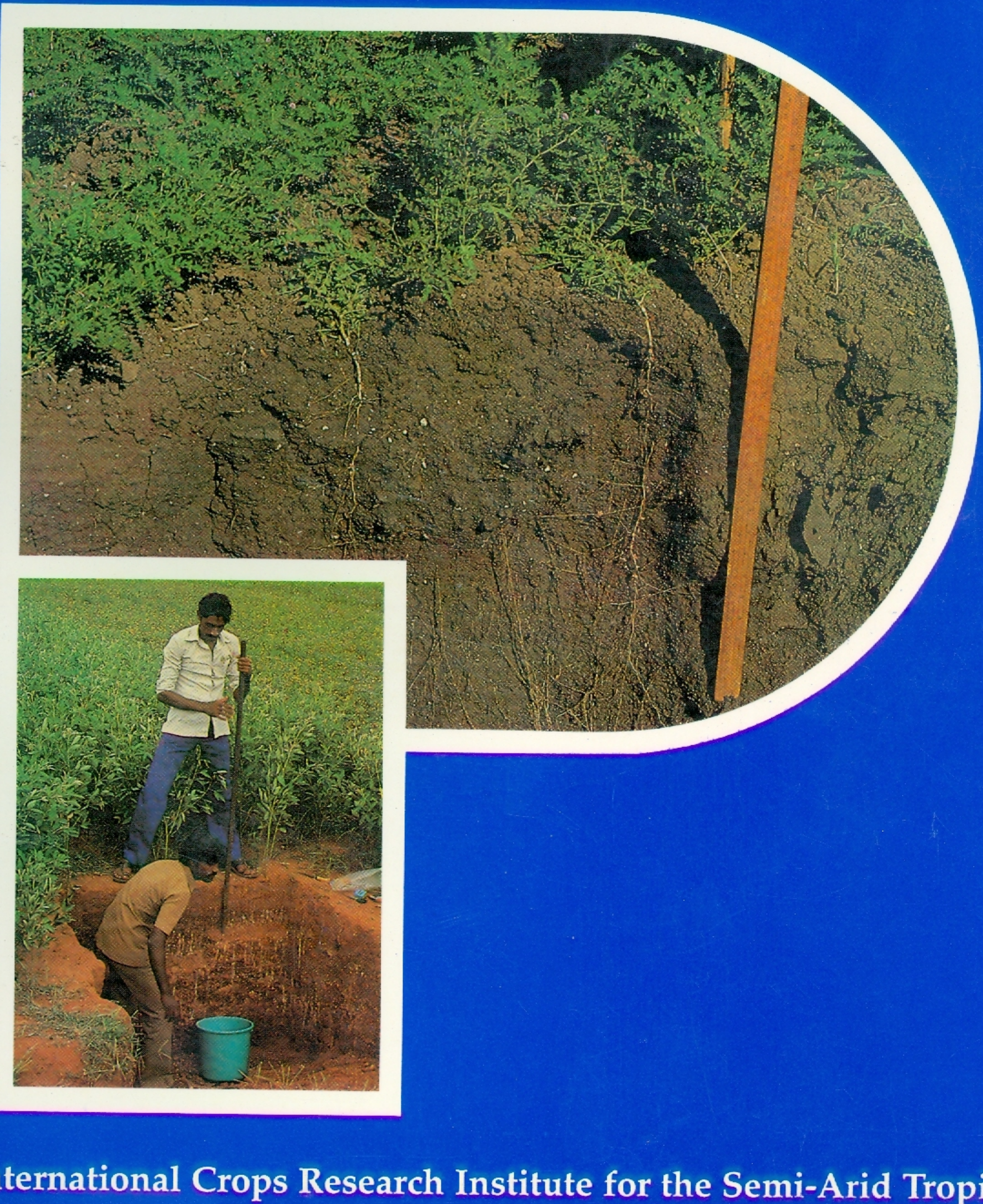
# Phosphorus Nutrition of Grain Legumes in the Semi-Arid Tropics



International Crops Research Institute for the Semi-Arid Tropics

# Abstract

**Citation:** ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1991. Phosphorus nutrition of grain legumes in the semi-arid tropics (Johansen, C., Lee, K.K., and Sahrawat, K.L., eds.). Patancheru, A.P. 502 324, India: ICRISAT. 264 pp. ISBN 92-9066-200-X. BOE 012.

This book contains papers presented at an international workshop on this topic held at ICRISAT Center on 8–11 Jan 1990. The workshop was the culmination of a 5-year special project at ICRISAT funded by the Government of Japan. The first part of the book covers phosphorus availability in soils of the semi-arid tropics (SAT), focusing on appropriate methods of measurement. Then follows a section on mechanisms by which plant roots take up soil phosphorus, highlighting the role of root exudates. Specific root exudates of chickpea (*Cicer arietinum* L.) and pigeonpea [*Cajanus cajan* (L.) Millsp.] are described in detail. Subsequent chapters deal with options for improving the phosphorus nutrition of grain legumes, particularly chickpea and pigeonpea, in the SAT. Noteworthy are discussions on how to manipulate favorably mycorrhizal associations. Final chapters cover phosphorus fertilization from the point of view of entire cropping systems. Recommendations are made for a better understanding of the dynamics of phosphorus cycling in target cropping systems, and the need for better use of current knowledge in improving phosphorus fertilizer-use efficiency in these systems.

# Résumé

**Référence**: ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1991. Nutrition phosphorée des légumineuses à grain dans les zones tropicales semi-arides (Johansen, C., Lee, K.K., et Sahrawat, K.L., éds.). Patancheru, A.P. 502 324, India: ICRISAT. 264 pp. ISBN 92-9066-200-X. BOE 012.

Cet ouvrage rassemble les communications du colloque international organisé sur ce thème au Centre ICRISAT du 8 au 11 janvier 1990. Le colloque a marqué le comble des recherches entreprises à l'ICRISAT dans le cadre d'un projet quinquennal spécial soutenu par le gouvernement du Japon. La première partie de l'ouvrage porte sur la teneur du sol en phosphore assimilable dans les tropiques semi-arides, en mettant l'accent sur les méthodes de mesure appropriées. La section suivante est consacrée aux mécanismes qui interviennent dans l'absorption du phosphore à partir du sol par les racines du plant; le rôle que les exsudats racinaires y jouent est souligné. Des exsudats racinaires spécifiques du pois chiche (*Cicer arietinum* L.) et du pois d'Angole [*Cajanus cajan* (L.) Millsp.] sont décrits en détail. D'autres chapitres traitent des options visant à l'amélioration de la nutrition phosphorée des légumineuses à grain, en particulier le pois chiche et le pois d'Angole dans les zones tropicales semi-arides. Il importe tout particulièrement, de noter les discussions sur les méthodes permettant de manipuler avec succès des associations mycorhiziennes. Les derniers chapitres abordent la fertilisation phosphorée du point de vue des système culturaux. Enfin des recommandations sont proposées afin de mieux saisir la dynamique du cycle du phosphore dans des systèmes de culture donnés. L'attention est accordée, à la necessité de mieux exploiter l'acquis actuel pour rendre plus efficace l'utilisation du phosphore dans ces systèmes.

# Resumen

**Citacion:** ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1991. Nutrición de fósforo de los legumbres granosos en los trópicos semi-áridos. (Johansen, C., Lee, K.K., y Sahrawat, K.L., eds.). Patancheru, A.P. 502 324, India: ICRISAT. 264 pp. ISBN 92-9066-200-X. BOE 012.

Este libro contiene las ponencias presentadas en un taller internacional sobre este tema que se celebró en el centro ICRISAT durante el 8-11 de enero de 1990. El taller fue la culminación de un proyecto especial de 5 años de duración, llevado a cabo en ICRISAT y financiado por el gobierno de Japón. La primera parte del libro abarca la disponibilidad de fósforo en las tierras de los trópicos semi-áridos (SAT), centrándose en métodos apropiados de medición. Después viene una sección sobre los mecanismos por los cuales las raíces de las plantas absorben el fósforo de la tierra, destacando el papel que desempeñan los exudados de las raíces. Los exudados específicos de las raíces de garbanzo (*Cicer arietinum* L.) y de guandul [*Cajanus cajan* (L.) Millsp.] están descritos detalladamente. Los capítulos subsecuentes se ocupan de las opciones para mejorar la nutrición de fósforo de los legumbres granosos, sobre todo de garbanzo y de guandul en los trópicos semi-áridos. Hay que destacar las discusiones sobre cómo manipular favorablemente las asociaciones micorrizales. Los capítulos finales se tratan de la fertilización de fósforo desde el punto de vista de todos los sistemas de cultivo. Se hacen recomendaciones para un mejor entendimiento de la dinámica de los ciclos de fósforo de los sistemas meta de cultivo, y la necesidad de la mejor utilización del conocimiento acutal sobre la eficacia del uso del fertilizante de fósforo en estos sistemas.

**Cover:** Above: roots of chickpea exposed in a Vertisol soil profile. Below: excavating an Alfisol soil profile to examine roots of a sole crop of short-duration pigeonpea.

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International Crops Research Institute for the Semi-Arid Tropics
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1991

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# Preface

This book was prepared from the proceedings of an international workshop held at ICRISAT Center, Patancheru, India, 8-11 Jan 1990. The workshop was organized as a culmination to a Government of Japan (GOJ) Special Project undertaken at ICRISAT during 1985-89. In this project, three Japanese scientists, N. Ae, J. Arihara, and K. Okada, studied the phosphorus (P) nutrition of chickpea (*Cicer arietinum* L.) and pigeonpea [*Cajanus cajan* (L.) Millsp.] growing on Alfisols and Vertisols at ICRISAT Center.

The aims of this workshop were to solicit views of international scientists with particular expertise in the subject matter covered by the project, facilitate detailed discussion on project research findings, and formulate future research requirements. The emphasis was on chickpea and pigeonpea, mandate legumes of ICRISAT, but examples to illustrate particular principles were also drawn from other grain legumes and other crop species.

The workshop sessions, and subsequently the parts of this book, were organized under four main themes: P availability in soil, P uptake by plants, methods of improving P nutrition, and a cropping systems perspective. The chairman of each session was requested to prepare an overview of the session, based on the workshop deliberations, and these are included as chapters herein. The meeting was organized so as to provide maximum discussion of the ideas presented, to permit a joint evaluation of present knowledge and encourage setting of priorities for further research.

We would like to express our appreciation to the other members of the Organizing Committee of the workshop, N. Ae, J. Arihara, K. Okada, Susan D. Hall, P.R. Murthy, and R. Narsing Rao. We are particularly grateful to R. Narsing Rao for his secretarial input at all stages, from planning of the workshop to publication of the book. We also thank other ICRISAT staff members who willingly contributed to organizational and logistic support, discussions during the workshop, and review of papers submitted. The active participation of non-ICRISAT delegates who were neither invited authors nor chairmen is also much appreciated. We appreciate the editorial input of Vrinda Kumble and the work of the ICRISAT Information Services in the publication process. We gratefully acknowledge the management of ICRISAT and the GOJ Special Project for sharing the costs of the workshop and the publication of this book. Finally, we thank the authors for their contributions herein.

**C. Johansen**
**K.K. Lee**
**K.L. Sahrawat**
Scientific Editors

# Foreword

Phosphorus deficiency is a major constraint to legume production in tropical and subtropical regions, particularly in acid soils. Responses of chickpea and pigeonpea to phosphorus in South Asia on predominantly neutral to alkaline soils, however, have been less than expected even when standard soil-test values indicate low availability of soil P.

This apparent enigma provided the theme for a special project conducted at ICRISAT Center from 1985 to 1989, in cooperation with the Tropical Agriculture Research Center, Ministry of Agriculture, Forestry, and Fisheries, Japan. The Government of Japan (GOJ) provided funding for employment and support of three Japanese scientists to work at ICRISAT Center to tackle this research problem. Such special projects allow more in-depth study of particular problems than would otherwise be possible with regular ICRISAT staff and resources and given the Institute's applied research priorities.

The workshop proceedings upon which this book is based marked the completion of this project. However, perhaps as an indication of the success of this collaboration, a second phase of the GOJ Special Project is now under way, concentrating on nitrogen dynamics of cropping systems incorporating the ICRISAT mandate legumes.

It is our hope that the contents of this book will provide an up-to-date assessment of knowledge on the subject of phosphorus nutrition of legumes and point the way to promising areas for future research.

**L.D. Swindale**
Director General
ICRISAT

# Foreword

The Government of Japan (GOJ) has supported activities at ICRISAT since its establishment, through funding and by posting Japanese scientists to work at the Institute. However, the establishment in 1984 of a GOJ Special Project, entitled "Methods of Soil Management and Pulses Cultivation in the Semi-Arid Tropics," marked an increased commitment of Japanese researchers to the problems of food production in semi-arid tropical regions. During the 6 years I spent as a member of ICRISAT's governing board (1983-88), the progress in ICRISAT's research activities has been gratifying, not only in relation to Japanese input but in general.

I was particularly interested in reports appearing in recent ICRISAT annual reports indicating that pigeonpea is better able than other crop species to absorb phosphorus from iron-bound P. The research proceeded to identify the mechanisms by which this occurred, particularly the role of P-solubilizing root exudates. This line of research has a parallel in other well-known research conducted in Japan on the role of phytosiderophores in enhancing the iron nutrition of cereal crops. A pioneer in this research, S. Takagi, was a contributor to the workshop and this volume.

During the workshop, discussions indicated an increased awareness that P uptake by plants could not be described solely by earlier-conceived equilibria between the plant root surface, soil solution, and P either adsorbed, fixed, or precipitated on soil particles. Exudation from plant roots appeared to be causing deviation of observed from expected values of P uptake, as discussed in detail in several chapters of this book.

As P deficiency is a major limitation to legumes grown in the tropics and subtropics, efficient use of soil and fertilizer P is an important consideration for low-input agricultural technology and sustainable agricultural systems. Of particular interest is the development of methods to tap sources of soil P normally considered unavailable for plant uptake. Here, the role of root exudates and mycorrhizae becomes important. This book examines recent concepts of how best to exploit these factors, along with other possible methods of improving P-use efficiency of grain legumes in the semi-arid tropics.

