3 Gene Expression Induced by Phosphorus Starvation

Phosphorus starvation modulates gene expression causing distinct morphological and physiological alteration. Modulated gene expression is supposed to be because of the interaction of *cis*-regulatory elements, regulate promoter and other DNA binding transcription factors (Li et al. 2012). It is well documented that several genes including RNases, phosphatases, β-glucosidase, P transporters, and others with uncharacterized functions are induced under P deficiency (Guo et al. 2013). A key positive regulator, *PHO4* encodes helix-loop-helix domain that controls the expression of several genes, P transporters, and phosphatases (Fig. 4.1c) (Yoshida et al. 1989). Under inorganic Pi sufficiency, two negative regulators *PHO80* and *PHO85* render *PHO4* inactive through hyper-phosphorylate, while under Pi deficiency another PHO regulon member *PHO81* impedes the activity of *PHO80/85,* thus permitting *PHO4* to interact with specific promoter sequences (Bun-ya et al. 1996; Secco et al. 2012).

4.3 Mechanisms of Phosphorus Acquisition and Homeostasis

Nitrogen, P, and S are vital macroelements that are frequently acquired from the soil solution to allow for plant growth and development (Maathuis 2009). Being an important component of various organic compounds, such as nucleic acids, ATP, nicotinamide adenine dinucleotide phosphate, sugar phosphates, phospholipids, and phosphoproteins. P plays an essential role in major plant processes comprising of biosynthesis of nucleic acid and phospholipid, photosynthesis, energy transfer and respiration (Battini et al. 2017; Sakuraba et al. 2018). Hence, plants need to acquire P to allow for efficient utilization and maintenance of homeostasis and metabolism in various habitats (Sakuraba et al. 2018).

Due to the fact that Pi which is the principal soluble source of P is available at reduced concentrations that are unevenly allotted and almost immobile in soils, its acquisition by plants is problematic (Maathuis 2009). More specifically in the tropics and subtropics, its insufficiency is considered a major limiting factor in crop

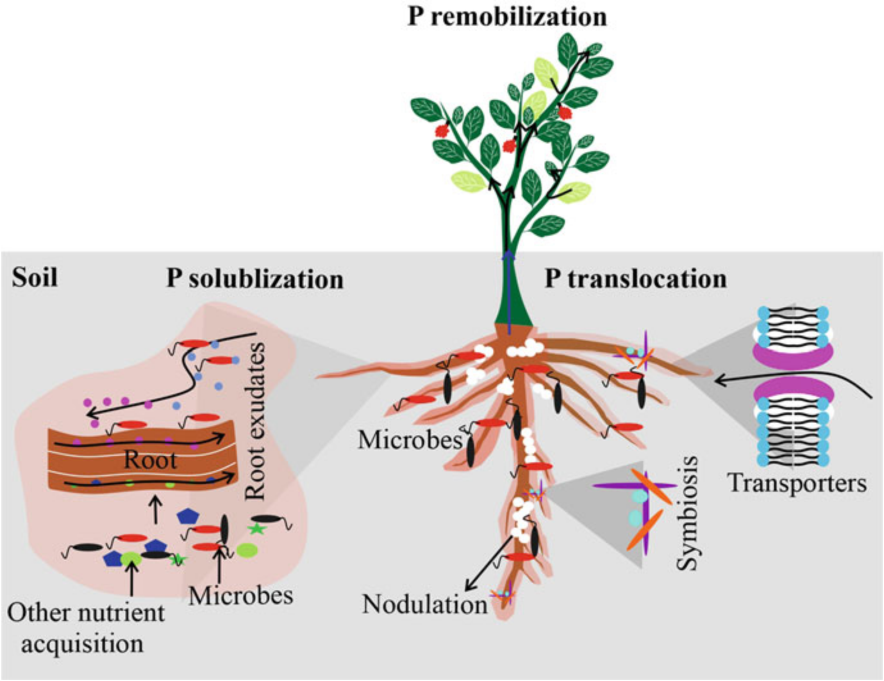

Fig. 4.2 Aspects of phosphorus and other nutrient use efficiency in crops mediated by nutrient transporters, root exudates, associated symbiosis, and bacterial communities, and root-nodule bacteria for phosphorus and soluble nutrient remobilization, translocation, liberating stored phosphorus/nutrients for remobilization

productivity (Ramaekers et al. 2010). High concentrations of P cause immobilization and precipitation with other soil minerals, such as iron (Fe) and aluminum (Al) in acid soils and calcium (Ca) in alkaline soils. Little amount ($<1\%$) is directly available for uptake by the plant (Battini et al. 2017). In most cases, the absorption of P by plants from soils is in the forms of primary orthophosphate (Pi) ion (HPO_4^{2-}) and secondary Pi ion (HPO_4^{2-}), and Pi ions react easily with clay, Fe, and Al compounds within the soils. Therefore, the abundance of P available for plant uptake in every habitat varied. Hence, plants often under P-deficiency need to adapt to the nutrient insufficiency of their living environment (Sakuraba et al. 2018). For sustainable production of crops with high yields, it is imperative to apprehend plants P acquisition and homeostasis mechanisms (Fig. 4.2).

4.3.1 Phosphorus Acquisition

There is a rapid progression in molecular characterization of the signaling pathways associated with P homeostasis. The regulatory mechanisms describing the integrated signaling cascade involved in vast responses of plants to P starvation, encompassing root Pi acquisition have been revealed (Liu et al. 2009). For instance, the transcriptional activators PHR1*,* PHL*,* and SPX (regulatory proteins) proteins play an important role in this mechanism. Various key Pi starvation-responsive genes such as *PHT1;1, IPS1*-miRNA399, *PHR1,* and *PHL1*; MYB-like GARP (GOLDEN2, ARR-B, Psr1) TFs bind to *cis*-acting regulatory elements thereby inducing their expression (Rubio et al. 2001; Bari et al. 2006; Bustos et al. 2010) (Table 4.1). Pi abundance hinders SPX proteins interacts with PHR1, PHL1 by interacting with the SPX-inositol polyphosphate complex. Meanwhile, when PHR1 and PHL1 are free, they activate Pi starvation-responsive genes under low-P (Puga et al. 2014). The interaction of nitrate sensor NRT1.1B with a phosphate signaling repressor SPX4 has been well described in rice. Nitrate perception stabilizes the NRT1.1B–SPX4 complex causing ubiquitination and degradation of SPX4 by recruiting NRT1.1B interacting protein 1 (NBIP1). PHR2, a key TF of phosphate signaling is then translocated to the nucleus thereby causing transcriptional activation of P utilization genes (Hu et al. 2019).

Genome evolution of white lupin has shown that cluster root formation under low-P. Soil-P remobilization, carbon fixation, and cellular P translocation are essential pathways for high PUE. Auxin modulation is especially vital for cluster root formation by relating *LaABCG36* and *LaABCG37* genes (Xu et al. 2020). Recently, *LaABCG29 was* reported to enhance P use when subjected to soil drying and P deficiency by increased root growth and rhizosheath formation in rice (Aslam et al. 2021a, b). The source of N, P, or S compounds of many plant species will support the normal growth of plants for limiting plant life span. Hence, even under unfavorable conditions, efficient root uptake is an absolute need for N, P, and S homeostasis in the plant (Maathuis 2009). Even though there is a significant difference in the root architecture of monocots and dicots, root traits correlated with intensified P acquisition are the main and common adaptive means among all vascular plant species (Niu et al. 2013). Therefore, maximal and continued soil exploration by proliferation and extension of the various root types with a preference for those roots that are metabolically effective and obtain P avidly is the major strategy for P acquisition utilized by plants (Ramaekers et al. 2010).

In addition, an abundance of plant root-associated microbiota is a sustainable means for exploiting and mobilizing soil P pool (Battini et al. 2017). In microbial biomass, the assimilation and accumulation of P is a vital building block for important cellular functions. In a situation whereby P is not directly available but there is adequate availability of other nutrients such as C and N, soil microorganisms effectively acquire and/or mobilize P from the environment to fulfill their needs (Raymond et al. 2021). For instance, the capacity of *Paenibacillus illinoisensis* IB 1087 and *Pseudomonas extremaustralis* IB-Ki-13-1A strains to mobilize phosphates was assessed. The bacterial inoculation to soil improve the level of P concentration in wheat plants, mobile phosphorus concentration within the soil was increased, further indicating their efficiency in enhancing the acquisition of phosphorus compounds (Kudoyarova et al. 2017). In maize plants, growth and P uptake was improved by arbuscular mycorrhiza fungi through the mycorrhizal pathway.

Table 4.1 Some important mechanisms regulated by phosphorus in plants

Pi homeostasis	Mechanism	Means	References
Acquisition	Molecular	Activation of P responsive genes; *PHT1*, *PHT1;1, IPS1* and miRNA399, transcriptional activators *PHR1/2* and *PHL1*, *PHR2* Proteins interaction; nitrate sensor NRT1 and phosphate signaling repressor SPX4), and activities of SPX protein.	Rubio et al. (2001), Bustos et al. (2010), Puga et al. (2014) Hu et al. (2019) Niu et al. (2013), Xu et al. (2020) Maathuis (2009), Ramaekers et al. (2010) Battini et al. (2017), Kudoyarova et al. (2017), Aslam et al. (2019) Selvi et al. (2017), Kalayu (2019) Bargaz et al. (2016) and Battini et al. (2017)
	Morphological (root architecture)	Cluster root formation Efficient root uptake	
	Ecological	Interaction of plant with root-associated microbiota such as *Paenibacillus illinoisensis* IB 1087 and *Pseudomonas extremaustralis* IB-Ki-13-1A strains, Arbuscular mycorrhizal fungi (AMF) Streptomyces sp. W94, *Piriformospora indica*. Hydrolysis of insoluble organic and inorganic P compounds to soluble P form by PSMs	
	Inter-cropping	Legume-cereal intercrops enhanced rapid root growth and higher P uptake (wheat and chickpea, faba bean and wheat, wheat and soybean)	
Translocation	Molecular (Pi transporters)	Allocation of pi ions by plants, pi transporters (PHTs) including PHT1/2/3/4/5 to organelles and tissues Phosphate transporter-1;3 (*OsPHT1;3*).	Rubio et al. (2001), Misson et al. (2004), Chen et al. (2008), Młodzińska and Zboińska (2016), Wang et al. (2017), Parra-Almuna et al. (2018), Sakuraba et al. (2018) and Chang et al. (2019)
Remobilization	Cellular processes	Remodeling of root architecture at physiological and biochemical levels, improving organic acid excretion, encourage symbiosis Activities of acid phosphatases, ribonucleases and cell wall modification Lipid bilayer remodeling, smaller P-esters in senescing organs, and hydrolysis of RNA	López-Arredondo et al. (2014) Yun and Kaeppler (2001), Tossi et al. (2009), Zhu et al. (2015) (Dissanayaka et al. (2018) Rubio et al. (2001), Uauy et al. (2006), Dai et al. (2012), Gao et al. (2017) and Yu et al. (2020)
	Molecular	Reprogramming transcriptional responses by *OsPAP26* protein, PHR1 and *AtMYB62*, R2R3 MYB TF, *OsMYB2P-1,* R2R3 MYB TF, *MYB103*, *NAM-B1* transcription factors	
Root exudation under P deficiency	Morphological	Release of organic acids and/or acid phosphatases by plant roots. Increased concentration of amino acids and organic acids including tartaric, malic and succinic acids in root exudates	Marschener (1998) Zhou et al. (1998), Tawaraya et al. (2014) Louw-Gaume et al. (2017), He et al. (2020)

(continued)

Table 4.1 (continued)

Pi homeostasis	Mechanism	Means	References
		Increased carboxylates (oxalate) and acid phosphatases (secreted-APases), and tartrate exudation Release of large amounts of organic acid anions Increased exudation of organic acid anions (OAs) including Citrate, iso-citrate, and malate in the root surfaces	Zhou et al. (1998) and Almeida et al. (2020)

Streptomyces sp. W94 efficiently facilitates P uptake by hyphae from a root-free soil compartment (Battini et al. 2017). *Piriformospora indica* establishes a mutual alliance with plant roots reminiscent under P limitation to promote plant growth by making available Pi through solubilizing soil inaccessible organic P P_o) (Aslam et al. 2019). More so, phosphate solubilizing microbes (PSMs) have the ability of hydrolyzing P_o and Pi insoluble phosphorus compounds to soluble Pi form which is easy for plants absorption. Provision of ecofriendly and economically sound approach by fungal genera (*Penicillium* and *Aspergillus*), bacterial genera (*Bacillus*, *Pseudomonas*, and *Rhizobium*), actinomycetes, and arbuscular mycorrhiza fungi. Phosphate solubilizing microbes pave the way to overcoming P scarcity and its subsequent uptake by plants (Kalayu 2019). In addition, seed or soil inoculated phosphate solubilizing microbes including *Bacillus sp*., *Aspergillus sp*., *Pseudomonas sp*., and *Penicillium sp*. enhanced solubilization of fixed and applied phosphates within the soil thereby increasing crop yield. In phosphate deficient soils, these phosphate solubilizing microbes are effective as biofertilizers in improving the yields of crop (Selvi et al. 2017).

However, intercrops are advantageous to both intercropped species such as legume-cereal offer niche differentiation effectual development of restrictive resources, and optimize rhizosphere biochemical (Bargaz et al. 2016). For instance, wheat and chickpea, faba bean and wheat, deficient resources acquisition, including P and water were significantly stimulated by legume nodulation (Betencourt et al. 2012; Bargaz et al. 2016). Moreover, in a similar instance, legume-cereal intercrops facilitated rapid root growth associated with higher P acquisition and were confined to cereal as compared to legume (Battini et al. 2017). P starvation-mediated root morphological and biochemical changes proportional to microbial diversity suggest positive rhizosphere heterogeneity and contribute to an enhanced aerial biomass and nutrient (P and N) acquisition in inter- and mono-cropped wheat and soybean (Betencourt et al. 2012). However, natural phyB variants had been shown to be essential for low Pi acquisition as demonstrated in Arabidopsis (Sakuraba et al. 2018). It has shown that microbes are integral to P acquisition in plants. Therefore, understanding the mechanisms underlying the acquisition and delivery of P facilitated by microbes is critical for apprehension of this interaction. This may provide more valuable insights and serve as the basis for breeding crops that are highly efficient in Pi acquisition and utilization.

4.3.2 Phosphorus Translocation

The acquisition and homeostasis of Pi rely on processes regulated by Pi transporters, known to be grouped into five families: PHT1, PHT2, PHT3, PHT4, and PHT5 (Wang et al. 2017). Following the absorption of Pi ions from the soil by the plants, Pi transporters (PHTs) allocate these ions to organelles and tissues (Sakuraba et al. 2018). For instance, PHT1s located within the plasma membrane (PM) function in Pi acquisition from the soil (Wang et al. 2018). This has been demonstrated in Arabidopsis, where *PHT1* genes had been highly expressed in roots (Chen et al. 2008). Pi is distributed within the plant against chloroplasts, mitochondria, golgi, and vacuole by the concerted activities of PHT2, PHT3, PHT4, and PHT5 family members (Wang et al. 2017), which has also been described in Arabidopsis and rice (Młodzińska and Zboińska 2016). Mutation of *PHT1-1* and *PHT1-4* decreased Pi uptake to 20% and 40%, respectively, as compared to the wild type (Misson et al. 2004; Chen et al. 2008; Młodzińska and Zboińska 2016).

There is complexity in the expression pattern of *PHT1* genes, but many of them had been induced rapidly due to P limitation. The promoter of *PHT1* genes has a P1BS-like *cis*-element that is essential for response to P-starvation (Table 4.1) (Rubio et al. 2001). In ryegrass (*Lolium perenne*), deficiency of P and the toxicity of aluminum resulted in up-regulation of *LpPHT1* and *LpPHT4* P transporters (Parra-Almuna et al. 2018). Pi uptake, translocation, and remobilization have been shown to be mediated by Pi transporter, *OsPHT1;3* was highly expressed in young leaf blades and the basal region of the shoot much obviously in roots and old leaf blades of rice plant (Chang et al. 2019). Pi transporters play a pivotal role in Pi homeostasis, thus genetic manipulation of plants (especially those that are severely affected due to Pi deficiency) to express Pi transporters genes may enhance Pi utilization.

4.3.3 Phosphorus Re-Mobilization

To curtail P deficiency and survive during its scarcity, plants have evolved various strategies including remodeling of root architecture at physiological and biochemical levels, root exudates, scavenging enzymes, activating membrane-associated P transporters, and symbiosis (López-Arredondo et al. 2014). In addition to improving the efficiency of P-nutrition, plant-internal engagement of acid phosphatases, ribonucleases, cell wall modification, and internally sequestered P can be remobilizing by plants under P limitation (Yun and Kaeppler 2001; Ticconi and Abel 2004; Zhu et al. 2015; Wang et al. 2018).

Under P deficiency, P in older leaves is remobilized to younger growing and other active sinks. At molecular level, several transcription factors (TFs) have been described to be reprogramming transcriptional responses of plant to P deficiency (Table 4.1) (Yu et al. 2020). Myeloblastosis (MYB) TFs constitute one of the largest gene families that are essential for plants response under P deficiency. For example, in Arabidopsis, *AtPHR1* and *AtMYB62* are involved in the transcriptional response to P deficiency (Rubio et al. 2001; Devaiah et al. 2009). In rice, an R2R3 MYB TF, *OsMYB2P-1*, improves the plant's tolerance to P starvation (Dai et al. 2012). Similarly, in cabbage (*Brassica oleracea*), *MYB103* has been involved in cell wall-based P remobilization under P deficiency by regulating ethylene production (Yu et al. 2020). In wheat grains, the NAC family TF, *NAM-B1* plays an essential role in P remobilization (Uauy et al. 2006). In rice, *OsPAP26* protein encoded by the purple acid phosphatase gene could remobilize Pi from senescing to younger leaves and utilize organic P under leaf senescence and deprivation of Pi, with an increase in abundance of *OsPAP26* (Gao et al. 2017). In another instance, lipid-bilayer remodeling coupled with the hydrolysis of RNA and smaller P-esters in senescing organs triggered P remobilization (Dissanayaka et al. 2018).

4.4 Plant Root Exudation Under Phosphorus Deficiency

The release of a vast number of compounds by plant roots into the soil is termed root exudation. These exudates take part in numerous biotic and abiotic interactions (Preece and Peñuelas 2020). However, plant nutritional status affected the composition of root exudates derived from plant metabolites (Tawaraya et al. 2018). Root exudation might be a nutrient starvation responsive strategy. For instance, P, Fe, and Zn deficiencies lead to the release of organic acids, acid phosphatases, or phytosiderophores by some species (Marschener 1998).

In response to P deficiency, active released and increased in concentrations of various metabolites including amino acids and organic acids in root exudates had been observed in soybean roots. Some of these metabolites are tricarboxylic acid (TCA) cycle intermediates, possibly accelerating carbon flow to the TCA cycle in P-deficient soybean root (Tawaraya et al. 2014). In radish plants, an increase in organic acid (including tartaric, malic, and succinic acids) exudation under P deficiency was noted (Zhang et al. 1997). In sweet potato cultivars, internal P is used effectively under P deficiency, it preferably allocates carbon to shoots, enhancing arbuscular mycorrhiza fungi and release of organic acid, instead of increasing the root mass or forming specialized root structures (Minemba et al. 2019). In signal grass and ruzigrass, carboxylates (oxalate) and acid phosphatases (secreted-APases) exudation increased with reduced P concentrations of the plant (Louw-Gaume et al. 2017). It has been shown that more than 33% of the metabolites are exudated by the roots of *O. sativa under* P deficiency, indicating the active release of metabolites in response to P deficiency by rice roots (Tawaraya et al. 2018). Under a low supply of P to the soil, the roots of alfalfa released more carboxylates (mainly tartrate) and phosphatase to the rhizosheath (He et al. 2020). Under P deflation, the discharge of high amounts of organic acid anions from specialized root structures (cluster or proteoid roots) to mobilize and acquire sparingly soluble phosphates from a restricted soil volume had been demonstrated in white lupin (Zhou et al. 2020). In response to low P availability, tropical grasses including *Urochloa ruziziensis* (ruzigrass), *Megathyrsus maximus* (Guinea grass), and *U. brizantha* (palisade grass), acquired P from gypsite and hematite by exudation organic acid anions such as citrate, malate, and iso-citrate in the soil surrounding root (Almeida et al. 2020). Crop production relies on sufficient P supply for plant growth. Molecular, and morphological traits of P acquisition are integral to P use by plants, however, much understanding of microbial behaviors that lead to root exudation is another promising means that will ensure P availability to plants.

4.5 Microbial Symbiotic Associations

Phosphate solubilizing microorganisms (PSM) employ varied biochemical processes to carry out the process. The microbes release different organic acids and enzymes to catalyze P conversion. Furthermore, studies have shown that P solubilizing microbes (PSMs) do not reflect in the laboratory condition as in the exact soil condition and have limitations since the soil in the fields is inhabited with many different microbes (Gyaneshwar et al. 2002). In a typical natural field condition, the process of solubilizing P is achieved by diverse microbes which interact by releasing varied metabolites (Fig. 4.2). The microbes therefore cohesively function in symbiotic relationships in the rhizosphere enabling plants to achieve maximum production by creating availability of nutrients in the soil (Bargaz et al. 2018).

Biofertilizers are often supplemented with a combination of both N and P supplementing microorganisms. Understanding microbial symbiotic relationships are key in designing and developing microbial-based biofertilizers formulations. Application of phosphate solubilizing microbes and arbuscular mycorrhiza fungi is generally associated with uptake of P in higher plants and increased yields in cereals and vegetables (Wu et al. 2012; Sawers et al. 2017; Bargaz et al. 2018). Kyei-Boahen et al. (2017) showed that rhizobia inoculated together with P fertilizer, *Bradyrhizobium*, agronomic efficiency was significantly enhanced compared to individual inoculants. Furthermore, fertilized field soil consisting of two mutualistic isolates, *Ensifer meliloti* and *Ensifer medicae*, was reported to confer higher benefits on *Medicago lupulina* (Simonsen et al. 2015).

4.6 Microbial Communities Mediated Phosphorus Dynamics

Microbial communities were reported to recycle soil P thereby, enhance P availability in soil and also contribute to plant P nutrition. In recent years, understanding the role of soil microbes in the P cycle has been on the rise due to the high deficiencies in soil P across the world and the high costs of P fertilizer (Mitra et al. 2020). The use of microorganisms to enhance P availability in soil therefore emerged as the most suitable in promoting sustainable agriculture (Richardson and Simpson, 2011a, b). Microorganisms mainly solubilize HPO_4^{2-} by producing organic acids such as gluconate, formic acid, citrate, oxalate, ketogluconate, lactate, succinate, pyruvate, malate, fumarate, glycolate, and acetic acids (Mardad et al. 2013), indicating the potential role of root secretion and microbial association to assist P dynamics.

According to Alam et al. (2002), bacteria are more effective in the solubilization of P than fungi species. *Bacilli* are among the most common soil bacteria that are involved in P acquisition (Fig. 4.2). Several studies have reported the ability of *Bacillus* species including *B. subtilis*, *B. fusiformis*, *B. cereus, B. megaterium, B. thuringiensis, B. pumilus, B. chitinolyticus, B. macerans, B. coagulans,* and *B. mycoides* contribute to P solubilization (Sharma et al. 2013; Meena et al. 2016; Ahmad et al. 2019). In a study by Sharma et al. (2015), *B. licheniformis* were shown to solubilize P in a medium containing insoluble tri-calcium P. Similarly, Delfim et al. (2018) demonstrated that inoculation of wheat plants with HPO_4^{2-} solubilizing *B. thuringiensis* was reported to increase P in the rhizosphere (11%), up-to 67% increase in aerial tissues, and 75% increase of P in root tissues. *Bacillus* mainly carries out P solubilization by producing organic acids especially acetic acids and lactic acids which chelate the cations bound on the insoluble phosphate (Saeid et al. 2018). Inoculation of *B. firmus* shown to significantly enhance P content in grains and to progressively increase P availability in soils with rock phosphate (Datta et al. 1982). Thus implies that *Bacillus* may play a critical role in both P solubilization and acquisition, and can also be used to enhance crop production and nutrition grown in soils with lower levels of P.

Pseudomonas strains have been described as effective solubilizers of HPO_4^{2-}, while *P. putida*, *P. striata*, *P. fluorescens*, was reported to increase the yield, seedling length, nutrient availability, and uptake of P in soybean, corn, and chickpea (Sharma et al. 2007; Yazdani et al. 2009). According to Buch et al. (2008), the majority of bacteria which include *Pseudomonas* solubilize P by producing gluconic acid from extracellular glucose in a reaction that is catalyzed by periplasmic glucose dehydrogenase. Henri et al. (2008) reported the ability of three *P. flourescens* strains to solubilize three different HPO_4^{2-} of Al, Ca, and Fe supplemented to growth media. Most studies consider *P. flourescens* strains as important P solubilizing bacteria that inhabit roots of plants and they possess bio-fertilizing and biocontrol properties (Qureshi et al. 2012).

Accordingly, *B. tuberum*, *B. unamae*, *B. silvatlantica, B. mimosarum*, and *Sinorhizobium meliloti* exhibited inorganic P solubilizing activity in the media supplemented with glucose as the carbon source. *Bulkhoderia* species possess an acid phosphatase gene (AcpA) used for the breakdown of P complexes. Several studies have reported the ability of various phosphobacteria to enhance P availability in soil and improve crop yield. Wu et al. (2009), was able to isolate 14 different phosphobacteria from eutrophic aquatic ecosystem and investigated their prospects as biofertilizers. Some of the identified bacteria in the study include *Aureobacterium resistents*, *Acidovorax temperans*, *Achromobacter xylosoxidans*, *Chryseobacterium sp*., *Enterobacteria sp*., *Acinetobacter sp*., and *Proteus sp.* which were reported to produce organic acids which are involved in P solubilization.

4.7 Conclusion

P deficiency is a major limiting nutritional stress affecting crop growth and productivity. Root architectural modifications play an imperative role in the acquisition of immobile P through the increased lateral root, root hair development, and soil strength. In addition, root-microbial associations can significantly contribute to improve nutrient uptake efficiency by reducing the extensive use of fertilizers. Moreover, a PHO4 regulon binds with key cis-regulatory elements to control the expression of P responsive genes, could potentially increase the PUE of crops by using alternative P sources from the soil. The adoption of crop species to P deficiency may use as a key adaptation tool to reduce the application of exogenous P fertilizers and improve agriculture sustainability.

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Chapter 5
Biochar for Sustainable Phosphorus Management in Agroecosystems

Komel Jehangir, Muhammad Riaz, Rashid Mahmood, and Muhammad Arif

Abstract Global production systems need revolutionary changes to meet food security while sustaining agroecosystems. Plants require macro- and micro-nutrients for their growth, development, and reproduction. As a consequence, crop production depends mainly on the availability of mineral nutrients provided as fertilizers. After nitrogen, phosphorous is the second most important growth-limiting macro-nutrient. Therefore, new agricultural practices are needed to improve phosphorus uptake. Here we review the role of biochar, a carbon neutral recycled material, as amendment to soils, in improving phosphorus availability. Biochar is an organic amendment produced by pyrolyzing biomass. Biochar amendments increase soil organic carbon contents and improve soil physical, chemical, and biochemical properties, which in turn leads to better soil fertility and quality. Biochar influences soil phosphorous dynamics by modulating the chemical and biochemical pathways of phosphorous cycling. Biochar addition has increased soil phosphorous content, resulting in higher phosphorous uptake and crop productivity in various cropping systems. Moreover, integrating biochar amendments with organic and mineral phosphorous fertilizers can enhance phosphorous uptake by plants and crop productivity.

Keywords Biochar · Organic fertilizer · Inorganic fertilizer · Phosphorus · Agriculture

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5.1 Introduction

Agroecosystems are fundamental elements of food security as they are the key determinant of food availability. According to FAO (2003), “food security is the situation that occurs when all population, always, have physical, social and economic access to safe, sufficient and nutritious food that fulfill their dietary needs and food preferences for healthy active life”. Therefore, the components of multi-layered food security concept include food production, food access, food utilization, and food stability. Despite the substantial evidence that the “green revolution” increased crop yields of major grain crops (maize, rice, and wheat) many-folds, sustaining and improving crop production requires fundamental changes at the crop, farm, and landscape levels (Fischer and Edmeades 2010; Spiertz 2012). New concepts and progress in improving crop production systems need to focus on factors to optimize yields by understanding climatic, soil, water, and nutrient (nitrogen, phosphorus, and potassium) constraints.

Phosphorous is among the growth limiting essential macronutrients in agricultural and natural ecosystems, and hence phosphorous is intrinsically linked to global food security (Cordell et al. 2009; Ashley et al. 2011; Glaser and Lehr 2019a, b; Rafique et al. 2020). Therefore, the quality and quantity of crop production generally depend on phosphorous fertilizer (Anwar et al. 2017; Amanullah et al. 2021). However, the overall use of mineral phosphorous fertilizers is greatly uneven on a global scale. The suboptimal application of mineral phosphorous fertilizers often results in low crop production and yields particularly in developing countries (Takahashi and Anwar 2007; Iqbal et al. 2019a, b). In contrast, in some regions in the world including Europe and China, phosphorous fertilizers are applied at much higher rates which results in phosphorous accumulation in soils (Cordell and White 2014). Nevertheless, the high rate of phosphorous is often recommended to increase phosphorous uptake by plants, phosphorous use efficiency, and crop yields (Withers et al. 2018; Swaney and Howarth 2019).

Most of the phosphorous fertilizers are naturally obtained from phosphate rocks via mining, which is a natural and non-renewable source. The use of phosphorous in the agricultural field has been increased since 1950s in order to meet the food and energy demands of the growing population. It becomes available to plants only in inorganic form and is sparingly mobile in soil (Amanullah et al. 2016a, b). Moreover, the orthophosphate ions are highly reactive and become unavailable to plants due to reaction with aluminum (Al) or iron (Fe) in acidic soils and calcium (Ca), potassium (K), magnesium (Mg), and sodium (Na) in alkaline soils or microbial immobilization (Zhu et al. 2018). Therefore, higher phosphorous concentrations from mineral phosphorous fertilizer become unavailable to plants under alkaline and acidic conditions, making phosphorous the most important limiting macronutrient (Nash et al. 2014; Amanullah et al. 2019). If the phosphorous fixed in soils could become available to plants globally, it would be sufficient for crop production for the next 100 years. The fixed amount of phosphorous fertilizer in the soil is sufficient to run off all the losses regarding freshwater bodies e.g. eutrophication

(Bennett et al. 2001). Therefore, it becomes imperative to find new and advanced phosphorous cycling mechanisms and new strategies which can help to optimize phosphorous to plants so that food production is enhanced to meet food security (Rafique et al. 2019). There are many techniques to support sustainable intensification in relation to phosphorous fertilization:

- Improvement in soil quality to increase phosphorous nutrition of plants at critical growth stages;
- Management of soil fertility to enhance phosphorous availability to crops under diverse conditions; and,
- Development of phosphorous fertilizers that ensure optimum phosphorous availability to plants.

Maximum phosphorous supply to plants could be achieved by improving phosphorous fertilizers' traits and functionality, crop characteristics, and soil quality that controls soil and plant interactions (Iqbal et al. 2017). In addition to soil and crop properties, fertilization regimes determine better crop yields (Khan et al. 2017). Higher amounts of phosphorous result in the accumulation of phosphorous in the soil, which leads to phosphorous leaching and runoff, and eutrophication of surface waters (Daniel et al. 1998). In tropical soils, high soil organic carbon content is used as an indicator of soil quality and is related to phosphorous availability (Sousa et al. 2017). In African regions, the deficiency of phosphorous in the soil is commonly found which contributes to lesser yields of crops (Cordell and White 2014). Due to this, adequate and sustainable use of phosphorous fertilizers is required most importantly to increase the production of crops of future and reduce the hazards of the environment.

Biochar is a carbon-rich organic amendment produced from pyrolysing the biomass waste under limited or no supply of oxygen. Biochar developed from crop residues such as rice husk and corncob has generally low nitrogen and phosphorous contents (Liu et al. 2019). Reduction in soil phosphorous content was observed when animal manure biochar was added to the soil (Wu et al. 2013). This could be due to the bonding of phosphorous with multivalent metal cations present in biochar (Dai et al. 2016). Therefore, it is apparent that nitrogen and phosphorous are supplied to soils from organic and inorganic inputs after biochar application. The studies on the combined application of biochar with inorganic fertilizer and organic fertilizer such as compost or poultry manure have shown promising positive effects on soil properties, nutrient availabilities, and crop yields (Naeem et al. 2018).

5.2 Phosphorus Dynamics in Soils

If the fixed phosphorous in soils is made available to plants on a global scale, it will be adequate to sustain crop production for the next 100 years (Zhu et al. 2018). However, the mobilization of this fixed soil phosphorous above crop requirements can be lost via leaching and surface runoff into freshwater bodies and cause algal growth and eutrophication (Bennett et al. 2001; Siddique and Robinson 2003).

The alkaline or acidic soils differ substantially in their chemical reactions relating to phosphorous availability in soils (Ara et al. 2018). Therefore, for sustainable crop production, site-specific phosphorous management is recommended. The situation of phosphorous availability is generally aggravated in the arid and semi-arid region soils because the soils are composed of calcareous parent material which is rich in Mg, K, Ca, and Na salts along with soluble bicarbonate (HCO_3) and carbonate (CO_3) and produces hydroxyl radicals (OH^-) that lead to increase in soil pH in the range of 7.5–8.5. As a result, the retention of phosphorous in alkaline soil is dominated by precipitation reactions, clay minerals, and the adsorption to calcium carbonate (Naeem et al. 2013).

Improving phosphorous mobilization and supply to the root zone on a sustainable basis by integration of physiological and morphological strategies can be proven an effective measure to maximize the plant root efficiency to access and acquire phosphorous more easily from the rhizosphere. Moreover, the uptake and utilization of phosphorous by the plants play an important role in the determination of the overall crop yield.

