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Intra-Specific Variations of Phosphorus Utilization Efficiency

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Abstract: Soils of Pakistan are frequently characterized as deficient in plant-available phosphorus (P). The option of fertilizer applications to cope the situation has proved cost-intensive for resource-poor farmers of the country. Under the circumstances, exploitation of genetic variations in crops for P-use efficiency and identification of P-efficient crop cultivars hold great promise. Experiments conducted at the University of Agriculture, Faisalabad indicated significant growth differences among varieties of wheat, rice, chickpea and cotton when grown under P-deficient as well as P-adequate conditions. Differences in relative adaptability of varieties to P-deficiency stress were also considerable. In this paper, work done in Pakistan and elsewhere on genotypic variations of P-nutrition of crops is briefly reviewed. Various physiological mechanisms responsible for such variations are also discussed.

Keywords: Phosphorus-use efficiency, genotypic variation, mechanism

Introduction

In Pakistan, inherent and management problems limit the use of cultivable lands. The soils are generally characterized as alkaline-calcareous in nature and widespread deficiencies of N and P are well-established (Rashid and Rafique, 1997). In addition, slow adoption of phosphatic fertilizers by the farmers especially in comparison with nitrogenous fertilizers has made fertilizer applications highly unbalanced (Ahmad *et al.*, 1992), and therefore less beneficial for the farmers. Cultivation of high yielding varieties at wide N:P₂O₅ application ratios further aggravate the problem. Sillanpaa (1982) reported that Pakistani soils, on average, are poorer in 0.5 M NaHCO₃-extractable P than the soils of any other country. Malik *et al.* (1984) reported on the basis of consolidated results from 136,161 soil samples from Punjab that about 93 per cent of these samples contained less than 10 mg kg⁻¹ Olsen P.

Unfathomable price hikes of phosphatic fertilizers and low P-use efficiency of crops have made P applications cost-intensive. The situation demands for producing more yields from each kg of applied P while maintaining quality of the produce and sustaining productivity of soils. The interest in selecting species and varieties adaptable to conditions of low soil P is to decrease the amount of phosphorus fertilizer necessary for adequate yields.

There is scope for identification of P-efficient crop cultivars in Pakistan (Ahmad *et al.*, 1998) but unfortunately the work done so far is very scarce and mostly confined to green-house studies (Gill *et al.*, 1994; Ashraf, 1996; Ahmad *et al.*, 1998). The need for filling this gap holds promises under existing socio-economic conditions: Efficient utilization of phosphatic fertilizers under otherwise unfavorable soil conditions being the most important. Besides providing basic insight into the subject of genetic variability among crops for P-use efficiency, this paper will also act as a source of references for those interested in this field of research.

Historical: The conventional approach to tackle soil problems had been "changing the soil to fit the plant" (Buol and Eswaran, 1993). The idea of tailoring plants to fit problem soils has been slow to receive acceptance (Foy, 1993), although references regarding research on genetic aspects of plant mineral nutrition are as old as thirties (Lyness, 1936). First collaborative efforts to arouse the interest of plant and soil scientists in the potential of genetic approach for solving mineral nutrition problems of plants were undertaken by USDA, Cornell University, USA, and ARS in mid seventies. The outcome of these efforts was the holding of first international meeting "Plant Adaptation to Mineral Stresses in Problem Soils" at Beltsville, USA (Wright and Ferrari, 1976) in 1976.

The momentum of the first meeting was kept and two years later, in 1978, second international meeting "Crop Tolerance to Suboptimal land conditions" was held which was sponsored by the American Society of Agronomy (Jung, 1978). These two conferences generated a large body of literature on genetic aspects of plant mineral nutrition and diverted the attention of many plant and soil scientists towards this subject. Christiansen and Lewis then edited a book "Breeding Plants for Less Favorable Environments" and thus provided a source for further insight into the subject (Christiansen and Lewis, 1982). During the following years number of conferences and seminars were held (Taylor, 1988; Wright *et al.*, 1991). Most of the work presented was confined to plant - soil interactions at low pH.

Increasing fertilizer prices and general awareness of the need for conservation of soil, water and energy and the control of ground water pollution further fueled the idea of modifying plants instead of soils for solving the problem of nutrient deficiencies of soils (Foy, 1993). The genetic approach of plant mineral nutrition was also found compatible with low input, sustainable agriculture (LISA) approach (Sanchez and Salinas, 1981). Besides, achievements made under international programs like INTSORMIL further endorsed the feasibility of genetic approach to tackle soil problems (Foy, 1993). INTSORMIL was designed to develop genotypes of sorghum and millet that are better adaptable to acid, infertile or dry soils of Africa and South America, where these crops are the main food sources for subsistence farmers. INTSORMIL also collaborated financially with the University of Nebraska (USA) and USAID in holding an international workshop "Adaptation of Plants to Soil Stresses" at Nebraska in 1993 (INTSORMIL, 1993). In addition, number of international symposia on "Genetic Aspects of Plant Mineral Nutrition" have also been held during last two decades of the current millennium (Saric, 1982; Randall *et al.*, 1993).