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# Part 1

# Phosphorus Availability in Soils of the Semi-Arid Tropics

# Potential Crop Productivity of Alfisols and Vertisols in the Semi-Arid Tropics

**S.A. El-Swaify[1] and R.C. Caldwell[1]**

## Abstract

*Alfisols and related soils (certain Aridisols, Entisols, and Ultisols) occupy the largest land area not only in the semi-arid tropics (SAT) but also worldwide. Vertisols are considerably less extensive globally but are the fourth most extensive soil order in the SAT. These soils often occur in close proximity along the landscape, but have widely contrasting properties that result in clear differences in both potential productivity and optimum management requirements. Such differences are more notable under rainfed conditions; both soil orders can be highly productive with adequate irrigation.*

*Substantial diversity exists within each of these orders; however, certain generalizations may be made on the soil-based attributes, constraints, and management requirements of each under rainfed conditions. The Productivity Index (PI) model was used to quantify how root-zone attributes, expressed as sufficiency values for meeting crop needs, determine potential soil productivity. PI comparisons were made between Alfisols (Rhodustalfs), Vertisols (Pellusterts), and Hawaii's SAT Oxisols (Eutrustox) with and without fertility sufficiency parameters, specifically phosphorus (P) status. Vertisols possessed the highest PI value in both cases. Alfisols and Oxisols had nearly equal values when nutrient sufficiency was not included in the PI index. However, Oxisols were far inferior to Alfisols when P sufficiency was considered, reflecting the low availability of P in Oxisols. Available data confirm the higher predicted productivity of SAT Vertisols as compared with Alfisols. Based on the PI model, it is hypothesized that SAT Oxisols, particularly those deficient in P, would be the least productive of the three soils.*

## Introduction

The semi-arid tropics (SAT) occupy nearly 20 million km$^2$ in at least 48 countries on 4 continents (Swindale 1982; Kanwar 1986). The largest SAT regions are in western Africa (24% of total land area), eastern Africa (18%), southern Africa (20%), South America (17%), Australia (10%), and South and Southeast Asia (11%, most of which is in India) (El-Swaify et al. 1985). These areas are characterized by certain similarities in climate, particularly the strictly seasonal rainfall, and staple crops.

Important crops are included in ICRISAT's mandate; namely, sorghum [*Sorghum bicolor* (L.) Moench], pearl millet [*Pennisetum glaucum* (L.) R.Br.], pigeonpea [*Cajanus cajan* (L.) Millsp.], chickpea (*Cicer arietinum* L.), and groundnut (*Arachis hypogaea* L.). According to Kanwar (1986), a large percentage of these crops—44% of the sorghum, 55% of the pearl millet, 90% of the pigeonpea, 96% of the chickpea, and 67% of the groundnut—are produced and consumed directly as human food in the SAT. Unfortunately, traditional dryland farming systems produce very low yields of all these crops,

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ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1991. Phosphorus nutrition of grain legumes in the semi-arid tropics (Johansen, C., Lee, K.K., and Sahrawat, K.L., eds.). Patancheru, A.P. 502 324, India: ICRISAT.

even in dependable rainfall regions. Estimates reported for peninsular India by El-Swaify et al. (1985) are 0.3-0.9 t $ha^{-1}$ for sorghum, 0.3-0.5 for pearl millet, 0.2-0.3 for pigeonpea, 0.2-0.5 for chickpea, and 0.4-0.6 for groundnut. There are indications, however, that many SAT sites possess a higher productivity potential than indicated by these figures. Improved cultivars and management have given up to tenfold yield increases (El-Swaify et al. 1985).

The objective of this paper is to discuss the extent to which soil-based attributes or constraints affect the realization of high crop yields under rainfed conditions in the SAT. Whenever possible, special emphasis will be placed on the performance of grain legumes, particularly pigeonpea, in Alfisols and Vertisols.

## Soils of the Semi-Arid Tropics

El-Swaify et al. (1985), Stewart et al. (1991), and Swindale (1982) have reviewed the distribution and extent of various soils in the SAT. Eight of the ten orders in the U.S. Soil Taxonomy are represented in these regions; five of them—Alfisols, Aridisols, Entisols, Oxisols, and Vertisols—account for more than two-thirds of the SAT land area (Fig. 1). Within these orders, SAT environments are identified at the suborder level by *ustic* moisture regimes in which "moisture is present at a time when conditions are suitable for plant growth" (USDA 1975). This moisture regime applies to tropical regions with a monsoon climate that has at least one rainy season lasting 3 months or more a year.

Emphasis in the following discussions will be placed on SAT Alfisols and Vertisols. However, we also refer to the Oxisols of Hawaii's SAT, as this will allow us to illustrate the applicability of the presented concepts to contrasting soils and to utilize the appreciable useful data available on these soils. El-Swaify (1980), Fox (1980), Fox and Searle (1978), and Theng (1980) have provided considerable information on the characteristics and management of Oxisols and other soils with variable-charge characteristics.

### Alfisols of the Semi-Arid Tropics

Alfisols occur extensively in southern Asia, western and central Africa, and many parts of South America (Fig. 1). These soils can be derived from many different parent rocks. Coarse-textured Alfisols are most likely to develop on granite, gneiss, schist, sandstone, mica, acid trap, quartzite, and shale. Fine-textured Alfisols are most often derived from such rocks as chanockite, diorite, basalt, or other materials that are rich in clay-forming minerals. Weathering of lime-bearing feldspars may produce lime concretions, which appear in the form of discrete nodules or thick veins. An important profile feature of many Alfisols is the "murrum" layer, which is a distinct layer of gravel and weathered rock fragments occurring at depths below the argillic horizon. The extent to which murrum impedes root development and growth is unclear, but appears highly dependent on water content (El-Swaify et al. 1984).

Characteristically, these soils have a coarse-textured surface horizon, and clay content increases with depth. By definition, Alfisols possess an argillic horizon, which constitutes the "control section" within the profile. Proposed revisions in Soil Taxonomy may identify some of these argillic horizons as *kandic* horizons, particularly where clay content undergoes a sharp increase over a short depth (van Wambeke 1989). The high base saturation of the control section (>35%) distinguishes Alfisols from Ultisols. Argillic horizons may compound the contribution of murrum layers in inhibiting root development and, in turn, prevent crops from withstanding even moderate droughts (Charreau and Nicou 1971). Because of the flexibility in the criteria that characterize the argillic horizon, many diverse soils are included in this taxonomic order (El-Swaify et al. 1984). To distinguish among these, criteria based on the definition of the eluvial horizon, different parent materials, and clay mineralogy must be used. For example, the Alfisols of peninsular India generally contain a higher percentage of clay-sized particles and active clays (e.g., 2:1 layer silicates) than those in western Africa. Clay mineralogy appears primarily kaolinitic, with varying sesquioxide contents. Using the scheme proposed by Fox and Searle (1978), the soils may be considered to have moderate potential for phosphorus (P) fixation.

Among Alfisols in the SAT, Haplustalfs, Paleustalfs, and Rhodustalfs are the most important agriculturally. Their profiles may be respectively designated as thin, thick, and eutrophic (derived from basic parent material) (Swindale 1982). Alfisols appear to belong to several of the soil map units in the FAO/UNESCO soil maps of the world (FAO/UNESCO 1974-1978), namely, Luvisols, Nitosols, and Arenosols. Those in India may be grouped under Chromic or Ferric Luvisols, while those in western Africa are probably Luvic or Ferralic Arenosols. El-Swaify et al. (1984) concluded that the characteriza-

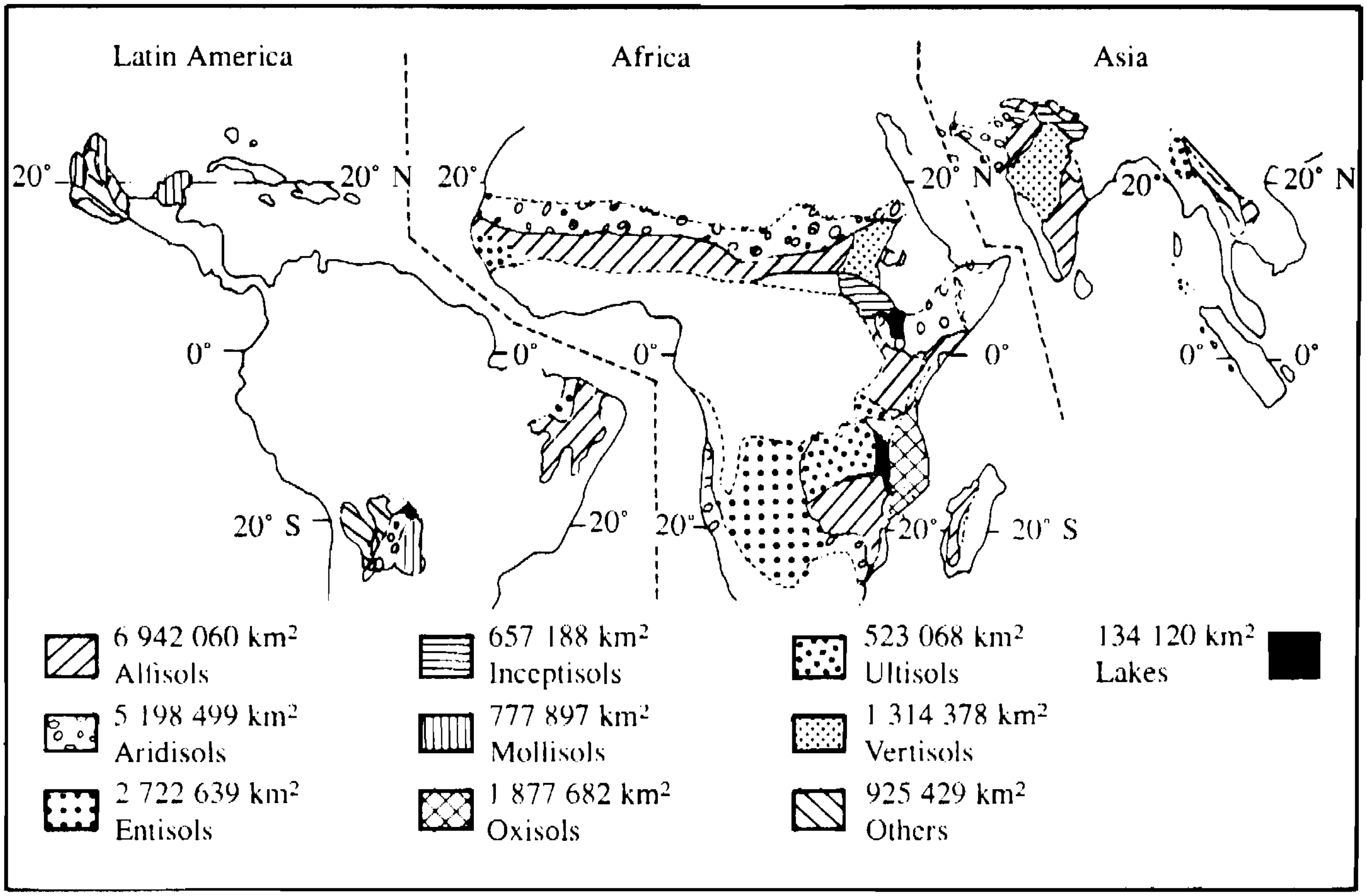

**Figure 1. Soil orders in the semi-arid tropics according to the U.S. Soil Taxonomy. Source: El-Swaify et al. (1984).**

tion and classification of SAT Alfisols are not sufficiently advanced to allow clear mapping and delineation. They considered these tasks to be of high priority for allowing the systematic establishment of research networks and reliable transfer of appropriate improvements in technology. Proposed changes in tropical soil classification and diagnostic horizons may ultimately remove some of these ambiguities (van Wambeke 1989).

Alfisols are represented in this discussion by the red soils at ICRISAT Center, Patancheru, India (Patancheru sandy loam, a Udic Rhodustalf) (Table 1).

### Vertisols of the Semi-Arid Tropics

These deep black soils, also known as Black Cotton Soils or Black Magnesium Clays, are abundant in India, Sudan, Ethiopia, Australia, the USA, and other countries. Vertisols, by the Soil Taxonomy's definition (USDA 1975) contain more than 30% clay-sized particles and are therefore heavy in texture. Vertisols may be derived from basalt, shale, limestone, volcanic rock, tuffs, gneiss, schist, and/or basic alluvium or collovium materials (El-Swaify et al. 1985). Their clay mineralogy is most often montmorillonitic, although some tropical Vertisols may be rich in halloysites and other minerals (El-Swaify et al. 1977). High clay contents and active mineralogy combine to provide Vertisols with relatively high, and permanent, cation-exchange capacities (up to 70 meq 100 $g^{-1}$). Except when they contain halloysites and sesquioxides, the soils have a low affinity for P sorption and, thus, have a low tendency for P fixation (Fox and Searle 1978). Appreciable contents of calcium carbonate ($CaCO_3$) and calcium sulfate ($CaSO_4$) are common in Vertisols. Murthy (1988) provided a comprehensive review of Vertisols in India.

High water-holding capacity is an important property of the Vertisols, and water retention is highly associated with shrinkage and swelling. Cracks that form upon drying and progressively increase in size during the dry season can achieve impressive sizes; it is believed that the roots of certain crops (including pigeonpea, Sheldrake and Venkataratnam 1983) can be damaged as a result. Such cracks enhance evaporation of moisture from the soil. In SAT Vertisols (Usterts), cracks remain open for 3-5 months or more but close when the soil reswells after the onset of the rainy season. Cracks allow high initial infiltration rates in dry Vertisols, but swelling reduces these rates several hundredfold in saturated soils. Bulk density varies from approximately 1.0 Mg m$^{-3}$ in wet (swollen) soils to 1.8 Mg m$^{-3}$ in dry soils; the bulk density at field capacity ranges between 1.6 and 1.8 Mg m$^{-3}$ (El-Swaify et al. 1985).

Physically, the most important attribute for rainfed farming of Vertisols is their high content of plant-available water (El-Swaify et al. 1985). This is tempered, however, by the slow rate of infiltration, impeded internal drainage, poor trafficability, and the sticky nature of the soils when wet as well as their excessive hardness and difficult workability when dry.

Vertisols are represented in this discussion by the Kasireddipalli series (a Typic Pellustert) at ICRISAT Center (Table 1).