The phosphorous present in soil generally exists in different organic or inorganic chemical forms. These chemical forms are different from each other in their behavior and function in soils (Turner et al. 2007). Inorganic phosphorous accounts for 35–70% of total phosphorous in soil (Harrison 1987). Stengite, apatite sand variscite are primary minerals and are very stable, and phosphorous release from these minerals is a slow process that occurs via weathering. This phosphorous is inadequate to meet the demands of plant growth. However, appetites are proved to be relatively enough for plant growth in acidic soil. Secondary minerals, such as Ca, Al, and Fe phosphates differ from each other in their pH, rates of dissolution, and size of mineral particles (Pierzynski et al. 2005; Oelkers and Valsami-Jones 2008). The solubility of Al and Fe phosphate is directly proportional to soil pH, but the solubility of Ca decreases when the pH value is increased to 8 (Hinsinger 2001). By desorption reactions, the adsorbed AlP and Al oxides can be released. The organic or inorganic forms of phosphorous generally exist in equilibrium with each other representing that they are sparingly available and stable to plant-available aluminum pools such as soil solution aluminum and labile aluminum.

In acidic soils, aluminum is absorbed by oxides of Fe and Al and available hydroxides such as hematite, goethite, and gibbsite (Parfitt 1989). Phosphorous is absorbed on the surface of the clay resulting in the formation of various complexes when bounded with oxides of Fe and Al. At soil pH of 4–9 protonated and non-protonated bidentate surface, complexes are likely to coexist; however, in acidic soil conditions, protonated bidentate soil complex is more dominant (Arai and Sparks 2007). Aluminum and Fe oxides along with clay minerals have large surface areas which facilitate phosphorus adsorption. Therefore, the absorption of phosphorous in the soil can be enhanced by increasing the ionic strength of the soil solution. As a result, soil phosphorous can be occulated in nanopores which are frequently found in Al and Fe oxides which makes soil phosphorous unavailable to plants (Arai and Sparks 2007). In neutral-to-calcareous soils, soil phosphorous retention is enhanced by precipitation reactions (Lindsay et al. 1989). Moreover, soil phosphorous can also be adsorbed on the surface of Ca carbonate (Larsen 1967) and clay minerals (Devau et al. 2010). Phosphate precipitates with Ca, generating dicalcium phosphate that is available to plants, and ultimately, it can be transformed into more stable forms such as octocalcium phosphate and hydroxyapatite which are less available to plants at alkaline pH (Arai and Sparks 2007). Soil physico-chemical properties are thus the most important determinant of soil phosphorous transformations and its availability to plants.

5.3 Biochar as a Soil Amendment

Biochar is a charcoal-like organic material that is produced by the pyrolysis of biomass with or without the presence of oxygen, which has a porous structure and great surface area (Lehmann and Rondón 2006; Atkinson et al. 2010). Besides higher surface area, biochar has high carbon contents which is resistant to decomposition via biochemical transformations, and it is of great importance for environmental scientists and agronomists. Biochar is generally used in agricultural and environmental applications because it is established that the biochar amendments increase soil organic carbon contents, improve soil physico-chemical and biological properties, provide essential nutrients to the soil, reduce greenhouse emissions, and facilitate the remediation of soil contaminated with organic and inorganic pollutants such as heavy metals (Hagemann et al. 2018; Kong et al. 2018). After application to soils, biochar reacts with soil particles through a wide array of reactions that include oxidation-reduction, acid-base, adsorption-desorption, dissolution, and precipitation reactions (Joseph et al. 2010). Many studies have confirmed that the application of biochar to soil improves soil fertility, enhances the production of crops, and promotes carbon sequestration (Lehmann 2007; Atkinson et al. 2010; Sohi 2010). The various qualities of biochar e.g. higher adsorption capacity, greater surface area coverage and presence of various contents of mineral nutrients (nitrogen, phosphorous, potassium, calcium, and magnesium), ion exchanges capacities make it a suitable material for soil and environmental applications under the wide majority of conditions (Lehmann and Joseph 2015). However, the application of biochar for benefits other than soil carbon sequestration can become non-consistent considering the complex properties of biochar amendments and soils to which they are applied particularly in terms of economic feasibility. For example, biochar obtained from manure and crop residues can be a good source of soil organic carbon and plant available nutrients (Mukherjee and Lal 2014). Glaser et al. (2002) also argued that biochar production and application to soil can be an effective and efficient strategy to improve soil organic carbon contents.

The addition of biochar to soils influences soil microbial activity and their functions, and resultantly, has enormous effects on soil nitrogen and phosphorous cycling by altering soil physical and chemical properties (Hagemann et al. 2017).

Effects of biochar on nitrogen cycling are evident as it increases nitrate and ammonium retention and reduced nitrogen losses to the environment from leaching and gaseous emissions (Cao et al. 2017). Moreover, biochar can modify the biochemical reactions pertaining to the soil phosphorous cycle such as mineralization and immobilization of organic and inorganic phosphorus present in the soil that directly control solubility, adsorption, and availability of phosphorous in the soil. However, given the differences in nature and properties of various biochar amendments, it is imperative to optimize the biochar production and application with a view of improving phosphorous availability, and reducing its loss to the environment to avoid pollution of the aquatic environment.

Biochar has a strong potential to alter the sorption and availability of phosphorous in soil by using different mechanisms such as changes in soil pH, adsorption of phosphorous ions, and precipitation of phosphorous minerals. Phosphorous can be sorbed on compounds and functional groups formed at biochar surface during pyrolysis that contain elements such as Mg, Ca, Fe and Al which may alter phosphorous availability in soils (Yao et al. 2013; Joseph et al. 2015; Shepherd et al. 2017), Highly porous structure of biochar is generally linked with enhanced water retention in soils (Singh et al. 2010). Biochar amendments can also increase root arbuscular mycorrhizal interactions to increase soil phosphorous availability (Vanek and Lehmann 2015; Zwetsloot et al. 2016). Thus, the changes mediated to the soil environment after the application of biochar can also alter the structure of the microbial community and this has a great effect on phosphorous mineralization and solubilization (Fox et al. 2014; De Oliveira Mendes et al. 2014; Deb et al. 2016). The increase in nutrient availability from biochar can improve seed germination, plant growth, and crop yields (Van Zwieten et al. 2010). Therefore, biochar also acts as a soil conditioner that enhances plant growth by supplying nutrients efficiently and increasing crop yields (Verheijen et al. 2009; Spokas et al. 2012). Biochar amendments improve soil physical, chemical, and biological functions in a wide variety of soils which enhance nutrient availabilities, soil organic carbon, water retention, and crop productivity while reducing greenhouse gas emissions to make the cropping systems climate-resilient.

5.4 Biochar and Soil Phosphorus Dynamics

5.4.1 Biochar-Mediated Effects on the Soil Phosphorus Cycle

Phosphorous is produced naturally in soil by the biogeochemical cycle from the hydrolysis of organic phosphorus and solubilization of inorganic phosphate which is mediated by the action of plant roots, root symbionts, and free-living microorganisms by releasing organic acids and hydrolytic enzymes (Fig. 5.1). Orthophosphorous in the soil can diffuse to nearby plant roots or can be intercepted by high affinity arbuscular mycorrhizal fungi transporters which, then, can transfer it to the host plant. The application of biochar to soil can change solubilization and hydrolysis reactions, and also the ortho phosphorous transport by mycorrhiza.

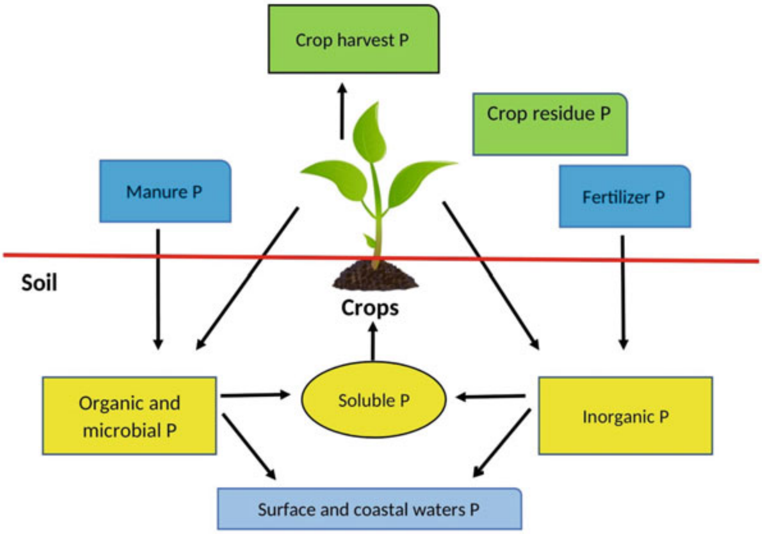

Fig. 5.1 Soil phosphorous cycle at the soil-plant interphase. P: Phosphorous

The hydrolysis of organic phosphorous can be mediated by extracellular enzymes such as phytase, phospholipase, and phosphatase which are produced naturally by plant roots and microorganisms present in the soil. Phosphorous mineralization directly depends on the microbial biomass and activity of enzymes, and the biochar addition to soil can enhance the process of phosphorous mineralization by increasing the microbial biomass (Masto et al. 2013). Lehmann et al. (2011) showed that biochar increased microbial biomass three-fold that resulted in a 21% increase in phosphorous availability in soil. Similar effects of biochar on soil phosphorous availability were found in a 20-day incubation study by Gul et al. (2015). However, these effects strongly depend on the nature of biochar amendments. For example, Mitchell et al. (2015) found that soil microbial biomass content was higher when crop residue and manure biochars were added to soil than with the wood biochar. This could be due to higher nutrient and labile carbon contents of crop residue and manure biochars than wood biochar. Gul et al. (2015) showed that microbial biomass increased from 13% to 80% within the range of fine-textured to coarse-textured soils amended with ~8–160 ton ha^{-1} of manure- and crop-based slow pyrolysis biochars (production temperatures 350–700 °C). As the demand for microbial biomass was high so there was more possibility of sustaining ortho phosphate's metabolic functions. A soil with biochar and with a high concentration of microbial biomass could have a higher rate of phosphorous mineralization and hence phosphorous availability in soil (Masto et al. 2013).

The modification of soil pH is another way that influences phosphorous hydrolysis, the higher the pH of soil there would be more alkaline phosphatase activity (Jin et al. 2016). A study by Du et al. (2014) reported ~2 to ~3 times increase in phosphatase activity in the surface soil under summer maize and winter wheat rotation that received four annual applications of the corncob biochar (360 °C pyrolysis temperature). In another study, Jin et al. (2016) found that the swine manure biochar (slow pyrolyzed at 400 °C) application at 25 ton ha^{-1} rate increased the alkaline phosphomonoesterase activity by 28.5% in clay soil due to an increase in soil pH from 6.8 to 7.6 whereas the alkaline phosphomonoesterase activity almost increased to double in the silt loam soil after application of the same biochar which increased soil pH from 5.3 to 5.9. In the same study, the authors found that the activity of phosphomonoesterase acid decreased in both soils suggesting the possible shift in the soil microbial community which can be related to the buffering of pH or input of nutrients from biochar made with swine manure. It was then concluded that the application of biochar is in favor of hydrolysis of organic phosphorous in the soil, which was due to larger demand of ortho-phosphate and production of extracellular enzyme by the microbial community of soil or due to modification in pH of the soil which results in an increase in activity of alkaline phosphatase. Thus, biochar amendments can be optimized to improve phosphorous availability in both acidic and alkaline soils. This can also be achieved by co-applying biochar with other organic amendments such as animal manures.

5.4.2 *Effects of Biochar and Phosphorus on Crop Productivity*

Biochar application improves soil physical, chemical, and biological properties which improve plant growth and development but these effects of biochar amendments vary strongly both on spatial and temporal scales. Jeffery et al. (2011) found that only 25–40% changes in plant production were observed after biochar addition to soils under diverse soil, crop, and environmental conditions. This reflects that biochar amendments yield different benefits which depend on biochar types, ecological conditions, and crop types (Lehmann and Joseph 2015). In mesic and humid zones, more research is conducted on a relative basis to explore the potential of biochar in improving soil nutrients and crop production. For example, in the humid tropics of Amazonia, biochar was used in combination with different fertilizers that resulted in better soil fertility and crop yields (Steiner et al. 2008). This was because of improvements in soil properties from biochar application in these highly weathered soils.

Phosphorus availability and phosphorous fertilizer use efficiency generally depend on soil properties. Plants depend on the continuous replenishment of phosphate ions in the soil solution. Moreover, phosphorous fertilizer when applied in a significant amount becomes unavailable to plants because phosphorous strongly sorbs to the soil particles and associated nutrients. The low availability of phosphorous is a global problem that results in reduced production of crops (Richardson and Simpson 2011; Syers et al. 2011). A significant body of knowledge reports the outcome of the different experiments and practices which were conducted to enhance the availability of phosphorous for plants under different soil and environmental conditions (Shenoy and Kalagudi 2005; Simpson et al. 2011; Table 5.1). Recent studies have suggested that biochar can increase phosphorous availability to crops both from organic and inorganic phosphorous fertilizer under diverse climatic conditions (Shen et al. 2016; Yeboah et al. 2016). However, manure-derived biochars are better in improving soil phosphorous availability than wood- and residue-based biochars because they have higher phosphorous contents. Understanding the effects of biochar amendments on soil phosphorous dynamics can provide an opportunity to find ways to enhance soil phosphorous availability in agroecosystems.

5.4.3 Effects of Biochar on Soil Phosphorus Dynamics

The application of biochar to soil has been shown to improve nutrient uptake and reduce nutrient leaching in various soil environments (Yoo and Kang 2012; Haider et al. 2015; Abbas et al. 2017). As a result, biochar is proved to have the potential to combat abiotic stress in plants by enhancement in nutrient uptake by plants as well as other mechanisms (Abbas et al. 2018; Rehman et al. 2020). The multifarious characteristics and functions of biochar amendments play a key role in soil phosphorous dynamics (Fig. 5.2). Biochar improves phosphorous availability in various soil environments with different magnitudes (Rizwan et al. 2016). In some cases, biochar amendments contain fractions of plant-available phosphorous, but it depends on the nature of feedstocks used to develop biochar and pyrolysis conditions, and application of such biochar can improve the availability of phosphorous in soils (Atkinson et al. 2010; Rehman et al. 2018). In calcareous soil, biochar improves phosphorous availability as biochar changes the soil microbial community and hence the chemical composition and processes that govern the phosphorous availability (Schneider 2012; Deb et al. 2016). However, the application of biochar can have both negative and positive effects on P dynamics in soils. Liu et al. (2017) reported that the rice hull biochar amendments at 40 ton ha^{-1} rate to red clay soil and alkaline soil increased the phosphorous availability by 53% and 33%, respectively.

Bai et al. (2015) concluded that biochar made from poultry litter at an application rate of 10 ton ha^{-1} increased the soil bioavailable phosphorous by $>$1000-fold. Moreover, various studies have shown that the biochar could increase the phosphorous content of the soil, while the other studies claimed that biochar obtained from maize straw, flax straw, and willow stems do not increase the phosphorous availability of soil (Li et al. 2016; Amendola et al. 2017). In contrast, some studies have shown that biochar can even reduce the phosphorous content in soil (Chintala et al. 2014; Vasconcelos et al. 2017). The mechanisms of positive and negative effects of phosphorous bioavailability in biochar amended soils are not clearly understood. However, it is reasonable to speculate that the effects of biochar on the phosphorous

Table 5.1 Effects of biochar amendments on soil phosphorus dynamics and crop productivity

Feedstock and pyrolysis conditions of biochar	Soils	Type of study	Application rates and treatments	Crops	Effects on soil phosphorus dynamics	References
Sewage sludge pyrolyzed at 600 °C for 2 h	Sandy loam	Laboratory incubation	Biochar added at 4% and 8% (w/w basis) rates	–	Biochar increased phosphomonoesterase activity	Paz-Ferreiro et al. (2012)
Commercial biochar developed from seed coat, chaff and wheat residues	Silt loam, clay loam and loam soils	Laboratory incubation	Biochar was added at 0.5, 1, 2, and 4% (w/w basis) in initial screening study whereas 1% in the main incubation study	–	Biochar increase soil soluble phosphorus fractions primarily through phosphorus binding sites and cationic flocculation	Parvage et al. (2013)
Chicken litter	Sandy loam	Laboratory incubation	Biochar alone or in combination with compost rates equivalent to 10 and 20 t ha^{-1}	–	Biochar without and with compost soil total, available, inorganic and organic phosphorus contents	Ch'ng et al. (2014)
Mixed maple and hickory sawmill waste pyrolyzed at 450 °C for 1 h	Weathered tropical soil	Greenhouse	Biochar applied without and with arbuscular mycorrhizal inoculants	Beans	Biochar increased arbuscular mycorrhizal by 6% and phosphorus uptake by beans from 3.1 to 3.8 mg $plant^{-1}$. Microbial and available soil phosphorus also enhanced.	Vanek and Lehmann (2015)
Bone meal and woodchip biomass co-pyrolyzed at 350 or 750 °C for 45 min	Silty clay	Laboratory incubation and pot	Biochar added at 1.2 and 0.9 g kg^{-1} soil in laboratory incubation for 350 and 750 °C biochar, respectively whereas 0.4 g kg^{-1} for 750 °C biochar in pot study	Maize	Biochar increased Olsen and resin phosphorus fractions, and also increased plant access to soil phosphorus through higher root-arbuscular mycorrhizal interactions	Zwetsloot et al. (2016)

Swine manure pyrolyzed at 400 °C for 4 h	Silt loam and clay loam	Laboratory incubation	Biochar applied at 0.5% and 1.5% (w/w basis)	–	Biochar increased soil total and Olsen phosphorus in both soils which increased with biochar rate	Jin et al. (2016)
Mixture of douglas fir, white fir and western red fir pyrolyzed using "Cylinder Burn" method	Sandy loam, loamy sand	Field study at 10 farms	Biochar and charged biochar (biochar treated with litter slurry) at 20 t ha^{-1}	Dry beans, green beans and cauliflower	Biochar enhanced soil extractable phosphorus on an average by 29% after one growing season and also increased phosphorus uptake in beans	Gao et al. (2016)
Corn straw pyrolyzed at 450 °C using slow pyrolysis process	Silt loam soil	Field	Biochar added at 5, 10 and 20 ton ha^{-1}	Cotton	Biochar increased cotton yield from by 18% and also increased soil available phosphorus	Tian et al. (2018)
Biochar from animal waste, biowaste, crop residue, wood and wastewater sludge	Acidic, neutral and alkaline soils	Meta-analysis of 25 laboratory incubation, pot and field studies	Low (<10 ton ha^{-1}) and high (>10 ton ha^{-1})	Agricultural soils	Biochar significantly increased soil available phosphorus by 4.6% but only those biochar amendments developed at <600 °C pyrolysis temperature and applied at >10 ton ha^{-1}	Glaser and Lehr (2019a, b)
Wheat, rice and maize straw pyrolyzed at 500 °C for 2 h	Paddy soil	Pot	Biochar added at 2% (w/w basis)	Rice	Biochar increased soil available phosphorus, phosphatase activity and grain and straw rice yields	Jing et al. (2020)
Rice husk pyrolyzed at 600–700 °C	Acidic sulfate soil	Laboratory incubation	Biochar applied at rates equivalent to 20 and 50 ton ha^{-1}	–	Biochar amendments increased soil phosphorus fractions but depended at biochar rates	Phuong et al. (2020)
Rice husk, wheat straw and sugarcane bagasse pyrolyzed at 450 °C	Silt loam	Laboratory incubation and pot studies	Pure and acidified biochar added at 120 kg ha^{-1}	Maize	Biochar amendments increased soil available phosphorus and phosphorus uptake by maize.	Qayyum et al. (2021)

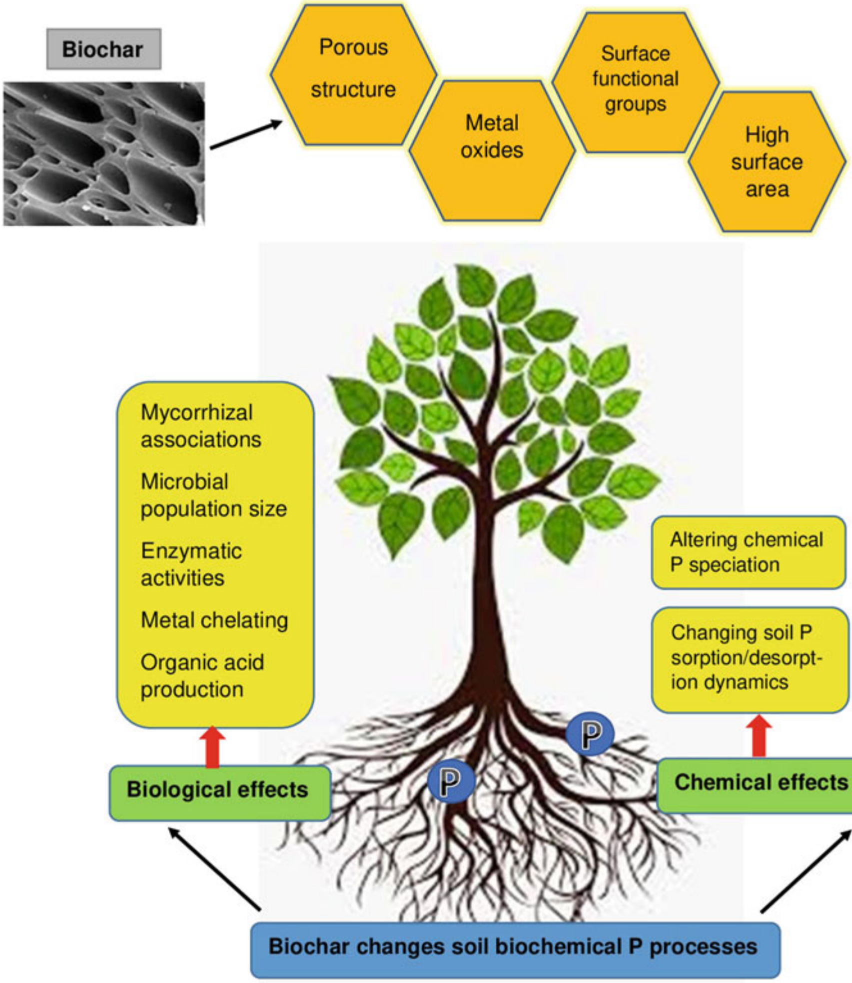

Fig. 5.2 Mechanisms of biochar-mediated changes in soil phosphorous dynamics. P: Phosphorous

bioavailable in soils is controlled by the inherent properties of both the biochar (e.g. pH and total phosphorous contents) and soil characteristics such as soil pH, soil inorganic and organic phosphorous fractions, soil type, ionic strength, and native microbial diversity. Therefore, the biochar amendments are being developed to suit local soil and crop conditions which can be integrated within the crop fertilization regimes.

5.4.4 Interactions of Biochar with Organic and Inorganic Phosphorus Fertilizers

When combinations of mineral and organic fertilizers are applied to soil, they improve soil quality by increasing soil organic carbon and macronutrients contents such as nitrogen, phosphorous, and potassium which increase plant growth and yields, and reduce negative impacts of mineral fertilizers on the soil environment, and also reduces the cost of production (Xia et al. 2017). Application biochar to soil enhances nitrogen and phosphorous availability in soils particularly applied with organic-inorganic fertilizers (Zhao et al. 2014; Arif et al. 2017). For example, Arif et al. (2017) showed that application of biochar with mineral and organic fertilizers improved wheat and maize yields by increasing nitrogen and phosphorous availability and soil organic carbon contents in nutrient-depleted alkaline calcareous soils. Biochar can increase soil phosphorous contents and availability to plants which increase the productivity of crops especially in areas where the soil is less fertile (Blackwell et al. 2010; Subedi et al. 2016). Moreover, the incorporation of biochar into the soil can increase phosphorous availability through direct phosphorous release by acting as a phosphorous source (Christel et al. 2016). However, the effects of biochar amendments on soil phosphorous dynamics directly depend on soil types (Scott et al. 2014). For example, biochar is more beneficial in increasing soil phosphorous availability in acidic soils than in alkaline soils (Parvage et al. 2013). Biochar rate is an important factor that determines its effects on phosphorous availability and crop production (Blackwell et al. 2010). Moreover, the biochar developed from animal manures supplies more phosphorous for the growth of plants than those derived from plants (Liang et al. 2014). In a field experiment, the biochar made from different feedstock has shown potential to increase soil phosphorous availability and crop productivity in highly weathered soils (Macdonald et al. 2014). Improving nutrient use efficiency promote crop yields and reduces nutrient losses to the environment particularly nitrogen and phosphorous (Zhang et al. 2010; Wang et al. 2012). Blackwell et al. (2010) found the improvement in wheat yield and phosphorous availability in southwestern Australia under dry weather when biochar made from wood chip was applied.

5.5 Biochar, Phosphorus Use Efficiency and Crop Productivity

Phosphorus use efficiency in an agroecosystem can be defined as the dimensionless ratio of the mass of harvested phosphorous in crop biomass to the mass of total phosphorous inputs in specific time duration for a specific crop (Zhang et al. 2020). Phosphorus use efficiency in crop production means that the conversion ratio of the total phosphorous inputs into useful plant exports, e.g. harvested crop biomass. Therefore, phosphorous use efficiency in the crop production system is an important indicator for measuring the phosphorous management status in the agricultural production system and its effects on food security and environmental protection (MacDonald et al. 2011; Wu et al. 2016a, b).

The low availability of phosphorous in soils is considered a major problem globally, especially in areas with less vegetation and low soil fertility (Syers et al. 2011). In order to deal with this issue, different agronomic practices have been suggested to enhance soil phosphorous availability and phosphorous use efficiency under different environmental conditions (Simpson et al. 2011). Moreover, relatively little work has been done to explore the potential of biochar to increase phosphorous use efficiency from organic and inorganic fertilizers. Biochar can increase soil phosphorous availability and phosphorous use efficiency because it can reduce phosphorous adsorption on Fe-oxides or by acting as a direct source of phosphorous to plants particularly at higher biochar application rates (Li et al. 2011). However, it is important to optimize the biochar rate for higher phosphorous use efficiency before large-scale application to increase crop yield. The more amount of biochar as amendment of soil is unfeasible at large scale because of uncertain increasing of crop yield (Liu et al. 2017). Glaser et al. (2015) suggested that the use of biochar with mineral fertilizer was a better option than the use of mineral fertilizer only. This was also suggested that the production of granulated biochar with phosphorous fertilizer can be a viable option to improve soil phosphorous in tropical soils. Therefore, combining water-soluble phosphorous fertilizer with biochar can improve phosphorous uptake by plants and phosphorous use efficiency. Recent studies have strongly suggested that biochar can increase phosphorous use efficiency when combined with organic-inorganic fertilizers such as Arif et al. (2021) found that biochar addition with organic and inorganic fertilizers improved soil phosphorous availability, soil organic carbon, and phosphorous use efficiency in maize agroecosystem under irrigated semi-arid climate. This study also suggested that the application of biochar with organic and inorganic phosphorous fertilizer was economically a profitable option. Similarly, Arif et al. (2017) also reported higher phosphorous availability and phosphorous use efficiency in wheat-maize cropping systems under a semi-arid environment by integrating biochar with organic and inorganic fertilizers. Biochar amendments improve phosphorous use efficiency by increasing soil organic carbon contents which increase soil phosphorous availability and phosphorous use efficiency leading to better soil fertility and quality on a long-term basis.

5.6 Conclusion

Phosphorus is the second most important macronutrient after nitrogen which limits crop production and threatens food security on a global scale. Availability of phosphorous in the soil is also challenging in a variety of soils under diverse climatic conditions. Biochar is organic amendments developed from biomass waste by pyrolysis process under limited or no supply of oxygen. Among other practices, biochar is gaining popularity to improve phosphorous availability in both alkaline and acidic nature soils. Biochar amendments developed from manure and crop residues are better options to improve soil phosphorous availability, phosphorous use efficiency, and crop production than wood-based biochars. Recent studies have also confirmed that the application of biochar amendments to improve soil phosphorous contents can also be an economically viable option particularly if biochar is combined with organic and inorganic fertilizers. However, the scale of biochar applicability remains a major challenge for its use in agricultural production.

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Chapter 6
Phenotyping for Assessing Genotypic Variation in Phosphorus Use Efficiency

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Abstract Phosphorus is a key element for improving yield and quality of crop plants. Since phosphorus is poorly available in the soil rhizosphere, phosphorus stress occurs in susceptible crop plants. Phosphorus use efficiency may be improved by adapting phenotyping characters such as root, shoot, plant height, canopy structure, rhizosphere, photosynthesis, chlorophyll contents, biomass, and leaf area index. Here we review sensors for plant phenotyping and applications. Phenotyping assessment can be done using red, green and blue wavelength cameras, multispectral and hyperspectral imaging cameras, and thermal infrared cameras. In some plants, young leaves, meristems, flowers, transfer approximately half of the phosphorus back to the xylem. The proliferation of the lateral and shallow roots in rice may enhance the exploration of inorganic phosphate in the topsoil. Many plant species use arbuscular mycorrhizal fungi to promote foraging and access to phosphorus. Vegetative and physiological traits are closely linked to phosphorus use efficiency. Phosphorus-efficient genotypes can be used for developing crop varieties by plant breeding.

Keywords Crop plants · Phosphorus · Phenotyping · Root · Shoot · Rhizosphere · Sensors

Abbreviations

AMF	Arbuscular mycorrhizal fungi
CCI	Chlorophyll concentration index
CSM	Crop surface phenotyping

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DSM	Digital surface phenotype
EVI	Enhanced vegetation index
GNDVI	Green normalized difference vegetation index
LAI	Leaf area index
LiDAR	Light sensors and distance sensors
NDRB	Normalized differential red boundary
NDVI	Normalized difference vegetation index
NGRDI	Normalized green-red difference index
NIR	Near-infrared
Nut%	Nutrient percentage
NutHI	Nutrient harvest index
P	Phosphorus
PC	Principal components
Pi	Inorganic phosphate
PSI	Phosphate starvation-inducing
RGB	Red green and blue
RMSE	Relative mean square error
RS	Root structure
RVM	Vector machine
SfM	Structure of motion
SPAD	Soil plant analysis development
UAV	Unmanned aerial vehicle
Y. seed	Seed yield

6.1 Introduction

Phosphorus is an important nutrient for crop production, mainly synthesized from phosphate rock in the form of mineral fertilizers (Anwar et al. 2017; Amanullah et al. 2016a, b). The development of phosphorus-tolerant crop varieties can increase the efficiency of phosphorus use, which is a key contribution to sustainable crop production (Iqbal et al. 2019a, b). The seed yield of crop plants, Y.seed, is based on the relationship between the nutrient use efficiency and the total nutrients accumulated in the plant, Nut accum, and the nutrient harvest index: NutHI, the distribution ratio of the total accumulated nutrients in the plant.

There are several vegetative and physiological mechanisms, which may be evaluated under phosphorus use efficiency. The major phenotyping components – vegetative and physiological – may be affected by root, root shoot ratio, soil conditions, etc. Special attention is paid to the roots phenotypes that are directly involved in phosphorus use efficiency. Under field conditions, the pressure generated by some soils will negatively affect the structural characteristics of the root system, which in turn affects the absorption of phosphorus, other nutrients, and water by crops (Khan et al. 2017; Amanullah et al. 2019).

Since phosphorus levels in different plant stages and plant parts are genetically complex (polygenic) traits affected by management and environmental factors (Amanullah et al. 2021; Iqbal et al. 2017). Therefore, the root structure is based on the adaptability characteristics of phosphorus uptake and crop yield. In addition, crop phenotyping is used to evaluate the long-term effects of phosphorus-efficient varieties, soil phosphorus levels, and crop production systems. Currently, several components of interdisciplinary research work are using the genetic diversity of plant phenotypes to develop new phosphorus-efficient crop varieties and planting systems.

Response to phosphorus deprivation, phosphorus is the main component of nucleic acids, phospholipids, phosphoproteins, and metabolites. All these molecules are involved in the physiological aspects of plant growth and development (Maathuis 2009; Mehra et al. 2018). The availability of different macronutrients in the soil is relatively higher than the concentration of soluble inorganic phosphate (Pi). This is due to its complex physical and chemical properties, making phosphorus the main limiting factor for plant growth (Schachtman et al. 1998). Phosphorus has low availability in the soil and slow diffusion, making its concentration in the soil solution of the root zone low (Pierre and Parker 1927). Plants are usually susceptible to phosphorus stress and adopt different survival mechanisms. Phosphorus is very important to the growth and development of plants, and its absorption and utilization need to be regulated. Under normal environmental conditions, the concentration of cytosolic phosphorus remains constant (Raghothama 1999), although short-term fluctuations are observed (Pratt et al. 2009). The transport of phosphate between and within various cells mainly occurs through membrane-bound transporters.

When phosphorus is abundant, its absorption rate may increase and exceed plant requirements. In this case, most crops prevent phosphorus poisoning by reducing the soil's absorption of phosphorus or increasing the storage of phosphorus in vacuoles (Schachtman et al. 1998). Some plant species, namely creeping hack, blue lupine, and underground clover, have a lower ability to down-regulate inorganic phosphate absorption during periods of high inorganic phosphate supply and exhibit symptoms of toxicity (Lambers and Plaxton 2015). Contrary to the situation under limited phosphorus conditions, some plants maintain cytosolic phosphorus levels in a variety of ways, that is, promoting external phosphorus, increasing absorption, circulation, and increasing consumption of non-essential phosphorus-containing molecules (Pratt et al. 2009). For example, OsPAP21b secreted from rice roots hydrolyzes the combined organic phosphorus source, thereby increasing the availability of soluble phosphorus (Mehra et al. 2017). This process takes place in three locations: above ground, roots, and rhizosphere, but the exact sequence and comprehensive effects are still unclear. In the case of shoots and roots, these processes occur on different biological scales, including morphology, anatomy, physiology, and biochemistry. This chapter reviews efficient phenotyping methods for improving the phosphorus use efficiency in crop plants.