Intra-specific variations for P-nutrition of plants: Intra-specific variations for P efficiency in crops are well documented (Gerloff, 1976; Gabelman, 1976; Fohse *et al.*, 1988; Gerloff and Gabelman, 1983) and have been proposed as a possible tool to tackle the problem of P-deficiency stress in soils (Fageria and Baligar, 1993) by optimizing the application of P fertilizers. Salinas and Sanchez (1976) have reviewed available information on the subject of intra-specific variations for P-efficiency of crops. They have demonstrated that these variations could be grouped into two classes: Differences in relation to external critical levels of P (in the soil) and internal critical levels (in the plant). They also discussed the possible physiological mechanisms that might explain the observed species and varietal

Ahmad *et al.*: Intra-specific variations of phosphorus utilization efficiency

Table 1: References to some papers dealing with P deficiency stress – plant genotype interactions.

Plant species	References
Wheat	Batten, 1986a,b; Jones <i>et al.</i> , 1989; Fohse <i>et al.</i> , 1991; Graham <i>et al.</i> , 1992; Battern, 1993; Gill <i>et al.</i> , 1994; Gahoonia and Nielsen, 1996; Schulthess <i>et al.</i> , 1997; Yaseen <i>et al.</i> , 1998
Rice	Ponnamperuma and Castro, 1971; Fageria <i>et al.</i> , 1988; Majumder <i>et al.</i> , 1990; Fageria <i>et al.</i> , 1991; Ni <i>et al.</i> , 1996
Maize	Elliott and Lauchli, 1985; Bottacin <i>et al.</i> , 1990; Jungk <i>et al.</i> , 1990; Sachay <i>et al.</i> , 1991; da Silva and Gabelman, 1992; da Silva <i>et al.</i> , 1993; Hajabbasi and Schumacher, 1994; Hedley <i>et al.</i> , 1994; Krisztina <i>et al.</i> , 1997
Cotton	Ashraf, 1996; Ahmad <i>et al.</i> , 1998
Barley	Clarkson and Scattergood, 1982; Gahoonia and Nielsen, 1996; Römer and Schenk, 1998
Sorghum and Millets	Brown and Jones, 1977; Wieneke, 1990; Payne <i>et al.</i> , 1995; Payne <i>et al.</i> , 1996;
Forage and tree	Jones, 1974; Sanginga <i>et al.</i> , 1989; Davis, 1991; Mugwira and Haque, 1991; Sanginga <i>et al.</i> , legume 1991; Aduayi and Haque, 1992; Caradus, 1992; Caradus <i>et al.</i> , 1993; Gourley <i>et al.</i> , 1993; Mugwira and Haque, 1993; Sanginga <i>et al.</i> , 1995; Mugwira <i>et al.</i> , 1997; Hamud-ur-Rehman <i>et al.</i> , 1998
Other crops	Whiteaker <i>et al.</i> , 1976; Coltman <i>et al.</i> , 1987; Baas and Bausichem, 1990; Helal, 1990; Krannitz <i>et al.</i> , 1991; Kirschbaum <i>et al.</i> , 1992; Ae <i>et al.</i> , 1993

differences related to low P tolerance. The work done by some other workers summarized in Table 1.

Physiological mechanisms involved in intra-specific variations for P-use efficiencies of crops:

P-acquisition from rooting medium: The availability of P to plant roots is diffusion limited (Tisdale *et al.*, 1984) and the diffusion of P through soil is the slowest of all macro nutrients (Fitter and Hay, 1987). Uptake of P by plant roots is a metabolically driven process which is evidenced by higher P contents of a tissue and xylem sap than the soil solution bathing the roots (Mengel and Kirkby, 1987). Major site of active P accumulation in the root is cortical cells and it is then transported across the root in the symplast pathway (Ferguson and Clarkson, 1975) through xylem.

Many workers have reported intra-specific variations for P-acquisition from rooting medium and their impact on adaptation to P stress (Jungk *et al.*, 1990; Krannitz *et al.*, 1991; Hajabbasi and Schumacher, 1994; Römer and Schenk, 1998; Krisztina *et al.*, 1997). Efforts for selecting crops or genotypes with greater ability to absorb P under P-limiting conditions have revealed that factors such as root morphology and physiology (Schenk and Barber, 1979; Hajabbasi and Schumacher, 1994), rhizosphere pH (Grinstead *et al.*, 1982) and root exudates (Hoffland *et al.*, 1992) are important in P uptake.