## Oxisols of the Semi-Arid Tropics

Although we are primarily concerned with Alfisols and Vertisols in this discussion, we also include an Oxisol for comparison and contrast. For this purpose, we have chosen an Oxisol from the SAT central region of the island of Oahu, Hawaii (Wahiawa silty clay, a Tropeptic Eutrustox). This soil is uniformly high in clay content with depth; is primarily kaolinitic, with a high content of sesquioxides; possesses a high degree of aggregation and microstructural stability; has a relatively weak macrostructure and is easily compactable; has high infiltration rates, low runoff

**Table 1. General characteristics of a selected SAT Alfisol (Rhodustalf), Vertisol (Pellustert), and Oxisol (Eutrustox)[1].**

| Depth (cm) | Horizon | Particle-size analysis (%)[2] Sand | Silt (<0.02 mm) | Clay (<0.002 mm) | Water content (%) 0.03 MPa | 1.5 MPa | Organic carbon (%) | CEC $NH_4OAc$ (meq 100 $g^{-1}$) | Base saturation $NH_4OAc$ (%) | pH[3] ($H_2O$) |
|---|---|---|---|---|---|---|---|---|---|---|
| Alfisol (Patancheru sandy loam) | | | | | | | | | | |
| 0- 5 | Ap | 79.3 | 6.4 | 14.3 | 16.2 | 6.3 | 0.55 | 4.8 | 74 | 6.0 |
| 5- 18 | B1 | 66.7 | 5.5 | 27.8 | 20.0 | 12.4 | 0.52 | 8.2 | 64 | 6.9 |
| 18- 36 | B21t | 14.6 | 6.8 | 51.6 | 21.9 | 13.9 | 0.63 | 14.8 | 69 | 6.9 |
| 36- 71 | B22t | 45.0 | 4.4 | 50.6 | 24.8 | 17.4 | 0.40 | 14.1 | 82 | 6.8 |
| 71-112 | B23t | 54.1 | 7.4 | 36.5 | 23.6 | 16.2 | 0.10 | 9.8 | 88 | 6.5 |
| 112-140 | B3 | 70.6 | 4.1 | 25.3 | 18.7 | 11.5 | 0.18 | 9.1 | 92 | 6.2 |
| Vertisol (Kasireddipalli clay) | | | | | | | | | | |
| 0- 16 | Ap | 43.6 | 16.3 | 40.1 | 32.5 | 18.7 | 0.27 | 34.9 | 93 | 8.1 |
| 16- 57 | B12 | 33.2 | 17.3 | 49.5 | 34.9 | 20.5 | 0.12 | 35.2 | 94 | 8.5 |
| 57-118 | B13 | 18.9 | 20.4 | 60.7 | 33.4 | 20.5 | 0.18 | 48.3 | 92 | 8.5 |
| 118-155 | B14 | 20.3 | 19.4 | 60.3 | 35.8 | 21.3 | 0.12 | 43.6 | 100+ | 8.2 |
| Oxisol (Wahiawa silty clay) | | | | | | | | | | |
| 0- 10 | Ap1 | 9.9 | 30.3 | 59.8 | 34.3 | 24.6 | 2.77 | 20.8 | 66 | 5.4 |
| 10- 27 | Ap2 | 8.5 | 28.6 | 62.9 | 32.0 | 23.6 | 1.72 | 18.4 | 45 | 5.0 |
| 27- 40 | AB | 8.5 | 35.7 | 55.8 | 33.4 | 23.9 | 1.41 | 17.6 | 53 | 5.3 |
| 40- 65 | B21 | 8.2 | 30.4 | 52.4 | 40.0 | 33.0 | 0.59 | 13.7 | 64 | 5.8 |
| 65- 90 | B22 | 1.6 | 24.8 | 73.6 | - | - | 0.36 | 13.0 | 67 | 6.1 |
| 90-120 | B23 | 4.2 | 20.9 | 74.9 | - | - | 0.27 | 14.1 | 62 | 6.3 |
| 120-150 | B24 | 6.4 | 23.7 | 69.9 | - | - | 0.24 | 14.4 | 65 | 6.4 |

1. Sources: Alfisol and Vertisol – El-Swaify et al. (1985); Oxisol – El-Swaify (1980).
2. International textural classification for the Alfisol and Vertisol (0.02 mm limit for silt); American textural classification for the Oxisol (0.05 mm limit for silt).
3. In 1:2.5 suspension for the Alfisol and Vertisol; 1:1 suspension for the Oxisol.

generation potential, and low erodibility; and has more exchangeable acidity and considerably higher capacity for P sorption than either the Alfisols or Vertisols (El-Swaify 1980; Fox and Searle 1978; Table 1).

## Constraints to Productive Rainfed Farming

### General Constraints

Climatic constraints are often the most critical determinants of productive agriculture in the SAT. Stewart et al. (1991) proposed a generalized scheme for assessing the difficulty of achieving agricultural sustainability as determined by the combined effects of temperature and moisture regimes. The scheme assumes that this difficulty is directly proportional to the amount of precipitation and inversely proportional to the temperature and potential evapotranspiration at a given site. These authors justified their reasoning in view of the various uncertainties and soil-degradation processes that come into play in different climatic regions, the most dominant being soil erosion and organic matter decline. They also suggested that the benefits that can be derived from soil-conservation practices in unfavorable (hot and arid) environments are lower than those in favorable (cool and wet) ones. Figure 2 shows an application of this concept to specific locations, including several in the SAT. Sustainability difficulty is estimated as a relative index, using the ratio of potential evapotranspiration to rainfall at a given site.

Elements of climatic risk in SAT regions have been previously analyzed (e.g., Virmani et al. 1978). These include strict rainfall seasonality, with nearly 90% of annual precipitation falling in a prescribed rainy season; wide rainfall fluctuations between and within rainy seasons; and highly uncertain dates of arrival and withdrawal of seasonal rainfall. Soil characteristics are critical for determining the extent to which productive and sustainable farming can be designed and realized in a particular climatic setting.

### Soil-based Constraints

The contrasting characteristics of Alfisols and Vertisols, which affect their respective productivity potentials, are basically attributable to differences in explorable rooting depth, particle-size distribution, gravel content, aggregation and structural characteristics, mineralogy, water-retention and transmission properties, and horizon differentiation and depth within the soil profile. These are reflected in differences in the retention, release, and availability of water and nutrients; accumulation and stabilization of organic matter; internal drainage; potential for runoff and erosion; and vulnerability to sealing, crusting, and compaction. Acidity can be a constraint in "borderline" Alfisols, such as those in West Africa (El-Swaify et al. 1984). Salinity can be a constraint in Vertisols, and the soils are quite sensitive to even low levels of sodicity (El-Swaify et al. 1977).

The following discussion focuses on soil attributes and does not directly include the impact of water losses as excess runoff in determining soil productivity. However, it is important to note that such losses can be critical, particularly under rainfed conditions. El-Swaify (1987a) estimated that current management practices allow runoff losses of 26%, 28%, and 15% of rainfall for selected soils representing Alfisols, Vertisols, and Oxisols, respectively. Reducing these losses and maximizing the use efficiency of rainfall are important to realizing the potential productivity of the soils.

## Potential Productivity of Soils in the Semi-Arid Tropics

Research on and modeling of erosion impacts on soil productivity have produced many tools that are applicable to assessing site productivity and spatial or temporal changes therein. This is particularly important in view of persistent threats of land degradation in tropical environments. Soil loss affects the physical, chemical, and biological quality of soils and, as a consequence, reduces soil productivity. El-Swaify (1989), reporting on the results of long-term studies on Oxisols, concluded that crop response to erosion is determined by:

- crop type, species, cultivar, rooting habits, and tolerance to nutritional and physical stresses;
- level of applied inputs, particularly fertilizers and amendments, tillage, and irrigation;
- the physical, chemical, and biological quality of the eroded soil in comparison with the uneroded soil;
- soil type, texture, rooting depth, mineralogy, and degree of weathering; and
- prevailing climatic conditions.

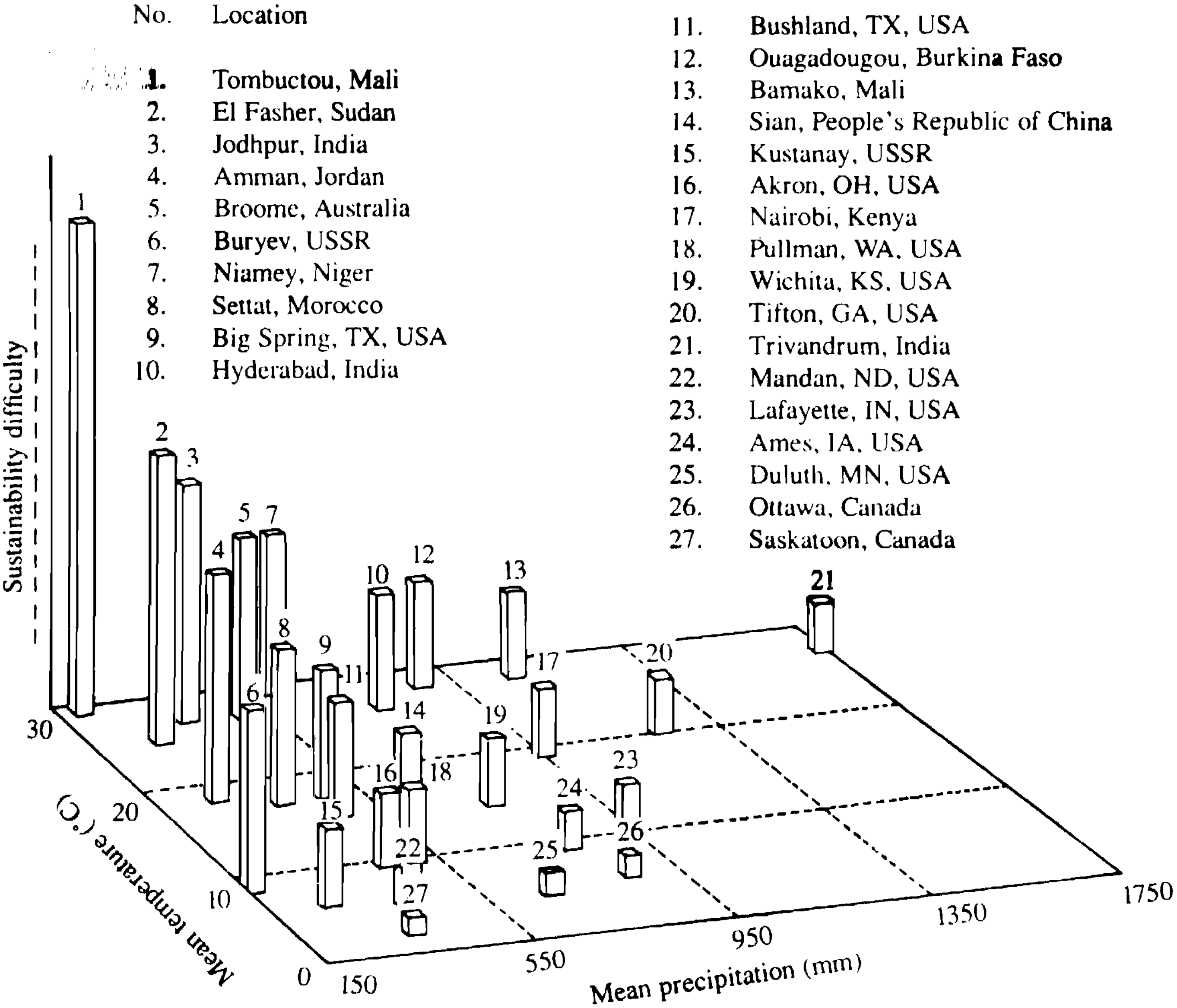

**Figure 2. Relationship between mean annual temperature and precipitation for various locations and temperature/precipitation as an index indicating difficulty of developing a sustainable agriculture system. Source: Stewart et al. (1990).**

It is evident that these are the very factors affecting overall site productivity. Changes in root-explorable soil depth, excessive runoff, and the limitations to plant-available water storage associated with both, dominate in determining the impacts of erosion on productivity, particularly in rainfed farming systems (Pierce et al. 1983; El-Swaify 1987a). All are often associated with or exacerbated by changes in the soil structure, both at the surface (by sealing or crusting) and below (consolidation, compaction, or exposure of inferior soil layers). In addition, depletion of organic carbon, nutrients, and nutrient-holding capacity are critical, particularly in coarse-textured and highly weathered (mineralogically inactive) soils, such as Alfisols, and when fertilizer supplements are absent or limited (as in low-input farming). Erosion also affects the abundance and efficacy of beneficial soil microorganisms such as *Rhizobium* (Habte and El-Swaify 1988) and mycorrhizae (Yost et al. 1985). Stocking (1984) observed that, in general, crop yield declined linearly with soil loss for soils with appreciable and uniformly distributed nutrient reserves and exponentially in texture-contrast soils and those with nutrients concentrated in the topmost layers. He estimated that the impact of a unit loss in soil on yield is at least 20 times greater for tropical than for temperate conditions. El-Swaify (1987b) reported similar conclusions, based on socioeconomic arguments as well as a large body of erosion-productivity data for Hawaii's Oxisols.

The two most widely available models that lend themselves to estimating potential productivity are the EPIC model (Erosion Productivity Impact Calculator—Williams 1983) and the PI model (Productivity Index—Pierce et al. 1983). EPIC is a comprehensive, complex, and primarily process-based model that has massive data requirements for the combined application of crop-growth and soil-loss prediction submodels (Williams 1983). The less complex PI model will be employed here to compare the relative potential productivities of important SAT soils.