6.2 Shoots

The vacuolar/cytoplasmic deficiency of phosphate stock reduces photosynthesis and ultimately inhibits plant growth and development (Foyer and Spencer 1986). Obvious symptoms of phosphorus deficiency include delayed growth and development of branches, dark to blue-green branches and leaves, weak/fine stems, low tillering rate, low pollination rate, few flowers, delayed maturation, poor grain quality, and low biological activity. Production (Kennelly et al. 2012). Phosphorus stress inhibits the natural opening of stomata and compartmentalization of phosphorus into the cytoplasm and chloroplasts, which may be caused by metabolic processes (Hernandez and Munne-Bosch 2015; Pratt et al. 2009). In the absence of phosphorus, old leaves will age to mobilize phosphorus into young leaves, meristems, flowers, and seeds (Smith 2002). In addition, plants under stress may transfer approximately half phosphorus of phloem-derived back into the xylem (Jeschke et al. 1997). The physiological mechanism of releasing vacuolar-bound phosphate may not be sufficient to compensate for the decrease in cytoplasmic inorganic phosphate levels (Jouhet et al. 2004; Zhang et al. 2014). In addition, the genetic expression for shoot specific and development was also observed (Hammond et al. 2003). For example, it has been shown that the expression of the OsHAD1 gene in buds increases phosphatase activities under low phosphorus in rice plants (Pandey et al. 2017). However, the molecular mechanism for local phosphorus detecting and signal transduction in shoots is still unclear.

Advances in high-throughput genotyping have provided rapid and inexpensive genomic information for tailoring the crop cultivars with the best genetic makeup. Though genotyping pay more attention to genotypic selection, they still require accurate phenotypic data. The phenotypic advancement is essential for the development of reproduction using traditional, molecular, and transgenic products.

6.3 Roots

Different crop plants have acquired adaptability to phosphorus-deficient root morphology and exudation ability (Niu et al. 2013). The phosphorus utilization rate in the root structure is still low, and some developmental changes have been adopted, namely increasing root length and expanding root surface area, including root hair length and density (cluster root) (Benjamin et al. 2011; Niu et al. 2013). Different varieties of the same crop reveal different root responses for phosphorus deficiency (Haling et al. 2018).

Generally, root structure is controlled by developmental and hormone-related genes (Jung and Susan 2013). Similarly, phosphate is required for cell division in growing organs, and its magnitude depends on the phosphate starvation-inducing (PSI) gene (Lai et al. 2007). Under low phosphorus conditions, it will reduce root cell elongation and root meristem cells (Ticconi et al. 2009), resulting in a decline in primary root growth of Arabidopsis. The primary roots meristem decreases, a mitotic activity that may shift to the formation of lateral roots to increase their number (Sanchez-Calderon et al. 2005). Then each lateral root may behave like a tap root, which will further grow more lateral roots (Lopez-Bucio et al. 2002). The proliferation of the lateral root system may result in a shallow root system, which enhances the better exploration of inorganic phosphate in the topsoil (Williamson et al. 2001).

It has recently been reported that in rice, the RMD1 gene controls the crown and root angle under low-phosphorus conditions in the soil. It has been observed that the expression of the RMD1 gene increases the response to low phosphorus, resulting in shallow roots, thereby improving phosphorus foraging ability (Huang et al. 2018). Root hair proliferation has characterized the response to phosphate stress, and it is also controlled by a series of cellular and genetic processes (Schiefelbein and Somerville 1990; Foreman and Dolan 2001). During the period of phosphorus deficiency, the appearance of root hairs near the root tip enhances the root surface area, thereby promoting the phosphorus level (Ma et al. 2001).

Studies on Arabidopsis and rice revealed root hair elongation, which was observed under low phosphate conditions as an adaptive response controlled by auxin (Bhosale et al. 2018; Giri et al. 2018). The levels of respiratory and metabolic activity in these cells indicate that in the absence of phosphate, the length of root hairs increases (Bates and Lynch 2000). When these root hair cells may die due to nutrition, they are used elsewhere in the plant. Similarly, certain plant species like Casuarinaceae, Leguminosae, Myricaceae, and Amoeba, form root clusters (Shane and Lambers 2005). Therefore, it is known that internal phosphate can regulate the formation of clusters/secondary roots (Niu et al. 2013). However, increasing inorganic phosphate absorption reduces the clustering of secondary roots, preventing energy and material investment in their growth. Therefore, it is very important to understand the response of each tissue against phosphate stress including the epidermis, periphery, and cortex, which will produce long root hairs. Therefore, the phosphorus uptake by lateral roots and aerated tissues is used elsewhere in the plant (He et al. 1992; Ma et al. 2003). Many adaptations regarding architecture, anatomy, and molecular mechanisms remain unclear.

6.4 Rhizosphere

Plants can reply to phosphate stress by changing the biochemical composition of the rhizosphere (Javot et al. 2007). This may involve the exudation of organic anions (malic acid, citric acid, and oxalic acid), enzymes (phosphatase, phytase), phenolic acid, protons, and other molecules (Richardson et al. 2011). In general, exudation increase the dissolution from insoluble phosphate to soluble compounds by competing with cationic phosphate partners and releasing inorganic phosphate ions from organic compounds (Dakora and Phillips 2002; Tomscha et al. 2004). Some exudates also promote the growth of soil microorganisms by providing carbon sources and acting as chemical attractants (McNear and Jr. 2003; Czarnecki et al. 2013).

These microorganisms act as inorganic phosphate traps for plants or may release exudates, dissolving organic and inorganic phosphate compounds (Richardson et al. 2011). In plant species, the fungal symbionts, arbuscular mycorrhizal fungi (AMF), get food nutrition and access to phosphorus and other nutrients. Arbuscular mycorrhizal fungi grows in root cells and extends the hyphae into the soil, eventually forming a seed root-hyphae network (Smith et al. 2011). The inorganic phosphate of the roots of mycorrhizal fungi developing colonies is 3–5 times higher than that of non-mycorrhizal fungi.

In response to phosphorus deficiency, strigolactone exuded from lotus roots and rice enhances the colonization of arbuscular mycorrhizal fungi mycelial branches and roots, thereby increasing the exploration of phosphorus (Besserer et al. 2006; Akiyama et al. 2006). During arbuscular mycorrhizal fungi colonization, some inorganic phosphate transporters are inhibited, especially in the epidermis. Although several phosphate starvation-inducing genes are activated, namely P-type H^+-ATPase, mycorrhizal-induced inorganic phosphate transporter, and phosphatase (Zhang et al. 2014). In addition, with the higher availability of phosphorus in the soil root zone, the AMF colonization rate decreases, which may be due to the increase in internal/cellular phosphate (Smith et al. 2011). The benefits of arbuscular mycorrhizal fungi are not so obvious in plants with longer root hairs, which may be an increase in cytoplasmic inorganic phosphate (Schweiger et al. 1995). In addition to absorbing inorganic phosphate, arbuscular mycorrhizal fungi also affects root structure by promoting lateral root formation (Chen et al. 2017). The mechanism of arbuscular mycorrhizal fungi colonization and its related effects on inorganic phosphate absorption and root structure have been strongly advocated (George et al. 1995; Gutjahr and Paszkowski 2013). Additional information provides more information about the dynamics of phosphorus in the soil.

6.5 Different Sensors for Plant Phenotyping

Different sensor types have different characteristics and functions. The spatial and spectral resolution and sensor cost characteristics should be considered according to the specific application. The red-green-blue (RGB) images have three types of bands: red, green, blue, and, while multispectral images have multiple bands, which are usually visible in the near-infrared spectral region. The hyperspectral images contain up to thousand continuous bands in the visible as well as near-infrared regions. Therefore, it is worth studying the potential effects of different sensors on the high-yield phenotype of plants.

Each sensor type has its advantages and disadvantages. It is highly recommended to practice appropriate sensors for a specific trait and use proper algorithms to build a more powerful phenotype. Swinfeld et al. (2019) proposed two linear phenotypes, which can fit the training data well and provide different skew modes. A non-linear phenotype describing the height deflection from the top of the canopy might be generated the best results. Some researchers used vegetation factors as another predictor to improve yield phenotyping (Geipel et al. 2014). The image resolution along with higher resolution can provide accurate phenotype recognition accuracy (Holman et al. 2016).

James and Robson (2014) suggested inserting the oblique image into the image at the lowest point, which may improve the perceptual accuracy of the 3D phenotype. Maimaitijiang et al. (2017) found that the best detection of nitrogen and chlorophyll a + b in soybeans can be achieved by combining data from different sensors such as red-green-blue, multispectral and thermal pigments. In addition, after taking drone images, ground data should be collected efficiently. For example, collecting leaf area index (LAI) data immediately after acquiring drone images to improve the accuracy of maximum solar angle detection (Mathews and Jensen 2013). Based on this sensor research, it is important to find that leaf area index prediction depends on the variability of the phenological stage, because the total canopy and low density may improve the accuracy of leaf area index detection. In addition, a few samples in the exercise kit help improve accuracy.

Images of plants mean more than “photography”. The purpose of the images is to measure the phenotype through the interaction between light and plants, such as reflex photons, absorption photons, or transmitted photons. Each component of plant cells and tissues is specific to the wavelength Absorbance, reflectance, and transmittance characteristics. Images with different wavelengths are used for different aspects of plant phenotyping (Table 6.1).

RGB cameras are digital cameras that are used to capture true-color images in the color spectrum. It is a cheap light sensor that can be easily installed on drones for data collection. Based on red-green-blue cameras, the 3D geometry of red-green-blue images can be used to create plant surface phenotypes to detect plant heights (Bendig et al. 2014). It provides information in the three bands in the form of blue, red, and green. Red-green-blue images of leaves, leaf area index, plant height, biomass, yield, etc. are often used to analyze plant phenotypes. The flow diagram for red-green-blue cameras analysis has been illustrated in Fig. 6.1.

6.5.1 Multispectral Imaging Cameras

The multispectral imaging camera can connect the interference filters in the front lens to transmit or block specific light. Multispectral image sensors can deliver various valuable bands, invisible in the near-infrared spectral region. Therefore, yield, biomass, nitrogen, and phosphorus content, etc. can be predicted by multispectral images. The multispectral image shows six bands, and the number of bands varies from sensor to sensor. Multispectral image sensors are usually small in size and light in weight, making it easy to work on drones.

However, the multispectral imaging data have few bands which are not continuous and show limited information.

Table 6.1 Comparison of different imaging techniques for plant phenotyping

Phenotyping technique	Sensor type	Resolution	Raw data	Phenotype parameters
RGB imaging	RGB cameras	The system measures RGB color information with per pixel depth information.	Gray or color value images	Plant biomass, shoot shape, growth dynamics and color index,
Hyperspectral imaging	Near-infrared instruments, spectrometers, hyper spectral cameras, thermal cameras	Crop vegetation cycles, indoor time series experiments	Continuous or discrete spectra	Leaf and canopy health status; leaf and canopy water status; coverage density; leaf growth; panicle health Status
Thermal imaging	Near-infrared cameras,	Pixel-based map of surface temperature in the infrared region	Whole shoot or leaf tissue, time series	Canopy temperature, infestation of insects on grain
Near infrared imaging	Near-infrared cameras, multispectral line scanning cameras, active thermography	Continuous or discrete spectra for each pixel in the near-infrared region	Time series or single-time point analyses of shoots and canopies, single-point assessment of seeds	Leaf area index, water contents composition parameters for seeds
Visible light imaging	Cameras sensitive in the visible spectral range	Whole organs or organ parts, time series	Colored value images	Shoot biomass, growth dynamics, panicle traits, yield traits, root architecture, early embryonic axis growth, height, imbibition and Germination rates, flowering time size morphology,
Laser imaging	Laser scanning instruments with widely different ranges	Whole-shoot time series at various resolutions	Depth maps, 3D point clouds	Shoot biomass and structure, canopy structure

RGB (red, green, and blue wavelengths) cameras
Li et al. (2014) and Liu et al. (2017)

6.5.2 Hyperspectral Imaging Cameras

Hyperspectral imaging cameras have increased the number of bands along with maximum information that can be available from its images. It is a costly sensor that

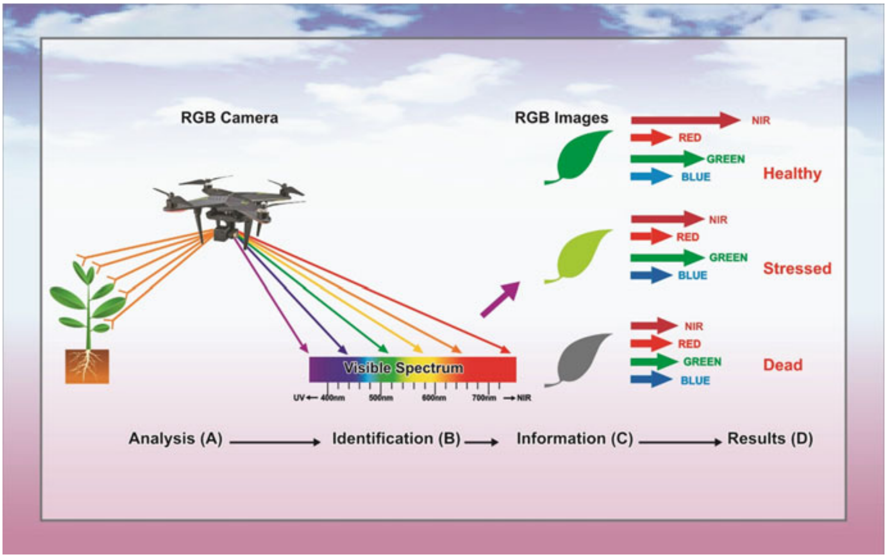

Fig. 6.1 Plant phenotyping using red-green-blue (RGB) wavelength cameras

can offer thousands of bands in the visible light and near infrared spectrum. It has continuous spectrum information. In case of hyperspectral imaging, each pixel has spatial and spectral characteristics. It has wider applicability in different research fields (Xie et al. 2017). There are generally four types of hyperspectral imaging cameras, namely (**a**) point scan, (**b**) line scan, (**c**) area scan, and (**d**) single scan (Wu and Sun 2013). The lines scanning is the most common in hyperspectral imaging cameras. The working of hyperspectral imaging cameras is highly complicated irrespective of multispectral imaging and wavelength sensors. This makes working on the drone more difficult. Most hyperspectral imaging research is conducted in laboratories and greenhouses. Hyperspectral imaging is commonly used for phenotypic plant characteristics, such as height, biomass, and chlorophyll contents, amount of nutrients absorption in leaves.

6.5.3 Thermal Infrared Imaging Cameras

Thermal imaging cameras are commonly used during drought stress to assess crop water status, after detecting plant's canopy temperature (Zarco-Tejada et al. 2012; Sepulveda-Reyes et al. 2016; Park et al. 2017; Santesteban et al. 2017; Poblete et al. 2018; Bian et al. 2019). Thermal images provide information's about canopy temperature, concerning plant transpiration under stress conditions and plant water status. The hot water pressure index can be calculated from the thermal image. The measurements of canopy temperature through drone-based thermal infrared imaging sensor, show the difference between irrigations levels. So, it is much useful for agronomists to manage irrigations schedule according to pressure. Light sensors and distance sensors such as light detection and ranging (LiDAR) emit their light energy. LiDAR can work efficiently during nighttime as compared to other sensors (Andujar et al. 2019). LiDAR sensors can make 3D canopy structures of plants and further estimate the plant height and biomass (Wang et al. 2017a, b).

6.6 Application of Plant Phenotyping

Compared with traditional phenotyping analysis, drone-based plant phenotyping analysis has several advantages. It is worth noting that many functions can be measured using drone-based technology.

6.6.1 Yield Phenotyping

The assessment of crop yield is a very important phenotypic trait. The radio-controlled helicopters are used for multispectral images to estimate rice yield (Swain et al. 2010). Various studies determined spectro-radiometers of wavelength 350–2350 nm were used to measure spectral reflectance of soil. The drones are used for normalized difference vegetation index (NDVI) based on the coefficient of determination ($R^2 = 0.897$). Finally, the correlation between the unmanned aerial vehicle (UAV) based NDVI value and the output is 0.728. Similarly, spectral observations collected through drone-based red-green-blue sensors are used to evaluate maize yield (Geipel et al. 2014). The phenotypes are created using a vegetative index with the highest $R^2 = 0.74$.

Multispectral images along with red-green-blue data were collected from the field and drone after monitoring the maize growth at various phosphorus concentrations. It was observed that vegetation index is correlated with grains yield and highly correlated with leaves phosphorus contents (Gracia-Romero et al. 2017). Multispectral images with different wavelengths (red = 520–570 nm, green = 600–690 nm & NIR = 750–850 nm) were obtained using drones to examine sunflower achene yield, total biomass, and level of nitrogen. Normalized difference vegetation index (NDVI) was measured with multispectral images during different dates. The comparison based on different images data collected at different times with several resolutions showed accuracy in results (Vega et al. 2015). Therefore, drones during higher flights may save time and may reduce the number of images. The reported NDVI is closely related to yield, aboveground biomass, and biomass nitrogen content. The above studies indicate that red-green-blue or multispectral imaging can be used to predict yield. Therefore, the recommendations of both sensors for phenotypic analysis of plant yield are better respectively. Unmanned aerial vehicle-based sensors are used for different plant characteristics, namely biomass, altitude, leaf area index, and chlorophyll contents.

6.6.2 Biomass Phenotyping

Plants producing above-ground plants parts are an important indicator reflecting the growth and light use efficiency which is important for carbon storage in the form of biomass (Swinfeld et al. 2019). Therefore, several research on plant biomass has been conducted using drone-based sensors. The spectral data collected by drones is used to estimate the dry biomass of wheat (Honkavaara et al. 2013). Digital surface phenotype (DSM) is also used to calculate biomass estimates and vegetation height. However, it has no linear relationship with dry biomass. The poor results may be due to the low signal-to-noise ratio along with the narrow band in the wheat study on fresh and dry biomass, as well as the other three traits viz., leaf area index (LAI), nitrogen levels, and plant height (Schirrmann et al. 2016). Red-green-blue image obtained through drone first converted into color spaces for distinguishing the area of plant population and empty soil. The pixel density is also calculated on red-green-blue images, namely the ratio of blue-green and the ratio of red-blue channels. A simple correlation of image index and biophysical characters increases with plant growth. The estimated yield height from the image is also closely related to the fresh, dried biomass, leaf area index, and measured height of each part. The correlation between the measured unmanned aerial vehicle production height and the dry biomass is weak, appearing in the first stage. This is due to maximum dry biomass being stored within leaves, not in the stem, and not also in many early leaves. At each stage, the correlation between nitrogen concentration and all biophysical parameters is weak.

Additionally, the principal components (PC) were analyzed for the image traits and determined as independent variables for linear regression of phenotype. Biophysical characters come under the values i.e., $R^2 = 0.70$–0.97 and 0.73–0.99 for verification data. However, the relationship between nitrogen and PCs is very low ($R^2 = 0.22$–0.65). Red-green-blue images collected by drones are also used to detect barley biomass (Brocks and Bareth 2018). The author uses crop surface phenotyping (CSM) to plot the maximum height of the plant canopy. Plant height collected from red-green-blue images may be used to justify the 3D monitoring system for biomass study (dry biomass; $R^2 = 0.55$–0.79, and fresh biomass; $R^2 = 0.34$–0.61).

Phenotyping of peas and oats performed by red-green-blue cameras that mounted on the drone to examine their biomass (Jannoura et al. 2015). The collected images were observed as normalized to the green-red difference index (NGRDI), which is based on the reflectance of green and red and subtracted from the true colour image. It is used to observe crop growth stages and above-ground biomass with nutritional levels. This study discussed a relationship between the normalized green-red difference index (NGRDI) along with above-ground dry biomass i.e., 0.65 for peas, 0.55 for peas/oats, and 0.55 for oats. 0.74. NGRDI is also positively correlated with plant biomass, 0.59 for peas, 0.58 for peas/oats, and 0.78 for oats.

According to the research results, the spatial variation map of upper-ground biomass was observed, which is significant for the management of each site. The map will enable farmers and researchers to discover and monitor the growth of crops, namely biomass, and diseases. The spatial pattern of biomass, monitor plant changes throughout the field, and adopt appropriate strategies based on the visual maps. However, traditional/older sensors may not be able to capture deep canopy observations effectively. Therefore, LiDAR is used to collect maximum canopy information. The LiDAR can offer sufficient soil reflection to produce digital terrain phenotyping of trees and forests. The LiDAR can perform data collection during the night, making this technology more robust. The airborne LiDAR estimates changes in forest carbon stocks. In this study, we present the association between soil storage-estimated carbon storage and LiDAR indicators. The total R^2 value of carbon is 0.74 and the R^2 value of above-ground biomass is 0.81. Thus, the study shows that unmanned aerial vehicle-based LiDAR can estimate plant biomass.

6.6.3 Plant Height Phenotyping

Among various crops, plant height is directly correlated with crop yield and acts as a major location for carbohydrate storage (Holman et al. 2016; Hassan et al. 2019). This is an important indicator about biomass and yield prediction during different growing stages of canopy structure (Aasen et al. 2015). The traditional method of measuring plant height with a meter-rod, is laborious, time-consuming, and least efficient. The drone's technology along with sensors may capture images of crop plants from the field to estimate plant height. There are several studies conducted on unmanned aerial vehicle remote sensing technology for measuring plant height. The combined application of unmanned aerial vehicle-based red-green-blue images and ground-based LiDAR is used to estimate wheat crop height (Holman et al. 2016 Madec et al. 2017).

Unmanned aerial vehicle technology determined the best results i.e., R^2 yield height is 0.99 and R^2 ground LiDAR is 0.97. Then using digital surface phenotype to create a spatial variability map of the field scale and individual crop height. The results show that the proficiency of drone technology can produce high-quality and large amounts of phenotypic information. Consequently, red-green-blue and LiDAR both are important for measuring the plant height under field conditions. Plant height assessment of barley through red-green-blue image shows growth variability (Bendig et al. 2013, 2014). It is believed that plant height measured through drones may be a good marker of above-ground biomass. LiDAR is also used to collect tree height by placing the multi-rotor unmanned aerial vehicle platform for collecting height, position, and canopy width of trees (Wallace et al. 2012). The evaluation cloud points are generated by the unmanned aerial vehicle-LiDAR technique, and the relative mean square error (RMSE) is 0.34 m (horizontal) and 0.14 m (vertical).

Generally, the standard deviation of the height generated by the point cloud is 0.05 m and the standard deviation is 0.44 m, while the standard deviation for canopy width is 0.25 m. Among the plant characteristics, height and canopy diameter may be used for the selection of new varieties in breeding programs. Therefore, Diaz-Varela et al. (2015) studied the use of an improved red-green-blue camera mounted on a unmanned aerial vehicle to predict height and canopy diameter. Modify the RGB camera to obtain the near-infrared band after removing the internal infra-red filter. Digital surface phenotype is created by image reconstruction of the structure of motion (SfM). The results showed relative RMSE value of the tree and hedge level was between 6.55% and 19.24%. The relative RMSE of crown diameter was 12.96–18.83%.

Hyperspectral imaging is also used in place of red-green-blue and LiDAR that can provide more information about bands of spatial characteristics. This hyperspectral imaging technique is used to predict the plant height parameter of barley using a visual map of wavelength between 450–950 nm (Aasen et al. 2015). The vegetative growth assessment through hyperspectral vegetation index also predicts chlorophyll, leaf area index, and green biomass. During low light/darkness LiDAR can be more powerful than red-green-blue. LiDAR is more expensive and complicated. The data analysis is much complicated using this hyperspectral image sensor system. However, it is estimated that red-green-blue and LiDAR sensors both can be used for the reliable assessment of plant height.

6.6.4 Leaf Area Index Phenotyping

The leaf area index (LAI) is calculated by the total leaf area per unit canopy area of the plant. Leaves are the most important characteristics in crop plants, which directly correlates with food synthesis and contributes to increasing crop yield. The leaf is the best indicator of plant health, and nutritional status (Liu et al. 2010; Wang et al. 2017b). It is studied that leaf area index is associated with the number of photosynthates that produce under photosynthesis (Potgieter et al. 2017). Therefore, several studies were conducted for the phenotyping of leaf area index using drone-based sensors. Three bands, green, blue, and near infra-red measure by cameras installed on the drone for assessing wheat production (Hunt et al. 2010). A positive correlation between leaf area index ($R^2 = 0.85$) and Green Normalized Difference Vegetation Index (GNDVI) was observed.

Subsequent results showed that these three bands, green, blue, and near infrared, have been used for production forecasts in different crops. The multi-spectral images (red, green, blue, and near infra-red) collected through drones were also used to estimate the leaf area index of sorghum (Potgieter et al. 2017). The enhanced vegetation index (EVI) and normalized difference vegetation index (NDVI) are assessed using spectral bands to analyze the plants per unit area, leaf area index, and canopy size. The vegetation indexes (NDVI and EVI) during the growth stage (before and during flowering) are closely related to the leaf area index. In addition, the growth patterns of sorghum genotypes are also used to determine the aging process of the crop. Senescence information at different growth stages is the best signal for breeders to screen out green genotypes as tolerant under water shortage conditions.

The normalized differential red boundary (NDRB) is used to determine the level of aging, which is closely related to chlorophyll content and photosynthetic activity. NDRB plays a key role to determine aging patterns for selecting the green genotypes. This study shows that high-throughput phenotyping following unmanned aerial vehicle-based can help to maximize yield after improving genotypes. Leaf area index phenotyping is predicted by many geneticists using red-green-blue images such as leaf area index in onion was predicted through red-green-blue images collected by drones (Corcoles et al. 2013). The association of leaf area index with plant canopy is calculated by three different phenotypes of leave and canopy like linear, polynomial, and exponential. The first two phenotypes indicate that R^2 is equal to 0.847 and 0.839, respectively.

Compared with traditional phenotyping methods used to measure leaf area index, drone-based phenotyping is time-saving. In another study, using drone-based red-green-blue images to check visualization of grape canopy leaf area index, the result was predicted as $R^2 = 0.57$. A 3D map created by structure of motion contains information about the vineyard. Red-green-blue images are most reliable for estimating leaf area index. Red-green-blue sensors are simple and easy to operate through drones and are recommended for phenotyping of leaf area index. Significant phenotypic variation in the leaf area index helps to adopt appropriate management strategies for improving the trait.

6.6.5 Chlorophyll Phenotyping

Chlorophyll contents are associated with the photosynthesis process and healthy plants have their higher contents to synthesize more photosynthates. Therefore, chlorophyll contents determine the rate of photosynthesis in leaves and photosynthetic products of plants (Peng et al. 2011). Chlorophyll content plays an important role in crop plants during different stresses to boost up nutritional status and crop yield (Martinelli et al. 2015; Maimaitijiang et al. 2017). The chemistry of chlorophyll molecule, reveals some chemical groups, including CIH and CO. Therefore, the variations in these chemical groups like CIH, OeH, NIH, and CO can be observed in the near infrared spectral region for detecting chlorophyll-a in a phenotype of the plant. Various studies have been conducted for assessing the chlorophyll phenotype following the vegetation index getting from multispectral and hyperspectral imaging.

Chlorophyll phenotyping using the drones with red-green-blue and near-infrared cameras, produce thermal and multispectral images to calculate the chlorophyll contents in oat crop (Elarab et al. 2015). The phenotypic analysis of the chlorophyll concentration was also performed using a correlation vector machine (RVM). The program first measures the Soil plant analysis development (SPAD) value and then uses the eq. $CCI = 1 + 0.00119 \times SPAD\ 2.67$ to calculate the Chlorophyll Concentration Index (CCI) based on SPAD. Finally, chlorophyll ($\mu mol \times m^{-2}$) $= -132 + 146 \times (CCI\ 0.43)$ can be used to calculate the chlorophyll mass of each leaf area. Various parameters, namely leaf area index, normalized difference vegetation index (NDVI), and heat are input variables to identify chlorophyll contents. NDVI, leaf area index, and chlorophyll with different values are displayed in different colors, based on the visual map, to discover and monitor changes in plants under field conditions.

In addition to the chlorophyll contents, this assay is also used for predicting phenotyping of traits like leaf area index and total biomass produced. Therefore, the combination of multispectral and thermal data can predict phenotyping of biochemical parameters including nitrogen and chlorophyll contents. For different biophysical parameters, leaf area index uses a combination of multispectral and thermal data for phenotypic analysis which provides color rendering, canopy shape, temperature, and biomass as the best predictor. They also calculate the phenotype of plant vegetation, which can provide information about plant density and structure. Hyperspectral images between wavelength 340–764 nm were collected by drones that can predict chlorophyll contents in rice cultivars (Uto et al. 2013). The results showed that the chlorophyll index may be associated with the density of chlorophyll contents. Hyperspectral imaging is effective due to the sensitive spectral wavelength for chlorophyll contents estimation. Therefore, phenotyping data of multispectral and thermal images determine the best results for chlorophyll contents prediction.

6.6.6 Phenotyping of Other Traits

Phenotyping of traits helps improve the knowledge, skills of plant breeders and biologists. Choosing stress-resistant cultivars can help increase farmers' yield and income. Therefore, some studies use drone-based sensors to focus on plant stress traits. The various water stress levels are assessed through multispectral thermal images that may range from 530 to 800 nm wavelength (Baluja et al. 2012). Assessment of thermal images of plant height and stomatal conductance index is used to assess water contents in stem and leaf cells. Different researchers have pointed out that thermal imaging can be the short-term answer to assess the state of the water body, whereas normalized difference vegetation index (NDVI) can be the long-term answer. Then, phenotyping of stem water potential and leaf stomatal conductance can be used for the health analysis of crop plants. Therefore, drone-based thermal imaging technology has been used for phenotypic analysis of changes in the moisture status of different fruit trees like almonds, apricots, peaches, lemons, and oranges (Gonzalez-Dug et al. 2013). According to the visual map of crop situation/health farmers can adopt precise strategies accordingly. Structure of motion technology is used to obtain digital surface phenotype from each plant. Digital surface phenotype then obtains information about the affected and missing vines in the form of grayscale images. The results showed that 9.5% and 7.3% of the plants were affected, respectively, and lack of vines, which cause abiotic stress affected 16.8% of the plants in total.

The biological stress-like diseases may analyze through unmanned aerial vehicle-based sensors following the multispectral images with a blue wavelength between 430 to 470 nm, green from 530 to 570 nm, red from 630 to 670 nm, and near infrared between 810–850 nm, and hyperspectral images from 397 to 995 nm. Unmanned aerial vehicle-based red-green-blueimages are also used to estimate the canopy size and canopy senescence in some crops (Makanza et al. 2018). The vitality of crops can be controlled according to the shape of the canopy and the senescence of the canopy. This is a physiological process that can be used as an indicator of the robustness and speed of crop canopy measurement and is significantly affected by genetic characteristics. According to the results, the total canopy area has medium to high heritability. In addition, the other four characteristics, namely dry, yellow and green canopy, all showed moderately heritability values. Studies have shown that effective high throughput phenotyping based on unmanned aerial vehicle imaging, by which at large scale ideal plants can be selected for ideal type breeding. All studies prove that the use of drone sensors/cameras is useful for analyzing the best tolerant characteristics against biotic and abiotic stresses.

6.7 Conclusion

Phosphorus is the main component of phospholipids, nucleic acids, metabolites, and phosphoproteins. All these molecules are involved in the physiological aspects of plant growth and development. Plant phenotype is still the bottleneck for selecting genotypes with higher phosphorus utilization efficiency. The main challenge is to produce an accurate phenotype. An accurate phenotype will produce correct data and interpretation. With the development of new sensors, an additional task is to develop a phenotypic system that can easily use by new types of sensors.

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Chapter 7
Advanced Biotechnological Tools for Improving Phosphorus Use Efficiency

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Abstract Phosphorous is an essential element for physiological and biochemical activities of living cells. Soil is the main source of plant phosphorous, but soils usually contain low levels of readily available phosphorous. As a consequence, phosphorous fertilizers are added to soils to enhance crop yields, though this is not a sustainable solution because fertilizer resources such as phosphate rock are depleting. Therefore there is a need for techniques to improve phosphorus use efficiency. Here we review biotechnological tools to improve phosphorus use efficiency. Plant physiological traits can be adapted by the utilization of phosphate transporters, membrane lipid remodeling to drive remobilization, targeting signaling pathways, and phenotyping and other genetic approaches. Biofertilization is also proving an efficient way to enhance phosphorus use efficiency. Phosphorous use efficiency can also be improved by transcriptomic and metabolomics.

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7.1 Introduction

Phosphorous is an essential element of every living cell, as phosphorus is required for their physiological and biochemical activities (Roberts and Johnston 2015; Iqbal et al. 2019a). The salient role of phosphorous in plants is protein metabolism and energy transfer (Fageria et al. 2010). Phosphorous is crucial for plant's structural integrity and regulation of metabolism as it is a potential component of adenosine triphosphate, nucleic acid, and phospholipids (Vance 2011; Amanullah et al. 2019). Plants obtain a large amount of phosphorous from the soil solution as phosphate ions (Amanullah et al. 2016a, b). But they are present in a very limited concentration in the soil, typically around 10–5 M. They are removed with crop harvesting and should be replaced to eradicate nutrient depletion and soil degradation.

The constant supply of readily available phosphorous in the soil is needed to maintain its concentration which can be taken up by the roots (Anwar et al. 2017; Iqbal et al. 2019b). This constant supply is maintained due to phosphorous fertilizers which come from the ores of phosphate rock, a nonrenewable and limited resource (Amanullah et al. 2021). According to Van Kauwenbergh (2010) and International Fertilizer Development Center, these exploitable reserves may last for about 300–400 years. Most of these phosphate rock reserves are mainly present in Morocco, followed by the USA, and China (Van Kauwenbergh 2010). This unequal global distribution is a grave concern.

Excessive phosphorous fertilization is being used in agricultural practices to ensure proper supply as approximately 5.7 billion hectares of land have poor available phosphorous for sustainable cropping (Fageria et al. 2017). Phosphorus mining then becomes the concern for low input cropping systems while, in the high input cropping system, higher phosphorous fertilizer demand is the reason for concern (Khan et al. 2017; Safdar et al. 2021).

Another important factor that increases the demand for phosphorous fertilizer is the removal of almost 10 million tons of phosphorous across the globe each year by harvested produce (Lott et al. 2000). Grain crops are the major culprit for phosphorous removal at harvest (Lott et al. 2001). Lott et al. (2009) reported that about 85% of phosphorous applied as fertilizer is removed from the fields through harvest produce each year. Phosphorous increases tillering and pods in cereals and legumes (Fageria et al. 2008; Fageria and Filho 2007) and its deficiency makes plants more susceptible to some diseases (Hay 1998) and thus, a large number of phosphate fertilizers are needed to improve crop yield (Withers et al. 2014).