Phosphorus solubility in soil and hence absorbability by plants is generally considered to be influenced by rhizosphere pH. Gill *et al.* (1994) observed a significant correlation between declining rhizosphere pH and P uptake by wheat varieties. However, Barber and Chen (1990) have shown their concern about generalization of such relationships and proposed inclusion of some other independent variables such as form of P ion (at pH level above 6.7), level of P in the medium and the amount of root growth, to understand relationship between pH and P uptake by plant. Their concern was confirmed by Gahoonia and Nielsen (1996) who observed differential P uptake by barley and wheat varieties even no pH changes were recorded in their rhizospheres. They have attributed differential P uptake to genetic variations in root hair formation and root exudation of these crop varieties.

Otani and Ae (1996) have reported significant positive correlation between root length and P uptake by crops, and suggested a hypothesis that P uptake depended largely on root length, and that crops like sorghum, which can develop a large root system are advantageous for P uptake. But such generalizations are not favored by other workers (Fohse *et al.*, 1991) and there seems a need for isolating/separating the influence of these factors under specific substrate conditions.

Phosphorus movement and translocation within plant: The ability of plants to retranslocate P from inactive to active sites is a strategy

adopted by some plants to tolerate low P supply (Loneragan, 1978). Some physiological and metabolic P-transformations may also take place in plants as a response to P deficiency. For instance, Rao *et al.* (1990) reported changed enzymatic pathways in P-starved plants such that the amount of phosphate tied up in phosphorylated-intermediates was reduced and the amount of phosphate free carbon compounds was increased. This physiological adjustment increased the amount of Pi available for photosynthesis and other essential physiological functions. Rao and Terry (1995) have shown that in spite of 88 percent reduction in leaf blade P concentration of sugar beets, low-P leaves were able to sustain photosynthesis, which was 75 percent of the control.

Efficient redistribution and reutilization of nutrients from deficient or senescent plant parts could also cause variations in nutrient utilization. Weak redistribution may result in elemental retention in inactive plant parts away from sites of metabolic activities. Adu-Gyamfi *et al.* (1989) had observed that the rate of absorption and translocation of P to leaf is an important factor for the increase of dry matter production under P-deficiency stress. In another study, Adu-Gyamfi *et al.* (1990) observed that a larger proportion of soluble P in shoot was retained in stem of a sensitive species (soybean) compared to the tolerant species (pigeon pea), while opposite was the case in leaves of these two species.

Similarly, relatively lower proportions of total P have been reported to be retained in roots and stems and higher proportions translocated to leaves in P-efficient crop genotypes compared to inefficient genotypes (Saric, 1981; Clarkson and Scattergood, 1982; Snapp and Lynch, 1996; Jeschke *et al.*, 1996). Such variations in compartmentation of P in various plant organs are reported to be inducible under conditions of P deficiency (Gerloff and Gabelman, 1983) and are under genetic influence (Saric, 1981). Gerloff and Gabelman, (1983) have also maintained that tissue P concentration rather than P concentration in the growth media control such inductions, and that the plant tissue concentration at which enhanced long distance transport is initiated under P deficiency, vary in different genotypes. Role of internal P concentration (or some metabolite derived from it) at a critical location in plant, as a regulatory force for initiating enhanced P uptake from the growth media under P deficiency has also been confirmed by some other workers (Lee, 1982; Lefebvre and Glass, 1982).

Phosphorus utilization efficiency: Tailoring plants to adapt to conditions of low P supply and yield more from each kg of applied P (high P use efficiency) is being considered a feasible alternative for current high input agriculture (Sanchez and Salinas, 1981). Phosphorus use efficiency is of special interest for developing countries, especially those having soils with unfavorable P dynamics (Sanchez, 1976). Different workers, giving quite variable interpretations of the term have used different definitions of PUE. Batten (1993) reviewed various definitions of P efficiency in wheat

and stressed for selecting a specific definition for each study, which is compatible with the objectives and conditions of the experiment, to avoid confounding of results. Recently, Römer and Schenk (1998) also compared various definitions of PUE and emphasized the need for including additional plant traits such as enzymatic activities or root growth parameters for better prediction of the ultimate yield by the use of PUE, especially when experiments are conducted in pots or in solution culture. Most widely used definition of PUE is the amount of biomass or harvestable plant part produced per unit of P absorbed by the plant – generally referred to as physiological P use efficiency (PPUE) (Siddiqi and Glass, 1981; Batten, 1993; Gourley *et al.*, 1994), and measured as the product of yield times the reciprocal of P concentration. Intra-specific variations for PPUE have been observed for number of crops including wheat (Batten, 1993), barley (Römer and Schenk, 1998), maize (Elliott and Lauchli, 1985; Krisztina *et al.*, 1997), rice (Hedley *et al.*, 1994), forage crops (Mugwira *et al.*, 1997), cotton (Ahmad *et al.*, 1998) and other crop species (Fohse *et al.*, 1988). An overall high PPUE of plants can be achieved through combined effect of P-uptake efficiency and P-utilization efficiency (Römer and Schenk, 1998). As both these traits are genetically heritable (Nielsen and Schjöring, 1983; Jones *et al.*, 1989), they should be included in genetic improvement programs through breeding.

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