## Applying the Productivity Index Model to Alfisols, Vertisols, and Oxisols

The PI model (Pierce et al. 1983) views soil productivity as an intrinsic property and has a special appeal because of its logic, simplicity, and modest data requirements, and the ease with which it can accomodate additional input variables. This model's formulation assumes that the productivity index (PI) is determined by sufficiency functions (SUF) for each of the soil's productivity attributes in each soil layer (i) and a weighting factor based on the fraction of total crop roots present in that layer ($WF_i$). The attributes originally included are plant-available water storage capacity (PAW), aeration (AER), bulk density (DB), pH (PHS), and electrical conductivity (EC). Thus:

$$PI = \sum_{i=1}^{r} (SUFPAW \times SUFAER \times SUFDB \times SUFPHS \times SUFEC \times WF_i) \quad (1)$$

where r is the number of soil layers. Following the work of Kiniry et al. (1983), Pierce et al. (1983) suggested specific sufficiency functions for each attribute (Fig. 3 and Table 2) and depth-dependent idealized root-distribution functions for estimating WF in various soil increments. The latter is based on Horn's equation for predicting the profile of fractional depletions from a moist soil:

$$L = 0.152 \log(R + \sqrt{R^2 + 6.45}) - 0.152 \log(D + \sqrt{D^2 + 6.45}) \quad (2)$$

where L is the fractional water depletion for a given depth, D the depth, and R the (plant-determined) rooting depth. Table 3 shows computed values of L and subsequent WF values for rooting depths of 100

**Table 2. Nonlimiting, critical, and root-limiting bulk densities and criteria for their determination for different texture classes (Pierce et al. 1983).**

| | Bulk density (Mg m$^{-3}$) | | |
|---|---|---|---|
| Texture class | Nonlimiting | Critical | Root-limiting |
| Sandy | 1.60 | 1.69 | 1.85 |
| Coarse loamy | 1.50 | 1.63 | 1.80 |
| Fine loamy | 1.46 | 1.67 | 1.78 |
| Coarse silty | 1.43 | 1.67 | 1.79 |
| Fine silty | 1.34 | 1.54 | 1.65 |
| Clayey: 35-45% | 1.40 | 1.49 | 1.58 |
| >45% | 1.30 | 1.39 | 1.47 |

| | Criteria for determining bulk density | | | | |
|---|---|---|---|---|---|
| | | | Air-filled porosity (%) | | |
| Texture class | AWC[1] (m$^3$ m$^{-3}$) | Clay (%) | Nonlimiting | Critical | Limiting |
| Fine loamy | 0.10 | 25 | 20 | 10 | 5 |
| Coarse silty | 0.20 | 10 | 20 | 10 | 5 |
| Fine silty | 0.15 | 25 | 20 | 10 | 5 |
| Clayey 35-45% | 0.10 | 40 | 15 | 10 | 5 |
| >45% | 0.10 | 50 | 15 | 10 | 5 |

1. Available water-holding capacity.

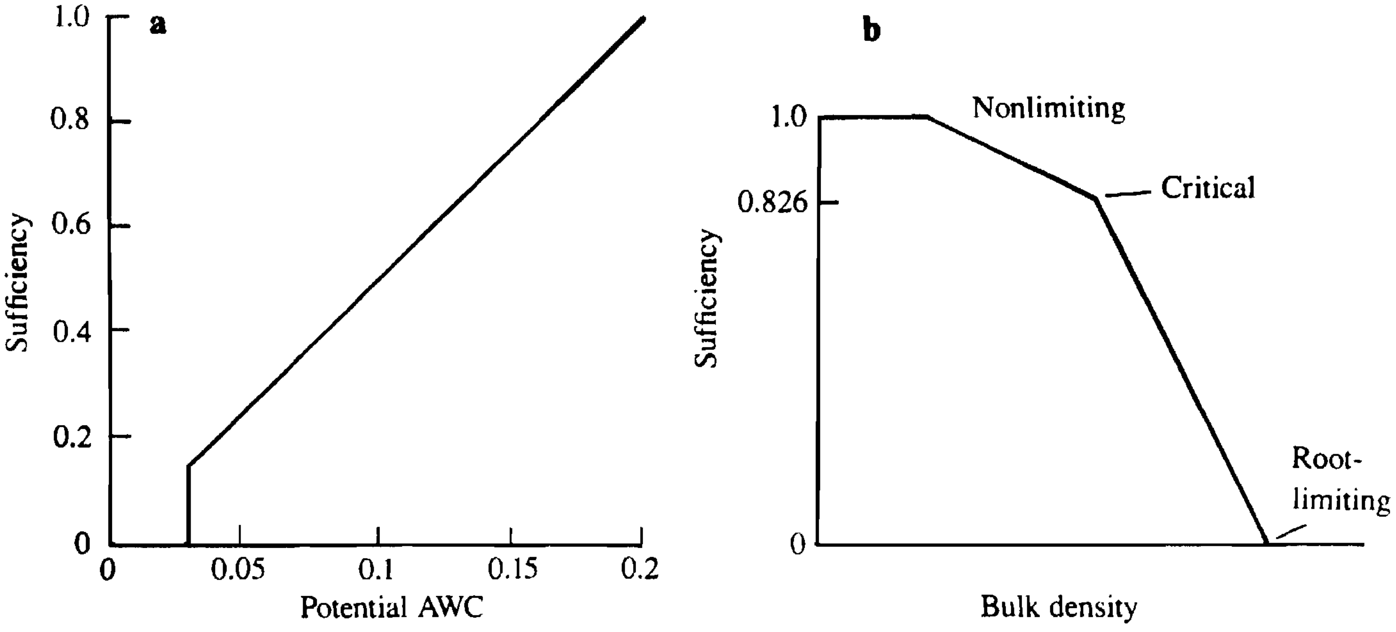

**Figure 3. Sufficiency of available water capacity (a) and sufficiency of bulk density (b) used in the Productivity Index model. Source: Pierce et al. (1983).**

**Table 3. Predicted soil water depletion and root fractions (RI) for an ideal soil with plant-determined rooting depths, R, of 200 cm and 100 cm (Kiniry et al. 1983).**

| | R = 200 cm | | R = 100 cm | |
|---|---|---|---|---|
| Depth increment (cm) | Depleted soil (cm) | RI | Depleted soil (cm) | RI |
| 0- 10 | 2.481 | 0.190 | 2.023 | 0.314 |
| 10- 20 | 1.717 | 0.132 | 1.260 | 0.196 |
| 20- 30 | 1.375 | 0.105 | 0.918 | 0.143 |
| 30- 40 | 1.152 | 0.088 | 0.694 | 0.108 |
| 40- 50 | 0.986 | 0.076 | 0.528 | 0.082 |
| 50- 60 | 0.853 | 0.065 | 0.395 | 0.061 |
| 60- 70 | 0.742 | 0.057 | 0.285 | 0.044 |
| 70- 80 | 0.648 | 0.050 | 0.190 | 0.030 |
| 80- 90 | 0.566 | 0.043 | 0.108 | 0.017 |
| 90-100 | 0.492 | 0.038 | 0.034 | 0.005 |
| 100-110 | 0.426 | 0.033 | | |
| 110-120 | 0.365 | 0.028 | 6.435 | 1.000 |
| 120-130 | 0.310 | 0.024 | | |
| 130-140 | 0.260 | 0.020 | | |
| 140-150 | 0.212 | 0.016 | | |
| 150-160 | 0.168 | 0.013 | | |
| 160-170 | 0.127 | 0.010 | | |
| 170-180 | 0.088 | 0.007 | | |
| 180-190 | 0.052 | 0.004 | | |
| 190-200 | 0.017 | 0.001 | | |
| | 13.037 | 1.000 | | |

and 200 cm. It is assumed that these values accommodate the range of ideal rooting depths for SAT grain legumes. The two selected depths appear to correspond to root-distribution patterns for short-duration and medium-duration pigeonpea, respectively (Chauhan, in press). It is important to note that the PI model is intended for use under rainfed conditions, as irrigation tends to mask most of the critical constraints, particularly physical parameters, that determine its value.

Table 4 shows results of PI calculations for the selected soils using applicable SUF values in equation 1 for the two plant-determined rooting depths (D values in equation 1). The index predicts that the productivity of Vertisols (Chromusterts or Pellusterts) for crop, including legume, production is superior to either the Alfisols (Rhodustalfs) or Oxisols (Eutrustox). The Alfisols and Oxisols rank almost equally when only the constraints/attributes included in equation 1 are considered. It is important to note that SUFAER, which was not determined here because data were unavailable, can be a major limitation for legumes growing in high-rainfall rainy seasons on Vertisols. This becomes clearly evident from ICRISAT's experience with short-duration pigeonpea (C. Johansen, 1990, ICRISAT, personal communication).

## PI Modification with Nutrient Sufficiencies

The soil attributes included in the original PI formulation (equation 1) did not include soil fertility as a constraint, as the authors assumed that it is a "replaceable" quality and that sufficient levels will always be provided by the farmer (Rijsberman and Wolman 1984). El-Swaify (1987b) argued that such assumptions rarely apply in tropical settings and resource-poor farming. This argument is supported by plentiful evidence for soils of the tropics (e.g., Biot 1987; El-Swaify 1987a, 1987b; Mbagwu et al. 1984; Stocking 1984; Yost et al. 1985). The absence of published and usable sufficiency indices for nutrients prevents a full treatment of the subject in the present context. However, there appears to be adequate information on internal (plant) and external (soil-solution) requirements for P to allow a preliminary treatment of the subject within the PI context.

The papers by Fox (1980), Fox and Searle (1978),

**Table 4. Computed sufficiencies (SUF) and productivity indices (PI) for Alfisols, Vertisols, and Oxisols according to equation (1).**

| Depth (cm) | Parameter[1] | Soil type |  |  |
|---|---|---|---|---|
|  |  | Alfisol | Vertisol | Oxisol[2] |
| 0- 15 | SUFPAW | 0.7 | 0.9 | 0.8 |
| 15- 30 |  | 0.6 | 0.9 | 0.7 |
| 85-100 |  | 0.5 | 0.9 | 0.6 |
| >100 |  | NA | 0.9 | 0.6 |
| 0- 15 | SUFDB | 0.9 | 1.0 | 1.0 |
| 15- 30 |  | 0.7 | 0.7 | 0.8 |
| 85-100 |  | 0.3 | 0.7 | 0.4 |
| >100 |  | 0.3 | 0.7 | 0.6 |
| 0- 15 | SUFPHS | 1.0 | 0.8 | 0.7 |
| 15- 30 |  | 1.0 | 0.7 | 0.7 |
| 85-100 |  | 1.0 | 0.7 | 0.9 |
| >100 |  | 1.0 | 0.7 | 0.9 |
| Profile | PI-100[3] | 0.42 | 0.56 | 0.40 |
| Profile | PI-200[4] | 0.35 | 0.53 | 0.34 |

1. PAW = plant-available water-holding capacity; DB = bulk density; PHS = pH; AER = aeration; EC = electrical conductivity. Neither SUFAER nor SUFEC in equation (1) were considered limiting.
2. PI values for the Oxisols were modified for gravel content and penetrometer resistance (see Rijsberman and Wolman 1984).
3. PI value calculated assuming a rooting depth (R in equation 2) of 100 cm.
4. PI value calculated assuming a rooting depth (R in equation 2) of 200 cm.

Juo and Fox (1977), Peaslee and Fox (1978), Silva and Fox (1977), and Yost et al. (1985) allow the estimation of adequate sufficiency functions for P, i.e., SUFP, to supplement the other parameters in equation 1. These papers utilize equilibrium sorption isotherms to estimate the soil-solution P level necessary for optimum crop yield (external P requirement). For most crops, this level ranged from approximately 0.05 to 0.5 mg $kg^{-1}$ (Fig. 4a) and does not appear to be soil-specific (Fig. 4b).

Phosphorus-sorption data published by Fox and Searle (1978) for many soils and by Juo and Fox (1977) for Alfisols were used to estimate the initial equilibrium P concentration in soil solution, i.e., without added P fertilizer. In the absence of similar data for pigeonpea, chickpea, groundnut, or similar legumes, 0.2 mg $kg^{-1}$ in soil solution was assumed as adequate for full sufficiency, and Figure 4a was used to approximate the sufficiency function (SUFP) for these crops. It is recognized that pigeonpea appears to respond less to P fertilization than other legumes (Johansen 1990). Available data, however, are not comparable with isotherm data and most often report fertilizer application rates rather than specific P levels in soil solution.

Table 5 shows estimated sufficiency evaluations for nonfertilized Alfisols, Vertisols, and Oxisols. Unfortunately, only a few sorption data were available for subsurface soil layers. Therefore, generalizations were made for applying the data to various depths; surface-soil isotherms were assumed applicable to depth increments in the top 15 cm (normal depth of plowing and mixing) and subsurface isotherms to deeper increments.

Applying SUFP data to the PI index for the various (nonmanaged or nonfertilized) soils entails appropriate combination of the data in Tables 4 and 5. The resulting respective PI (termed PI-p) values for the Alfisols, Vertisols, and Oxisols, are: 0.35, 0.53, and 0.15 at R = 100 cm; 0.30, 0.51, and 0.12 at R = 200 cm. Incorporating P sufficiency left the PI value for the Vertisol essentially unaltered, slightly lowered the value for the Alfisol, but drastically lowered the value for the Oxisol. Clearly, appropriate nutrient in-

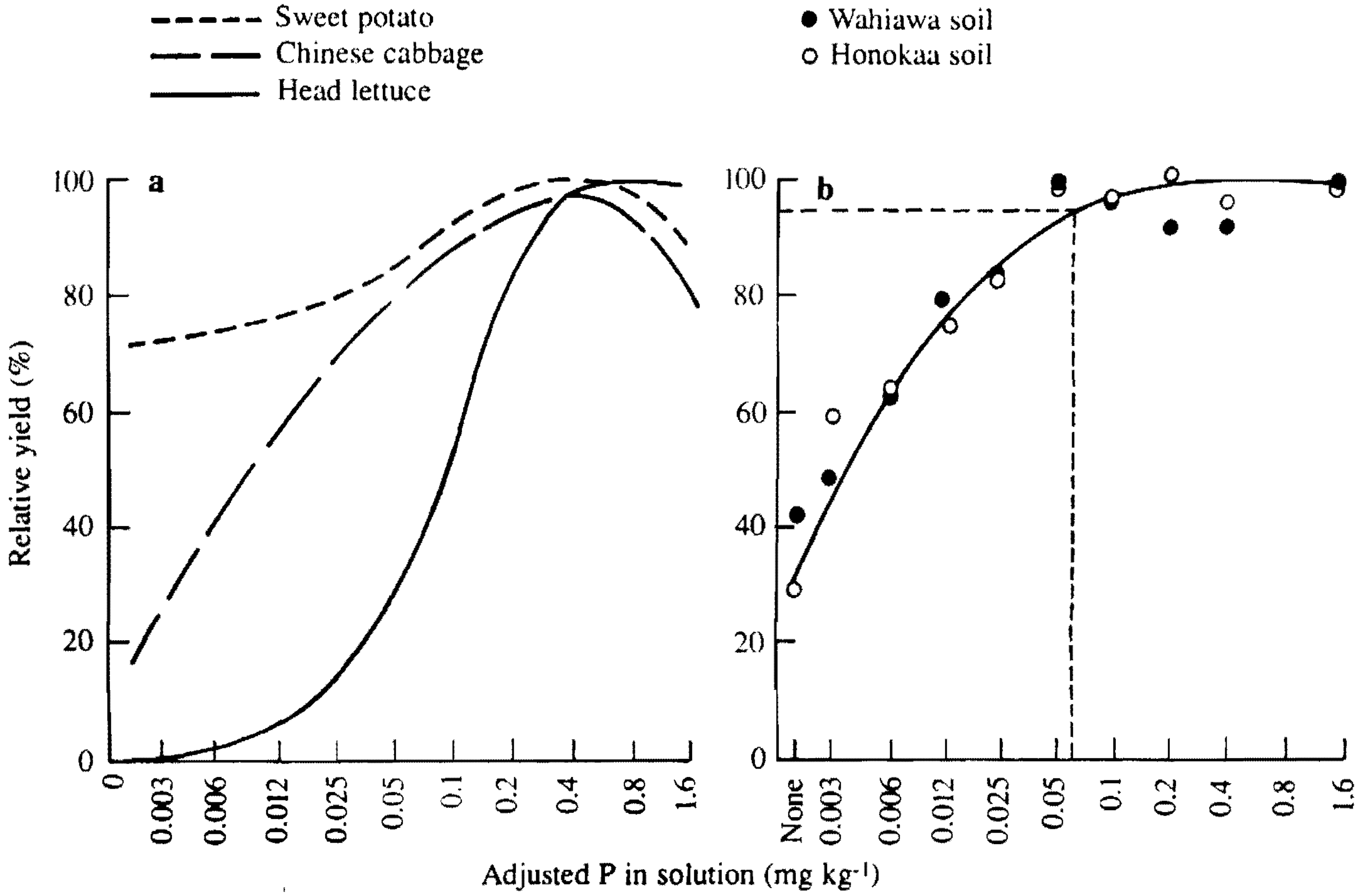

**Figure 4. Comparative growth-response curves for (a) Chinese cabbage, sweet potato, and lettuce growing on a Wahiawa soil (Typic Eutrustox) and (b) corn in soils of contrasting mineralogy in relation to adjusted concentrations of phosphorus in the soil solution. Source: Peaslee and Fox (1978).**