Phosphorous is one of the most important limiting nutrient factors for plant growth. The deficiency of plant available phosphorous is the main constrain in plant growth in over 5.7 billion hectares of land globally (Batjes 1997). A large amount of soil phosphorous is locked up in recalcitrant organic phosphate fractions or nonlabile inorganic phosphorous pools in the form of complexes with calcium in alkaline soil and with iron (Fe^{2+}) or aluminum (Al $^{3+)}$ in acid soils. Attempts at amelioration of this situation are the utilization of phosphorous fertilizers (Baligar et al. 2001; Rose and Wissuwa 2012).

Thus, improvement of phosphorus utilization efficiency is the need of the hour although it is a highly complex character that complements phosphorous uptake and ultimately results in the better yield of grain (Rose and Wissuwa 2012). There is a significant phenotypic variation of phosphorus use efficiency in the various genotype of the same species (Ozturk et al. 2005; Yuan et al. 2017). Phosphorus use efficiency can be improved by either increasing uptake capacity or optimizing its utilization (Parentoni & Souza Júnior 2008). Different approaches are needed to improve the phosphorus use efficiency for high and low input agricultural systems. For low input conditions, crops with high-affinity inorganic phosphate uptake potential and high internal phosphorus use efficiency are needed (Rose and Wissuwa 2012).

Breeding programs based on high throughput genomic approaches are needed to improve food production and thus overcome the use of fertilizers and other agrochemicals (López-Arredondo et al. 2013). Phosphorus use efficiency is an important index in determining the applied fertilizer by a crop species (Fageria et al. 2013).

Phosphorous efficiency mainly comprises phosphorous uptake efficiency and phosphorus use efficiency. Phosphorus use efficiency is not widely understood as compared to phosphorous uptake efficiency and many factors are responsible for this. The first and foremost reason is that the researchers failed to address is the definition of phosphorus use efficiency (Rose and Wissuwa 2012; Shenoy and Kalagudi 2005). According to Wang et al. (2010), phosphorous uptake efficiency is the propensity of plants to obtain inorganic phosphate from the soil, and phosphorus use efficiency is the capacity for biomass production measuring absorbed phosphorous (Wang et al. 2010).

7.2 Definition of Phosphorus Use Efficiency

Along with the poor definition, phosphorous deficiency of plants, multiple definitions, acronyms, and terms are used by various authors, for example, phosphorous utilization efficiency (Sepehr et al. 2009), and internal phosphorous utilization efficiency (Rose et al. 2011). The lack of specific terminology given for this specific criterion and range of definitions are unequivocally the reason for some apparent contradictions in the literature and made it more difficult to draw some conclusions. In this chapter, phosphorus use efficiency is defined as the biomass produced per unit phosphorus accumulated in tissue, and phosphorus efficiency relevance is defined as grain yield per unit of phosphorus accumulated in above-ground plant material.

The most cogent criteria used to quantify the internal phosphorus use efficiency is broadly classified into those having agronomic relevance and physiological relevance. If criteria measure the grain yield as a component, then phosphorus efficiency relevance has more agronomic implications as compared to phosphorus use efficiency measurement as it has no strong direct agronomic application. Phosphorous fertilizer use efficiency is approximately 10% in wheat and mostly applied phosphorous is fixed in the soil (Schröder et al. 2011).

7.3 Important Traits for Enhancing Phosphorus Use Efficiency

Plants have developed highly advanced mechanisms and regulatory systems to access and control nutrient hemostasis. They have evolved adaptive mechanisms in response to inorganic phosphorus deficiency, and transudation of organic acids to solubilize phosphorous complexes and phytases and phosphatases to access organic phosphorous (Hammond et al. 2004; López-Arredondo and Herrera-Estrella 2012). In rice (*Oryza sativa*), the phosphorus use efficiency is about 25% which gives a wide scope for improvement (Dobermann and Fairhurst 2000). In the rice production system, aluminium toxicity is the main constrain as it inhibits root growth and phosphorus use efficiency only then can be improved when plants are aluminium toxicity tolerant (Haefele et al. 2014).

A premise of this chapter is to identify loci and superior alleles within germplasm and use marker-assisted introgression to breed high-yielding varieties with specific phosphorus use efficiency traits/genes by using advanced biotechnological tools to improve the phosphorus use efficiency of modern crop cultivars, at present.

7.4 Physiological Traits Related to Phosphorus Use Efficiency

A wide range of physiological traits is involved in phosphorus use efficiency. These traits enhance phosphorus use efficiency by phosphorus scavenging and uptake and optimizing allocation within the plant. Some of these physiological responses are compounded and some are relatively straightforward and can be assessed for breeding purposes.

For the uptake of released phosphorous, high-affinity phosphate transporters and transporter proteins situated in cell membranes are up-regulated at the low phosphorous level. Internal phosphorus use efficiency improvement leads to rich resource-efficient use of phosphorous than increased phosphorous uptake efficiency. A broad range of metabolic integrations is intricated in phosphorus use efficiency. The main aspect of phosphorus use efficiency is the potent mobilization of phosphorous within the plants. It includes recycling phosphorus from senescing parts of plants to actively growing tissues and from vacuoles (Akhtar et al. 2008). Seedlings obtain stored phosphorus from seeds at the early growth phase (White and Veneklaas 2012). Seed phosphorus concentration can be decreased through harvest index in grain by using breeding efforts. But with decreased phytate level, seed vigor is affected.

Phosphatases are also important in phosphorus use efficiency as well as phosphorous uptake efficiency because they are involved in internal phosphorous reallocation in plants. Little work is done on internally localized phosphatases, but Tang et al. (2013) reported LaSAP1 expression has been increased in white lupin. High-affinity transporters also play an integral part in internal phosphorous mobilization, for example, specific transporter genes are upregulated in sensing tissue (Vance et al. 2003).

7.4.1 Utilization of Phosphate Transporters for Breeding Phosphorous Efficient Plants

From inorganic phosphorous uptake to its translocation within a plant is coordinated by a set of proteins having phosphate transport activities. Inorganic phosphorous distribution within the plants by translocation into mitochondria, chloroplasts, and golgi apparatus is mediated by PHT2, PHT3, and functionally diverse PHT4 gene family. Other transporter families have also been facilitated by transgenic approaches (Ai et al. 2009; Wang et al. 2012; Zhang et al. 2015). The regulation of phosphate transporters gene expression, function, and intracellular localization are multilayered and highly sophisticated (Gu et al. 2016). The regulatory genes which are affecting inorganic phosphorous homeostasis by direct or indirect regulation of phosphate transporters at different levels are targeted mostly at the transcriptional, post-transcriptional, translational, and post-translational levels.

According to the literature, overexpression of phosphate transporters might be propitious to a larger extent (Heuer et al. 2017). For breeding phosphorous efficient genetically modified crops, phosphorus use efficiency has practically more potential than phosphorous uptake efficiency in fertilized plants (Gu et al. 2016). Phosphorous uptake efficiency is more important in inorganic phosphorous-deficient soils. In various studies, phosphorus use efficiency is neglected and more concentration is given to measure inorganic phosphorous accumulation, inorganic phosphorous uptake, and both of these factors are used in determining the changes in inorganic phosphorous homeostasis (Rose et al. 2011).

Inorganic phosphorus transporters influence phosphorus use efficiency as they are related to inorganic phosphorous recycling, but phosphorus use efficiency is a more complicated trait. Under phosphorous-deficient conditions, the efficiency of metabolic shifts like alternative pathways of cytosolic glycolysis and mitochondrial electron transport chain and substitution of phospholipids by polar lipids (Hammond and White 2008).

To overcome the gap between molecular mechanisms and the practical application of phosphate transporters to improve phosphorus use efficiency in plants, some strategies can be taken into account. One strategy includes overexpression of some genes results in enhanced growth and yields under low inorganic phosphorous conditions (Wu et al. 2013) while some other genes hinder the growth. Tissue-specific promoters can be used along with constitutive strong promotors. Promoters with shoot-specific expressions should be considered (Li et al. 2015). In the second strategy, inorganic phosphorous -starvation specific promotors should be used to reduce the inorganic phosphorous toxicity caused by inorganic phosphorous over accumulators to regulate phosphate transporters gene expression. *OsPHT1;6*, the rice promotor is a potential candidate as it gives inorganic phosphorous -starvation specific expression in monocots as well as in dicots and can be used in crops cultivated in inorganic phosphorous -starvation conditions (Li et al. 2014). In the third strategy, artificial promotors can be designed by fusing minimal promotors with DNA fragments or *cis*-elements to generate inorganic phosphorous -starvation specific expression (Lota et al. 2013). In the fourth strategy, the genomic copy number of a single gene of a specific trait responsible for phenotypic variation can be considered. Native promotors of some phosphate starvation-induced phosphate transporters genes that mimic increased gene copy numbers should be used but not the ono-native promotors as they produce unfavorable side effects and change the gene spatio-temporal expression. For example, Ruan et al. (2015) reported that AT-type-PIBS has a better affinity for *OsPHR2*.

To engineer the plants under inorganic phosphorous-deficient conditions, having the ability to maximize the usage of inorganic phosphorous reserve in plants can be done by re-orchestrating the gene expression profile. Thus, normal shoot growth is achieved in this way. *Arabidopsis pho1–4* mutant has provided the proof for this theory (Wege et al. 2016).

7.4.2 Membrane Lipid Remodeling to Drive Phosphorous Remobilization

In response to inorganic phosphorous starvation, membrane phospholipids are substituted by lipids lacking phosphorous in major plants species including cultivated crops (Plaxton and Carswell 2018). Lipids remodeling pathway consists of many steps and any step can be targeted to modify the metabolic pathway to lower the phosphorous requirement and enhance the phosphorus use efficiency. Mainly phospholipids are targeted in membranes and replaced by sulfolipids and galactolipids (Lambers et al. 2012) because these are the hallmark of phosphorous -starvation (Tjellström et al. 2008). Transcription of genes related to the manufacture of sulfolipids and galactolipids is up-regulated in inorganic phosphorous-deficient leaves of *A. thaliana* (Morcuende et al. 2007). In phosphorous-free polysaccharides, mainly cellulose is targeted for adaptation of cell walls in low phosphorous conditions (Byrne et al. 2011).

In *Proteaceae* species, adapted to phosphorous impoverished landscapes, lipid remodeling takes place in mature leaves (Kuppusamy et al. 2014). Maintenance of a high level of phospholipids during leaf growth and development is a necessity. Rice genotype constructed by lipidome and transcriptome can express lipid remodeling genes under low inorganic phosphorous conditions (Mehra et al. 2016). The fact that phospholipids concentration decrease from 46.0% to 9.6% from young to mature leave can be used to develop the mechanism to increase phosphorus use efficiency in crop plants (Lambers et al. 2012).

7.4.3 *Signaling Pathways*

Under stressed conditions, signaling pathways and hormones are potent integrators in plants (Chiou and Lin 2011). Auxins and ethylene signaling take part in lateral root initiation mainly under low phosphorus conditions, however, cytokinin production is suppressed in low phosphorus conditions and it inhibits phosphorus starvation-induced (PSI) genes. When phosphorus mobilization is reduced from roots to shoots, shoot growth is inhibited even in the presence of vacuolar phosphorus pools. Veneklaas et al. (2012) suggested that phosphorus use efficiency can be enhanced by targeting these signaling pathways and hormones to make more efficient utilization of the shoot's phosphorus pool. For example, in *Arabidopsis*, modifying the gene expression of *PHOI*, uncoupling of shoot growth and phosphorus deficiency can be obtained. Strigolactones enhance mycorrhizal branching. Sugar signaling and phosphorus responsiveness are also connected. Hammond and White (2011) proposed that under low phosphorus conditions, starch formation is increased in shoots due to decreased photosynthesis. Phosphorus-responsive genes are activated upon the increase of the root to shoot ratio. This ratio is increased when sugar is allocated in roots after reaching into the phloem (Chiou and Lin 2011).

7.5 Phenotyping

To obtain plants with improved phosphorus use efficiency, high throughput selection of the desired genotype is requisite. Although field trials are the main thing, but these traits are hindered by variable environmental conditions which can provide false-positive results, or which can obscure the desired genetic variations. More controlled conditions overcome this issue and provide more clear results of phosphorus use efficiency linked traits in the tested plants. The plants should be cultivated in such a way that makes the assessment of traits easier and more reliable.

Soil and water-based systems are used in the cultivation of transgenic plants. In soil-based systems, the simple system is based on the pots in greenhouses with controlled conditions and different systems can be used to control the experimental conditions, for example, the system used previously by scientists (Da Silva and Gabelman, 1992). Rhizosphere study container technique (Zoysa et al. 1999), robotic rhizotron system (Nagel et al. 2012) for automatic imaging of both roots and shoots, and (Fang et al. 2009) recorded the total root system by coupling transport root growth medium with phytagel with 3D laser scanning.

The water-based system comprised of hydroponic culture techniques. From the simplest hydroponic culture technique, applied hydro-aeroponics (Lrsquo et al. 2012) to ingested-based hydroponics can be used on the plants. The ingested-based concept is more appropriate for phosphorus use efficiency than phosphorous uptake efficiency as the scavenging ability of the root system will not contribute to phosphorus use efficiency.

7.6 Genetics and Breeding to Improve the Phosphorus Use Efficiency

In recent research, plenty of quantitative trait loci for phosphorous efficiency and associated phenotypic have been found and mapped for wheat under field trials (Su et al. 2009), hydroponic cultures (Zhang and Wang 2015), and pot trials (Ryan et al. 2015; Su et al. 2006). The main objective is to locate the stable and important quantitative trait loci clusters that can be employed in quantitative trait loci cloning and crop breeding program mainly in most cultivated crops (Yuan et al. 2017).

Identification of targeted quantitative trait loci for a specific trait is a key point in boosting the phosphorus use efficiency of plants. Plants in a deficient phosphorous environment, improve their phosphorus use efficiency through reduction of organic phosphate pools, by alternative metabolic pathways, lipids remodeling, and enhancing phosphorous distribution from senescing tissues to developing tissue for maximum plant biomass production (Fig. 7.1) and allocation to seed yield (Chen et al. 2011; Wiel et al. 2016). Phosphorous uptake efficiency and phosphorus use efficiency differ substantially among and within species which can be manifested to improve crops by breeding. With the help of genetic mapping, complex traits are dissected into quantitative trait loci to get elite varieties with improved phosphorus use efficiency. Biotechnological tools for example marker-associated selection and other genetic engineering techniques are more efficient, precise, and easier than conventional breeding (Wang et al. 2019).

7.6.1 *Mapping Populations*

To map quantitative trait loci to improve phosphorus use efficiency in various crops, primary mapping populations including recombinant inbred lines or double haploid lines and advanced mapping populations including introgression lines and chromosomes segment substitution lines have been constructed. These constructs increase the precision of quantitative trait loci mapping by removing the diverse genetic background (Chao et al. 2015; Li et al. 2009; Zhang et al. 2014; Zhao et al. 2013).

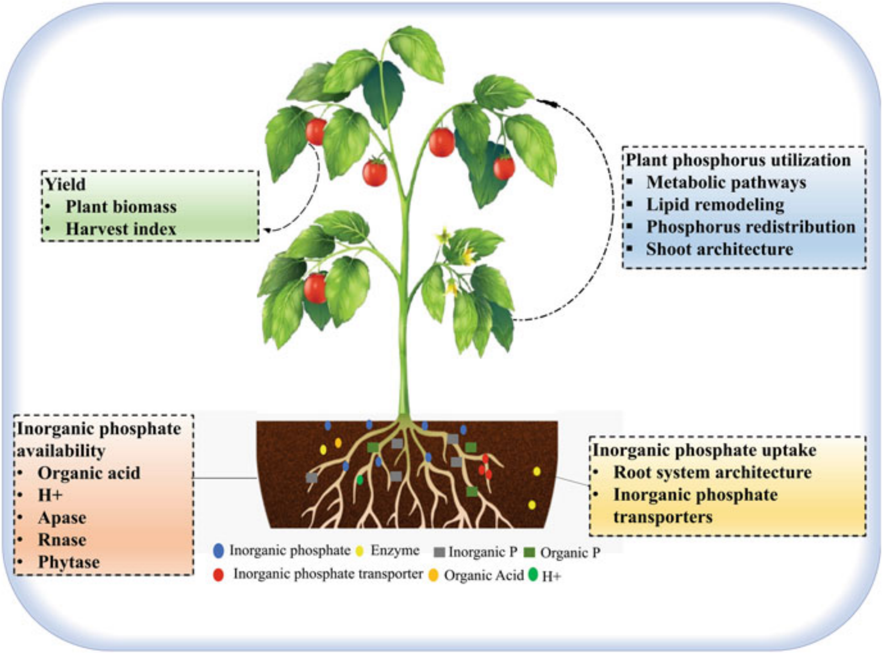

Fig. 7.1 Physiological phosphorous utilization efficiency is improved by limiting organic phosphorous pools via lipid remodeling, alternative metabolic pathways, and phosphorous redistribution from senescing tissues to developing tissues. Another strategy is to maximize biomass allocation to harvest index

7.6.2 Molecular Marker and Genetic Linkage Map

With regard to previous literature, simple sequence repeat, amplified fragment length polymorphism, random amplified polymorphic DNA, and restriction fragment length polymorphism have been used originally to construct the genetic linkage maps for phosphorus use efficiency related characteristics. But, recently, with state-of-the-art technologies, single nucleotide polymorphism markers have been used more broadly. For example, to genotype 202 lines of the BnaTNDH population, the 60 K Brassica Infinium single nucleotide polymorphism array (Illumina, USA) is being utilized (Zhang et al. 2016).

By using whole-genome sequencing, the bulk segregation analysis has widely been used to identify targeted traits to improve phosphorus use efficiency in many plants (Fu et al. 2015; Hua et al. 2016; Lu et al. 2014).

Genome-wide association study has also been used extensively for mapping phosphorus-efficient genes. Genome-wide association study has some advantages over other technologies as it increases the reliability of quantitative trait loci mapping and detection efficacy. But this method has some restrictions too due to complex population structures and false-positive results are obtained and due to low diversity, there is a reduction in the statistical capability of association analysis (Flint-Garcia et al. 2005). Association analysis along with linkage analysis are being used to identify targeted genes for desired traits in recent research (Flint-Garcia et al. 2005; Liu et al. 2015; Xiao et al. 2017).

7.6.3 Breeding of Phosphorous-Efficient Crop Varieties

Most identified quantitative trait loci affecting phosphorus use efficiency-related characteristics are environmental dependent, so there are limited, robust quantitative trait loci for effective mapping and cloning. There are limited marker-associated breeding programs to enhance phosphorus use efficiency because of epistatic interaction among quantitative trait loci and identified quantitative trait loci with very limited effect. Though, multiple system atrophy has been reported as most effective for introgression of stable quantitative trait loci of good impact (Miklas et al. 2006; Wang et al. 2019).

The major constrain to improve crop efficiency is the limited knowledge regarding the genetics of phosphorus use efficiency (Wang et al. 2010), mainly due to the confounding effect of phosphorous uptake efficiency on phosphorus use efficiency (Rose et al. 2011). A recent review of literature on this topic suggests that a better insight on the molecular mechanism of phosphorus use efficiency can be obtained by calculating phosphorus use efficiency indices based on the metabolically active phosphorous pools (Rose et al. 2011) and quantitative trait loci related to phosphorus use efficiency should be identified under conditions in which phosphorus use efficiency should be equal for cultivars understudies (Veneklaas et al. 2012).

For producing plants with improved phosphorus use efficiency, targeted traits associated with phosphorus use efficiency are investigated using high throughput technology, and most commonly used are hydroponic culture systems at the seedling stage (Adu et al. 2014; Dupuy et al. 2017; Shi et al. 2013) and rhizoboxes are used to determine root surface area (RSA) at maturation stage (Li et al. 2017). Automatic phenotyping platforms are being used to determine the above-ground traits of plants (Fig. 7.2). In the second step, to determine appropriate population genotype, next-generation sequencing technologies are being used commonly to boost efficiency in a limited time (Crossa et al. 2017). In the third step, casual genes of targeted quantitative trait loci are identified through targeted mutations (Zhu et al. 2017) or transcriptomics. In the fourth step, by using marker-assisted selection approaches flanking markers or functional markers of major quantitative trait loci are used in breeding programs. In the last step, novel crop genotypes are tested in the field trials with reduced phosphorous input. Some successful examples are present in the literature (Gao et al. 2020; Wissuwa et al. 2015) in which knowledge of targeted quantitative trait loci for phosphorus use efficiency improvement has been achieved but more novel plant varieties with greater phosphorus use efficiency are needed of the hour to overcome the problems of food security and agriculture sustainability.

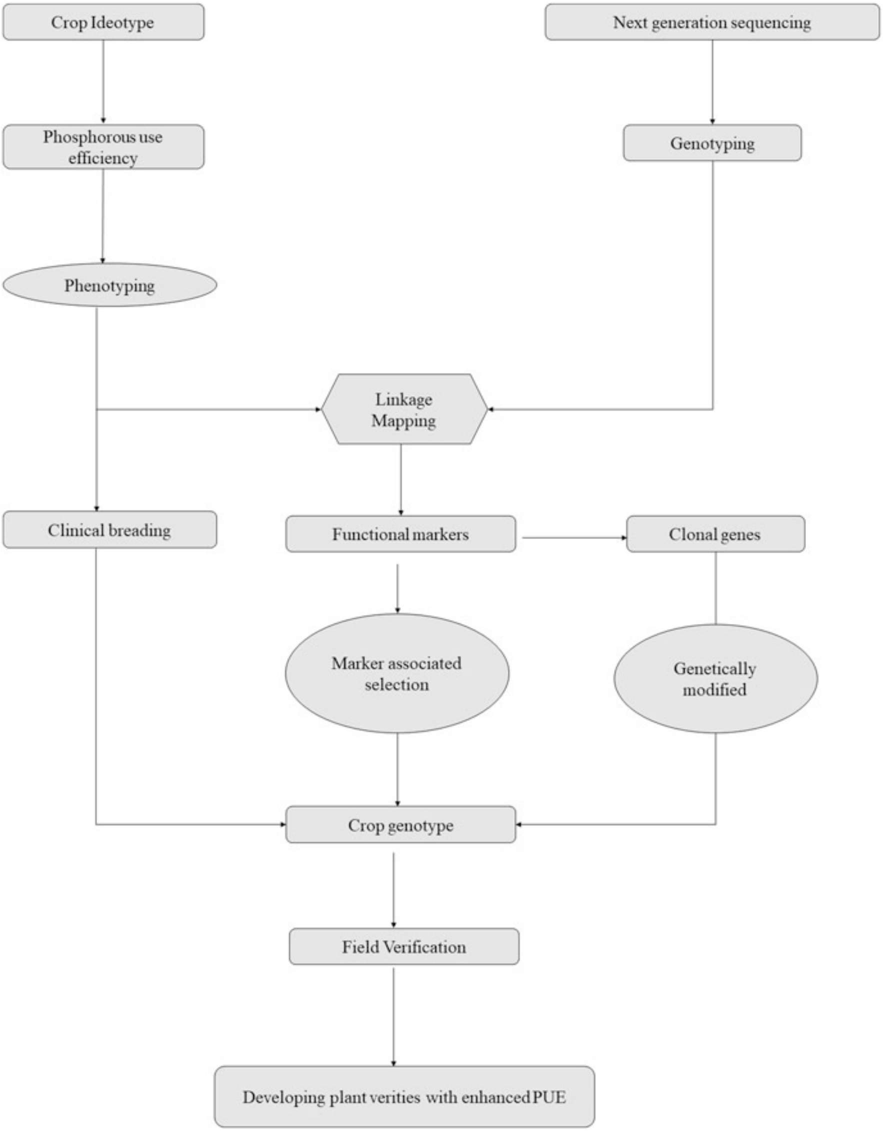

Fig. 7.2 Classical breeding and modern biotechnological approaches for improving phosphorous use efficiency

7.7 Genes Related to Phosphorus Use Efficiency

A broad array of the genes to enhance phosphorus use efficiency can be identified by using complementary DNA (cDNA) libraries (Tian et al. 2007), microarrays, and mutations in phosphorous utilization. In recent years, genes involved in phosphorus use efficiency are identified in tomato, maize, wheat, and rice (López-Arredondo et al. 2014). To increase phosphorus use efficiency, genes involved in transcription factors, signal transduction, hormonal pathways, metabolic pathways, and genes related to proteins involved in phosphorous scavenging mainly phosphorus transporters and acid phosphatases, are targeted. These identified genes linked to phosphorus use efficiency can be characterized by integrating them into other plants. However, their balance expression for the optimal effect might not be forthright because no genetically modified phosphorus use efficiency crop variant has been reported in the commercial pipeline.

7.8 Microbial Inoculants, Biofertilization and Phosphate Fertilizers

Dryland agriculture can use biofertilizers more efficiently (Clair and Lynch 2010) and there will be more dryland areas globally due to ongoing climate change so there is a need for biofertilizers to combat these challenges.

To optimize the effectiveness of phosphorous fertilizers, a technology established on metabolic engineering has been used to allow plants to metabolize phosphite. This technique converts phosphite to inorganic phosphate through the expression of bacterial phosphite oxidoreductase in plants which enables plants to produce inorganic phosphate for their growth and reproduction (López-Arredondo and Herrera-Estrella 2012). Phosphite uses the same tri-phosphate as inorganic phosphate although, cellular machinery cannot use phosphite as they don't have the enzyme needed to convert it into inorganic phosphate. These transgenic crops have the ability to express phosphite oxidoreductase, they can outcompete weeds as weeds cannot use phosphite as their phosphorous source, and thus there is no need to apply herbicides for weed control in these plants (López-Arredondo et al. 2014).

Field trials have been conducted to determine the robustness of the phosphite system in different soil types. In these trials, phosphite inhibited the growth of naturally occurring weeds and these weeds could not give competition to phosphonate dehydrogenase,-engineered plants (Heuer et al. 2017). This technology has been reported for transgenic *Nicotiana tabacum* and Arabidopsis transgenic plants.

7.9 Conclusion

An array of genotypic along with phenotypic traits have been assessed for enhanced phosphorus use efficiency in a broad array of crops. Quantitative trait loci have been identified for these traits and have been successfully used in different breeding approaches. Knowledge of genes involved in phosphorus use efficiency has been reported using marker-assisted breeding approaches. The economical and sustainable advanced biotechnological approaches may be utilized to improve the phosphorus use efficiency in plants. These approaches may include metabolic shifts like using alternative pathways for cytosolic glycolysis and mitochondrial electron transporter. There is also a need for more work on lipid remodeling to enhance phosphorus use efficiency, particularly the replacement of phospholipids by galactolipids and sulpholipids. Still very little is known about the mechanisms of how to improve phosphorus use efficiency and this knowledge gap has to be filled to make commercial genetically modified phosphorus efficient plants to make sustainable global phosphorous cycle.

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Chapter 8

Role of Arbuscular Mycorrhizal Fungi in Plant Phosphorus Acquisition for Sustainable Agriculture

Muhammad Riaz, Muhammad Tehseen Azhar, Muhammad Kamran, Omar Aziz, and Xiurong Wang

Abstract Mycorrhizae are essential for the acquisition of phosphorus (P) and are critical in the acquisition of nutrients that are not readily available to plants. Soil P can be classified into organic and inorganic P. Plant nutrient uptake occurs in two ways: the acquisition by root epidermis and root hairs, which is the direct root absorption method; and mycorrhizal association. Arbuscular mycorrhizal fungi are rhizosphere microorganism that are widely distributed in nature and have important ecological functions. Arbuscular mycorrhizal fungi form a symbiosis with vascular plant roots. Arbuscular mycorrhizal fungi provides plants with essential nutrients including P and nitrogen, and at the same time obtains the required carbon from the plant root system. This chapter presents the mechanisms of arbuscular mycorrhizal fungi for the acquisition of P and promoting plant growth.

Keywords Arbuscular mycorrhizal fungus · Phosphorus · Microorganisms · Mycorrhizal association · Phosphorus absorption · Symbiotic relationship · Mycelium

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Abbreviations

AMF	Arbuscular mycorrhizal fungi
Ca	Calcium
K	Potassium
N	Nitrogen
P	Phosphorus
Pi	Inorganic phosphate
Zn	Zinc

8.1 Introduction

Phosphorus (P) is a crucial macronutrient in the ecosystem, and essential for plants (Khan et al. 2017; Iqbal et al. 2019a). The P in the soil that can be absorbed and utilized by plants is called soil available P (Amanullah et al. 2019; Iqbal et al. 2019b). Many soils are deficient in P in a form usable by plants. As a result, P-based fertilizers are often used for increasing agricultural output and to feed the world's rising population (Richardson 2001; Richardson et al. 2009). Since the soil has a strong adsorption and fixation effect on P, the applied phosphate fertilizer can soon be fixed by the soil, resulting in lower soil available P content, and soil P stress greatly limits productivity (Richardson et al. 2009; Anwar et al. 2017). As a result, this deposit of P in the soil, commonly known as "fixation," increases the input cost of phosphate fertilizer for producers, but it also brings environmental threats.

The use of manure-based fertilizers or organic fertilizers is not usually encouraged due to their cost, insufficient supply, and limited effectiveness in broad-scale agricultural production. It is important to replace the P extracted by crops with a sufficient P supply available to plants to make the farming system sustainable. As a consequence, there is a buildup of net P in the soil, (Burkitt et al. 2007; Richardson et al. 2009; Riaz et al. 2020), and a large portion of it remains in the soil. Therefore, more in-depth knowledge of the methods by which plants may access soil P and/or alter the quantity of P in the soil is also desired. The arbuscular mycorrhizal fungi are considered an efficient strategy to supply P to plants in order to sustain agricultural production under P deficient/stress conditions (Riaz et al. 2020).

8.2 Soil Phosphorus and Acquisition by Plant Roots

Phosphorus is acquired by plants as inorganic phosphate (Pi, $H_2PO_4^-$, HPO_4^{2-}, or PO_4^{3-}) via the roots (Fig. 8.1) (Plassard and Dell 2010). Unfortunately, P supply is limited due to the poor diffusion rates of Pi (Shen et al. 2011), and aluminum hydroxides and iron adsorb this P to calcium (Ca) in alkaline soil with different

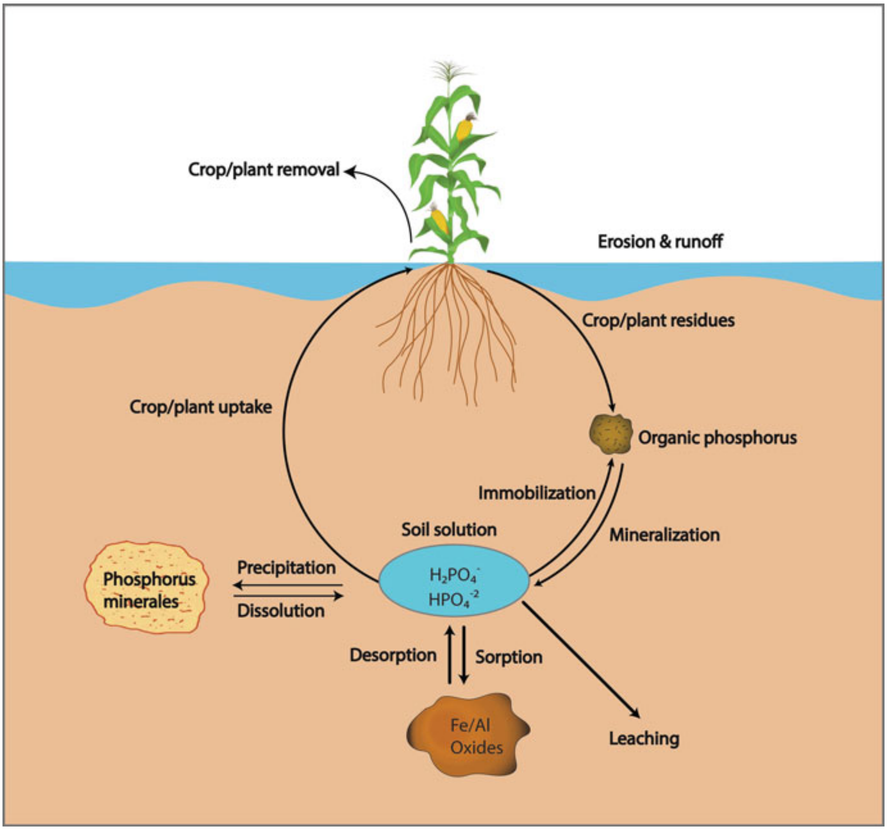

Fig. 8.1 Phosphorus cycle illustration, sources, and plant uptake

solubility (Prietzel et al. 2016), and some of them are bonded to organic matter present in the soil in a different environment (Lambers et al. 2015). Furthermore, the amount of P that enters the soil by deposition is quite low. Thus, changes in P availability are caused by weathering and P utilization in soils throughout the geological aging process (Turner and Condron 2013). As a consequence, the quantity of P available differs dramatically in various soils (Lang et al. 2016).

Most of the soil has a large amount of accumulated P (Amanullah et al. 2016a). The total amount of P in the soil is made up of both organic and inorganic sources. However, only a few plants can access this P (usually 1%). Most of the inorganic P is absorbed by soil components, including clay, sesquioxide, and organic matter, or appears in the form of precipitation of the mineral P (Amanullah et al. 2016b). Organic P accounts for at least 30% to as much as 80% of the total P in the soil. It is mainly composed of monoesters (up to 90%), of which the concentration of diesters, teichoic acid, and phosphonates are small (Condron et al. 1990). It was found that monoester P is mainly a cationic derivative of phytate (mainly oxalate), and a small part (5%) exists as sugar phosphate and diester P (phospholipids and nucleic acids).

The factors that affect the accumulation and transformation of several kinds of organic and inorganic P in the soil are intricate and are exaggerated by numerous challenging courses. The desorption or dissolution of inorganic P from the reservoir of total soil P is required, as is the mineralization of organic P, in order to release ortho-P into the soil solution and make inorganic P more readily available for plant uptake (Amanullah et al. 2021). However, the proportional role of organic P in supplying ortho-P for plant uptake and mobilizing P directly from soil mineral components remains unidentified (Frossard et al. 2000).