**Table 5. Estimated phosphorus sufficiency (SUFP) values for selected soils (Data adapted from Fox and Searle 1978; Juo and Fox 1977; Peaslee and Fox 1978; Silva and Fox 1977; and Yost et al. 1985).**

| | Equilibrium P in soil solution (mg kg$^{-1}$) | | Estimated SUFP | |
|---|---|---|---|---|
| Soil type | Surface | Subsurface | Surface | Subsurface |
| Alfisols<br>(Paleustalfs, Haplustalfs) | 0.09 | 0.006 | 0.90 | 0.65 |
| Vertisols<br>(Chromusterts) | 0.33 | 0.09 | 1.0 | 0.90 |
| Oxisols<br>(Eutrustox) | 0.005 | 0.002 | 0.55 | 0.20 |

puts, in this case P, are more critical for realizing the productivity potential of Oxisols than of Alfisols or Vertisols. Since pigeonpea has displayed low response to P fertilization in Alfisols and Vertisols at ICRISAT Center in India, it would be valuable to ascertain whether this crop responds differently on Oxisols.

### Erosion-induced Productivity Changes

Application of the PI model allows an approximation of the effects of erosion on soil productivity. El-Swaify (1987a) showed that, among the soils discussed here, Alfisols of limited depth are the most vulnerable to erosion impacts, with a PI loss of nearly 1% for every 1 cm of soil loss. Vertisols and Oxisols were predicted to undergo less than half of this loss, primarily because of more uniform soil profiles.

### Reconciling Relative and Absolute Productivity

El-Swaify et al. (1985) summarized results of village-level crop yield surveys in India. Sorghum was the only crop reported for both Alfisols and Vertisols; average grain yields for this crop are 0.3-0.5 t ha$^{-1}$ on Alfisols and 0.5-0.9 t ha$^{-1}$ on Vertisols. Few data are available on yields of sole-cropped pigeonpea on a field scale. Yields of rainfed pigeonpea grain have been reported to reach 3.0 t ha$^{-1}$ or more under ideal management conditions (C. Johansen, 1989, ICRISAT, personal communication). Srivastava et al. (1984) summarized operational-scale yield data for maize/pigeonpea intercrops; maize yield was 1.8-3.2 t ha$^{-1}$ on Vertisols and 1.4-2.6 t ha$^{-1}$ on Alfisols; corresponding pigeonpea yields were 0.9-1.6 and 0.6-0.8 t ha$^{-1}$. These data support the predicted relative productivity as estimated by the PI values for these soils. Although no similar data are available for Oxisols, it is hypothesized that yields on these soils would be either comparable to or less than those on Alfisols, depending on the extent to which P fertility is provided.

It is instructive to refer to Figure 2 again if the concepts discussed here are to be applied more generally. Climatic constraints to crop performance and threats to sustainability impose strong influences on the short- and long-term potential productivity of a given soil.

## Predicting and Improving Productivity

### Data Requirements for Estimating Potential Productivity

The above discussion points to the need for specific data and information beyond those collected in the course of conventional land/soil/crop management research. Particularly urgent is the need to document root characteristics and development patterns during the crop cycle. Standardization of these studies is needed to allow uniform and transferable expressions of data on root density with depth within the soil profile. In addition, assessments of soil fertility and other soil-productivity determinants should not be confined to the top soil horizon, as is conventionally done in diagnostic analyses. It is also critical that soil- and crop-specific data be collected for quantifying sufficiency values for all important productivity-determining attributes and constraints, particularly those in equation 1 and other relevant parameters as identified by informed researchers.

### Utility of Models

The importance of modeling in assessing soil productivity cannot be overemphasized. Modeling, as illustrated by the PI model, allows systematic and quantitative productivity estimates, provides guidance to the identification and quantification of productivity determinants and specific data requirements, sharpens the focus of research, and increases the transferability of research results by avoiding trial and error and unnecessary collection of field data. Sound modeling, theoretically or empirically based, provides a reliable basis for the formulation of testable hypotheses on the constraints or attributes to be targeted for improved soil management. Modeling also facilitates the formulation of preventive or conservation measures against soil degradation and associated threats to short- and long-term productivity. Clearly, as we have illustrated in this paper, models would need modification before they are applied to specific situations in the SAT.

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# Clay Minerals of Alfisols and Vertisols in the Semi-Arid Tropics in Relation to Phosphorus Behavior in the Soil

G. Uehara[1]

### *Abstract*

*The Alfisols and Vertisols of the semi-arid tropics are mostly Ustalfs and Usterts. Ustalfs are the reddish Alfisols with mixed or kaolinitic clay mineralogy; Usterts are the dark-colored Vertisols with montmorillonitic (smectitic) mineralogy. The specific surface of montmorillonite is about two orders of magnitude greater than that of kaolinite. This difference accounts for much of the behavioral difference between Usterts and Ustalfs. In the usual pH range of these soils, kaolinite and montmorillonite react only weakly with soluble phosphorus (P). Accessory minerals such as iron oxide in Ustalfs and noncrystalline materials with varying silica:alumina ratios in Ustalfs and Usterts are the major reactants with P. Organic and inorganic anions compete with phosphate ions for adsorption sites to maintain P in the soil solution. Phosphorus adsorbed on minerals increases net negative surface charge, which leads to deep-seated, long-lasting beneficial changes. These same effects can be partly achieved by soluble silicates and organic matter.*

## Introduction

Soil mineralogy is important only insofar as it aids in the interpretation of soil behavior and performance. When crop performance is constrained by phosphorus (P) deficiency, questions about the soil's capacity to behave as a source and sink for P come to mind. Owing to their high specific surface and chemical reactivity, the minerals in the clay fraction are considered very early in the diagnostic stage. The purpose of this paper is to explain the reasoning behind the rules and procedures that experienced agronomists employ to diagnose mineralogy-related P behavior.

## Clay Mineralogy of Alfisols and Vertisols

The range of clay mineralogy of the Alfisols is as wide as the mineralogy of the Vertisols is narrow; however, if we restrict our discussion to the semi-arid tropics (SAT), the mineralogy of the Alfisols is simplified considerably. The vast majority of Alfisols in the SAT are Ustalfs of mixed or kaolinitic mineralogy. Ustalfs are the mostly reddish Alfisols of warm subhumid to semi-arid regions that have a warm rainy season (USDA 1975). As a rule, the clay mineralogy of soils becomes increasingly kaolinitic and oxidic with increasing proximity to the equator (Millot 1979). As one moves away from the equator and enters the dry edges of the tropics (subtropics), smectitic soils, formerly called tropical black earths, occur more frequently. These mostly dark-colored soils are the Usterts of the Vertisol order of the semi-arid regions. They cover extensive areas of Mexico and Texas in North America; Morocco, Chad, and Sudan in northern Africa; and the Indian subcontinent in Asia. In the southern hemisphere, they occur in Australia, the countries of southern Africa, and the subtropical regions of South America. As a rule, one can say that the Alfisols of the semi-arid tropics and subtropics are the red Ustalfs with kaolinitic mineralogy. The Vertisols in this region are the dark Usterts with

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montmorillonitic (smectitic) mineralogy. Between pH 5.5 and 7.5, soils with kaolinitic mineralogy are generally expected to show P deficiencies more frequently than soils with smectitic mineralogy. In this pH range, kaolinite and smectite are not strong adsorbers of P, so that the differences in P chemistry observed between Ustalfs and Usterts must be attributed to accessory minerals. While it is possible to have identical accessory minerals in Ustalfs and Usterts, more generally the accessory minerals will reflect the geochemical factors that determine whether a soil evolves into an Ustalf or an Ustert. These geochemical factors result in Alfisols and Vertisols, which differ in surface-charge characteristics of the crystalline and noncrystalline minerals.

## Surface-charge Characteristics and Phosphorus Adsorption

Surface charges on soil particles arise from defects in the interior of the particles or from adsorption of potential determining ions. When the charge arises from internal defects, the charge is permanent, constant, almost always negative, and ranges from 1 to 2 × $10^{-4}$ cmol $m^{-2}$. Vertisols are the prime examples of soils with these types of clay minerals; the charge on the clay mineral is permanent, constant in value, and negative. The charge per unit mass of clay, or cation-exchange capacity, is high in Vertisols because the specific surface of clays commonly found in them is high. The relationship between cation-exchange capacity, specific surface, and surface-charge density is

$$\mathrm{CEC} = S\sigma \qquad (1)$$

where CEC is the cation-exchange capacity in cmol $kg^{-1}$, S is the specific surface in $m^2$ $kg^{-1}$, and $\sigma$ is the surface-charge density in cmol $m^{-2}$. Approximate ranges for these properties are given for montmorillonite and kaolinite in Table 1. The constant negative charge on montmorillonite and other smectites reduces their capacity to adsorb anions such as phosphate. More importantly, the high specific surface of smectite imparts to Vertisols many of their unique properties, such as their high shrink-swell potential.

In contrast, kaolinitic Ustalfs are noted for their low CEC and low shrink-swell potential. This feature of Ustalfs is largely attributable to the low specific surface of kaolinite. Although kaolinite offers less surface area for P adsorption than smectite, its variable-charge characteristic enables kaolinite to accommodate more P, particularly along its crystal edges.

**Table 1. Cation-exchange capacity (CEC), specific surface (S), and surface charge density ($\sigma$) of montmorillonite and kaolinite.**

| Mineral | CEC (cmol $kg^{-1}$) | S($m^2$ $kg^{-1}$) | $\sigma$(cmol $m^{-2}$) |
|---|---|---|---|
| Montmorillonite | 100-200 | 6- 8×$10^5$ | 1.3-2.0×$10^{-2}$ |
| Kaolinite | 5- 20 | 3-16×$10^3$ | 2.0×$10^{-4}$ |

In smectite, the surface-charge density ($\sigma$) is a constant; in kaolinite, where the charge originates from adsorption and desorption of protons along the crystal edge, $\sigma$ varies with electrolyte concentration, temperature T, and the pH of the soil solution, according to the relationship

$$\sigma = \left(\frac{2n\Sigma kT}{\pi}\right)^{1/2} \sinh \frac{ze}{2kT}\,\Phi \qquad (2)$$

where $\Sigma$ is the dielectric constant of water, k is the Boltzman constant, z is the counter ion valence, e is the electron charge, and $\Phi$ is the surface potential (Uehara and Gillman 1981).

In variable-charge minerals such as kaolinite, the surface potential ($\Phi$) varies with pH according to the expression

$$\Phi = \frac{kT}{e} \ln \frac{H^+}{H^+_0} \qquad (3)$$

where $H^+$ is the hydrogen ion concentration and $H^+_0$ is the hydrogen ion concentration corresponding to a surface charge of zero.

Equation 3 can be expressed in terms of pH

$$\Phi = \frac{kT}{e}\, 2.303\,(pH_0 - pH) \qquad (4)$$

and combined with equation 2 to give

$$\sigma = \left(\frac{2n\Sigma kT}{\pi}\right)^{1/2} \sinh z(1.15)\,(pH_0 - pH) \qquad (5)$$

where $pH_0$ is the pH at which net surface charge is zero. In kaolinite, $pH_0$ is less than pH 3, so that in Ustalfs with soil-solution pH nearly always greater than 5.0, the last term in equation 5 ($pH_0$ – pH) is always negative in value. This means that the surface charge is negative and the surface is a cation exchanger. Equation 5 also implies that as pH is lowered, the charge on kaolinite becomes less negative, thereby enabling phosphate ions to be more readily adsorbed. The pH-dependence of P adsorption by kaolinite has been known for some time (Muljadi et al. 1966). Phosphorus adsorption by both kaolinite and smectite, however, increases sharply below pH 5, not so much from changes in surface charge, but from solubilization of aluminum. Since the solution pH of Ustalfs and Usterts is normally above 5.5, reactions between phosphate and aluminum ions should not normally be a problem unless a weakly buffered Ustalf is acidified with nitrogen (N) fertilizers.

## Accessory Minerals

### Crystalline Accessory Minerals

The red Ustalfs derive their color from the iron oxide, hematite. Hematite formation is favored in soils with low moisture, high temperature, low organic matter content (Kampf and Schwertmann 1983), and high pH in the weathering environments (Schwertmann 1985). In more humid and acid environments, the iron oxide would be goethite and the soil color brownish or yellowish rather than red. Hematite and goethite are the two most common iron minerals in soils, and in the more weathered soils constitute the bulk of the iron. Interestingly, Norris and Rosser (1983) found a high correlation between percent $P_2O_5$ and percent $Fe_2O_3$ in several soils of Australia. They also showed that in goethites a high correlation exists between percent $P_2O_5$ and the degree of aluminum substitution for iron in the goethite crystal. High aluminum substitution results in smaller crystal size, and it is likely that $P_2O_5$ content of goethite is related to crystal size and specific surface. The work of Norris and Rosser (1983) indicates that particle size—and therefore the specific surface—of iron oxide is important to P chemistry.

The dark color of Usterts is also believed to be attributable to iron oxide. Raymundo (1965) examined the particle-size fractions of several benchmark Vertisols from Hawaii and concluded that the magnetic, opaque minerals in the silt and sand fractions were perhaps the main contributors to the dark color of the soils. The low reactivity of P with iron oxide in Vertisols can be attributed to the large size, low specific surface, and high crystallinity of the oxide. The oxides were mainly magnetite and ilmenite. It is also likely that, in Vertisols, these oxides are coated with amorphous silica.

Equation 5 also applies to iron oxides. However, unlike kaolinite, hematite has a $pH_0$ that occurs at about pH 8.5 (Parks and de Bruyn 1962). Thus, even for an Ustalf of pH 7, the quantity ($pH_0$ – pH) will still be positive, and the charge on hematite will be positive. Thus, while kaolinite and hematite are both variable-charge minerals, the position of the $pH_0$ renders their reactions with P very different. A small quantity of hematite can have a major effect on P chemistry, particularly if the soil is coarse-textured and the hematite is finely divided. In fact, this is commonly so in coarse-textured Ustalfs, wherein the sand particles are often coated with red hematite. In this way, inert sand particles become more reactive, so that the U.S. Soil Taxonomy (USDA 1975) recognizes classes of coatings on sands to account for variability in the behavior of sands. Coated sands hold more water and nutrients. If the coating is hematite, adsorption of P by the hematite markedly alters the chemistry of the hematite surface and therefore of the sand. The charge on the hematite surface can be reversed from positive to negative by P adsorption (Mekaru and Uehara 1972). This occurs because adsorbed P lowers $pH_0$ of hematite from pH 8.5 to values lower than the prevailing soil pH. In this condition, the hematite, which was originally an anion exchanger, becomes a cation exchanger. A small amount of iron oxide can be very beneficial to the chemistry and physics of sandy soils. In such soils, iron oxide increases the soil's capacity factors: its buffering capacity, CEC, and water-holding capacity. Because of the importance of coatings on sand grains in coarse-textured soils, Soil Taxonomy (USDA 1975) differentiates coated from clean sands on the basis of water retention. In coated sands, the moisture equivalent or the water held at a tension of 0.05 MPa is 2% or more. In clean or uncoated sands, the water content is less than 2%.

### Noncrystalline Accessory Minerals

Under the electron microscope, the surfaces of kaolinite particles appear to be coated with a gel-like material (Jones and Uehara 1973). In smectite samples, amorphous silicic acids seem to abound. Hashimoto and Jackson (1958) determined that 6.9% of a standard montmorillonite was free silica that could be readily dissolved in mild alkali, and Uehara and Jones (1974) observed noncrystalline silica precipitated from a water extract of montmorillonite.

An important difference between the noncrystalline components associated with kaolinite and smectite is their silica:alumina ratio. In data presented by Hashimoto and Jackson (1958), the silica:alumina ratio of the noncrystalline components was 39 for montmorillonite, 3-8 for kaolinite, and less than 1.5 for allophane. The silica:alumina ratio of a soil's noncrystalline fraction must be important to soil P chemistry. Experience shows that P adsorption is lowest in montmorillonitic soils, intermediate in kaolinitic soils, and highest in allophanic and oxide soils. Equation 5 can again be applied to explain this observation.

The $pH_0$ of silica is near pH 2, and that of alumina, above 8 (Yopps and Fuerstenau 1964). Mattson (1932) showed that the isoelectric point ($pH_0$) of his synthetic silica-alumina gels decreased when the silica:alumina ratio was increased. Since this ratio is higher in smectitic Usterts than in kaolinitic Ustalfs, at any pH (e.g., pH 7), the noncrystalline gel on smectite particles will be more negative, and therefore have less affinity for P than in the Ustalfs.

Up to this point, differences in P behavior among soils in general, and between Ustalfs and Usterts in particular, have been explained on the basis of surface-charge characteristics of soil colloids. The theory embodied in Equation 5 applies at low salt concentrations (<0.01 N) and at pH values within one unit of $pH_0$. However, its usefulness lies mainly in enabling one to look for alternative ways to manage and control P behavior in soils.

## Managing P Behavior

Of the three major nutrient elements, N, P, and potassium (K), P is the least mobile and has the longest residual effect. These attributes reflect the intrinsic role P plays in governing soil colloidal chemistry. Understanding this role can help us find alternative ways to define and overcome P problems.

The key factor in this approach depends on managing the surface charge of soil colloids. The important colloids are not necessarily the layered silicates that make up the bulk of the clay fraction, but the free oxides, noncrystalline gels, and organic matter. From equation 5, we can see that surface-charge density ($\sigma$) may be altered by varying (1) electrolyte concentration in the soil solution, (2) soil temperature, (3) valence of the counter ions, (4) soil pH, and (5) $pH_0$. In practice, only the last two options are feasible, and for the Alfisols and Vertisols of the SAT and subtropics, even soil pH is not as frequently a problem as in the humid tropics. This leaves $pH_0$ as the primary variable with which to manipulate surface charge and P behavior.

If we examine equations 3 and 4, we note that the surface potential approaches zero as $H^+ \rightarrow H^+_0$ or $pH \rightarrow pH_0$. It also follows that $\Phi$ can be negative, zero, or positive, depending on whether $H^+ < H^+_0$ ($pH > pH_0$), $H^+ = H^+_0$ ($pH = pH_0$), or $H^+ > H^+_0$ ($pH < pH_0$). Under intense leaching, pH tends toward $pH_0$, which is to say that surface potentials tend towards zero and stability. Mattson (1932) recognized this phenomenon and called it isoelectric weathering. Mattson's isoelectric point corresponds to $pH_0$ in equation 5. Although Mattson did not have the benefit of knowing equation 5, he predicted that with leaching, salt concentrations would decrease, and pH would shift towards $pH_0$. Both effects lead to net zero charge. If Mattson was right, we should see examples of this phenomenon in soils. The best examples are found in organic soils, quartz sands, and acric Oxisols. The same rules can be applied to modify P behavior in Ustalfs and Usterts.

It is widely known that highly leached quartz sands and organic soils are acid. However, it is not always realized that the pH of acric Oxisols increases with increasing leaching. Quartz sand and organic soils tend to be acid because quartz ($SiO_2$) and organic matter possess $pH_0$ between pH 2 and 3. If leached with rainwater, the pH of these soils tends toward $pH_0$. On the other hand, acric Oxisols, such as the Acrorthox of humid areas or the Acrustox of the semi-arid tropics, contain oxides with $pH_0$ near pH 7. When these soils are leached, the soil-solution pH again tends toward $pH_0$. Many of the most highly leached Oxisols have very low surface charge (effective CEC of <1.5 cmol $kg^{-1}$) and pH very near $pH_0$. Alfisols with pH close to $pH_0$ are evolving into Oxisols and possess some of the attributes of highly weathered soils. Vertisols, on the other hand, behave differently and become more acid with leaching. Table 2 shows the soil pH in water and 1 N KCl of an Oxisol.

The important points to note in Table 2 are (1) the increase in pH with depth and (2) the increasing positive value of the $\Delta$ pH or [pH(KCl) - pH($H_2O$)] value with depth.

It suffices to say that the sign and magnitude of $\Delta pH$ correspond to the sign and magnitude of the surface charge on the soil colloid. In the example, the horizons near the soil surface contain colloids that are negatively charged, but the charge turns positive in the deeper horizons. The data represent an example of isoelectric weathering; the soil pH in water and 1N KCl is governed by $pH_0$. But why does $pH_0$ vary so much within a soil profile? The answer lies in the organic matter (% carbon) content. Organic matter

**Table 2. Isoelectric weathering in an acric soil. (Data for a Typic Acrorthox from Puerto Rico, USDA Soil Survey Staff 1967).**

| Depth (cm) | Carbon (%) | pH<br>$H_2O$ | pH<br>1N KCl | pH(KCl) - pH($H_2O$) | $pH_0$ |
|---|---|---|---|---|---|
| 0- 28 | 6.0 | 5.1 | 4.3 | -0.8 | 4.2 |
| 28- 46 | 2.0 | 5.0 | 4.4 | -0.6 | 4.3 |
| 46- 71 | 1.3 | 5.0 | 4.7 | -0.3 | 4.5 |
| 71- 97 | 0.9 | 5.2 | 5.7 | +0.5 | 5.4 |
| 97-122 | 0.7 | 5.5 | 6.1 | +0.6 | 5.7 |
| 122-157 | 0.6 | 5.7 | 6.4 | +0.7 | 5.9 |
| 157-178 | 0.2 | 5.8 | 6.7 | +0.9 | 6.1 |

has a low $pH_0$, and a small amount in the soil can have a significant effect on surface charge. Without organic matter, the pH of the first horizon would be near that of the deepest horizon. The P chemistry of the first and last horizons differs because the horizons differ in organic matter content. Although P adsorption is generally thought to be pH-dependent, organic matter alters the rule in this case.

In the Usterts, $pH_0$ is already very low (<pH 4). This condition is a direct consequence of the high silica:alumina ratio of the colloidal fraction. Even though the $pH_0$ of Vertisols is low, their pH remains high because Vertisols occur in places where leaching intensity is low. While P deficiency is not uncommon in Vertisols, their high silica:alumina ratio renders them less likely to be P-deficient than most other soils.

The red Ustalfs of the semi-arid tropics are a different matter. They generally have lower buffering capacity and can be acidified through intensive cultivation. In such situations, additions of organic matter can counter the detrimental effects of excessive soil acidity. Organic matter improves soil conditions by (1) increasing surface charge to minimize phosphate adsorption, (2) detoxifying aluminum ions (Hue et al. 1986), and (3) improving soil structure and water retention.

## Conclusion

The surface-charge density of soils can be manipulated by varying the $pH_0$. Phosphorus added to soils and adsorbed by soil colloids shifts $pH_0$ to lower values, thereby increasing negative charge and reducing phosphate adsorption. Phosphorus is too expensive to be used as an amendment to reduce P fixation. In some instances, calcium silicate ($CaSiO_3$) has been added to soils to improve P nutrition; $CaSiO_3$ succeeds in lowering P adsorption by increasing the silica:alumina ratio of soil particles and increasing soil pH. It is a less expensive amendment than P fertilizers, but is bulky and not available everywhere. Even so, the sugarcane producers of Hawaii routinely apply $CaSiO_3$ to the more highly weathered, silica-poor soils, but never to the silica-rich Vertisols (Plucknett 1971).

Organic matter remains the most feasible material to increase surface charge. It does so by coating soil particles and imparting its chemical characteristics to the soil. These characteristics are (1) high surface charge and (2) low affinity for phosphate ions.

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# Appropriate Measurements of Phosphorus Availability in Soils of the Semi-Arid Tropics

**E.J. Kamprath**[1]

### *Abstract*

*Availability of soil phosphorus (P) can be described by the quantity-intensity relationship. The quantity factor in acid soils is the phosphate sorbed by aluminum hydrated oxides and some iron oxides; in neutral soils, it is phosphate bound to exchangeable calcium; and in calcareous soils, it is phosphate sorbed on the surface of calcium carbonate. Phosphate is taken up by the plant from the soil solution, and the critical concentration (intensity) for growth is related to soil texture, being higher for sandy soils than for clay soils. Soil tests for the most part measure a portion of the quantity factor, ideally, the solid-phase phosphate that controls the soil-solution P concentration.*

*In acid soils, the ideal extractant is one that extracts aluminum phosphates. Extractants containing fluoride (i.e., Bray 1), which complexes aluminum and releases the P, provide estimates of P availability well correlated with P uptake by crops. Sodium bicarbonate also is effective in extracting aluminum phosphate and is used to measure phosphate availability in acid soils.*

*On neutral soils containing no free calcium carbonate, acid solutions can be used to extract the calcium phosphates (primarily dicalcium phosphate), which control P availability. Where P is sorbed by calcium carbonate, the phosphate extracted with alkaline solutions, such as sodium bicarbonate, is well correlated with P uptake.*

*Interpretation of soil-test results requires taking into account the phosphate buffering capacity of the soil, which is correlated with soil texture. Thus higher soil-test values are required on sandy soils than on clayey soils to supply the same amount of P.*

## Introduction

The available phosphorus (P) supply of soils depends upon the amounts and forms of P present in the soil. Various extractants have been developed to extract the available soil P that plants would take up. Daubeny (1845) suggested that soil nutrients exist in the "active" and "dormant" forms. He advocated the use of carbonic acid to extract the active forms of nutrients. His thesis was that roots give off carbon dioxide, which reacts with water to form carbonic acid and solubilizes the active forms in the rhizosphere.

The studies of Dyer (1894) resulted in the development of the 1% citric acid solution as an extractant for available P. Dyer postulated that the ideal extracting solution should have a pH similar to that of root sap. His examination of a large number of plant species indicated that the acidity of plant root sap was similar to that of a 1% solution of citric acid.

Further advances in soil tests for P took place with the studies of Russell and Prescott (1916-1917). They found that dilute solutions of weak acids, such as citric and oxalic acid, extracted more P from soils than dilute solutions of strong acids, such as hydrochloric and nitric acid, at the same concentration. The citrate and oxalate anions reduced the readsorption of phosphate ions from the extracting solutions.

Methods were developed in the 1950s to fractionate the soil P into various chemical forms. Equilibra-

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tion of $^{32}P$ with soil made it possible to determine which chemical forms were being extracted by the various soil-test solutions. The concepts relating P availability to the relationships between quantity, intensity, and buffering capacity were formulated in the 1960s. Knowledge of these principles regulating P availability have made it possible to select appropriate extractants for available P, depending upon the chemical properties of the soils.

## Common Soil-test Extractants

Three soil-test extractants, Mehlich 1, Bray 1, and Olsen, are widely used to measure available soil P (Kamprath and Watson 1980). The Mehlich 1 extractant, 0.05 N HCl + 0.025 N $H_2SO_4$, was developed for kaolinitic soils in the southeastern USA. It is used where soil P is associated with aluminum (Al) and iron (Fe) compounds but is not suited for soils with pH higher than 7 (Fitts 1956).

The Bray 1 extractant, 0.05 N HCl + 0.03 N $NH_4F$, was developed to measure adsorbed P, primarily aluminum phosphates. It is suitable for a wide range of soils, but not calcareous soils (Fitts 1956; Kamprath and Watson 1980).