Plant roots uptake P in orthophosphate anions from the soil solution, and are absorbed by P transporters in the roots. The concentration of ortho-P (usually 5 μ M) in the soil solution is very low in the majority of soils, and the soil solution P must be quickly replenished from other soil P pools. Therefore, the shortage of P in plants is caused by a low concentration of ortho-P in the soil solution, a slow rate of P diffusion in the soil, and a limited potential for P replenishment in the soil solution (Conyers and Moody 2009). The concentration of ortho-P in the soil solution is influenced by a variety of physical and chemical parameters (Conyers and Moody 2009). P absorbed by plants from soil is dependent not only on the diffusion rate of orthophosphate into the roots (Barber 1995) but also on the growth of the root system, which will allow it to intercept additional sources of P. The low P diffusion from soil to root fundamentally reduces P absorption and inhibits plant growth (Silberbush and Barber 1983; Tinker and Nye 2000). As a result, the application of phosphate fertilizer is beneficial to plant growth by increasing the diffusion rate of P to roots and promoting the development of roots in unexploited soil (Wissuwa 2003).

The maximum concentration of plant-available P is typically present in the 0–0.10 m surface layer of the soil profile. In a study on traits related to the absorption of more P by wheat, it was found that the density of root length in the topsoil was the most significant P absorption attribute. Furthermore, since the majority of the P is found in the topsoil, drying this layer will impair the absorption of P, resulting in “nutrient deficiency”. However, when it comes to relatively fixed nutrients in the soil (such as P) and plants competing for the same nutrient, the situation is different, and root proliferation may be the most effective way to develop nutrient-rich patches.

8.2.1 Microorganism in the Acquisition of Phosphorus

Microorganisms mediate the supply of P to plants by a number of methods, including direct root expansion (Mycorrhizal association), and increased mobilization of orthophosphate by soil organic and inorganic P (Riaz et al. 2020). A significant quantity of fixed P assets is also present in the microbial biomass, which, according to estimates, contributes to about 5% of the total P in the soil. Microorganisms can easily immobilize P from soil solutions and fertilizers, but they often release large amounts of P back into the soil in the form of orthophosphate or organic forms that are readily mineralized are examples of such substances, which may be utilized by the plant (Oberson and Joner 2005). The P turnover rate in biomass of microbes is very fast, and P turnover may occur regardless of the size of the microbial pool. Higher turnover rates were reported in unfertilized soils containing organic inputs, particularly soils that have received readily accessible carbon e.g., glucose. This means that the ability of microorganisms that supply P to plants in the root zone has been significantly improved.

In the rhizosphere, a significant quantity of metabolizable carbon originates from plant roots (Kouno et al. 2002). A variety of bacteria and fungi has been discovered that soil microbes can mineralize organic P and dissolve precipitated inorganic P. These bacteria and fungi have the potential to offer significant pathways for the release of P from different soil P pools. Related microbes have been isolated and utilized as inoculants in the industrial setting in a few instances. Further understanding of rhizosphere microorganisms and their contribution to plant P nutrition is essential (Chen et al. 2002). Although the content of organic and inorganic P in the root zone is significantly reduced, when compared to plant systems, the proportional involvement of microbes in these activities is still unclear (George et al. 2002). In contrast, the unique relationship between roots and mycorrhizal fungi and their role in plant P uptake has been widely known. Mycorrhizal fungi form an interrelationship with most plant species.

Arbuscular mycorrhizal fungi (AMF) are very beneficial to several plant species. The main advantage of mycorrhizal interaction for the absorption of P and a number of other nutrients is that it has the potential to enhance the surface area of plant roots, which can extract a larger volume of soil (Fig. 8.2). Mycorrhizae have the potential to improve the use of organic P and use of nutrient-rich regions (Riaz et al. 2020). Because P is a macronutrient, it involves a significant effect on productivity (Becquer et al. 2014). Even if inorganic P concentrations are low in the soil, plants have limited ability to use it. Plants have evolved a number of strategies for dealing with the P shortages in their environment, including strengthening the soil-root interaction to boost P transport and establish a symbiotic partnership with AMF are just a few of the initiatives (López-Arredondo et al. 2014). AMF inoculation seems to boost nitrogen (N) and P absorption, which results in greater plant development and growth (Balliu et al. 2015). According to Garcés-Ruiz et al. (2017) and Begum et al. (2019), P absorption in the AMF inoculation maize was much improved than in control treatments. AMF has been revealed to improve seedling weight in *Leymuschinensis* by increasing, intercellular CO_2, contents of water and N, and P (Lin et al. 2018). It is believed that AMF inoculation speeds up the uptake and transfer of nutrients specifically P (Zarei et al. 2006; Clausing and Polle 2020). The present data support the notion that the management of P uptake by mycorrhizal interaction is critical for the provision of root P. Dalla Costa et al. (2021) confirmed that AMF significantly increased the nutrient use efficiency of apples. The inoculation of *G. albida* with acerola cherry enhanced the nutrient use efficiency of P (Balota et al. 2011), while nutrient use efficiency of N, P, and potassium (K) was reduced in olive trees after *Funneliformis mosseae* was introduced (Porras-Soriano et al. 2009). So, the AMF affects the nutrient use efficiency of woody plant species as well. A significant increase in nutrient use efficiency in mycorrhizal plants was seen

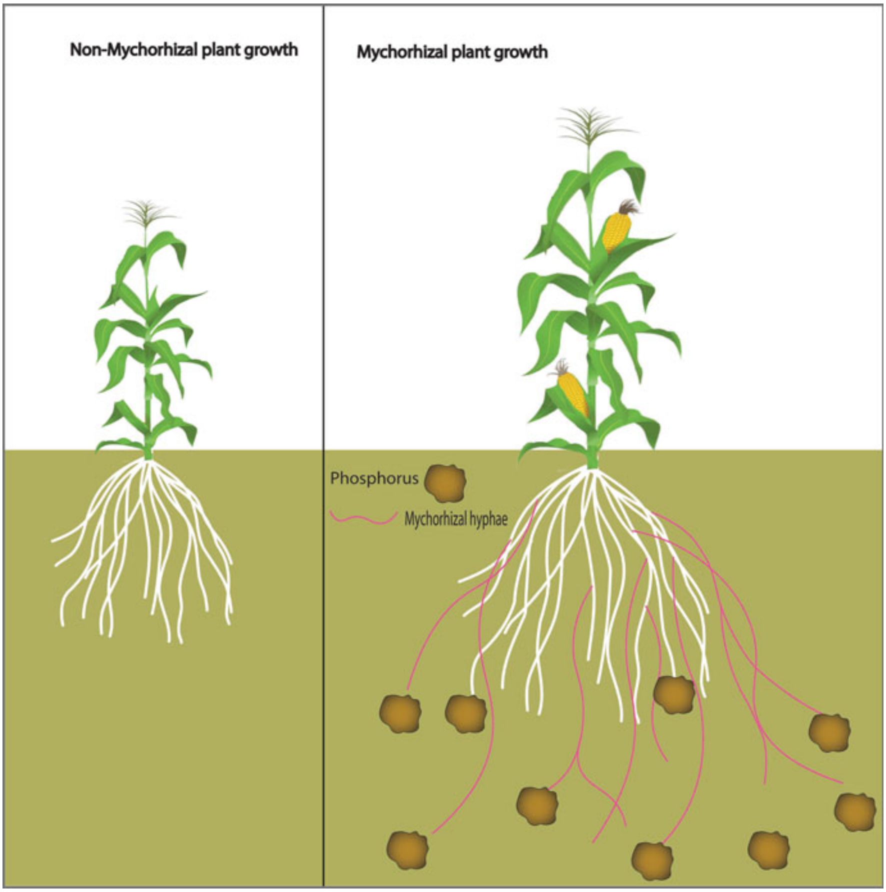

Fig. 8.2 Plant growth difference between mycorrhizal and nonmycorrhizal plants

in plants growing in the presence of *Acaulospora morrowiae* and *Gigaspora albida* in the absence of 50% P. When growing under carbon-limiting circumstances, the buildup of P on AMF hyphae might be ninefold more than on the roots (Hammer et al. 2011). P was improved if shoot of non-mycorrhizal plants by threefold in relation to mycorrhizal plants, demonstrating that AMF enhances nutrient acquisition underneath restrictive P soil conditions and control the delivery of P to plant metabolism within narrow boundaries (Nazeri et al. 2014). As a result of the increased nutrient use efficiency due to AMF inoculation, the requirement for fertilization is reduced, which has an influence on both production costs and environmental pollution.

Due to low soil nutrient levels, AMF is also believed to have a significant role in plant P nutrients in other low-P input systems (Ryan et al. 2000). Different plants depend on mycorrhizal infection to varying degrees, and the P status of the plant as well as the availability of P in the soil influence the degree of infection of the host. In agricultural systems with large amounts of accessible soil P for plants, the plants' need for mycorrhizal infections is also substantially decreased. When the mycorrhizal plant has almost no nutritional benefit in the absorption of P, AMF (although it is widely referred to as a beneficial symbiont) can harm the growth of the plant by consuming host carbon (Ryan et al. 2000). In the colder subtropical crop growing areas of northeastern Australia, where the input of phosphate fertilizer is low, to obtain sufficient nutrients for various crops, high levels of AMF colonization are often required.

8.2.2 Role of Arbuscular Mycorrhizal Fungi in the Acquisition of Phosphorus

The improvement of P efficiency is essential to encourage plant development, crop yields, and decrease the environmental pollution. The soil microbial resources can efficiently relieve P stress in the soil environment (Cibichakravarthy et al. 2015), among which AMF can improve the absorption of P, by the mycorrhizal plant via infecting plant roots which then increase the nutritional status of plants, promote their growth and development, and increase stress resistance (Table 8.1) (Xie et al. 2014). AMF forms a mutually beneficial symbiotic partnership with most plants in more than 80% of terrestrial plant roots (Hooker et al. 1992; Sharif and Claassen 2011; Manaut et al. 2015). In the soil, AMF combines with plant roots to form mycorrhiza, which can form a dense mycelial network system, which has an impact on the morphological structure, physiology, and cell level of mycorrhizal plants, which improve plant water metabolism and nutritional status and increase plant stress resistance (Liu et al. 2014), among which AMF improves the absorption and utilization of P by plants, which has attracted the attention of many researchers (Chen et al. 2017).

AMF help mycorrhizal plants in absorbing P in the soil, and plants provide some products of photosynthesis to help the growth and development of AMF, that is, AMF and plants form arbuscular branches in the mycorrhizal symbiosis (Fig. 8.3) (Smith et al. 2011; Smith and Smith 2011). Rice, in a symbiotic relationship with AMF, absorbs more than 70% of the P available (Yang et al. 2012). As the amount of P present in the soil rises, the efficacy of the AMF symbiosis and P translocation diminishes as well (Miao et al. 2009). Compared with plant roots, AM fungi increase the root surface area of plants and increase the absorption area of nutrients, which ultimately promotes plant growth (Sharif and Claassen 2011). The capacity of mycorrhizal plants to absorb and use P is considerably greater than that of non-mycorrhizal plants, and this difference is substantial (Cui et al. 2019). AMF stimulates the roots of the mycorrhizal plant to produce acid phosphatase and organic acids, activates some insoluble P, and improves plant P acquisition. For example, polyphosphate can be utilized by florae through the transformation of polyphosphatase, which can alleviate the deprivation of P in the rhizosphere of plants.

Table 8.1 Arbuscular mycorrhizal fungi in the uptake of phosphorus under different stress conditions

Serial number	Arbuscular mycorrhizal fungi	Plant type	Stress condition	Effect	References
1	*Rhizophagus irregularis*	*Zea mays*	Low phosphorus	Larger root hair and AMF inoculation increased P uptake	Ma et al. (2021)
2	*Rhizolive consortium*	*Picholine Marocaine*	Nutrient deficiency and Verticillium wilt	AMF increased Ca, K, Na, and P uptake	Boutaja et al. (2020)
3	*Claroideoglomus etunicatum, Rhizophagus intraradices, Funneliformis mossea*	*Glycine max*	P- deprivation under field conditions	AMF enhanced the soybean growth under P deficient condition	Adeyemi et al. (2021)
4	*Glomus* species	*Zea mays*	Regulation of P and Zn	AMF increased plant growth parameters	Saboor et al. (2021)
5	*Glomus intraradices*	(Fenugreek)	Drought stress	AMF showed good effect on diosgenin content and has significant effect on P uptake	Irankhah et al. (2021)
6	*Arbuscular mycorrhizal fungi*	*Zea mays*	Zn deficient and toxic condition	AMF increased Zn contents under bother Zn deficient and toxic conditions	Saboor and Ali (2021)
7	*Funneliformis mosseae*	*Zea mays*	Red soil, rainfall	*R*educes p losses	He et al. (2021)
8	*Glomus intraradices*	*Zea mays*	Field condition	Increased P concentrations	Cozzolino et al. (2013)
9	*Glomus intraradices*	*Hordeum vulgare*	Uranium stress	AMF enhanced the P uptake while decreased uranium uptake	Chen et al. (2005)
10	*Funneliformis mosseae*	*Zea mays*	N/A	AMF enhanced the P uptake	Sawers et al. (2017)
11	*Mixture of AMF strains*	*Glycine max*	Natural field conditions	Increased plant growth parameters and enhanced nutrient uptake	Adeyemi et al. (2020)
12	*Glomus intraradices Scutellospora calospora, Glomus mosseae*	*Vitis vinifera*	Two soils with contrasting P levels	AMF enhanced P, Ca and S uptake,	Schreiner (2007)
13	*Arbuscular mycorrhizae*	*Triticum aestivum*	Calcareous soil, Zn uptake	AMF and P application affected Zn uptake in plant parts	Zhang et al. (2016)

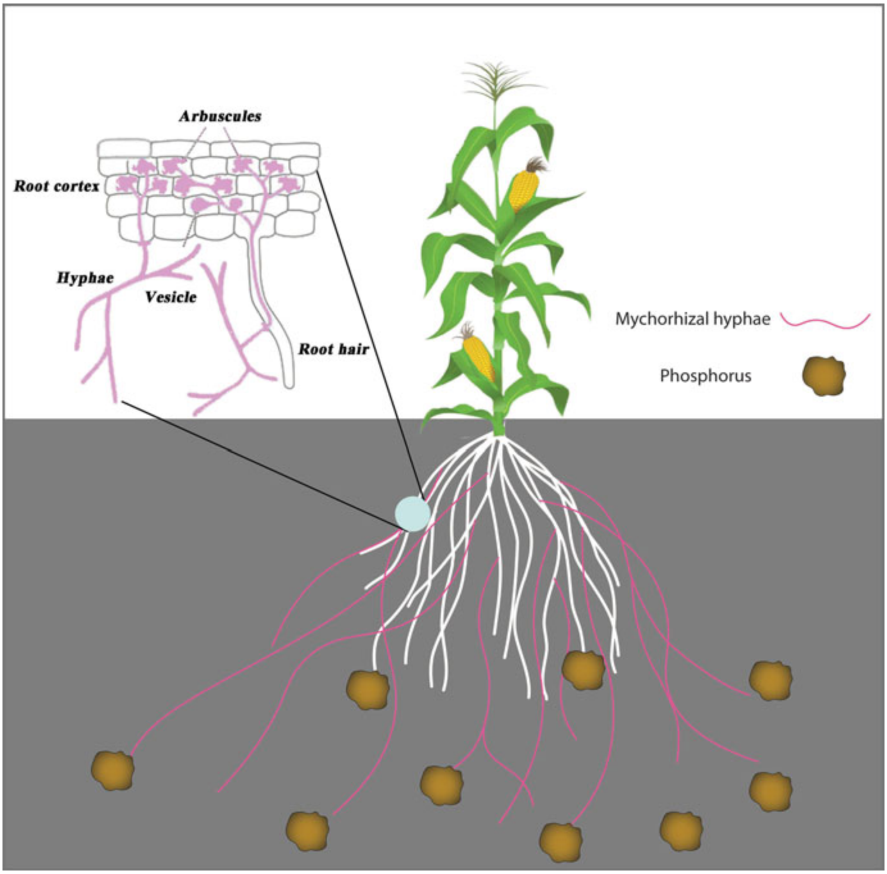

Fig. 8.3 Mechanisms of phosphorus uptake by arbuscular mycorrhizal fungi

The formation of mycorrhiza is affected by soil P levels. When the soil suffers from low P stress, the P supply can be increased by applying P fertilizers to promote plant growth and development; but when the P level exceeds a certain limit, it will inhibit the growth of AMF (Liu et al. 2014). In soils having high fixing ability and low P, AMF can mineralize organic P or help plants effectively use insoluble inorganic P, improving the availability of P in the rhizosphere soil. Therefore, inoculation with AMF can effectively promote changes in soil P form and the uptake of nutrients by the host, and colonization with appropriate AMF can better promote the conversion of soil P in the direction that is beneficial to the mycorrhizal plant absorption. AMF promotes the uptake of P by plants. AMF and P facilitated improvements of *N. tabacum* traits during drought circumstances were shown to be connected with higher absorption of important mineral ions, including N, K, and P, according to the research of (Begum et al. 2020).

AM fungi and plants have a certain level of sensitivity when they establish a symbiotic relationship. Based on results from a bait-plant method (Delavaux et al. 2017) discovered there were statistically noteworthy correlations between AMF and soil P (negative), N (positive), and rarefied tree diversity (Positive), indicating that soil P and N nutrient have had an impact on AMF levels. Fall et al. (2015) found that after 4 months of experiment in sterilized soil and under greenhouse conditions, grass seedlings colonized by AMF produced considerably more total biomass as compared to non-inoculated plants. Franco et al. (2019) demonstrated for the first time that AMF influences the mobilization of P, Fe, Ca, B, Zn, Mn, K, Cu, Mg, and N, in gymnosperms. A significant decrease in nutrient absorption (NPK) was seen in non-inoculated plants due to drought.

Plants infected with AMF had elevated levels of NPK, which was similar to earlier studies on the subject (Calvo-Polanco et al. 2014). The studies showed a considerable upsurge in the absorption of important nutrients such as NPK, magnesium, and Ca under normal and shortage irrigation circumstances due to AMF addition (Abbaspour et al. 2012; Armada et al. 2015). Sitko et al. (2019) have proven that increasing the accessibility of P increases the growth of maize by increasing the intake of other important minerals such as K, magnesium, and Ca. This increase in mineral uptake may be attributed to the effects of minerals on the morphology and hydraulics of roots, respectively (Armada et al. 2015). AM fungal isolate produced favorable results in apple micro when colonized by 4 different isolates of AMF with varying amounts of P (Dalla Costa et al. 2021). Indigenous AMF in the soil has the most significant promotion effect on plants. At present, research on the improvement of P uptake by the mycorrhizal plant by AMF has been extensively carried out, and the research on improving crop yield and the plant survival rate has made great progress, but the research on the mechanism is still in its infancy.

8.2.3 Arbuscular Mycorrhizal Fungi Effect on the Roots of Mycorrhizal Plants

AMF are abundant in the environments. They can form a symbiosis with plants-arbuscular mycorrhizas, thereby changing the plant's root morphology and expanding the range of nutrient absorption by the root system, in that way enhancing the mycorrhizal plant absorption and utilization of nutrients such as P and N. After the plant is infected by AMF, its biomass increases, and the root morphology of the plant changes (Liu et al. 2014).

AM-plants have two mechanisms for extracting P from soil solution at a fast rate and with great efficiency. The root epidermis and root hairs are responsible for direct P uptake in the plant body and in the 2nd pathway which is facilitated by AM, P is absorbed by exterior AM hyphae and delivered to colonized root cortical cells through the AM route (Smith and Smith 2011). Furthermore, mycorrhizal hyphae can collect soil P, which is inaccessible to the majority of nonmycorrhizal plants (Aparna et al. 2011; Sharif and Claassen 2011). As a result, the formation of mycorrhizal symbiosis with suitable fungus species may be used as an alternative technique for reducing plant P deficit. AMF regulates plant auxin signaling pathways by secreting sesquiterpenes to encourage mycorrhizal plants' lateral root growth (Sugiyama and Yazaki 2014). The mycorrhization of clover plants significantly increased primary and secondary lateral roots in the root system (Chen et al. 2017). When subjected to environmental stress, the roots of plants inoculated with AMF will be adjusted accordingly to enhance plant resistance. For example, under drought stress, citrus inoculated with *Funneliformis mosseae* significantly improved root growth parameters including root volume, root area, and root diameter (Liu et al. 2016).

Different types of AMF have differences in the colonization time and colonization effect of the mycorrhizal plant. The higher the adaptability of the two, the greater the contribution of AMF to the mycorrhizal plant. Because there are often multiple strains in the natural environment, molecular biology methods must be used to determine whether the infection impact of AMF on the mycorrhizal plant is better than that of a single strain when used in a mixed application of different strains, in order to be more in line with ecology. The extra-root hyphae, arbuscular branches, and vesicles produced by inoculation with AMF can expand the absorption range and promote the acquisition of P. A five-year field study was conducted on *Lonicera confusa* colonized by AMF, *G. intraradices,* and *G. etunicatum.* AM inoculation resulted in substantial increases in the number of new branches, crown diameter, and plant height. The concentrations of P in leaves and flowers rose, and the absorption of nutrients by plants increased after the administration of AM (An-Dong et al. 2013). The majority of dicotyledons often respond positively to AM inoculation, with improvements in growth and enhanced P absorption, as opposed to cereal crops, which are often believed to be nonresponsive (Grace et al. 2009). Gao et al. (2020) reported that AMF species have a strong symbiotic relationship i.e., *Rhizophagus irregularis* with the cotton.

The expression of specific phosphate transporter family genes and phosphate in cotton biomass were both dramatically increased during the symbiotic relationship between AMF and cotton. These data indicate the advantages of AMF-based inoculation on the uptake of P in cotton. It is important to note that trait flexibility, or the capacity of a species to modify the values of its traits in response to changing environmental circumstances, is an important component influencing a plant's capacity to endure environmental stress (Callaway et al. 2003). Fort et al. (2015) discovered that *Fabaceae* family increased their root/shoot ratio and root surface phosphatase activity when there was a lack of P available. AMF also affect the flexibility of root characteristics. According to a meta-analysis, AMF often increase biomass and length of the root while decreasing the ratio of root/shoot in most cases (Veresoglou et al. 2012), however, the mycorrhizal impact on root/shoot ratio remained non-significant. Additionally, Ryan et al. (2016) discovered that AMF dramatically reduced the root mass ratio of *Trifolium subterraneum.*

A large number of experiments (Guo et al. 2011) have proved that the supply of different concentrations and forms of P can cause significant changes in plant root morphology, including total root length, main root length, lateral root length, root projection area, specific surface area, and volume. When plants are subjected to low-P stress, the root system will undergo morphological changes under the influence of genetic factors, and the root system changes involved in different plants and different genotypes are complex.

8.2.4 Uptake Mechanism of Soil Phosphorus by Mycelium

Arbuscules are considered to be the most critical part of the symbiosis system. It is the place where AMF and the mycorrhizal plant exchange substances, and is regarded as the core of the functional structure of AMF (Gutjahr and Parniske 2017). The arbuscule double-membrane structure separates and combines the AMF and the mycorrhizal plant. From the aspect of form, AMF is located on the side of the arbuscule membrane, and the mycorrhizal plant is located on the side of the arbuscule precursor plasma membrane; from the functional aspect, the double membrane structure is the ion channel and the transporter attached to it are the places for material exchange between symbionts. After the arbuscule branches mature into the plant cells, the survival time is only 1–3 days before they begin to senesce and die. At the same time, the host cells return to the most primitive state and can be colonized by new arbuscule branches which export mineral nutrients while acquiring carbon sources to maintain symbiotic efficiency (Gutjahr and Parniske 2017). Compared with the direct acquisition of plant roots, mycelium has more advantages. Due to its huge biomass and surface area, it enhances the interaction with the soil and expands the absorption range of the mycorrhizal plant roots.

The average diameter of the mycelium is smaller than that of the root system. Therefore, it can enter the soil pores that the root system cannot penetrate (Qiang-Sheng et al. 2011). The extra-root hyphae (often called extra hyphae, extraradical hyphae, or mycelium.) can replace the root hair to uptake P. However, because the specific surface area of hyphae in roots is far less than that of arbuscule branches, although intracellular hyphae and intercellular hyphae are also involved in the transfer of P, their transport efficiency is not as good as that of arbuscule branches. Since AMF and plants do not have firm specificity when forming symbiosis, when the extra-root hyphae encounter other plants during the outward extension process, the root system will be infected again to form a hyphae network (Kytöviita et al. 2003). These mycelial networks can transfer nutrients between the same species and different plants and play an important role in the process of nutrient transfer between plants and natural nutrient cycling (Yao et al. 2003). The mycelial network infects different plants and connects plants with different nutritional statuses to transmit nutrients so that the distribution of nutrient resources forms a dynamic balance (Simard et al. 2003).

Under the premise of the difference in P nutrition between donor and recipient plants, the uptake of P can also be completed through the migration of the hyphae network. In an environment where soil nutrients are relatively scarce, the transfer effect of mycelium on P is more significant. Increased P fertilization, protracted fallow periods, and the growth of non-host crops may result in a reduction in mycorrhizal inoculum levels. The use of appropriate AMF in agricultural systems is essential because it not only makes use of the biopotential for effective P mining and uptake, but also minimizes P fertilizer usage and contamination in the environment. Regardless of the P levels in the soil, inoculating maize plants with AMF lead to a significant enhancement in P absorption as well as grain output (Zhang et al. 2012). AMF and strains that infect effectively, use less carbon, and deliver more P to the host are other key considerations for selecting crop species-preferred AMF and strains.

8.2.5 Arbuscular Mycorrhizal Fungi Modulate the Expression of Phosphorus Related Genes

P deficiency in the mycorrhizal plant encourages infection and AMF symbiosis. AMF induces high-affinity P transporter expression in itself and plants roots to enhance the uptake of available P in the soil and transport it to the desired part of the plant (Table 8.2) (Karandashov and Bucher 2005). At present, there are three kinds of P transporters detected in AMF: *GvPT*, *GiPT,* and *GmosPT*. When subjected to low P stress, the extra-root hyphae will increase the expression of the P transporter gene and promote P absorption in the soil. When P is transported from hyphae to arbuscule branches, AMF induces the expression of some members of the mycorrhizal plant's *Pht 1* family on the plasma membrane of the arbuscule precursor to enhance the plant's uptake of P in mycorrhiza, such as inoculation on *Medicago truncatula, G. radiata* significantly enhanced the expression of certain P transporters in arbuscule branches (Fiorilli et al. 2013).

OsPHT1.11 is the first AM-specific P transporter identified in rice, and a homologous (*MEDtr; PHT1.4*) in *Medicago truncatula* (Paszkowski et al. 2002). *OsPHT1.11* is also required for the establishment of AMF symbiosis in rice. Both *OsPHT1.11* and *OsPHT1.13* are essential for the establishment of an AMF symbiosis, indicating that grasses have developed a particular strategy for P acquisition via symbiosis with the AMF (Sun et al. 2012). In a symbiotic system, the P transporters of AMF influence P absorption and the expression levels of the transporter genes in the mycorrhizal plant. In the root periphery, mycorrhiza-inducible *PHT1* is involved in P absorption, and its loss causes P deficit in the plant (Rausch and Bucher 2002; Tian et al. 2013). In relation to non-infected control, AMF infection increases *ZmPHT1.3* expression 44-fold and reduces *ZmPHT1.6* expression 135-fold in maize (Tian et al. 2013). AMF colonization also has an effect on auxin and ethylene levels in the mycorrhizal plant, which are important regulators of lateral root and root hair formation (Rubio et al. 2009).

Table 8.2 Transporters in plants and arbuscular mycorrhizal fungi involved in nutrient uptake

Sr. No	Name	Transporter	Fungal/plant	References
1	*Glomus mosseae*	GmosPT	Fungal phosphorus transporter	Balestrini et al. (2007)
2	*Lotus japonicus*	LjAMT2;2	Plant N transporters	Guether et al. (2009)
3	*Glomus intraradices*	GiPT	Fungal phosphorus transporter	Maldonado-Mendoza et al. (2001)
4	*Lotus japonicus*	LjPT4	Plant phosphorus transporter	Volpe et al. (2016)
5	*Solanum lycopersicum*	StPT3	Plant phosphorus transporter	Rausch et al. (2001)
6	*Glycine max*	GmAMT4.1	Plant N transporters	Kobae et al. (2010)
7	*Petunia hybrida*	PhPT5	Plant phosphorus transporter	Breuillin et al. (2010)
8	*Oryza sativa*	OsPT2, 6, 11	Plant phosphorus transporter	Paszkowski et al. (2002)
9	*Gigaspora margarita*	GigmPT	Fungal phosphorus transporter	Xie et al. (2016)
10	*Medicago truncatula*	AMT2;3	Plant N transporters	Breuillin-Sessoms et al. (2015)
11	*Medicago truncatula*	MtPT4	Plant phosphorus transporter	Breuillin Sessoms et al. (2015)
12	*Glomus intraradices*	GintAMT 2,	Fungal N transporter	Perez Tienda et al. (2011)
13	*Glomus versiforme*	GvPT	Fungal phosphorus transporter	Harrison and Vanbuuren (1995)

The mycorrhizal plant can absorb substantial amounts of P nutrients via symbiosis with fungus. Both symbiosis and mycorrhizal P absorption are unaffected by tomato *PHT1.4* (a tomato homolog of the *PHT1.11*) (Bari et al. 2006). In dicots, direct P absorption is the dominant mode of absorption. The isolation of StPT3 protein from potato mycorrhiza enhanced P absorption (Rausch et al. 2001). The expression of *MtPT4* P transporter gene was significantly enhanced after the mycorrhization of *Medicago truncatula* (Pumplin and Harrison 2009). Through gene sequence and transcription analysis of multiple plants, it is found that there are differences in the number of Pht 1 family members in different plants, and the regulation mechanism of Pht1 family genes by AMF is also different, such as *A. thaliana* and rice genome determination. It was shown that there were 9 and 11 Pht 1 transporter family members for soil available P uptake and plant P transport (Goff et al. 2002), among the 11 Pht 1 transporter family members of rice, *OsPT11* was only used when AMF invaded.

Through the study of the P transporter promoter in *Arabidopsis thaliana* (Mudge et al. 2002), it was found that the *Pht1; 3* and *Pht1; 4* promoters in this family are responsible for the uptake of P from the soil by the roots of the plant. Chiou et al. (2001) studied specific binding alfalfa and found that when P is deficient, it stimulates the roots to increase the abundance of *MtPT1* P transporter, and this protein is significantly related to the P concentration in rhizosphere soil. These genes will respond when P is deficient, but there is no obvious positive correlation with AMF infection, and they may even be inhibited due to the establishment of a symbiotic relationship. For example, the *MtPT2* gene in *Medicago truncatula* inoculated with fungi (Harrison et al. 2002) and the *ZEAma: Pht1; 3* genes after maize mycorrhization (Benedetto et al. 2005).

8.3 Conclusion

Phosphate rock deposits are expected to be depleted in the next 80–100 years, and the inherent inadequacy of phosphate fertilizers is low. It is important to improve the P absorption efficiency of agricultural plants and agricultural systems. Agricultural practices, such as using soluble P fertilizers instead of poorly soluble fertilizers, designing fertilizer granules, and using liquid P fertilizers instead of granular fertilizers (highly Ca) should all be improved and all these are examples of methods for improving phosphate fertilizer absorption efficiency. Research has worked on the relationship between annual crops and AMF inoculation in the greenhouse. A deeper knowledge of the interplay between AMF and perennial plants, particularly under natural field conditions, is necessary to investigate its potential. AMF and plants have a certain degree of selectivity when they establish a symbiotic relationship. Different types of AMF may have completely different effects on the same plant. Indigenous AMF in the soil has the most significant promotion effect on plants. Different types of AMF have differences in the colonization time and colonization effect of the mycorrhizal plant. The higher the adaptability of the two, the greater the contribution of AMF to the mycorrhizal plant. Because there are often multiple strains in the natural environment, molecular biology methods must be used to determine whether the infection impact of AMF on the mycorrhizal plant is better than that of a single strain when used in a mixed application of different strains, to be more in line with ecology.

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Chapter 9
Phosphorus Cycle Enzymes to Remedy Soil Phosphorus Deficiency

Alhassan Idris Gabasawa

Abstract Phosphorus is indispensable for the production of crops and is the most expensive of all macro-nutrients. Phosphatase enzymes allow to maintain the soil phosphorus fertility, notably in phosphorus-deficient soils. Some soil properties impair phosphorus utilization by crops. For instance, sesquioxides in acidic soils fix phosphorus into insoluble iron and aluminium precipitates and, in turn, make phosphorus unavailable to plants. This chapter reviews phosphorus-cycle enzymes with focus on remedying problems of soil phosphorus fertility. Soils contain up to 100–3000 mg P kg^{-1} soil, mostly in orthophosphate forms. Phosphorus in agricultural soil solution usually ranges from 0.01 to 3.0 mg P kg^{-1}. About 30–65% of the total soil phosphorus is present in organic forms. Most soil organic P is present in organic complexes that must be cleaved by enzymes to release inorganic P available for plant uptake. Dynamics of water-soluble and labile soil organic phosphorus fractions in the rhizosphere are connected with the activities of the extracellular phosphatase enzymes. The amount of phosphorus available in the soil solution represents a small portion of plants' need. Therefore, soil P should be constantly solubilized by abiotic and biotic processes, including enzymatic hydrolyses, to provide available P to plants.