The Olsen extractant, 0.5 M $NaHCO_3$, was developed for measuring labile P in calcareous soils (Olsen et al. 1954). It has also been found effective for estimating available P in soils where aluminum phosphates are the main source of plant-available P (Kamprath and Watson 1980).

## Mechanisms of Phosphorus Extraction

Soil-test extractants used to measure available P remove P from the solid phase. There are essentially four reactions that remove a portion of the solid-phase P.

### Solvent Action of Acids

Several common soil-test extractants are acid in reaction. The Bray 1 solution has a pH of 2.6, and the Mehlich 1 a pH of 1.32 (Sharma and Tripathi 1984). These acid extractants solubilize inorganic P bound in Ca, Al, and Fe compounds. The calcium phosphates are the most soluble in acid solutions, dicalcium phosphate being more so than tricalcium phosphate. Aluminum phosphates are next, and iron-phosphates are the least soluble.

### Anion Exchange

Some of the soil P is adsorbed on the surfaces of $CaCO_3$ and hydrated oxides of Fe and Al. These adsorbed phosphates can be replaced by anions such as hydroxyls, acetate, citrate, lactate, sulfate, and bicarbonate (Dean and Rubins 1947; Olsen et al. 1954). The adsorbed P is generally associated with the labile P.

### Complexing of Cations Binding Phosphorus

Phosphorus bound by Al can be released by adding an anion that complexes the Al. Fluoride added as ammonium fluoride ($NH_4F$) is very effective in complexing Al (Chang and Jackson 1957). The organic anions, citrate and lactate, also complex Al. Solutions containing F ions will also extract P from $CaHPO_4$, since F ions will complex Ca and release the P (Thomas and Peaslee 1973).

### Hydrolysis of Cations Binding Phosphorus

Alkaline solutions are effective in extracting P bound by Al. The OH ions hydrolyze the Al, which releases the P. Sodium bicarbonate buffered at pH 8.5 is an excellent extractant of Al-P and, to some extent, Fe-P (Tyner and Davide 1962).

## Forms of Inorganic Phosphorus in Soils

Inorganic P in highly weathered soils is associated with Al and Fe compounds. These soils are generally acid, and added phosphate fertilizers react with exchangeable Al to form precipitated Al-P. Phosphate is also adsorbed on the surfaces of hydrated oxides of Al and Fe. With time, some of the adsorbed P diffuses into the interior of the Al and Fe oxides and becomes occluded. Most of the P in cultivated Ultisols is present as Al-P and Fe-P (Novais and Kamprath 1978); Al-P and Fe-P are also the main forms of inorganic P in highly weathered virgin soils (Table 1) and in the acid Himalayan hill soils and Alfisols and Oxisols of India (Table 2).

Calcium phosphates are the predominant form of inorganic P in slightly weathered and calcareous virgin soils (Table 1) and in Vertisols and Inceptisols in India (Table 2). Generally, soils in India with pH higher than 7.0 have a high proportion of their inorganic P in the form of Ca-P (Table 2). Exceptions to

**Table 1. Forms of soil phosphorus in calcareous, slightly weathered, and highly weathered virgin soils (Sharpley et al. 1984).**

| | Form of P (mg $kg^{-1}$) | | | | |
|---|---|---|---|---|---|
| Soil | Available | Al-P and Fe-P | Ca-P | Occluded | Organic |
| Calcareous (41 soils) | **25** | 17 | **285** | **6** | **36** |
| Slightly weathered (40 soils) | 34 | 49 | **85** | **12** | **78** |
| Highly weathered (39 soils) | 40 | 63 | 16 | 28 | 112 |

this are the red Vindhyan soils, which have relatively high amounts of Fe-P, and the Gangetic alluvial soils, which have high amounts of reductant-P (Table 2).

Phosphorus applied to acid Indian soils was adsorbed by Fe and Al oxides, while that applied to alkaline soils was 40% saloid-bound (Vig and Dev 1984). In soils with appreciable sesquioxides and pH higher than 7.0, almost 60% of the added phosphate was associated with Al-P and Fe-P and only 4-26% with Ca-P, even though as much as 2.4% $CaCO_3$ was present in the soil (Misra and Ojha 1968). This illustrates the strong affinity of Fe and Al compounds for P.

## Correlation of Soil Tests with Inorganic Forms of Phosphorus

### Calcareous and Alkaline Soils

The Olsen extractant, 0.5 M $NaHCO_3$, was developed for measuring available P in calcareous soils (Olsen et al. 1954). The $HCO_3^-$ replaces the $HPO_4^{2-}$ adsorbed on the surface of $CaCO_3$. The amount of P extracted by $NaHCO_3$ was highly correlated with the exchangeable P as measured by equilibration with $^{32}P$ (Cole et al. 1953). The $NaHCO_3$-extractable P of calcareous and slightly weathered soil was correlated

**Table 2. Forms of phosphorus in soils from various regions of India.**

| | | Form of P (mg $kg^{-1}$) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Soil | pH | Saloid | Al-P | Fe-P | Ca-P | Reductant | Total inorganic | Organic | Reference |
| Himalayan acid | | | | | | | | | |
| (25 soils) | 5.1-6.4 | 3.5 | 29 | 77 | 29 | 106 | | 82 | Sharma and Tripathi (1984) |
| Gangetic alluvial | | | | | | | | | |
| Recent | 7.7 | - | 5 | 9 | 13 | 337 | 372 | 27 | Gupta and Misra (1968) |
| Upland | 7.9 | - | 3 | 8 | 15 | 292 | 332 | 18 | |
| Dhankar | 7.3 | - | 4 | 8 | 13 | 302 | 350 | 25 | |
| Vindhyan | | | | | | | | | |
| Red | 7.7 | 2.5 | 16 | 80 | 85 | 41 | 229 | 27 | Gupta and Singh (1972) |
| Alluvial | 7.2 | 13 | 32 | 68 | 215 | 18 | 391 | 33 | |
| Dhankar | 8.7 | 38 | 8 | 98 | 220 | 16 | 409 | 54 | |
| Black (clay) | 7.8 | 5 | 22 | 60 | 290 | 24 | 412 | 150 | |
| Karnataka | | | | | | | | | |
| Inceptisols | - | - | 19-46 | 9-21 | 41-105 | 39-48 | 148-212 | 292-510 | Doddamani and Seshagiri Rao (1988) |
| Vertisols | - | - | 28-47 | 6-19 | 58-110 | 26-50 | 145-231 | 215-321 | |
| Alfisols | - | - | 39-73 | 20-39 | 8- 15 | 28-42 | 121-167 | 126-270 | |
| Oxisols | - | - | 42-74 | 37-90 | 3- 8 | 42-67 | 145-240 | 108-310 | |

**Table 3. Correlation (r = correlation coefficient) of soil tests with resin P of calcareous, slightly weathered, and highly weathered virgin soils (Sharpley et al. 1984).**

| | Soil test | | |
|---|---|---|---|
| Soil | Bray 1 | Mehlich 1 | Olsen |
| Calcareous | 0.44 | 0.30 | 0.85 |
| Slightly weathered | 0.95 | 0.78 | 0.83 |
| Highly weathered | 0.95 | 0.78 | 0.57 |

with resin P, a measure of exchangeable P (Table 3). Exchangeable P, that which is adsorbed on the surface of $CaCO_3$, is the major source of plant-available P in alkaline soils (Holford 1983, 1988).

The amounts of P extracted by the Bray 1 and Mehlich 1 extractants from calcareous soils were poorly correlated with the resin-extractable P (Table 3). The high $H^+$ concentration of these extractants results in the dissolution of relatively unavailable calcium phosphates (Holford 1983). In slightly weathered soils, however, P extracted by Bray 1 and Mehlich 1 solutions was significantly correlated with resin-extractable P (Table 3). In these soils, the main source of inorganic P is dicalcium phosphate ($CaHPO_4$), which is dissolved by the acidic solutions.

### Highly Weathered Soils

Plant-available forms of P in highly weathered soils are phosphates associated with hydrated oxides of Al and Fe. The amount of Olsen P in weathered Indian soils was significantly correlated with Al-P (Table 4). Extraction of acid soils with $NaHCO_3$ buffered at pH 8.5 results in hydrolysis of aluminum phosphates and release of P. Thus the Olsen extractant, which was developed for calcareous soils, is an excellent extractant for measuring available P in acid soils as well.

The Bray 1 P extracted from highly weathered soils was correlated with resin-extractable P (Table 3). Phosphorus extracted by the Bray 1 solution was shown to be significantly correlated with Al-P for highly weathered soils (Kamprath and Watson 1980). The $NH_4F$ in the Bray 1 solution effectively extracts P from Al-P because of the high affinity of F ions for Al, which results in release of P.

In highly weathered soils, the Mehlich 1 P was correlated with Al-P (Kamprath and Watson 1980). The low pH of the solution dissolves P from the reactive surfaces of Al and Fe hydrated oxides (Holford 1983). The Mehlich 1 extractant will also dissolve Ca-P, which can result in high values of P where unreacted rock phosphate is present in the soil.

## Availability of Soil Phosphate

The availability of soil P has been described by the quantity-intensity relationship (Gunary and Sutton 1967). The quantity factor is the amount of P required to give a certain soil-solution concentration of P (intensity). The change in the intensity values brought about by a given change in the quantity factor is defined as the P buffering capacity. For highly weathered soils, the P buffering capacity is determined by the amounts of hydrated oxides of Fe and Al. Because these sesquioxides are associated with the clay fraction, the buffering capacity is correlated with the clay content of the soil. Fifty-four percent of the variation in the P-fixing capacity of red and lateritic soils of West Bengal was accounted for by the percentage of clay in the soils (Dolui and Gangopadhyay 1984). The buffering capacity of slightly weathered soils, those neutral to alkaline in reaction, is associated with the amounts of exchangeable Ca and $CaCO_3$ (Olsen and Watanabe 1963).

Although essentially all of the soil P is associated with the solid-phase P (quantity), plants take up P from the soil-solution phase. Considerable attention

**Table 4. Form of soil phosphorus correlated (r) with phosphorus extracted by various soil tests.**

| | Soil test | | | |
|---|---|---|---|---|
| Soil | Bray 1 | Mehlich 1 | Olsen | Reference |
| Himachal Pradesh Alfisols | Al-P<br>0.557 | Ca-P<br>0.655 | Al-P<br>0.635 | Sharma et al. (1985) |
| Northwestern India acid soils (pH 5.1-6.4) | Al-P<br>0.575 | Ca-P<br>0.859 | Al-P<br>0.811 | Sharma and Tripathi (1984) |

has been given to the soil-solution P concentration required for optimum plant growth. Kamprath and Watson (1980) reported that as the clay content increased, the critical soil-solution P levels required for optimum growth decreased from 0.40 mg $kg^{-1}$ for coarse-textured soils to 0.06 mg $kg^{-1}$ for clayey soils.

Concentration of soil-solution P is one of the factors affecting diffusion of P in soils, the mechanism by which P moves to plant roots (Olsen and Watanabe 1963). Other factors are volumetric water content and tortuosity. Because sandy soils have lower volumetric water contents and more tortuous diffusion paths than clayey soils, higher concentrations of P are required to move a given amount of P to plant roots in sandy soils than in clayey soils. Sandy soils also have lower P buffering capacities and therefore soil-solution P concentrations decrease more with a given amount of P uptake.

The amount of plant-available soil P is controlled by the complex relationships between the quantity, intensity, and buffer capacity factors and their effect on P diffusion. Since for routine determinations of available P it is not practical to measure the intensity and buffer capacities, soil tests for P should ideally measure the portion of the soil P (labile P) that is in equilibrium with the soil-solution P and also compensate for the effect of buffering on P availability.

Holford (1980) has pointed out that a soundly based soil test should extract a proportion of the labile P, which is inversely related to the P buffer capacity. At any particular level of labile P, the concentration of soil-solution P decreases as the buffer capacity increases. Therefore in a successful test, increasing buffer capacity will decrease the extraction of labile P to the same extent as it decreases P uptake by plants.

## Correlation of Soil-test Values with Phosphorus Availability

An ideal soil test should extract a proportionate amount of plant-available phosphate from soils with differing chemical properties. For soil tests that meet this criterion, there will be high correlations between amounts of soil-test P extracted and various measures of plant response, such as P uptake, dry matter produced, and relative plant growth. Table 5 shows the correlations of soil-test P extracted from a range of soils with Olsen, Bray 1, and Mehlich 1 solutions with plant measurements of P availability. The Olsen extractant, $NaHCO_3$, gave consistently higher correlations than the other two extractants for a wide range of crops: white clover (*Trifolium repens* L.), lentil (*Lens culinaris* Medic.), barley (*Hordeum vulgare* L.), ryegrass (*Lolium* sp), and millet (*Pennisetum* sp).

The Olsen extractant is equally effective on calcareous and acid soils: on calcareous soils, it extracts exchangeable P associated with $CaCO_3$; on acid soils,

**Table 5. Correlation (r) of soil-test phosphorus levels measured by three extractants with plant measurements of soil phosphate availability.**

| Soil | Crop | Plant parameter | Soil test<br>Olsen | <br>Bray 1 | <br>Mehlich 1 | Reference |
|---|---|---|---|---|---|---|
| Australian<br>pH 5.4-8.1 | White clover | P uptake | 0.90 | 0.70 | 0.46 | Holford (1980) |
| Himachal Pradesh<br>Alfisols | Lentil | P uptake and<br>dry matter | 0.766 | 0.654 | 0.285 | Sharma et al. (1985) |
| pH 4.5-6.7 | | | 0.604 | 0.500 | 0.344 | |
| Australian | White clover | Relative yield | | | | Holford (1983) |
| <pH 5.6 | | | 0.87 | 0.60 | 0.62 | |
| >pH 5.6 | | | 0.89 | 0.84 | 0.41 | |
| Punjab<br>pH 8.0 to 8.4 | Barley | Relative yield | 0.80 | 0.62 | - | Sidhu and Dev (1985) |
| English<br>calcareous | Ryegrass | Relative yield | 0.98 | - | - | Holford and Mattingly (1979) |
| Moroccan | Wheat | Relative yield | 0.81 | - | - | Azzaoui et al. (1989b) |
| calcareous | | and P uptake | 0.93 | - | - | |

it extracts the Al-P. The Bray 1 and Mehlich 1 extractants are less effective on neutral to calcareous soils, because (a) the acid solutions dissolve unavailable calcium phosphates and (b) the free $CaCO_3$ in calcareous soils neutralizes the H ions and decreases the extraction of P. Buffering can also affect P extraction. As previously discussed, a given amount of labile P will be less available as buffering increases. The Olsen method tends to compensate for differences in buffer capacity, while the Bray 1 tends to overcompensate (Holford 1980, 1983, 1988).