Keywords Acid phosphatase · Alkaline phosphatase · Phosphorus · Phosphorus cycle enzymes

Abbreviations

ADP	Adenosine diphosphate
ATP	Adenosine triphosphate
DMRT	Duncan's multiple range test
SAMNUT	Samaru groundnut
SPAD	Soil plant analysis development

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9.1 Introduction

Phosphorus is a fundamental element for rhizobium bacteria in the transformation of atmospheric nitrogen (N_2) into an ammonium (NH_4), the plant-available nitrogen form (Anwar et al. 2017; Khan et al. 2017; Amanullah et al. 2021). Rhizobium is capable of synthesizing nitrogenase, an enzyme that catalyzes the conversion of dinitrogen (N_2) into two ammonia (NH_3) particles. An effective nodule is pink coloured which is due to the presence of a protein called leghaemoglobin. This uncommon protein is composed of iron (Fe) and molybdenum (Mo) and functions in restricting oxygen thereby ensuring a nodule environment that is relatively low in oxygen. This judiciously allows the bacteria (rhizobium) to grow and conveniently fix atmospheric nitrogen. As an important energy source, phosphorus gets included when an adenosine diphosphate (ADP) is formed due to a conversion of 16 molecules of adenosine triphosphate (ATP) when every molecule of atmospheric nitrogen is reduced to ammonia (NH_3). The photosynthetic process generated adenosine triphosphate is stored for plants' subsequent utilization. Via its essential functions in plants as an energy source, phosphorus, in phosphates form, impacts nodule development. Suboptimal phosphorus level, on the other hand, limits root development, photosynthetic process, sugar translocation, and other functions that, directly and/or indirectly, control leguminous nitrogen fixation capacities.

Availability of phosphates for plants' assimilation, from phytate, is strictly subject to its (phytate's) hydrolysis by phosphatases, which term is a general name that is being used in describing a wide array of groups of soil enzymes that are responsible for a hydrolytic breakdown of various ester-phosphate bonds of organic anhydrides of orthophosphoric acid (H_3PO_4) and other phosphates into inorganic phosphatic types (Iqbal et al. 2017). Rhizosphere phosphatase types may either be from soil microorganisms or plant roots that were believed to have been playing essential functions in fertilizer phosphorus cycles in the soil ecosystems. This was as duly perceived via their interrelationships with plant growth vis-à-vis phosphorus stressed environments (Amanullah et al. 2016a, b). They are also a vital indicator of fertile soils as they affect the acquisition and use efficiency of phosphorus in plants (Iqbal et al. 2019a, b).

9.2 Soil Enzymes

9.2.1 Soil Enzymes and Enzyme Activity

Nutrient cycling in soils involves physical, chemical, and biochemical reactions. The biochemical processes are mediated by microorganisms, plant roots, and soil animals (Tabatabai 1994b). All biochemical reactions are catalyzed by enzymes, which are proteins with catalytic properties due to their power of specific activation. Enzymes are substances that, without undergoing permanent alteration, cause chemical reactions to proceed at faster rates (Tabatabai 1994b). All metabolic processes of all living materials (microbes, animals, or plant roots) in the soil depend on these processes. Many classes of enzymes exist, such as respiratory (concerned with energy generation) and those concerned with cell synthesis. Soil enzyme production and its control on nutrient availability and soil fertility are controlled by the factors influencing soil microbial activity (Sinsabaugh et al. 1993). The microbial enzymatic activity contribution to phytate hydrolysis within the rhizosphere is insignificant. This is in comparison to root-derived enzymes mediated breakdown of the enzymes (Martin 1973). Availability of organic compounds for soil organisms is needed for the effective decomposition of pesticide residues, which mechanisms are termed co-oxidation. Soil reaction may, on the other hand, influence enzymatic sorption while its (the soil pH) effect on the enzymatic sorption has only been currently realized to be an important measurement tool for phosphatase activity (Li et al. 2004).

On the other hand, soil enzyme activity makes information on its biochemical processes available. It is a pH and microbial biomass regulated (Dick et al. 1988) process. The activity of soil enzyme is a time variable that is limited by a supply of substrate availability (Degens 1998). It may also provide a useful interrelationship between carbon processing and the composition of a given microbial community (Waldrop et al. 2000). Soil enzymatic activity information being utilized in determining microbiological features of soils are paramount for soil health and quality and in detecting soil changes (González et al. 2007) and are therefore soil degradation "sensors" as they readily concatenate soil microbial status (Aon and Colaneri 2003) and physicochemical information (Baum et al. 2003). They are also part of the cycling and availability of plant nutrients to crops and can be utilized as one of the important soil functioning indices (Nannipieri et al. 2003).

9.2.2 Nitrogen Cycle Enzymes

Nitrogen cycle enzymes are called amidohydrolases. There exist diverse amidohydrolases in the soil all of which involvement in hydrolyzing added organic and native nitrogen to soils (Tabatabai 1994a) is clearly important and essential in maintaining soil fertility (Wick et al. 1998). They also catalyze the hydrolysis of substrates with peptide bonds, using simple peptides and dipeptides (Pascual et al. 1997). More so, Wick et al. (1998) suggested that the proteolytic potential of soil, which they reflect, indicates their capacity to degrade proteins. Among these, however, amidase, urease L-asparaginase, and L-glutaminase are the most important as reported by Tabatabai (1994a).

9.2.2.1 Ureases

The enzyme, urease, is accountable for urea fertilizers' hydrolysis, after application into the soil, to ammonia (NH_3) and carbon dioxide (CO_2) with the resultant soil reaction (pH) rise (Andrews et al. 1989). This results into a rapid nitrogen loss to the atmosphere via NH_3 volatilization (Simpson and Freney 1988). Urease activities in soils have received a lot of attention due to this role, ever since it was first reported by Rotini (1935). This process is considered vital in the regulation of nitrogen supply to plants after urea fertilization. Majorly, soil urease originates from plants (Polacco 1977) and microorganisms found as both intra- and extra-cellular enzymes (Burns 1986). Zantua and Bremner (1977) reported that the plants- or microorganisms-extracted urease, on the other hand, is rapidly degraded by proteolytic enzymes in the soil. This suggests a significant fraction of ureolytic activity in the soil being carried out by extracellular urease, which is stabilized by immobilization on organic and mineral soil colloids. The soil urease activity is influenced by many factors, including soil depth, amendments, cropping history, organic matter content, heavy metals, and such environmental factors as temperature (Yang et al. 2006).

9.2.2.2 Amidase

The soil enzyme amidase catalyzes amides and ammonia hydrolysis and the corresponding carboxylic acid and acts on such bonds as carbon-nitrogen but for linear amides peptide bonds. It is specifically for aryl and aliphatic amides, which cannot act as substrates as reported by Kelly and Clarke (1962). The enzyme is in wide distribution in nature and it is being detected in microbes and animals (Bray et al. 1949). It is also reported to be available in the foliage of maize (*Zea mays L.*), sorghum (*Sorghum bicolor L.*), Alfalfa (*Medicago sativa L.*), and soybean (*Glycine max L.*) by Frankenberger and Tabatabai (1980a, b, 1982). Amongst the microbes that were shown to have amidase activity include: yeast (Joshi and Handler 1962), bacteria (Clarke 1970), and fungi (Hynes 1975). Cantarella and Tabatabai (1983) reported that the substrates of the amidase enzyme are rich sources of nitrogen for plant assimilation.

9.2.2.3 L-Asparaginase

The activity of the L-Asparaginase enzyme was first detected in soils by Drobni'K (1956). The enzyme is reported as catalyzing L-aspartic acid and ammonia hydrolysis. It is in wide distribution in nature. Wriston (1971) reported its detection both in microbes and plants and the enzyme has also been shown to widely vary in different strains of microbes.

9.2.2.4 L-Glutaminase

The enzyme L-Glutaminase is one of the amidohydrolases that play a significant role in nitrogen supply to plants. It is a hydrolase that specifically acts upon all carbon-nitrogen bonds but for linear amides peptide bonds. The reaction that is catalyzed by the enzyme includes L-glutamine hydrolysis to yield ammonia and L-glutamic acid. L-Glutaminase has been reported to have been detected in many animals (Sayre and Roberts 1958), microbes (Imada et al. 1973), and plants (Bidwell 1974). The ones detected in plants and microbes are, however, the most probable L-glutaminase activity sources in the soil, although Roberts et al. (1972) reported the main source as being microbial.

9.2.2.5 Proteases

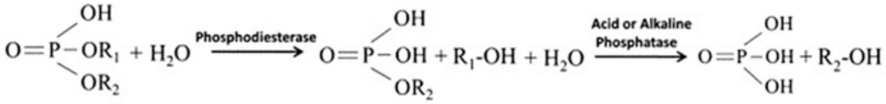
The nitrogen cycle enzymes Proteases play a significant role in soil nitrogen mineralization as reported by Ladd and Jackson (1982). It is, therefore, a vital process that regulates the quantity of plant-available nitrogen and, consequently, plant growth and development. The enzyme, within the soil, is reported by Nannipieri et al. (1996) to generally be related to organic and inorganic colloids. The level of activity of this extracellular enzyme may be an indication of the biological capacity of a given soil for the enzymatic conversion of the substrate, which is independent of the extent of microbial activity. It also plays a vital role in the microbial ecology activities of the ecosystem (Burns 1982).

9.3 Phosphorus Cycle Enzymes

The general name phosphatase has been employed to describe a wide group of enzymes catalyzing esters and anhydrides of H_3PO_4 hydrolysis (Schmidt and Laskowski 1961). Phosphatases include phosphoric monoester hydrolases, phosphoric diester hydrolases, triphosphoric monoester hydrolases, enzymes that act upon phosphoryl-containing anhydrides, and such enzymes that act on phosphorus-nitrogen bonds as phosphoamidase. Phosphomonoesterases (*i.e.,* acid and alkaline phosphatases), have extensively been studied. The enzymes are classified as acid and alkaline phosphatases due to the optimum activities they respectively show under acid and alkaline ranges (Speir and Ross 1978). Many structural and enzymatic adaptations have been developed by plants in order to adapt to low phosphate availability. Acid phosphatases transcription activity, which tends to increase under phosphorus-limited conditions (Ndakidemi 2006) is an example of such adaptations.

9.3.1 Phosphomonoesterases

As earlier stated, phosphomonoesterases happened to be the soil phosphatases that are studied most. The phosphomonoesterases such as acid phosphatase (orthophosphoric monoester phosphohydrolase, EC 3.1.3.2) and alkaline phosphatase (orthophosphoric monoester phosphohydrolase, EC 3.1.3.1) are classified according to the optimum pH of their activities. This readily varies towards acid and alkaline ranges, respectively for the two phosphomonoesterases (Dick 2011). Phosphomonoesterases are particularly known to hydrolyze a variety of such phosphomonoesters in the soil as *p*-nitrophenyl phosphate, phenylphosphate, β-glycerophosphate, and β-naphthyl phosphate. The general equation involved in the hydrolysis of phosphomonoesters into orthophosphates in the presence of acid or alkaline phosphatase as a catalyst is:



$$O{=}P(OH)(OR_1)(OR_2) + H_2O \xrightarrow{\text{Phosphodiesterase}} O{=}P(OH)(OH)(OR_2) + R_1\text{-}OH + H_2O \xrightarrow{\text{Acid or Alkaline Phosphatase}} O{=}P(OH)(OH)(OH) + R_2\text{-}OH$$

Where R represents either alcohol or phenol groups or nucleosides (Privat de Garilhe 1967).

As earlier partly introduced, they are classified into five, as follows: (i) phosphoric monoester hydrolases, (ii) phosphoric diester hydrolases and (iii) triphosphoric monoester hydrolases. The other two are (iv) enzymes acting on phosphoryl-containing anhydrites, and (v) such enzymes acting upon phosphorus-nitrogen bonds as the phosphoamidases (Florkin and Stortz 1964). A phosphatase is generally, an enzyme that removes a phosphate group from its substrate by hydrolyzing phosphoric acid monoesters into a phosphate ion and a molecule with a free hydroxyl group, as explained by Makoi and Ndakidemi (2008).

Specifically, and in terms of soil environment, phosphatase indicates an enzymes group that produces inorganic phosphate forms by hydrolytically breaking a wide array of ester-phosphate bonds of anhydrides of orthophosphoric acid (H_3PO_4) and organic phosphates (Harrison 1983). Yadav and Tarafdar (2003) reported that such types of phosphatases as phytases can increase the dephosphorylation (hydrolysis) rate in organic phosphorus (P_o).

Rhizosphere phosphatases may either be of soil microbial origin (Richardson et al. 2001) or plant roots' (Hayes et al. 1999). The hydrolysis of soil organic phosphorus is chiefly mediated by the soil microbial activity (Li et al. 1997), although roots of plants still have phytase and phosphatase activities as reported by Tarafdar and Jungk (1987). Phosphatases are known to play significant roles in phosphorus cycles within soil environments (Speir and Ross 1978). This is as evidenced by their correlation with plant growth and phosphorus starvation. Other than being a good soil fertility indicator, phosphatases also significantly contribute to various systems of the soil (Eivazi and Tabatabai 1977; Dick et al. 2000). Whenever a soil phosphorus deficiency symptom is perceived, for example, secretion of acid phosphatase by plant roots is enhanced in order to increase solubilization and remobilization of phosphates, thereby promoting the plants' ability to adapt to the noxious phosphorus-deprived situation (Karthikeyan et al. 2002). These enzymes, therefore, affect the phosphorus-acquisition and phosphorus-use efficiency potentials of crop plants. This was in part reaffirmed by a study of Gabasawa et al. (2012), as indicated in Tables 9.1 and 9.2 below.

They also catalyze the hydrolysis of phosphorus-ester bonds from organic matter, resulting in the release of inorganic phosphorus, as reported by Garcia et al. (1995). They are the key enzymes in phosphorus cycling in soils (Pascual et al. 1998). They show changes in the quantity and quality of soil phosphorated substrates (Rao and Tarafdar 1992). The aforesaid enzymes are good at releasing phosphates from extracellular and cellular organic compounds as, respectively, reported by Duff et al. (1994) and Bariola et al. (1994) at different stress levels.

Table 9.1 Effect of groundnut cultivar and phosphorus rate on acid and alkaline phosphatases (μmol g^{-1} soil ha^{-1})

Treatment	Acid phosphatase	Alkaline phosphatase
Cultivar (C)		
SAMNUT 10	0.0044^{a}	44.52^{a}
SAMNUT 11	0.0042^{a}	37.99^{a}
SAMNUT 21	0.0030^{c}	14.56^{c}
SAMNUT 22	0.0035^{b}	29.11^{b}
SAMNUT23	0.0040^{ab}	19.34^{c}
SE±	1.7E-4	2.220
Phosphorus (kg P_2O_5 ha^{-1})		
0	0.0035^{b}	23.09^{b}
60	0.0041^{a}	35.12^{a}
SE±	1.0E-4	1.404
Interaction		
G × P	**	**

**Significant at 1% level of probability; Means followed by the same letter(s) within treatment in a column do not differ significantly according to Duncan's multiple range test

Table 9.2 Interaction of groundnut cultivar and phosphorus rate on acid phosphatase activity (μmol g^{-1} soil ha^{-1})

	Phosphorus rate (kg P_2O_5 ha^{-1})	
Treatment	0	60
Cultivar (C)		
SAMNUT 10	0.0049^{ab}	0.0038^{cd}
SAMNUT 11	0.0049^{ab}	0.0035^{de}
SAMNUT 21	0.0023^{f}	0.0036^{de}
SAMNUT 22	0.0026^{f}	0.0044^{bc}
SAMNUT 23	0.0027^{f}	0.0053^{a}
SE±	2.38E-4	

Means followed by the same letter(s) within treatment in a column do not differ significantly according to Duncan's multiple range test

The activities of phosphate transporters are increased to optimize uptake and remobilization of phosphate in phosphorus-deficient plants. The amount of acid phosphatase secreted by plants is genetically controlled and differs with crop species and varieties as well as crop management practices (Wright and Reddy 2001).

It was reported by Yadav and Tarafdar (2001) that several studies indicated the quantity of secreted enzymes by legumes as being higher than that by cereals to the tune of up to 72%. Chickpea roots, for example, secreted higher quantities of acid phosphatase than maize. The acid and alkaline phosphatase activity was observed to correlate with organic matter in various studies (Aon and Colaneri 2003).

9.3.1.1 Acid and Alkaline Phosphatases

Acid and alkaline phosphatases, in particular, hydrolyze the ester bonds that bind phosphorus to carbon (that is, C-O-P ester bonds) available in organic matter. In the process, inorganic phosphorus is summarily discharged from the phosphorus that is bound organically, such as dead root systems, leaf litter other organic debris without an accompanying C release (Harrison 1983). Phosphorus from organic sources can then be utilized by the plant after it must have been phosphatase-hydrolyzed (George et al. 2002).

Acid Phosphatase

Acid phosphatase is a type of enzyme, used to free attached phosphate groups from other molecules during digestion. It is stored in lysosomes and functions when these fuse with endosomes, which are acidified while they function; therefore, it has an acid *pH* optimum (Baldwin et al. 2001). These enzymes are also used by soil microorganisms to access organically bound phosphate nutrients. An assay on the rates of activity of these enzymes may be used to ascertain biological demand for phosphates in the soil (Dick et al. 2000). Acid phosphatase secreted from roots was increased under phosphorus-deficient conditions (Hayes et al. 1999) and in hydroponic and soil cultures (Li et al. 2003, 2007) and, consequently, the hydrolysis of phytate was also increased.

Alkaline Phosphatase

Alkaline phosphatase is a hydrolase enzyme in charge of detaching phosphate groups from many molecule types, such as alkaloids, nucleotides, and proteins. The phosphate group detachment process is termed dephosphorylation. Alkaline phosphatases, as hinted by the name, are highly effective in alkaline environments (Baldwin et al. 2001). Therefore, it has been attributed to soil bacteria, due to its absence from the rhizosphere of axenically grown plants (Tarafdar and Claassen 1988). Its activity was also reported to be highest in soils that contained increased amounts of organic matter and it was least in soils with little or no organic matter addition (Joner and Jakobsen 1995).

9.3.1.2 Soil Phosphatase Activity

The use of certain crop plants tends to enhance the activity of phosphatase for the fact that acid phosphatase and other exudates are secreted by their roots (Jones 1998) just the way cultivation of some plant types may change potential phosphatase activity in soils. Studies indicated that plants living in phosphorus-deprived soils do actively secrete enzymes into their rhizosphere (Ozawa et al. 1995). Yadav and Tarafdar (2001) reported, in a study, that plants, especially in phosphorus-limiting soils, are known to secrete acid phosphatase immediately after roots emergence. Phosphatases are, probably, best known for their capacity for nucleic acid degradation (Razzell and Khorana 1959). This explains their obvious significance in the transformation and cycling of phosphorus in the soil. Acosta-Martinez and Tabatabai (2000) also reported soil pH and inductive enzymes as affecting their synthesis strongly.

It was observed in a study by Gabasawa (2021) that there were differences between two Nigerian agro-ecological zones, in terms of groundnut yields. This was due to acid and alkaline phosphatase activity differences of the agro-ecologies as respectively indicated in Figs. 9.1 and 9.2.

Quality of soil organic matter may, however, dictate the rate of extracellular phosphatase production, with the aid of arbuscular mycorrhizal fungi (AMF) hyphae as the activity phosphate is chiefly controlled by the availability of organic phosphorus to hydrolytic breakdown (Stewart and Tiessen 1987; Joner and Jakobsen 1995). Hence, the capacity of roots to secrete phosphatase extracellularly may readily be aroused when simply hydrolyzable substrates are available (Tarafdar and Claassen 1988). It may, however, be muffled by non-hydrolyzable organic phosphorus forms, as observed by Azcon and Elatrash (1997). Phosphatase activities may also be markedly influenced by the host plant (Azcon and Elatrash 1997) and the species of fungi available (Rao and Tarafdar 1993). An even increased phosphates' activity is, however, more commonly observed in the rhizosphere as reported by Tarafdar and Jungk (1987). Roots of plants that have a higher phosphatase activity also have greater chances of utilizing soil organic phosphorus (Helal 1990). This activity does not, however, directly serve as a phosphorus-status measurement, it rather suggests a potential release of phosphorus from organic sources as reported by McCallister et al. (2002). Phosphatase enzymes, which majorly originate from microbes, are broadly spread in nature thereby playing a significant function in the phosphorus nutrition of plants (Tabatabai 1994b). Also, they play very essential roles in chemically inclined transformations that aid orthophosphate discharge from diverse organic phosphorus compounds (Cookson 2002). Phosphatases persist in soils, due probably to humic materials' adsorption and hence they might be representatives of an important soil property history. Their evaluation might suggest a summed estimate of potential in phosphorus mineralization (McCallister et al. 2002).

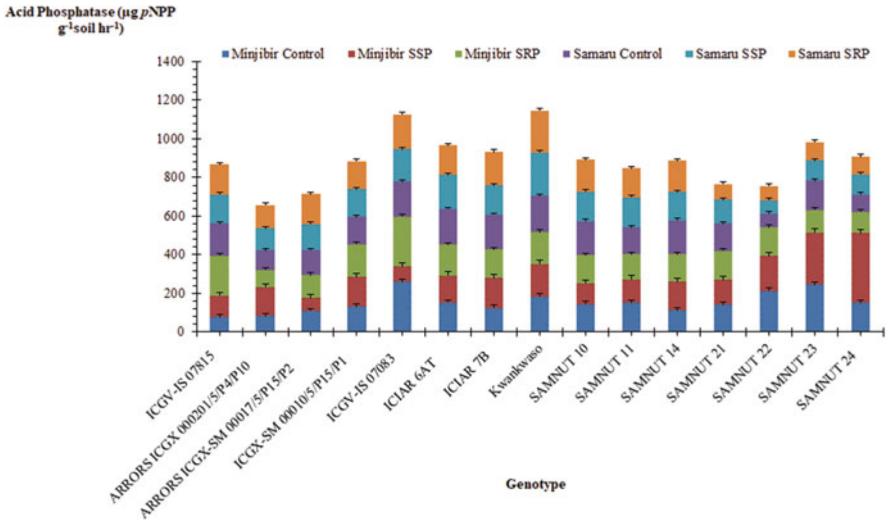


Fig. 9.1 Genotype by phosphorus versus location interaction on acid phosphatase activity

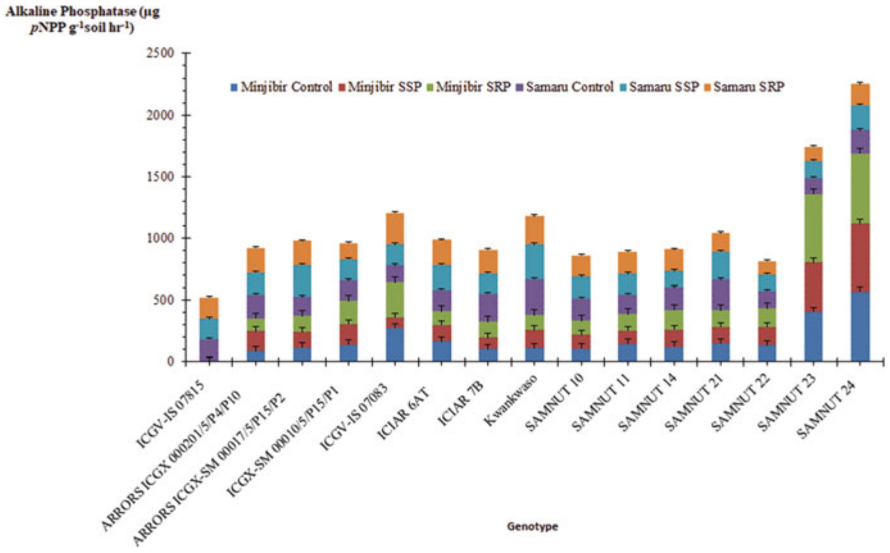


Fig. 9.2 Genotype by phosphorus versus location interaction on alkaline phosphatase activity

Phosphatase is higher in the topsoil and the rhizosphere. This is where the majority of the just-produced and less humified soil organic matter mostly exists (Tarafdar et al. 2001) and plays vital roles in the plants and microbial phosphorus acquisition, and consequently, in its cycling within the soil environment as observed by Nadgórska-Socha et al. (2006).

9.3.2 Role of Fertilizer Phosphorus in Biological Nitrogen Fixation

Fertilizer phosphorus is a fundamental element for rhizobium bacteria that transforms atmospheric nitrogen into ammonium (NH_4), which is the plant-available form of nitrogen. Rhizobium is capable of synthesizing the nitrogenase enzyme, which catalyzes the atmospheric nitrogen conversion into the two ammonia (NH_3) particles. The pinkish colour peculiar to viable nodule (called effective), is due to a protein presence that is known as leghaemoglobin. This uncommon iron (Fe)- and molybdenum (Mo)- contained protein functions in restricting oxygen thereby ensuring nodule with a low oxygen environment. This permits the bacteria to live comfortably and fix atmospheric nitrogen. Phosphorus gets included as an important source of energy when the 16 adenosine triphosphate molecules are converted into an adenosine diphosphate due to the reduction of every atmospheric nitrogen molecule into ammonia. The adenosine triphosphate is generated during the photosynthesis process when light energy is converted and stored as adenosine triphosphate for later utilization by the plant. Phosphorus impacts nodule development via its essential functions in plants as a source of energy. Suboptimal phosphorus levels limit root development, photosynthetic process, sugar translocation, and other functions that, directly and/or indirectly, control leguminous nitrogen fixation capacities. The important practice of liming acidic soils to 6.5–7.0 pH range is important to the phosphorus and symbiotic nitrogen fixation relationship. It improves the accessibility of soil phosphorus for plant assimilation and makes the soil environment more conducive for such beneficial bacteria as the diverse strains of rhizobium.

9.4 Biological Nitrogen Fixation

Biological nitrogen fixation is the process in which, in the presence of nitrogenase, atmospheric nitrogen ($N{=}N$) is reduced to ammonia. Nitrogenase is, however, a biological catalyst that is found, naturally, only in certain microbes such as the symbiotic *Rhizobium* and *Frankia,* or the free-living *Azotobacter* (Brockwell et al. 1995). Biological nitrogen fixation is the principal source of agricultural nitrogen input into agrarian systems (Gabasawa and Yusuf 2012). Rhizobia (synonymously called nitrogen-fixing bacteria) (Moreira et al. 2008), are symbiotic bacteria that evolve on the roots of specific legume hosts thereby forming new organs, called nodules. Within these nodules, the bacteria proliferate, differentiate into bacteroids, and subsequently fix the atmospheric nitrogen into NH_3 as highlighted by Denarie et al. (1992).

The biological nitrogen fixation process is brought about by both free-living soil microorganisms and symbiotic associations of microorganisms with higher plants.

Groundnut, like other leguminous counterparts, fixes atmospheric nitrogen by symbiotically working with the root nodules rhizobia. The rhizobia initially infect root hairs of the legume to produce these nodules (Tate 1995), and the nodule becomes an abode for the bacteria. It is from the nodules that the bacteria now access their energy via their plant host thereby taking free atmospheric nitrogen from the soil air and process same into combined nitrogen. In return, however, the plant receives the fixed nitrogen from the nodules and from which it produces food and forage protein. Biological nitrogen fixation is, therefore, an efficient source of nitrogen (Peoples et al. 1995a, b).

About 100–200 kg of atmospheric nitrogen fixed by groundnuts per hectare under diverse field conditions has been reported by Boddey et al. (1990). Both, the amount of atmospheric nitrogen fixed and the proportion of total crop nitrogen derived from atmospheric nitrogen-fixation, can, however, be controlled by a cultivated variety (Giller et al. 1987) and/or water deficit level (Peoples et al. 1992). Some studies revealed that the amount of atmospheric nitrogen-fixed exceeded the pod growth nitrogen need; hence, the atmospheric nitrogen-fixed leftover available in the vegetative parts would be distributed into the soil following pod harvest (McDonagh et al. 1993). Other studies have, contrarily, hinted at the fact that despite the elevated atmospheric nitrogen-fixation levels, net nitrogen-balance that follows pod harvest can be negative such that nitrogen reserves in the soil can be exhausted due to *Arachis* cropping (Peoples et al. 1992). Some locally sourced soybean varieties were observed to have obtained larger percent nitrogen derived from the atmosphere (% Ndfa) (65%) than Nasoko (53%), an ‘improved’ variety, in a study by van Vugt et al. (2018) in which variability in percent nitrogen derived from the atmosphere, atmospheric nitrogen-fixed and grain yields were compared.

9.4.1 The Nitrogen Fixation Process

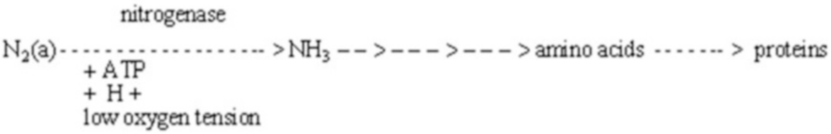
The element nitrogen or ‘azote’, meaning ‘without life’, as Antonie Lavoisier called it about 200 years ago, has proved to be anything but lifeless, as it is a component of poisons, explosives, food, and fertilizers (Schoot Uiterkamp 1990). The atmosphere contains about 10^{15} tonnes of atmospheric nitrogen, and the nitrogen cycle involves the transformation of some 3×10^{9} tonnes of atmospheric nitrogen year^{-1} on a global basis as reported by Postgate (1982). However, transformations, like atmospheric nitrogen-fixation, are not exclusively biological. Fertilizer industries provide very important quantities of chemically fixed nitrogen. Lightning also provides, probably, about 10% of the global fixed-nitrogen supply (Havlin et al. 1999).

9.4.2 Significance of Biological Nitrogen Fixation to Soil Fertility

Much land has been degraded worldwide due to agronomic practices during tillage, bush burning, fertilizer and pesticides applications, and other human influences (Balfour 1977), and it is time to stop the destructive uses of land and to institutionalize a serious reversal of land degradation (Burris 1994). Biological nitrogen fixation plays a key role in land remediation. The total per annum input of nitrogen from biological nitrogen fixation into the terrestrial environment ranged from 139 to 175 million tonnes of nitrogen as reported by Burns and Hardy (1975) and Paul (1988). The biological associations in arable lands account for a range between 25% and 30%. This represents 35–44 million tonnes of nitrogen as reported by Sprent and Sprent (1990). The symbiotic system of *rhizobia* and legumes associations has the highest quantitative impact on the nitrogen cycle. This is a gigantic avenue for fixed nitrogen contribution to soil ecosystems from the legumes (Tate 1995). The plant's benefit from bacterial nitrogen fixation appears to be highest in symbiosis, for example, between legumes and rhizobia, while associative bacteria do not form nodules but use plant exudates (Cristina et al. 2007).

9.4.3 Nitrogen-Fixing Organisms

Microbial atmospheric nitrogen-fixation can take place in association with higher plants and/or the free-living state (Jones and Jacobsen 2005a). The mechanisms of atmospheric nitrogen-fixation appear to be quite similar in most atmospheric nitrogen-fixing procaryotes (Zahran et al. 1995), however, the atmospheric nitrogen-fixation mechanism can, biochemically, in its simplified form be written as follows:



$$N_2(a) \xrightarrow[\substack{+\,\text{ATP} \\ +\,\text{H}+ \\ \text{low oxygen tension}}]{\text{nitrogenase}} NH_3 \dashrightarrow \dashrightarrow \dashrightarrow \text{amino acids} \dashrightarrow \text{proteins}$$

This mechanism, above, indicates that atmospheric nitrogen-fixing systems can survive in nitrogen-deficient soils. Adenosine triphosphate is the source of energy necessary for the cleavage and reduction of atmospheric nitrogen into ammonia (NH_3). In *rhizobia*, for instance, adenosine triphosphate results from oxidative degradation of sugars and related molecules. These sugars are produced, during photosynthesis, by the host plant, and then transferred to the root nodules. In general, therefore, for each gram of atmospheric nitrogen fixed by rhizobium, the plant fixes 1–20 grams of carbon, via photosynthesis. This is an indication that biological nitrogen fixation requires additional energy which can be used to produce more photosynthates in NO_3-fed plants. However, the extra energy cost of atmospheric nitrogen-fixation can be safely carried by a majority of field-grown legumes, with little or no production loss (Takishima et al. 1989).

All organisms capable of fixing atmospheric nitrogen (that is, converting the stable nitrogen in the atmosphere into a biologically useful form) belong to a biological group named prokaryotes. A wide range of organisms can fix atmospheric nitrogen, however, only a very small proportion of species are capable of doing so. Zahran et al. (1995) reported that an estimated 87 spp. in 2 genera of *Archaea*, 38 genera of bacteria, and 20 genera of *Cyanobacteria* have been identified as *Diazotrophs* that are capable of fixing atmospheric nitrogen. This wide variety of *Diazotrophs* guarantees one or two representatives in most of the ecological niches and also ensures ready replenishment of lost nitrogen (Sprent and Sprent 1990).

9.4.4 Factors Limiting Biological Nitrogen Fixation

Interactions between microsymbionts and plants are complicated by numerous environmental factors/conditions included in climatic, edaphic, and managerial issues. A rhizobium-legumes symbiosis may excellently be achieved in loamy but not sandy soils, in a sub-humid but not the Sahel region, or in tilled but not zero-tilled plots, and/or vice-versa. These factors may either affect the microsymbionts, the host plants, or both, such that crop production level can be not higher than that allowed by the highest limitation factor (Brockwell et al. 1995).

9.4.4.1 Physical Constraints

- *Temperature*: Surface soil temperature in some parts of the tropics can occasionally reach 65–70 °C and that of the sub-surface (at 5 cm depth) can be above 50 ° C (Dudeja and Khurana 1989). This temperature can sufficiently be as high as to restrict germination and destroy a lot of bacteria. Although lots of cyanobacterial species can form akinetes (spore types), which are highly desiccation-resistant, most of the free-living heterotrophic rhizobia and other atmospheric nitrogen-fixers are seldom heat resistant. This surmises that deleterious soil temperatures can destroy a majority of the surface layer bacteria, although all the same, some rhizobia can survive for some periods in dry soil temperature under 70 °C (Marshal 1964). Clay particles and soil organic matter are, however, a helpful refuge for bacteria against the desiccative high temperature such that sandy soils are types commonly with high temperatures (Giller and Wilson 1991).

In Samaru, northern Guinea savannah of Nigeria, for example, a rhizobial population of only 4–40 cells g^{-1} of soil was found in the upper 5 cm depth of the soil, whilst a population of up to 10^4 cells g^{-1} of soil was observed at a 20–25 cm depth by Day et al. (1978). In general terms, therefore, bacteria are less tolerant to high temperatures in moist than dry soils. Higher temperatures can restrict root nodulation, and consequently, prevent atmospheric nitrogen-fixation activities of legumes (Day et al. 1978) even when soil insulates the root nodules against the highest deleterious temperatures (Giller and Wilson 1991).

- *Soil texture*: As stated under temperature (above), depending on how finely textured soil is, the piercing heat due to high temperatures can, more or less, be insulated from vulnerably reaching the bacteria such that clay soils are best at protecting the rhizobia against the harsh solar rays, whereas sandy soils are relatively the worst.
- *Drought*: Rhizobial population in the soil is proportional to soil moisture (Bushby and Marshal 1977). Stressful drought affects atmospheric nitrogen-fixation of legumes, negatively, as the atmospheric nitrogen-fixation rate is more sensitive to soil moisture content reductions than such other processes as photosynthesis, transpiration, or leaf growth. Deep rooting grain legumes, such as cowpea, relatively do well in water-stressed environments than their shallow rooting counterparts if they successfully penetrate deeply before the drought starts or become noxious (Sinclair et al. 1987).
- *Soil salinity and sodicity*: Saline soils are measured as having electrical conductivity (EC) of >4 dS m^{-1} or due to mismanaged irrigation practices (Nortcliff 1988), while sodic soils are those as sodium (Na)-rich as to constraint growth and/or development of most crop plants that may or may not be saline. The soil reaction of both saline and sodic soils is normally >8.5, which property can result in a reduced availability of phosphorus, iron (Fe), zinc (Zn), manganese (Mn), and boron (B) needed for plant growth. Water stress, due to osmotic potential, is, however, the main problem with saline soils. Salinity-caused is more permanent than drought-caused as the former is always over when the drought is gone (Sprent 1984). The legumes hosting the *rhizobia* are very much more sensitive to saline conditions than the *rhizobia* themselves, as some (*rhizobial*) strains are adapted to saline conditions, although they still are sensitive to salt stress in a prevailing alkaline soil reaction condition. The ions of chloride (Cl^{-1}) are exceptionally deleterious to *rhizobial* survival (Elsheikh and Wood 1989).

Sprent (1984) reported that groundnut nodulation is, relatively, not sensitive to salinity effect due, probably, to the mode of *rhizobial* infection that is a direct type. A wild relative of pigeon pea (*Cajanus cajan*), *Atylosia platycarpa*, is also more insensitive to salinity such that no setback is observed in its nodule record even at NaCl and $CaCl_2$ salinities of up to 8 dS m^{-1} while even at 12 dS m^{-1}, effective nodules were still observed to be formed. The nodulation in *C. cajan* was, however, reduced even at 4 dS m^{-1} as reported by a study of Subbarao et al.'s (1990b). Once its initial nodulation is successfully completed, *C. cajan* can also grow in higher (8 dS m^{-1}) saline soil conditions without symptoms of injurious consequences featuring on development or functioning of the next nodule as observed by Subbarao et al. (1990a).

- *Waterlogging*: As *rhizobia* are normally aerobic, a waterlogged soil condition that necessitates a rapid use of free oxygen by organic substrates, especially at high soil temperatures, threatens a habitable environment for the *rhizobia*. Nevertheless, some strains of *Bradyrhizobium* and *Rhizobium meliloti* possess dissimilatory nitrate reductase, an enzyme that functions as an acceptor of electrons. This enables the bacteria to thrive in oxygen-depleted environments (Daniel et al. 1982). Lack of oxygen is also a major constraint to root respiration, as it can result in an immediate loss of nitrogenase activity (Witty et al. 1986). Even legumes that can grow in waterlogged conditions such as *Aeschynomene* and *Sesbania* some species, their root nodules do not develop in watered conditions. Stem nodules are, however, not affected even by submerged conditions, presumably, as oxygen is transported to the nodules via *Lacunae* within the shoot (Eaglesham and Ayanaba 1984).

de Willigen and van Noordwijk (1989) reported that some legumes can still transfer some air (oxygen-laden) to their roots from the shoot; while some roots respond, adaptively, to increase oxygen supply from shoot to themselves as their root porosity is increased. Nodules can also develop enlarged "lenticels" and a thick cortex which assist in an exchange of gasses across the surface of nodules (Minchin and Summerfield 1976). Accumulation of Mn and Fe, to a toxic level, that may inhibit *rhizobia* and plants, are among others, additional hitches related to water-logged environments (Giller et al. 1989a).

9.4.4.2 Chemical Constraints

- *Toxicity*:
- *Soil acidity*: Low soil reaction (pH) is important, especially, in tropical soils, which are majorly acidic, and the problem can arise, either, from low pH survival medium troubles or that of chemical changes in soil, which is caused by high acidity, especially due to large amounts of aluminium (Al) or Fe and Mn in solution, on one hand, and decreased phosphorus and molybdenum; and the lack of calcium (Ca), in most acidic soils as reported by Giller and Wilson (1991). Low soil reaction (*pH)* is reported to usually affect bacterial symbionts, although there are still those that can regulate the pH of their internal environment as reported by O'Hara et al. (1989). This category is reported to have a higher rate of survival potential under the prevailing low pH. A number of *Bradyrhizobium* strains were, for example, tested to be more Al tolerant than their *Bradyrhizobium japonicum* counterparts as observed by Johnson and Wood (1990).

Arachis hypogaea and *Vigna unguiculata* are reported to be the lowest soil pH tolerant legumes. This is, especially, in comparison to *Phaseolus vulgaris* and/or *Glycine max* (Munns 1978), although *A. hypogaea* still indirectly suffer some problems, in the acid soil, due to the high need of pod for Ca, which is deficient in such (acid) soils. High available nitrogen levels can, in addition, greatly retard nitrogen fixation because the plant, automatically, stops releasing a chemical that attracts the bacteria to the roots, and the plant, consequently, disallows nodules formation (Jones and Jacobsen 2005b).

- *Nutrient deficiencies*: Deficiency in nutrients that are critical for the growth and development of plants and/or bacteria can tantamount to tremendous declination in the number and physical features of the root nodules that are to be formed including its size, and hence the fixed atmospheric nitrogen amounts. In majorly weathered and highly leached acid soils, many essential nutrients (*e.g.*, phosphorus and molybdenum) are deficient as they are bound into plant-unavailable forms, whereas other nutrients, like Fe and Zn, are inherently unavailable at high soil reaction conditions. Nutrient deficiency can, however, be in vogue in semi-neutral pH soils due to leaching or continuous cropping (Giller and Wilson 1991). Guerinot (1991) reported that several such other nutrients as micronutrients (for example cobalt, boron, copper, or molybdenum) can be deficient, thereby limiting nodulation and therefore constraining the biological nitrogen fixation.
- *Pollution*: Edwards (1989) and Roberts (1991) reported that a number out of the various agricultural pesticides can have deleterious repercussions on *rhizobial* survival and, consequently, the legumes' nodulation. Graham et al. (1980), therefore, cautioned *rhizobia* inoculators to pay unique attention while inoculating seed coats of legumes and while applying agrochemicals to the seed surface. Polluting agricultural soils, with sewage sludges that are contaminated with heavy metals, has drastically and completely undermined atmospheric nitrogen-fixation in many crops. Giller et al. (1989b) emphasized that this is sequel to the vulnerability of rhizobium to the toxic features of heavy metals.

9.4.4.3 Biological Constraints

The fixation process, in the atmospheric nitrogen-fixing system, is strongly related to the physiological state of host-plant, such that pruned and lopped leguminous plants, for example, have a decreased photosynthetic ability (Thies et al. 1995). It impairs atmospheric nitrogen-fixation and can cause nodule decay, which in turn results in the shedding of a big number of root zone *rhizobia* as observed by Brockwell et al. (1995). The absence of the required rhizobium, presence of crop competition, nematodes, and insects are some other biotic factors that drastically limit atmospheric nitrogen-fixation in an otherwise efficient nitrogen-fixing legume as reported by Thies et al. (1995). According to Roughley (1985), competition and antagonism, from other organisms, are also highly influential in the thriving chances of free-living atmospheric nitrogen-fixing *rhizobia*.

9.5 Nitrogen-Phosphorus Dynamics and Root Nodulation

The capacity of leguminous crops to improve soil nitrogen fertility may be hampered by low concentrations of inherently available soil phosphorus (Buresh et al. 1997). This is because good nodulation and atmospheric nitrogen-nitrogen fixation levels, among which soil nitrogen fertility depends, require huge amounts of phosphorus (Giller 2001). Knowledge of phosphorus dynamics in the soil is, therefore, fundamental in predicting its bioavailability and the risk of its transport from soil to water bodies (Zheng et al. 2004). Lajtha and Harrison (1995) highlighted that plants adopt two main strategies to promote *nitrogen* and phosphorus acquisition and use, including (a) those directed towards the improved acquisition and/or uptake, and (b) those targeted to conserve use.

9.5.1 Root and Root Nodules

Nitrogenase, as earlier mentioned, is an enzyme that is very sensitive to oxygen. Limited oxygen condition is identified via compartmentation in cyanobacteria (through heterokysts in *Anabaena azollae*), active respiration (in *Azotobacter*), synthesis of *leghaemoglobin* in a macro-molecule synthesized by the symbiotic partners (*i.e.*, *rhizobia* and host plant). The *rhizobium* synthesizes the '*haeme*' portion; and the plant, the '*globine*'. Like human *haemoglobin*, *leghaemoglobin* fixes O_2. It is responsible for the red or brown colour of active (that is: nitrogen-fixing) nodules. Non-nitrogen-fixing nodules have white or green nodule contents when the *globine* has degenerated as reported by Tripathl and Psychas (1992). Generally, therefore, nodules' effectiveness can best be evaluated by the degree of pink, brown or red colouration of atmospheric nitrogen-fixing bacteroid and; would, consequently, not be considered when classifying currently active nodulation (Peoples et al. 1989; Tripathl and Psychas 1992).

9.5.2 Chlorophyll Content of Plant Leaf

Chlorophyll, one of the most vital plants' chelates, has the capacity of directing solar energy into chemical energy through the photosynthesis process. In addition to being a plant nitrogen status indicator, chlorophyll content (CC) is also an important leaf senescence indicator (Noodén et al. 1997). The chlorophyll content can also be adjusted due to response to possible stresses of the environment (Neufeld et al. 2006). Several CC examining methods exist, including the extraction method, which involves extraction of the chlorophyll in a solvent followed by spectrophotometric in-vitro measurements. This method is, however, laborious, costly, destructive, and time-consuming. Alternatively, however, the use of chlorophyll meters (*e.g.*, the SPAD-502, from Spectrum Technologies, Plainfield, Illinois, USA), provides a quick, non-destructive and simple method for estimating the chlorophyll content of a given leaf (Xiong et al. 2015).

Chlorophyll meter, therefore, provides a non-destructive and rapid diagnosis of plant nitrogen status is easily applicable even in field experiments (Uddling et al. 2007; Vollmann et al. 2011) and has widely been tested for many crops (Turner and Jund 1991; Follett et al. 1992; Peterson et al. 1993; Varvel et al. 1997). Chlorophyll meter measurements of a crop are correlated with its petiole nitrate-nitrogen, leaf nitrogen, and yield, and they (the measurements) are less variable than petiole nitrate (Bronson et al. 2001). Enhanced mineral nutrition is known to assist in increased chlorophyll content of plants and consequently helps in achieving a higher photosynthetic rate (Feng et al. 2002). A close interrelationship exists between the content of chlorophyll of plants versus their nitrogen concentration (Richardson et al. 2001). This implies the possibility of using its measurement to compliment atmospheric nitrogen-fixation measurement (Vollmann et al. 2010).

Using soil plant analysis development (SPAD) meter to assess leaf chlorophyll concentration has, relatively, become common, although calibrating SPAD meter readings into direct units of chlorophyll concentration remains difficult. A comprehension of the relationship between these two parameters, as necessity is another hitch (Markwell et al. 1995). Diverse studies have estimated the SPAD readings and chlorophyll content relationships per leaf area in different plant species. This relationship (between SPAD readings and chlorophyll content per leaf area) has, however, been found to differ widely among plant species, and even within the same species in some cases (Uddling et al. 2007; Parry et al. 2014; Lin et al. 2015). This difference is presumed to be due to variation in conditions of measurement (Hoel and Solhaug 1998) and to leaves' structural differences that cause a difference in reflection and/or scattering effects of light. About 80% of leaf nitrogen is attributed to chloroplasts and about 50% of the leaf nitrogen is utilized in photosynthetic proteins in leaves. Only 0.5–1.5% of the leaf nitrogen is, however, allocated to chlorophyll, depending on the growth environment and species of plant (Le Roux et al. 1999). An increased leaf nitrogen content allocated to chlorophyll–protein complexes, due to decreased irradiance has been reported for many plant species (Evans and Poorter 2001). More so, the allocation ratio of leaf nitrogen to chlorophyll is reported to be affected by nitrogen supplementation conditions (Makino and Osmond 1991). Comprehending the leaf characteristics and environmental factors' effects on the SPAD readings, and the relationship between chlorophyll content and leaf nitrogen content per leaf area will be questions of critical importance when the SPAD is used to guide nitrogen management practices in agriculture systems.

9.6 Conclusion

Phosphorus occurs in soils as mineral phosphates as well as organic compounds. The importance of organic phosphorus in plant nutrition is reported to still be relatively vague. However, it is reported to possibly account for about 30–80% of the total agricultural phosphorus in soils. The soil organic phosphorus sources, on the other hand, must first be hydrolyzed by phosphatases before judiciously being assimilated by the plant, thereby circumventing against noxious phosphorus deficiency. Legumes' access to phosphorus may, therefore include an increase in acid phosphatase (orthophosphoric monoester phosphohydrolase; EC 3·1.3·2) secretion, especially under phosphorus-deficient conditions. There is also reported hydrolysis of mono-ester soil organic phosphorus at low soil reaction (pH), and hence an increased availability of orthophosphate. Acid phosphatases are known to differ from alkaline phosphatases by displaying an optimal enzyme activity below pH 7·0, and by generally being characterized by low substrate specificity. As such, a wide range of plants and/or plant tissues show a non-specific acid phosphatase enzyme activity.

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Chapter 10
Phosphorus Nutrition Enhancement of Biological Nitrogen Fixation in Pastures

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Abstract Nitrogen (N) is the most limiting plant nutrient in agroecosystems. The increasing use of N-containing fertilizers increases greenhouse gas emissions and groundwater contamination. Biological nitrogen fixation is an eco-friendly source of N that can reduce the use of mineral fertilizers. Biological nitrogen fixation potentially accounts for half of the total N on earth and has been reported to supply

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approximately 50–128 × 10^9 kg N $year^{-1}$ in different agroecosystems. However, optimal biological nitrogen fixation depends on phosphorus (P) nutrition. For instance, the conversion of dinitrogen to ammonia by nitrogenase enzyme depends on P as adenosine triphosphate. Here, we review the role of P in biological nitrogen fixation with focus on the increase in the productivity of pasture crops, and the use of mycorrhization in pastures. Mycorrhization, the symbiotic association between arbuscular mycorrhizal fungi and plants, can account for 80% of total P uptake by plants. Mycorrhization provides optimal soil P required for N transfer from N_2-fixing forage legumes to non-N_2 and N_2-fixing forage grasses during intercropping. Intercropping N_2-fixing forage legumes and non-legumes can fix up to 16—-124 kg N ha^{-1} and contribute about 475–700 kg N ha^{-1} $year^{-1}$ on pasture fields. Further, the inclusion of N_2-fixing and P-mobilizing forage crop species with non-N_2-fixing and non-P-mobilizing species facilitates root interaction and acquisition of N and P. The association of pasture crop mixtures, arbuscular mycorrhizal fungi, and N_2-fixing bacteria further promotes crops' tolerance to biotic and abiotic stresses.

Keywords Biological nitrogen fixation · Phosphorus · Arbuscular mycorrhizal fungi · Pasture productivity · Legumes · N_2-fixing bacteria · Non-N_2-fixing forage crops · P-mobilizing pasture species · Tripartite association

Abbreviations

N	Nitrogen
N_2	Dinitrogen
NH_4^+	Ammonium
NO_3^-	Nitrate
P	Phosphorus

10.1 Introduction

Biological nitrogen (N) fixation is a globally known eco-friendly source of N in agroecosystems that can reduce the contribution of agriculture to climate change. Biological N fixation harnesses the abundant atmospheric dinitrogen (N_2) for crops utilization and improved productivity of the agroecosystems (Gupta et al. 2019). The biological N fixation process involves the conversion of N_2 to ammonia (NH_3) by microbes, mainly bacteria, with the aid of an enzyme known as nitrogenase (Galloway et al. 2008; Sprent 2009; Bargaz et al. 2018; Taylor et al. 2020). Biological N fixation accounts for approximately half of the total N on earth and serves as the most abundant source of natural N in the terrestrial biosphere (Angus and Grace 2017; Ramírez-Puebla et al. 2019; Taylor et al. 2020). The adoption of biological N fixation-promoting practices in cropping systems could drastically reduce the use of N-containing chemical fertilizers and consequently prevent the loss of an excessive amount of mineral N into the environment (Foley et al. 2011; Lannetta et al. 2016; Sulieman and Tran 2016; Mahmud et al. 2020). Thus, increased exploration of biological N fixation in agroecosystems could be a highly viable and healthy option in providing adequate N for increased crop productivity compared to the excessive use of inorganic fertilizers.

Pastures cover about 68% of the global agricultural fields (FAO 2019) and are one of the terrestrial landscapes where biological N fixation could reach its climax (Vitousek et al. 2013). Pasture fields offer important ecological functions and services including biomass production, carbon sequestration, climate regulation, and conservation of crops' and microorganisms' biodiversity (Jimoh et al. 2020). Pasture crops mainly provide forages for livestock and are well adapted to broad climatic conditions (Allen et al. 2011; Mahmud et al. 2020). Several pasture legumes and grasses can fix a substantial amount of N (Neyra and Döbereiner 1977; Bustamante et al. 2006; Lopez-Hernandez et al. 2006; Herridge et al. 2008; Cech et al. 2010; Marques et al. 2017; Aguirre et al. 2020). Despite biological N fixation being an eco-friendly source of large amounts of renewable N, it is still an under-exploited phenomenon in pasture fields (Peoples et al. 2009a). Hence, there is a need for the deliberate exploitation of biological N fixation in pastures for optimal productivity and sustainable ecosystem functioning.

Many reports of biological N fixation-driven increase in crop productivity suggest that optimal phosphorus (P) availability is important for optimal biological N fixation (Ormeño-Orrillo et al. 2013; Khan et al. 2017; Míguez-Montero et al. 2020). For example, several studies have indicated that low biological N fixation under low P was reversed when P inputs were increased (Benner and Vitousek 2012; Alkama et al. 2012; Míguez-Montero et al. 2020). The underlying mechanism is adduced to the essentiality of P on optimum performance of N_2-fixing bacteria within the rhizosphere (Aziz et al. 2016; Bello et al. 2018; Rurangwa et al. 2018). In addition, P plays regulatory functions in N cycling in the agroecosystems which also have impacts on biological nitrogen fixation (Smith 1992). As P is the most limiting plant nutrient after N (Amanullah et al. 2016a, b; Pérez-Fernández et al. 2017; Lopez-Delacalle et al. 2020), inadequate P nutrition disrupts carbon cycling within plants, reduces nutrient uptake (Iqbal et al. 2019), causes poor nodule membrane biosynthesis, and increases the permeability of the nodule to oxygen which all consequently leads to poor biological N fixation (Ribet and Drevon 1995; Vance et al. 2001; Jemo et al. 2017). Hence, to optimize the impacts of biological N fixation in the agroecosystems, there is a need for an increased understanding of the processes and factors inhibiting or promoting biological N fixation due to low or optimal P availability.

Among all the known sources of P for improved plant growth, mycorrhization, the symbiotic associations between arbuscular mycorrhiza fungi and plants has high ecological importance (Sawers et al. 2017; Iqbal et al. 2017; Amanullah et al. 2019). Arbuscular mycorrhizal fungi are obligate symbionts that form extra radical hyphae on plant roots and thus increase the surface area of the root for the improved acquisition of immobile nutrients, including P, from the rhizosphere (Farzaneh et al. 2009; Wang et al. 2017). In addition to arbuscular mycorrhizal fungi, other P-solubilizing microorganisms enhance P availability and uptake from the soil through association with plant roots (Bello 2021). The provision of P by arbuscular mycorrhizal fungi and P-solubilizing microorganisms is achieved by the hydrolysis of organic P-pools to inorganic P forms ($H_2PO_4^-$ and HPO_4^{-2}) that are readily available for plant uptake (Bello 2021). Consequently, arbuscular mycorrhizal fungi are complementary sources of P that could enhance biological N fixation in the agroecosystems, however, arbuscular mycorrhizal fungi contributions to biological N fixation and associated processes, e.g., N cycling, have not been adequately studied in pastures. This could be partly due to under-exploitation of the biological N fixation potentials, uneven distribution of N_2-fixers, and/or under-exploitation of mycorrhizal association in P nutrition. Despite the ecological importance of arbuscular mycorrhizal fungi, it is important to note that the addition of a little amount of inorganic P, like single super phosphate, further enhances the contribution of arbuscular mycorrhizal fungi to crop productivity (Bello and Yusuf 2021). Therefore, there is a need for more scientific investigations to increase our understanding of how arbuscular mycorrhizal fungi associations under low to moderate P soil conditions could promote biological N fixation and productivity in pastures.

Here, we reviewed how optimal P availability could optimize biological N fixation in pasture systems for improved forage productivity. We further discussed how biological N fixation could be enhanced via intercropping and crop rotation between forage legumes and grasses under different soil P conditions. The recent advances in biological N fixation, mycorrhization, and potential merits of the tripartite symbiotic association involving pasture crops, N_2-fixing bacteria, and arbuscular mycorrhiza in improving forage productivity are also discussed. Conclusively, we anticipate that this review would trigger an increase in empirical studies to unravel the detailed physiological, biochemical, agronomic, and genetic mechanisms, as well as microbial associations regulating the influence of P on biological N fixation in pastures.

10.2 Potentials of Biological Nitrogen Fixation in Pasture Swards

Biological N fixation is a cheap, sustainable, and environment-friendly phenomenon that could supply a significant amount of N required for optimum functioning and service delivery of agroecosystems (Herridge et al. 2008; Peoples et al. 2009b; Lazali and Bargaz 2017; Taylor et al. 2020). Galloway et al. (2004) estimated that about 128×10^9 kg N year^{-1} is fixed through biological N fixation worldwide. Similarly, Herridge et al. (2008) reported an estimate of $50–70 \times 10^9$ kg N year^{-1} in global cropping systems. Vitousek et al. (2013) recently reported that biological N fixation contributed 58×10^9 kg N year^{-1} in terrestrial ecosystems. Thus, there is a high potential for sufficient N provision in pastures through the increased exploitation of biological N fixation.

10.2.1 Types of Biological Nitrogen Fixation

10.2.1.1 Symbiotic Biological Nitrogen Fixation

Symbiotic biological N fixation involves a mutual relationship between microbes, mostly from rhizobium genus, and plants such as legumes to fix atmospheric dinitrogen into the agroecosystems. It is a conserved association controlled by biochemical and genetic pathways, e.g., the encoding of nitrogenase enzyme complex by *nif* genes (Mahmud et al. 2020). In symbiotic biological N fixation, nodules containing substances such as nutrients from both the microbes and plants are formed by the host plant as a medium of exchanging the plant's photosynthates for the microbe's N (Graham and Vance 2003; Unkovich et al. 2008; Udvardi and Poole 2013). Biological N fixation by legumes is a natural source of N, and a deliberate introduction of N_2-fixing legumes into pastures could enormously increase available soil N via rhizodeposition of the fixed N, and the decomposition of roots and nodules (Khan et al. 2002; Dahal et al. 2018). Cumulatively, symbiotic biological N fixation simultaneously nourishes crops with the required N during growth and increases the amount of available N in the soil.

The biological N fixation-driven increase in the soil available N increases assimilation of N into the organic components of plant cells such as nucleic acids and proteins (Unkovich et al. 2008; Sengupta et al. 2011; Pérez-Fernández et al. 2016; Míguez-Montero et al. 2020). Biological N fixation-driven increase in soil available N also improves the productivity and quality of forage crops in N limiting ecosystems (Nasto et al. 2014). Several studies have demonstrated that symbiotic biological N fixation can contribute almost an equal amount of N as N-containing chemical fertilizers in pastures (Ta and Faris 1988; McNeill and Fillery 2008; Unkovich et al. 2010; Schlesinger and Bernhardt 2013). Unlike nitrogenous fertilizers, some of the N from symbiotic biological N fixation that remain in the soils as organic matter are less susceptible to leaching and volatilization (Reckling et al. 2016; Mahmud et al. 2020). Harnessing optimal symbiotic biological N fixation is vital for ecologically sustainable N-cycling and improved functioning of the terrestrial ecosystems (Gerber et al. 2010; Taylor et al. 2020). Thus, symbiotic biological N fixation between rhizobia and leguminous crops should be promoted in pastures for optimal agroecosystem functioning.

10.2.2 Non-symbiotic Biological Nitrogen Fixation in Pastures

The non-symbiotic biological N fixation also has the potential to contribute significantly to N inputs in pastures. Unlike the symbiotic biological N fixation, the non-symbiotic or free-living or associative biological N fixation does not necessarily require an intimate connection between the microbes and host plants. Associative

N_2-fixing bacteria live around the root of the plants, mainly grasses or non-legumes, or as endophytes to access photosynthates from the plants in exchange for N (Pankievicz et al. 2015). Examples of free-living bacteria genera are *Azospirillum*, *Azotobacter*, *Klebsiella*, *Beijerinckia*, *Burkholderia*, *Clostridium*, *Herbaspirillu*m, *Nitrosospira*, *Cyanobacteria*, *Pseudomonas,* and *Paenibacillus* (Baldani et al. 2000; Van Dommelen et al. 2009; Setten et al. 2013; Bageshwar et al. 2017; Bargaz et al. 2018; Rosenblueth et al. 2018; Morris and Schniter 2018; Table 10.1). Several studies have reported the contributions of the non-symbiotic biological N fixation in pastures. For example, forage grasses in association with free-living, associative, and endophytic bacteria in tropical grasslands reportedly fix 14–42 × 10^9 kg N annually (Cleveland et al. 1999; Herridge et al. 2008). Studies have also shown that non-symbiotic biological N fixation contributed about 35%, 55–78%, 31.4%, and 27% N required by maize (Alves et al. 2015), sorghum (Barros et al. 2020), sorghum genotype BRS655 (Santos et al. 2017), and rice (Rodrigues et al. 2008) crops, respectively. Cereal crops such as sorghum, maize, and rice are among the major crops that are capable of non-symbiotic biological N fixation and are sometimes sowed as pasture crops. Therefore, more efforts should be geared towards the

Table 10.1 Nitrogen-fixing forage grasses and their microbial partners

Forage grass(es)	Microbial partner(s)	References
Leptochloa fusca L. Kunth	*Azoarcus* sp. BH72	Hurek et al. (2002)
Panicum coloratum L. Bambatsi, *Chloris gayana* L. Katambora, and *Digitaria eriantha* Steud. cv. Premier	*Burkholderia* sp. and *Polaromonas naphthalenivorans*	Gupta et al. (2019)
Sorghum bicolor L. (forage genotype)	*Burkholderia kururiensis* (16 and 109) and *Herbaspirillum seropedicae* (ZMS176)	Santos et al. (2017)
Brachiaria brizantha, *B. decumbens*, and *B. humidicola*	*Azospirillum amazonense*, *Azospirillum lipoferum* and *Azospirillum brasilense*	Reis et al. (2001)
Panicum maximum		
Digitaria decumbens	*Spirrillum lipoferum*	Neyra and Döbereiner (1977)
Triticum aestivum cv. Schöndorfer	*Azospirillum brasilense* FP2	Stets et al. (2015)
Zea mays	and *Herbaspirillum seropedicae* ZAE94	Alves et al. (2015)
Cynodon dactylon (coastcross-1)	*Azospirillum brasilense* (Ab-v5 and Ab-v6)	Aguirre et al. (2020)
Pennisetum purpureum	*Herbaspirillum frisingense* 84B-DSM13129	Kirchhof et al. (2001)
Oryza sativa	*Azospirillum amazonense* Y2	Rodrigues et al. (2008)
Axonopus affinis, *Andropogon lateralis*, *Paspalum notatum*, and *Aristida laevis*	*Azotobacter* sp. (*A. paspali*), *Azospirillum* sp. *and Herbaspirillum* sp.	Marques et al. (2017) and Döbereiner and Campelo (1971)

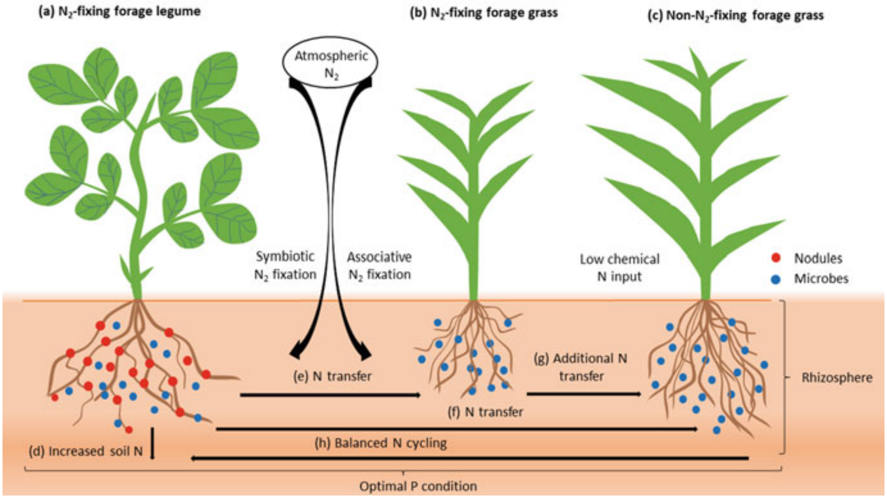

Fig. 10.1 Nitrogen transfer from N_2-fixing forage legume and grass to non-N_2-fixing forage grass in an intercropped pasture system. (**a**) N_2-fixing forage legume, (**b**) N_2-fixing forage grass growing optimally due to an adequate supply of P, and (**c**) non-N_2-fixing forage grass growing optimally under low chemical N fertilizer input. (**d**) Increased N in the rhizosphere of N_2-fixing forage legume due to the decomposition of the entire root system, including the nodules; abundance of N-rich root exudates such as amino acids, ureides, and peptides; and rhizodeposition of fixed N_2. (**e**) N transfer from N_2-fixing legume to N_2-fixing grass, (**f**) N transfer from N_2-fixing legume to non-N_2-fixing grass, and (**g**) additional N transfer from N_2-fixing grass to non-N_2-fixing grass. (**h**) Under optimal P conditions, balanced N cycling is achieved by optimal utilization of N in the agroecosystem for increased fodder production. N_2, N, and P represent dinitrogen, nitrogen, and phosphorus, respectively

improvement and discovery of non-symbiotic biological N fixation associations that could result in significant N inputs in pastures.

There are indications that the amount of N_2 fixed through non-symbiotic biological N fixation is usually less efficient than symbiotic biological N fixation, insufficient to meet the needs of crops, and varies with genotype and environment (Bargaz et al. 2018; Rosenblueth et al. 2018; Barros et al. 2020). However, the symbiotic biological N fixation by forage legumes, e.g., *Centrosema pubescence*, *Medicago sativa*, *Trifolium repens*, *Glycine max*, rotated or intercropped with grasses could augment the N from non-symbiotic biological N fixation (Thilakarathna et al. 2016; Clúa et al. 2018; Fig. 10.1). The availability of P could also potentially increase N inputs derived from non-symbiotic biological N fixation since P is a core component of the nitrogenase enzyme which regulates both the symbiotic and non-symbiotic biological N fixation (Postgate 1998). Consequently, there is a need for an in-depth understanding of how simultaneous exploitations of both non-symbiotic and symbiotic biological N fixation under varying levels of soil P availability affect N_2 fixation and pastures productivity. Therefore, it is suggested that non-symbiotic biological N fixation should be explored alongside symbiotic biological N fixation and eco-friendly sources of P for enhanced N_2 fixation and sustainable pasture productivity.

10.3 Optimization of Biological Nitrogen Fixation in Low-Input Agriculture

10.3.1 Optimizing Biological Nitrogen Fixation via Intercropping and Crop Rotation Systems

The cultivation of high N-demanding forage grasses, e.g., *Lolium perenne* or *Pennisetum purpureum*, with high biological N fixation legumes and grasses is a promising technique for a balanced N cycling in pastures (Aldana and Berendse 1997; Martha et al. 2004; Anglade et al. 2015; Fig. 10.1). Intercropping increases soil fertility level of cultivated pastures via N transfer from 'N donors', e.g., N_2-fixing forage legumes and grasses to 'N receivers', e.g., non-N_2-fixing or high N-demanding forage grasses (Thilakarathna et al. 2016). The N_2 fixed via biological N fixation in mixed pastures is useful to the host plants and other companion or follow-on crops that are grown in rotation through below-ground N transfer (Bullock 1992; Loreau and Hector 2001; Giller 2001; Fustec et al. 2010). The N-donors transfer the fixed N_2 through decomposition of the entire root systems, including the nodules and exudation of N-rich substances like ureide and amino acids from the legume roots (Heichel et al. 1981; Ledgard and Steele 1992). About 16–-124 kg N ha^{-1} has been reportedly fixed in intercropping systems involving different forage legumes, e.g., pea, faba bean, pigeonpea and rice bean, and non-legumes, e.g., sorghum, barley, oat, and maize (Danso et al. 1987; Rerkasem et al. 1988; Cowell et al. 1989; Jensen 1996; Adu-Gyamfi et al. 1997). In the absence of high N-demanding grasses, the fixed N_2 from N_2-fixing legumes could be lost to the environment via volatilization of nitrous oxide (N_2O) or nitrate leaching which leads to the contamination of groundwater. Thus, the intercropping of N_2-fixing and non-N_2-fixing species and/or rotation could promote optimum N cycling in the agroecosystems (Fig. 10.1).

Multispecies swards are known to be more productive than the monocultures due to the complementarity, niche differentiation, e.g., nutrient acquisition, and interspecific facilitation, e.g., nutrient availability, between the crop species (Hector et al. 1999; Hauggaard-Nielsen and Jensen 2005; Li et al. 2014; Suter et al. 2015; Lannetta et al. 2016). For instance, the presence of shallow-rooted legumes, e.g., soybean, in mixed pastures could offer more P benefits to deep-rooted grasses, e.g., ryegrass, by avoiding competition for subsoil P acquisition. More importantly, some investigations have further suggested that biological N fixation from intercropping or rotation could completely halt the use of N fertilizer and its contribution to greenhouse gasses e.g., NO_2, methane – CH_4, and carbon dioxide – CO_2, emission (Van Kessel and Hartley 2000; Rochester et al. 2001; Hauggaard-Nielsen et al. 2012; Barneze et al. 2020). Lannetta et al. (2016) reported that a rye-clover mixture added a higher amount of N (475–700 kg N ha^{-1} $year^{-1}$) into the cropping system than that (150–-350 kg N ha^{-1} $year^{-1}$) obtained from chemical N fertilizer application. It has also been estimated that N transfer from companion forage legumes through below-ground processes could contribute about 73% of N need for forage grasses in mixed pasture fields (Thilakarathna et al. 2016). Although, low N transfer in some mixtures like red clover-bluegrass (Thilakarathna et al. 2012) and pea-oat intercrop (Van Kessel and Hartley 2000) indicate the need for the identification of best pairs to promote functional diversity under different climatic conditions or environments. Overall, harnessing the benefits of growing different species of forage crops in pastures would lead to better utilization of ecological resources and interrelationships for improved pasture productivity with less or no chemical N inputs.

10.4 Optimizing Biological Nitrogen Fixation in Pastures via Ecofriendly Phosphorus Nutrition

Phosphorus (P) plays essential roles in different plant physiological processes, including photosynthesis, respiration, root development, seed production, and cell division as well as improved biological N fixation (Murrell and Munson 1999; Krishnaraj and Dahal 2014; Chekanai et al. 2018). P in the form of adenosine triphosphate plays an important role in the formation of nodules and the active transport of N in the form of nitrate (NO_3^-) or ammonium (NH_4^+) to plant roots (Lopez-Delacalle et al. 2020). P deficiency affects the productivity of N_2-fixing legumes-microbes association due to the high adenosine triphosphate requirement for nitrogenase reaction (Ritchie et al. 1998; Vitousek and Field 1999; Cabeza et al. 2014; Sulieman and Tran 2015). P deficiency often leads to a reduced rate of metabolism, nutrient acquisition, and utilization as well as a reduction in the growth and yield of pasture legumes (Goufo et al. 2017; Jemo et al. 2017; Fig. 10.2). Its addition alleviates the negative impacts of high soil N on biological N fixation in pastures (Smith 1992). The synergy between P and symbiotic N_2-fixing bacteria increases nodulation, N_2 fixation and improves productivity in pastures (Verma and Singh 2008; Messele and Pant 2012; Nyoki and Ndakidemi 2014; Kyei-Boahen et al. 2017; Bargaz et al. 2018; Table 10.2). Therefore, achieving a high biological N fixation efficiency and an improved overall plant growth requires optimal P availability (Fig. 10.2).

10.4.1 Inclusion of Phosphorus-Mobilizing Species in Pasture Swards

One of the important strategies for optimizing biological N fixation, in low-input agriculture, is the inclusion of P-efficient or P-mobilizing species in pasture swards. P-efficient legumes can grow optimally under a low soil available P condition because they have root systems that enhance access to the low P-pool in soils. It has been suggested that harnessing the organic P-pool of pastures or grasslands could provide adequate inorganic P required for optimum plant performance (Nash

Table 10.2 Effects of P on biological nitrogen fixation systems for improved forage crop productivity

Forage crop	N_2-fixing bacteria	Source of P	Output	References
Common bean (*Phaseolus vulgaris*)	*Rhizobium tropici*	Single superphosphate	Increased nodulation, biomass, and grain yield	Chekanai et al. (2018)
	Rhizobium tropici CIAT899 and PR-F81	Ammonium dihydrogen phosphate ($NH_4H_2PO_4$)	Improved nodulation and N_2 fixation	Chagas et al. (2010)
	Rhizobium tropici CIAT899	Potassium dihydrogen phosphate (KH_2PO_4)	Increased leaf area, whole plant dry weight, nodule biomass, shoot and root P content	Olivera et al. (2004)
Soybean (*Glycine max*)	*Bradyrhizobium japonicum*	Triple superphosphate	Increased nodulation, growth, and grain yield	Tarekegn and Kibret (2017)
	Bradyrhizobium japonicum (USDA 110)	Potassium dihydrogen phosphate (KH_2PO_4)	Increased nitrogenase activity, nodulation, P and N assimilation, and biomass production	Israel (1987)
Groundnut (*Arachis hypogaea*)	*Bradyrhizobium yuanmingense*	Triple superphosphate	Increased nodulation, haulm, pod, and seed yield	Asante et al. (2020)
Cowpea (*Vigna unguiculata*)	*Rhizobia* spp.	Single superphosphate	Increased N_2 fixation	Bello et al. (2018)
Alfalfa (*Medicago sativa*)	*Rhizobium* sp.	Calcium phosphate ($CaHPO_4$)	Increased N_2 fixation and biomass production	Crews (1993)
	Rhizobium sp.	P fertilizer	Increased nodulation and yield	IPNI (1999)
White lupin (*Lupinus albus*)	*Bradyrhizobium lupini*	Monocalcium phosphate $Ca(H_2PO_4)_2$	Increased photosynthesis, N_2 fixation and P concentration in shoots, roots and nodules	Schulze et al. (2006)
	Indigenous soil population	Monocalcium phosphate $Ca(H_2PO_4)_2$	Increased root growth, shoot P and N concentration	Wasaki et al. (2018)
Pigeonpea (*Cajanaus cajan*), Sunn hemp (*Crotalaria juncea*), White Jack bean (*Canavalia ensiformais*),	Indigenous soil population	Triple superphosphate	Increased root growth and dry weight; Increased N-use efficiency and micronutrients (Mn, Zn and Cu) uptake	Fageria et al. (2014)

(continued)

Table 10.2 (continued)

Forage crop	N_2-fixing bacteria	Source of P	Output	References
Mucuna bean (*Mucuna cinereum*), and Lablab (*Dolichos lablab*)				
White clover (*Trifolium repens* L. Milkanova)	*Rhizobium leguminosarum* (biovar *trifolii* strain)	Sodium dihydrogen phosphate NaH_2PO_4	Increased nodulation and N_2 fixation	Høgh-Jensen et al. (2002)
Berseem clover (*Trifolium alexandrinum*)	Indigenous soil population	Arbuscular mycorrhizal fungi (*Rhizophagus irregularis* and *Funneliformis mosseae*)	Increased biomass production, N_2 fixation, P and N uptake under drought stress	Saia et al. (2014)
Subterranean clover (*Trifolium subterraneum* cv. Seaton Park)	*Rhizobium trifolii* (TAI)	Finely ground (lower than 200 pm) superphosphate (10% P)	Increased nodulation, N fixation, plant growth	Robson et al. (1981)
Leguminous shrubs (*Cytisus balansae, C. multiflorus, C. scoparius,* and *C. striatus*)	*Bradyrhizobium* spp.	Sodium phos phate monobasic dihydrate ($NaH_2PO_4 \cdot 2H_2O$)	Increased nodulation, plant biomass and shoot	Míguez-Montero et al. (2020)
Young pea plants (*Pisum sativum*)	*Rhizobium leguminosarium* RisØ strain la	Sodium dihydrogen phosphate (NaH_2PO_4)	Increased nodulation and P concentration in the shoot	Jakobsen (1985)
Chickpea (*Cicer arietinum* L.)	*Rhizobium* sp	Superphosphate	Increased nodulation, leaf area, and shoot dry weight	Yahiya et al. (1995)

Forage crops as used in this table refers to crops that are used as animal feeds directly or indirectly

et al. 2014). Some well-known P-mobilizing forage legumes, e.g., *Lupinus albus*, *Ornithopus sativa*, *Vicia faba*, *Trifolium purpureum*, *Lotus corniculatus*, and *Ornithopus compressus*, facilitate P availability and acquisition by neighboring non-P mobilizing species (Li et al. 2014; Simpson et al. 2017; Dissanayaka et al. 2017). In addition to P-mobilizing pasture crops, the inclusion of P-mobilizing bacteria such as *Pseudomonas* spp. also makes more inorganic P available for crop uptake (Nassal et al. 2018). Thus, it is suggested that the holistic inclusion of both P-mobilizing pasture crops and microorganisms would greatly improve biological N fixation and productivity in pastures (Fig. 10.2).

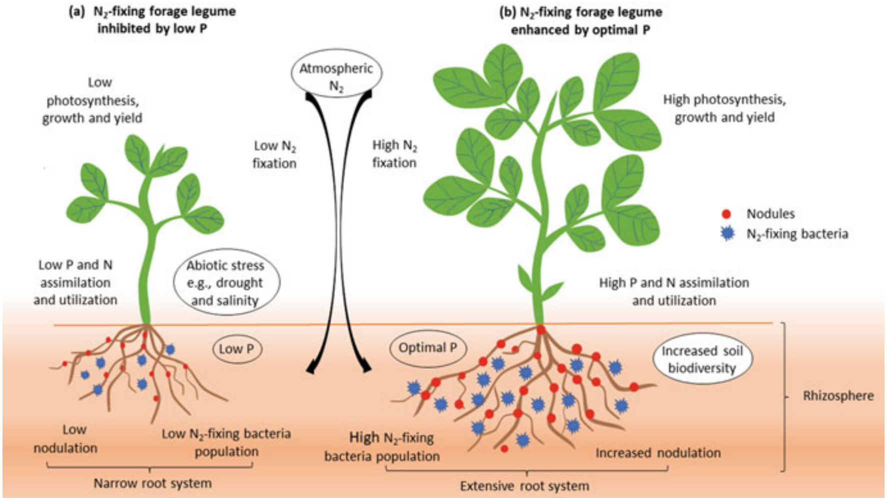

Fig. 10.2 Effects of P availability on biological N fixation and other associated mechanisms leading to increased pasture productivity. (**a**) Low P causes a low population of N_2-fixing bacteria, poor nodulation, P and N assimilation, as well as reduced photosynthesis, growth, and yield of pasture legumes. (**b**) Optimal P enhances N_2-fixing bacteria population, nodulation, P and N assimilation, as well as photosynthesis, growth, and yield of legumes. Optimal P nutrition also enhances tolerance of legumes to other abiotic stress such as drought and salinity. Similarly, P availability in the rhizosphere increases soil biodiversity, thereby enhancing other beneficial microbial associations with forage crops for optimal growth and yield. N_2, N, and P represent dinitrogen, nitrogen, and phosphorus, respectively

10.4.2 *Phosphorus Nutrition Through Arbuscular Mycorrhizal Fungi Associations for Improved Biological Nitrogen Fixation*

In low-input agriculture, sufficient soil phosphorus (P) could be made available to plants via inoculation of microorganisms that solubilize and/or mineralize organic P for plant uptake. These microorganisms may include bacteria, fungi, algae, or actinomycetes, but arbuscular mycorrhizal fungi and phosphate solubilizing bacteria are the most prominent in plant P nutrition. These microbes produce organic acids, siderophores, and enzymes that hydrolyze P from the organic form into a bioavailable form to improve the efficiency of P uptake and utilization by plants (Alori et al. 2017; Bargaz et al. 2018; Wei et al. 2018; Sawers et al. 2017). Both arbuscular mycorrhizal fungi and phosphate-solubilizing bacteria do not only nourish crops with P but also associate with N_2-fixing bacteria for improved biological N fixation efficiency (Afzal et al. 2010; Bargaz et al. 2018; Fig. 10.3). Significantly improved N and P uptake have been linked to the integrated use of P solubilizing bacteria such as

Pseudomonas striata, arbuscular mycorrhizal fungi, and *Rhizobium* spp. (Zaidi et al. 2003; Khan and Zaidi 2007). Thus, P provision by arbuscular mycorrhizal fungi and other P solubilizing microorganisms in low-input pastures is of great potential (Fig. 10.3).

Arbuscular mycorrhizal fungi are ubiquitous in nearly all agricultural ecosystems. Over 80% of terrestrial plants associate with arbuscular mycorrhizal fungi and this association accounts for up to 80% of plants total P uptake (Li et al. 2006; Farzaneh et al. 2009; Wang et al. 2018; Bargaz et al. 2018). Through the arbuscules of arbuscular mycorrhizal fungi, P is transferred from the fungi hyphae into the root cortex cell of plants (Aslam et al. 2019). Just as biological N fixation cost N_2-fixing plants to expend a lot of photosynthates, the mycorrhizal association also requires that plants exchange sugar for P from arbuscular mycorrhizal fungi (Luginbuehl and Oldroyd 2017; Rosenblueth et al. 2018). Consequently, under sufficient P and N conditions, plants tend to uptake these nutrients directly instead of relying on the biological processes of mycorrhization and biological N fixation (Coelho et al. 2009; Weese et al. 2015; Liu et al. 2016; Míguez-Montero et al. 2020). A recent study has shown that N transfer from forage legumes to grasses is regulated by arbuscular mycorrhizal fungi or root exudates, depending on the N status of the soil (Zhang et al. 2019). Arbuscular mycorrhizal fungi were actively involved in the transfer of N from alfalfa to maize under zero N-containing fertilizer application, while root exudates regulated the transfer of N after the application of 165.5 kg N ha^{-1} (Zhang et al. 2019). Therefore, it is essential to deepen our exploration of the abundant arbuscular mycorrhizal fungi in pastures for higher N and P provision under poor soil fertility conditions (Fig. 10.3).

Some plants can form both nodules and mycorrhizal associations, thereby having multiple mechanisms for essential nutrient acquisition and survival in N and P limiting environments (Fig. 10.3). The integrated inoculations of N_2-fixing bacteria and arbuscular mycorrhizal fungi increase nitrogenase activity, uptake of macro, e.g., P, and micro, e.g., iron, nutrients in adverse environmental conditions (Meng et al. 2015; Zhu et al. 2016). The concurrent presence of both N_2-fixing bacteria and arbuscular mycorrhizal fungi also promotes higher N transfer from forage legumes to grasses (Abd-Alla et al. 2014). N_2-fixing legumes experience an increase in accumulation of tissue N as a result of P supply by arbuscular mycorrhizal fungi (Subba Rao et al. 1986; Biro et al. 2000). Similarly, reduced P uptake from low available soil P has been linked to reduced arbuscular mycorrhizal fungi colonization (Wang et al. 2018). It has been hypothesized that biological N fixation enhances higher arbuscular mycorrhizal fungi colonization, thereby enhancing increased P uptake (Nasto et al. 2014). Thus, harnessing the tripartite association among pasture crops, N_2-fixing bacteria, and arbuscular mycorrhizal fungi could help to maximize or maintain optimal agroecosystem functioning in pastures.

For example, in a grass – *Trachypogon* spp.- dominated savanna ecosystem, six forage legumes including *Desmodium intortum*, *Indigosfera pascuorum*, *Mimosa pudica*, *Cassia cultrifolia*, and *Stylosanthes* spp. formed symbiotic associations with both arbuscular mycorrhizal fungi and N_2-fixing bacteria (Mora et al. 2017).

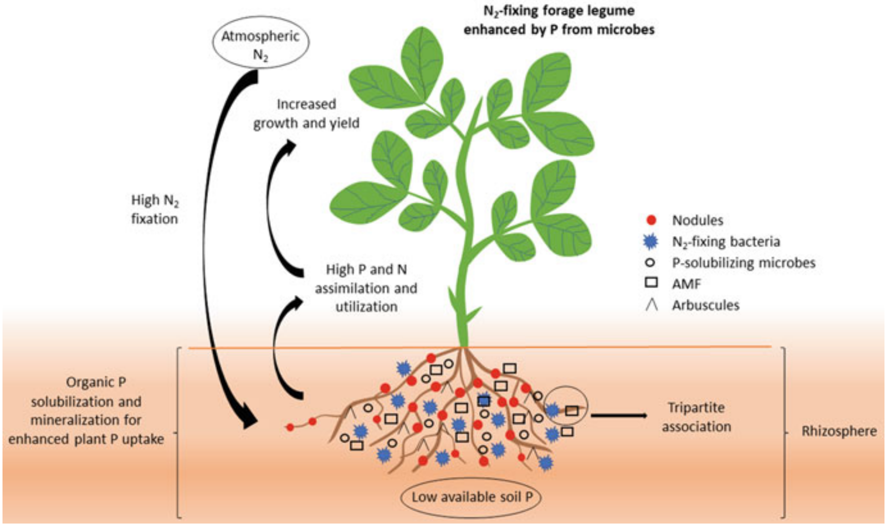

Fig. 10.3 Microbial provision of P for improved biological N fixation. Due to low soil P, there is an increased association between the plant root system with specific P-solubilizing or mineralizing rhizospheric microorganisms. The associations between the plant root system and P-solubilizing microorganisms lead to the establishment of processes, such as the production of organic acids, siderophores, biosynthesis, and secretion of enzymes, that enhance plant P uptake by hydrolyzing organic P to plant bioavailable forms. In addition, plant root-P-solubilizing microorganisms associations lead to increased surface area for immobile soil P acquisition, increased tolerance to abiotic stresses such as heavy metal toxicity and salinity, and biotic stresses such as pathogen infestation. The tripartite association among the plant root, mycorrhiza, and N_2-fixing bacteria ultimately promote pasture crop productivity, especially in low fertilizer input systems. N_2, N, and P represent dinitrogen, nitrogen, and phosphorus, respectively

Piptadenia gonoacantha, a leguminous tree, also formed nodules and exhibited biological N fixation only when colonized by arbuscular mycorrhizal fungi (Júnior et al. 2017). This phenomenon was attributed to the dependency of *Piptadenia gonoacantha* on arbuscular mycorrhizal fungi for P nutrition. Soybean inoculated with both arbuscular mycorrhizal fungi and rhizobia under low P and N field conditions had enormous growth, as well as P and N concentrations compared to the non-inoculated soybean (Wang et al. 2011). This positive outcome is linked to the adaptability of the soybean deep root structure which facilitated arbuscular mycorrhizal fungi colonization in low soil P and higher nodulation when P was sufficient in the soil (Wang et al. 2011). Therefore, the dynamics of the tripartite association involving pasture crops, N_2-fixing bacteria, and arbuscular mycorrhizal fungi in pastures have the potential to improve agroecosystems functioning and merits further studies.

10.5 Conclusion and Future Perspectives

Efficient biological N fixation can improve pasture productivity by increasing the soil N and tissue N contents of plants. The intensive exploitation of biological N fixation in pastures also has the potential to reduce the contributions of agriculture to climate change through the reduced use of chemical N-containing fertilizers. However, the efficiency of biological N fixation depends on optimal availability of P which influences several factors that regulate biological N fixation including N_2-fixing bacteria, nodulation, and nitrogenase enzyme activities. Rather than the incessant use of inorganic P fertilizers, natural or environment-friendly sources of P could be harnessed to provide the required P for optimal biological N fixation and pasture productivity. An abundant amount of organic P is present in the soil and is only accessible to plants when converted to the inorganic form. The conversion of the soil organic P-pool to the inorganic P-pool in pastures can be sustainably achieved by the deployment of arbuscular mycorrhizal fungi. However, the environment-friendly provisioning of P for plants through arbuscular mycorrhizal is less exploited for the improvement of biological N fixation and productivity in pastures.

Our review of available literature has shown that the holistic exploitation of arbuscular mycorrhizal fungi and N_2-fixing bacteria is an important strategy needed for the improvement of plant nutrition and productivity in the pasture agroecosystems. The concurrent exploitations of arbuscular mycorrhizal fungi and biological N fixation complementarily provide plants' most required nutrients, P and N. This arbuscular mycorrhizal fungi- N_2-fixing bacteria association could also be exploited to reinforce plants against adverse growing conditions by aiding the production of plant defense hormones against pest and diseases, salinity, and drought. Overall, the exploitation of plant-microbial associations such as arbuscular mycorrhizal fungi and P solubilizing bacteria in conjunction with intercropping and crop rotation among different pasture species could optimize biological N fixation for increased pasture productivity. In conclusion, we suggest that there is a need for the continued promotion of the use of eco-friendly microbial sources of nutrients in conjunction with sustainable farming practices to achieve increased productivity in pastures.

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Index

A
AbdelHakam, M.R., 31
Abdel-Hamid, M.A., 61
Abdel-Salam, M.A., 25–40
Abobatta, W.F., 25–40
Acid phosphatases (APases), 55, 73, 77–80, 82, 148, 161, 181–186, 196
Adeel, M., 49–62
Adeyemi, N.O., 162
Agriculture, v, 2, 5–7, 12, 13, 15–18, 29, 31–32, 52, 53, 55, 56, 74, 82, 83, 146, 148, 155–169, 208, 214–215, 218, 221
Agroecology, 2, 6, 17
Aguirre, P.F., 211
Ahmad, M.A., 49–62
Ahmad, N., 137–149
Ahmed, W., 60
Akande, M.O., 62
Akbar, F., 137–149
Alam, S., 82
Ali, S., 137–149
Ali, S.S., 137–149
Ali, W., 61
Alkaline phosphatase, 31, 99, 100, 181–186, 196
Almeida, D.S., 78
Alves, G.C., 211
Arbuscular mycorrhizal fungi (AMF), v, 37, 61, 71, 73, 76–78, 80, 81, 98, 120, 155–169, 185, 209, 210, 217–221
Arif, M., 93–107
Asante, M., 216
Aslam, M.M., 69–83
Azcon, R., 185
Azhar, M.T., 115–130, 155–169
Aziz, O., 155–169

B
Bach, S., 6
Badr, M.A., 30, 62
Bai, S.H., 101
Balestrini, R., 168
Bargaz, A., 77
Bariola, P.A., 183
Battini, F., 77
Begum, N., 159
Bello, S.K., 207–221
Biochar, v, 93–107
Biofertilization, 148
Biological nitrogen fixation, v, 187–193, 207–221
Blackwell, P., 105
Boddey, R.M., 188
Bouajila, K., 59
Boutaj, H., 162
Bremner, J.M., 180
Breuillin, F., 168
Breuillin-Sessoms, F., 168
Brockwell, J., 193
Buch, A., 82
Burns, R.C., 189
Bustos, R., 77

C
Campelo, A.B., 211
Cantarella, H., 180

A. Iqbal et al. (eds.), *Sustainable Agriculture Reviews 58*, Sustainable Agriculture Reviews 58, https://doi.org/10.1007/978-3-031-16155-1

Chagas, E., 216
Chang, M.X., 77
Chattha, W.S., 115–130
Chekanai, V., 216
Chen, C., 162
Chen, L., 8
Chen, Y.F., 77
Chiou, T.J., 168
Ch'ng, H.Y., 102
Clarke, P.H., 180
Commoner, B, 4, 16
Condron, L.M., 60
Corporate social responsibility, 5, 12
Cozzolino, V., 162
Crews, T.E., 216
Crop plants, 116–118, 127–129, 143, 183, 185, 191
Crop productivity, 31, 37, 38, 62, 98, 102, 105, 209, 210, 216, 220

D
Dai, X., 77
Dalla Costa, M., 159
Daly, H.E., 14
Davis, J.G., 55
Day, J.M., 190
Delfim, J., 82
Denarie, J., 187
de Willigen, P., 192
Diaz-Varela, R.A., 126
Dissanayaka, D., 77
Döbereiner, J., 211
Drobni'K, J., 180
Duan, A., 49–62
Duff, S.M.G., 183
Du, Z., 99

E
Ecovillage, 2, 9–12, 18
Edwards, C.A., 193
Elatrash, F., 185
El Kinany, S., 61

F
Fageria, N.K., 216
Fall, F., 164
Fang, L.-P., 60
Farooq, A., 115–130
Ferguson, R.S., 6
Fort, F., 165
Francis, C.A., 6
Franco, A., 164
Frankenberger, W.T. Jr., 180
Furlani, A.M.C., 61

G
Gabasawa, A.I., 177–196
Galloway, J.N., 210
Gao, S., 103
Gao, W., 77
Garcés-Ruiz, M., 159
Garcia, C., 183
Gawad, A.M.A., 25–40
Genus, A., 11
Giller, K., 193
Giller, K.E., 192
Gizaw, B., 37
Glaser, B., 97, 103, 106
Graham, P.H., 193
Grilo, F., 8
Guerinot, M.L., 193
Guether, M., 168
Gul, S., 99
Guo, L., 59
Gupta, V.V.S.R., 211

H
Hammond, J.P., 143
Hardin, G., 4, 18
Hardy, R.W.F., 189
Harrison, A.F., 194
Harrison, M.J., 168
Hashim, T.A., 25–40
Hathaway, M.D., 6
Hedley, M.J., 57
He, H., 77
Hellal, F.A., 31
Henri, F., 82
Herridge, D.F., 210
He, Y., 162
Høgh-Jensen, H., 217
Holistic environmentalism, 2
Holmgren, D., 2, 3
Huang, W., 31
Hu, B., 77
Hurek, T., 211
Husnain, S.R., 30
Hussain, Z., 137–149

I
Idris, A.L., 69–83
Indra's Net, 16, 17
Inorganic fertilizer, 51, 54, 61, 95, 106, 107, 209
Iqbal, A., 49–62, 137–149
Irankhah, S., 162
Israel, D.W., 216
Israr, M., 137–149

J
Jackson, R., 181
Jakobsen, I., 217
James, M.R., 121
Jeffery, S., 100
Jehangir, K., 93–107
Jimoh, S.O., 207–221
Jing, Y., 103
Jin, Y., 100, 103
Johnson, A., 192
Jungk, A., 185

K
Kaeppler, S.M., 77
Kalayu, G., 77
Kamran, M., 155–169
Kelly, M., 180
Khalil, A., 30
Khan, A.I., 115–130
Kibret, K., 216
Kirchhof, G., 211
Kobae, Y., 168
Krebs, J., 6
Kudoyarova, G.R., 77

L
Ladd, J.N., 181
Lajtha, K., 194
Lannetta, P.P., 214
Legumes, 78, 138, 184, 187–193, 196, 209–211, 213–215, 217–219
Lehmann, J., 102
Lehr, V.I., 103
Leinweber, P., 60
Li, J., 49–62
Li, L., 122
Litfin, K.T., 9
Liu, S., 101, 122
López-Arredondo, D.L., 77
Lott, J.N., 138
Louw-Gaume, A.E., 77
Lovell, S.T., 6

M
Maathuis, F.J.M., 77
Mahmood, R., 93–107
Maimaitijiang, M., 121
Mäkelä, P.S., 60, 61
Makoi, J.H.J.R., 182
Maldonado-Mendoza, E.A., 168
Malik, M.A., 137–149
Malik, W.A., 49–62
Maqbool, S., 49–62
Marques, A.C.R., 211
Marschener, H., 77
Ma, X., 162
Maxey, L., 8
McCallister, D.L., 185
Microorganisms, 27, 31, 32, 36–38, 40, 73, 76, 81, 82, 99, 119, 120, 158–161, 178, 180, 184, 187, 209, 210, 217–220
Míguez-Montero, M.A., 217
Mineral phosphorous, v, 27, 38, 53, 62, 94
Misson, J., 77
Mitchell, P.J., 99
Młodzińska, E., 77
Mollison, B., 2, 3
Mondini, C., 61
Muraina, T.O., 207–221
Murphy, J., 58
Mycelium, 166–167
Mycorrhizal association, 158, 210, 219

N
Nadgórska-Socha, A., 186
Nannipieri, P., 181
Ndakidemi, P.A., 182
Negassa, W., 60
Neyra, C.A., 211
N_2-fixing bacteria, 187, 209, 210, 212, 215, 217–221
Niu, Y.F., 77
Non-N_2-fixing forage crops, 212–214
Norberg-Hodge, H., 5

O
Odum, H.T., 15
O'Hara, G.W., 192
Okal, E.J., 69–83
Olasupo, I.O., 207–221

Olivera, M., 216
Organic fertilizer, 38, 51, 54, 61, 95, 105, 156
Organic phosphorous, v, 27, 31, 34, 36, 39, 49–62, 98–100, 102, 104, 117, 139–141, 182, 185, 196
O'Riordan, T., 14

P
Parra-Almuna, L., 77
Parvage, M.M., 102
Pasture productivity, 213, 215, 218, 221
Paszkowski, U., 168
Paz-Ferreiro, J., 102
P deficiency, 51, 70, 71, 73–75, 77, 79, 80, 83, 156, 162, 165, 167, 215
Perez Tienda, J., 168
Permaculture ethics, 2–5, 7, 15–18
Phenotyping, v, 115–130, 143–144, 146
Phosphate fertilizers, 32, 156, 158, 161, 169
Phosphate transporters, 77, 120, 140–142, 165
Phosphorus, 6, 26, 50, 69, 94, 116, 138, 156, 178, 209
  absorption, 33, 70, 96, 116, 117, 158, 159, 161, 165, 167–169
  availability, 27, 28, 31, 33–36, 38, 39, 70, 73, 81, 209, 210, 213, 217, 218, 221
  cycle enzymes, v, 177–196
  deficiency, v, 51, 69–83, 118, 120, 139–142, 167, 177–196, 215
  fertilizers, 6, 28, 29, 31, 32, 38–39, 53–55, 70, 81, 83, 105, 163, 167, 169, 216, 221
  uptake, 61, 69–72, 74, 76–78, 94, 106, 139–141, 144, 146, 159, 162, 164, 168, 218–220
Phosphorus-efficient crop, 74, 117, 146–147
Phosphorus-solubilizing bacteria, 36, 38, 218, 221
Phuong, N.T.K., 103
Pickerill, J., 8
Pierzynski, G.M., 37
Pilkington, B., 8
Plant growth, 26–28, 32, 37–39, 56, 61, 72–74, 78, 81, 96, 98, 100, 105, 117, 118, 130, 138, 158, 160–163, 178, 181, 182, 191, 209, 215, 217
P-mobilizing pasture species, 217
Postgate, J.R., 188
Psychas, D.J., 194
Puga, M.I., 77

Q
Qayyum, M.F., 103

R
Rahman, A.U., 137–149
Ramaekers, L., 77
Rasha, R.A., 31
Rasool, A., 137–149
Rausch, C., 168
Rawls, W., 59
Reis, V.M., 211
Rhizosphere, 32, 36, 60, 71, 73, 74, 78, 81, 82, 96, 117, 119–120, 143, 159, 161, 163, 169, 178, 179, 182, 184–186, 209, 213, 218
Riaz, M., 93–107, 155–169
Riley, J.P.J.A.C.A., 58
Roberts, E., 181
Roberts, J.M.F., 193
Robson, A.D., 217
Robson, S., 121
Rochayati, S., 62
Rock phosphate, v, 29–33, 38–40, 51, 52, 55, 60, 82
Rodrigues, E.P., 211
Root, 26, 61, 70, 96, 138, 156, 178, 209
Root exudates, 28, 70, 75, 77, 79–81, 213, 219
Rotini, O.T., 180
Roughley, R.J., 193
Roux-Rosier, A., 2
Rowe, H., 31
Roy, R.N., 32
Ruan, W., 141
Rubio, V., 77
Ryan, M.H., 165

S
Saboor, A., 162
Saia, S., 217
Sakuraba, Y., 77
Salem, H.M., 25–40
Sanaa, M., 59
Sanchez-Monedero, M., 60
Santos, C.L.R., 211
Sawers, A., 162
Schreiner, R.P., 162
Schulze, J., 216
Schumacher, E.F., 5
Selvi, K.B., 77
Sensors, 76, 77, 120–130, 179
Shah, M., 137–149
Shakeel, A., 115–130
Shakoor, N., 49–62
Sharing economy, 5, 10, 12, 13, 18
Sharma, S.B., 36, 82

Shoot, 26, 61, 79, 80, 116–118, 122, 142, 143, 160, 165, 192, 216, 217
Silva, U.C., 60
Sims, J.T., 37
Slay, R.M., 2, 3
Soil health, 38, 54, 62, 179
Soil microbes, 27, 34, 55, 70, 73, 74, 81, 97, 99–101, 159, 161, 179, 182
Spatial scale, 5
Sprent, J.I., 189, 191
Sprent, P., 189
Stets, M.I., 211
Subbarao, G.V., 191
Suh, J., 1–18
Suleman, M., 137–149
Sun, R., 8
Swinfeld, T., 120
Symbiotic relationship, 161, 164, 165, 169

T
Taalab, A.S., 30, 62
Tabatabai, M.A., 179, 180
Tang, H., 140
Tarafdar, J.C., 182, 184, 185
Tarekegn, M.A., 216
Taşkın, M.B., 61
Tawaraya, K., 77
Testing techniques, 53, 55–59
Thiele, L.P., 17
Thies, J.E., 193
Tian, X., 103
Tossi, V., 77
Transgenic plants, 143
Tripartite association, 200, 219
Tripathl, B.A., 194

U
Uauy, C., 77
Ur-Rahman, S., 49–62
Usman, S., 207–221

V
Vanbuuren, M.L., 168
Vanek, S.J., 102
Van Kauwenbergh, S.J., 138
van Noordwijk, M., 192
van Vugt, D., 188
Veneklaas, E.J., 143
Vinci, G., 61
Vitousek, P.M., 210
Volpe, V., 168

W
Wang, D., 77
Wang, X., 139, 155–169
Wasaki, J., 216
Waseem, M., 69–83
White, P.J., 143
Wick, B., 179
Widada, J., 37
Wilson, K.J., 192
Wood, M., 192
Wriston, J.C. Jr., 180
Wu, G., 82

X
Xie, X., 168
Xu, M., 49–62
Xu, W., 77

Y
Yadav, R.S., 182, 184, 185
Yahiya, M., 217
Yi, Y., 38
Yu, F., 77
Yun, S.J., 77

Z
Zahran, H.H., 190
Zain, M., 49–62
Zaman, N., 137–149
Zantua, M.I., 180
Zapata, F., 32
Zboiñska, M., 77
Zhang, M.-K., 60
Zhang, W., 162
Zhong, C., 31
Zhou, J.-J., 77, 78
Zhu, X.F., 77
Zwetsloot, M.J., 102