Changes in soil-test values for Mehlich 1 and Bray 1 P as phosphate was removed by cropping were highly correlated with the clay content of five Ultisols in North Carolina, USA (Novais and Kamprath 1978). The results clearly illustrate that as the buffer capacity increases, the amount of P extracted by the Mehlich 1 and Bray 1 extractants decreases. However, with the Olsen extractant, changes in soil-test P after cropping were not correlated with clay content, indicating that buffer capacity had less effect on the amount of P extracted by the Olsen solution than that extracted by the Bray 1 and Mehlich 1 extractants.

## Response of Chickpea and Pigeonpea to Phosphorus Fertilization

Some examples of response of chickpea to P fertilization on neutral to calcareous soils in India are given in Table 6. On soils with Olsen-P values of 5-15 mg $kg^{-1}$, yields of chickpea grown without added P were only 74-88% of those obtained with P fertilization. Yields increased 214-700 kg $ha^{-1}$ with P fertilizer, and optimum rates of P ranged from 12 to 52 kg $ha^{-1}$.

Yields of pigeonpea without P fertilizer varied from 62 to 85% of those obtained with P fertilizer on Indian calcareous soils with Olsen-P values of 3-6 mg $kg^{-1}$ (Table 7). Yields increased 270-490 kg $ha^{-1}$ with P fertilization on these soils, and optimum rates of P fertilizer ranged from 30 to 90 kg P $ha^{-1}$.

On an acid Paleudult in Africa with a Bray 1 value of 6 mg P $kg^{-1}$, the relative yield of pigeonpea without P fertilizer was 60% of that with P fertilizer (Table 7). Application of 26 kg P $ha^{-1}$ gave a yield increase of 285 kg $ha^{-1}$.

These data do not provide definitive critical values for Olsen P above which no response to P fertilization would be obtained for chickpea and pigeonpea. However, the reported soil-test P values at maximum yield are generally below critical soil-test values for Olsen P reported by other researchers for a range of crops and soils (Table 8).

The high relative yield of chickpea and pigeonpea without P fertilization at low soil-test P values may be partially explained by the P-uptake characteristics of the two legumes; their uptake was more rapid at low solution-P concentrations than that of corn, a crop more responsive to P fertilization (Itoh 1987). Pigeonpea had an external solution-P requirement simi-

Table 6. Response of chickpea to phosphorus fertilization in India as related to soil-test phosphorus.

| Soil | Olsen P (mg $kg^{-1}$) | Yield without P (kg $ha^{-1}$) | Relative yield (%) | Fertilizer P at maximum yield (kg $ha^{-1}$) | Yield response (kg $ha^{-1}$) | Reference |
|---|---|---|---|---|---|---|
| Sandy loam | | | | | | |
| pH 7.7 | 5 | 2080 | 84 | 17 | 350 | Singh et al. (1984) |
| Vertisol pH 8 | | | | | | |
| Nonirrigated | 6 | 1578 | 88 | 40 | 214 | Kulhare et al. (1988) |
| Irrigated | | 1772 | 88 | 13 | 235 | |
| Vertisol | | | | | | |
| Clay loam pH 8.2 | 6 | | | | | |
| Expt. 1 | | 1260 | 81 | 12 | 290 | Khandkar et al. (1985) |
| Expt. 2 | | 1170 | 74 | 26 | 410 | |
| Calcareous | | | | | | |
| pH 7.8 | 11 | 1750 | 74 | 34 | 620 | Singh and Yadav (1985) |
| Calcareous | | | | | | |
| pH 8.1 | 15 | | | | | |
| Nonirrigated | | 1150 | 62 | 52 | 700 | Sharma and Yadav (1976) |
| Irrigated | | 2270 | 78 | 52 | 650 | |

**Table 7. Response of pigeonpea to phosphorus fertilization as related to soil-test phosphorus.**

| Soil | Soil-test P (mg kg$^{-1}$) | Yield without P (kg ha$^{-1}$) | Relative yield (%) | Fertilizer P at maximum yield (kg ha$^{-1}$) | Yield response (kg ha$^{-1}$) | Reference |
|---|---|---|---|---|---|---|
| | Olsen | | | | | |
| Sandy loam<br>pH 7.8 | 3 | 1500 | 76 | 30 | 400 | Singh et al. (1983) |
| | 4 | 1320 | 79 | 30 | 270 | |
| Sandy loam<br>pH 8.3 | 4 | 2140 | 85 | 44 | 380 | Manjhi et al. (1973) |
| | 4 | 1770 | 85 | 44 | 320 | |
| Sandy loam | 5 | 850 | 66 | 90 | 430 | Ahuja (1984) |
| | 6 | 810 | 62 | 90 | 490 | |
| | Bray 1 | | | | | |
| Paleudult<br>pH 4.8 | 6 | 425 | 60 | 26 | 285 | Rhodes (1987) |

lar to that of soybean (*Glycine max* L.) and cowpea (*Vigna unguiculata* L. Walp.) (Fist et al. 1987). This suggests that critical soil-test levels of P for soybean may also apply to pigeonpea.

## Conclusions

In calcareous soils, the source of P, which controls P availability to the crop, is that adsorbed on the surfaces of $CaCO_3$. Phosphorus extracted with the $NaHCO_3$ extractant (Olsen P) is correlated with surface P of calcareous soils. The acid extractants are not satisfactory for use on calcareous soils because they dissolve unavailable calcium phosphates.

In acid weathered soils, such as Alfisols and Ultisols, the aluminum phosphates are the main source of plant-available P. In these soils, the P extracted with the Bray 1 and Olsen extractants is correlated with the amounts of aluminum phosphate in the soil. In regions with both acid and calcareous soils, the Olsen extractant, which is effective on both, would be the most suitable for measuring available soil P.

When Olsen-P levels were in the range of 9-12 mg kg$^{-1}$, the relative yield of chickpea without P fertilization was 74-88% of that with P fertilization. Relative yields of pigeonpea with Olsen-P levels of 7-12 mg kg$^{-1}$ were 62 to 85% of those obtained with P fertilization.

**Table 8. Critical soil-test values for $NaHCO_3$-extractable (Olsen) phosphorus in various soils.**

| Soil | Crop | Critical value (mg kg$^{-1}$) | Reference |
|---|---|---|---|
| Calcareous soils<br>USA | Alfalfa, cotton, wheat | 10 | Olsen et al. (1954) |
| Calcareous soils<br>Punjab, India | Barley at 90% maximum yield | 14 | Sidhu and Dev (1985) |
| Acidic tablelands<br>New South Wales, Australia | Clover at 85% maximum yield | 21 | Holford and Crocker (1988) |
| Calcareous soils<br>Morocco | Wheat | 10 | Azzaoui et al. (1989a) |

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# Phosphorus Response of Chickpea and Evaluation of Phosphorus Availability in Indian Alfisols and Vertisols

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### *Abstract*

*Olsen's sodium bicarbonate extraction method is generally recommended for evaluating phosphorus (P) availability to crops in calcareous and alkaline soils. However, the method fails to predict growth responses when we consider the P fertility of both Alfisols and Vertisols. Olsen's method sometimes underestimates P uptake from Vertisols, which have been considered to have high P-fixation capacity. The roots of several crop species, by secreting organic acids and hydrogen ions, may lower rhizosphere soil pH by 1.0-1.5 units from a bulk-soil pH of 8.7 in calcareous Vertisols. The amount of acid exudates from roots would influence the thickness of the rhizosphere that is acidified, and thus the volume of soil in which P is solubilized and made available for uptake by the roots.*

*As measured by the agar plate technique, chickpea was found to have two to three times more rhizosphere soil from which P could be solubilized than any other crop species tested. A major fraction of inorganic P in Vertisols is associated with calcium (Ca); in Alfisols, P is mainly associated with iron (Fe). Thus, we obtained a better correlation between P uptake by chickpea and Truog P (obtained by an acid extraction method) than between P uptake and Olsen P (obtained by using an alkaline extractant). Further, by considering the thickness of rhizosphere that is acidified, we could obtain good correlations between P uptake and Truog P for sorghum, which exudes less acid than chickpea.*

## Introduction

The extent of phosphorus (P) deficiency in India has been previously assessed in extensive surveys, either of the available P status of the soil or of the responses of crops to added P. For example, Tandon (1987) reported that the soils in 45% of the 372 districts surveyed were low in available P.

Olsen's sodium bicarbonate extraction method (Olsen et al. 1954) is generally recommended for evaluating P availability of soils, especially calcareous and/or alkaline soils (Whitehouse 1970; Banger et al. 1979; ICRISAT 1985; Kamprath 1991). But the response of different crops to P varies greatly on Vertisols where P becomes limiting (Venkateswarlu 1987). Additionally, some leguminous crops (e.g., chickpea and pigeonpea) appear to be much less responsive to fertilizer P than cereals such as sorghum and millet (Rao et al. 1982). Another reason for this lower response to fertilizer P on Vertisols is the high P-fixation (adsorption) capacity of these soils, resulting from a high content of free calcium carbonate ($CaCO_3$) (Kunze and Templin 1956).

This paper examines the appropriateness of particular soil tests for predicting available P status of contrasting soils, Vertisols and Alfisols. This is considered in relation to forms of P in the soil and effects of root exudates in modifying the rhizosphere

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ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1991. Phosphorus nutrition of grain legumes in the semi-arid tropics (Johansen, C., Lee, K.K., and Sahrawat, K.L., eds.). Patancheru, A.P. 502 324, India: ICRISAT.

environment and thus solubility of soil P, particularly for chickpea.

## Comparative Response to Phosphorus on Vertisols and Alfisols

At ICRISAT Center (near Hyderabad, in southern India), Vertisols generally have lower P status, at least to 60-cm soil depth, than Alfisols (Table 1). Even on Vertisols of low apparent P status, response of chickpea to P application is minimal (Fig. 1). A high yield can be obtained even without P application.

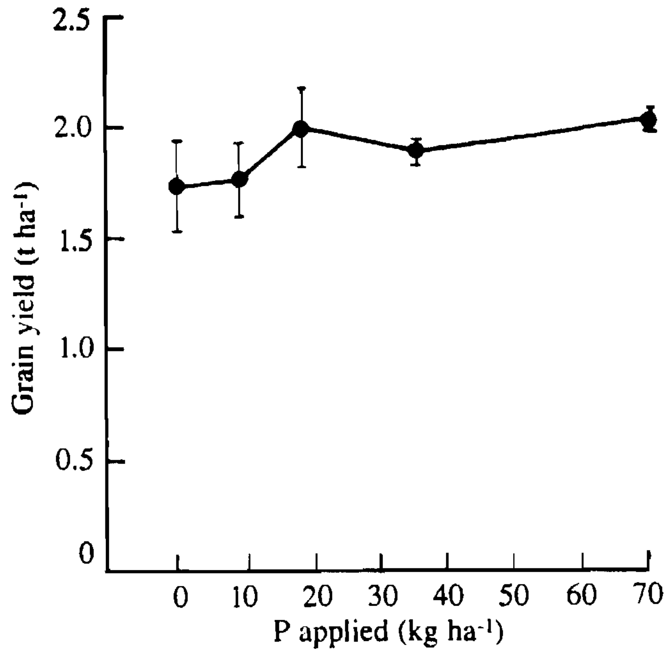

**Figure 1. Response of chickpea grain yield to P application in a Vertisol field (BR 4J) of low P status (1.5 mg P kg$^{-1}$ by Olsen's method) at ICRISAT Center, postrainy season 1988/89. Standard errors indicated.**

**Table 1. Phosphorus fertility and pH (with standard errors) of Vertisols and Alfisols at ICRISAT Center, Patancheru, India.**

| Soil type | Depth (cm) | pH | Olsen P (mg kg$^{-1}$) |
|---|---|---|---|
| Alfisol | 0-15 | 7.3 (±0.06) | 9.8 (±0.64) |
| (n = 241) | 15-30 | 7.3 (±0.06) | 4.6 (±0.44) |
| | 30-60 | 7.3 (±0.06) | 3.5 (±0.43) |
| Vertisol | 0-15 | 8.3 (±0.02) | 3.5 (±0.23) |
| (n = 301) | 15-30 | 8.4 (±0.03) | 1.5 (±0.11) |
| | 30-60 | 8.4 (±0.03) | 1.0 (±0.08) |

As chickpea is not normally grown on Alfisols, because of their low water-holding capacity, comparisons of crop response in the field between soil types were made using sorghum, which can grow in the rainy season on both soil types. Two field sites each on an Alfisol and a Vertisol were chosen for study. Their chemical characteristics are given in Table 2. An NPK factorial experiment (150 kg N, 65 kg P, and 125 kg K ha$^{-1}$) was conducted in the rainy season of 1986. On the Alfisol of lowest P status (RCW 8), dry-matter production without applied P was only 37% of that with P (Table 2). However, on both Vertisol fields, dry-matter yields without P were about 90% of those with P, even though the P status according to Olsen's test is much lower on the Vertisols than the Alfisols. Thus, in the absence of separate calibration

**Table 2. Soil chemical characteristics[1] and dry-matter production of sorghum (cv CSH 5) at the harvesting stage in four fields at ICRISAT Center, rainy season, 1986.**

| | | | | | Inorganic P (mg kg$^{-1}$) | | | Available P (mg kg$^{-1}$) | | | Dry matter (g m$^{-2}$) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Soil type | Field | pH | EC (dS m$^{-1}$) | P fixation[2] (mg kg$^{-1}$) | Ca-P | Al-P | Fe-P | Olsen | Bray 2 | Truog | NPK | NK (-P) |
| Alfisol | | | | | | | | | | | | |
| | RCW 8 | 7.2 | 0.05 | 1340 | 4 | 5 | 48 | 3.5 | 1.5 | 6.5 | 776 | 289 |
| | RCE 14 | 6.9 | 0.05 | 1110 | 14 | 24 | 72 | 8.5 | 14.5 | 18.8 | 1112 | 1063 |
| Vertisol | | | | | | | | | | | | |
| | BR 4J | 8.3 | 0.16 | 7380 | 58 | 20 | 55 | 1.5 | 18.1 | 49.2 | 1494 | 1337 |
| | BP 1 | 8.3 | 0.11 | 5870 | 45 | 19 | 87 | 2.5 | 12.3 | 36.2 | 1216 | 1092 |

1. See Olsen and Sommers (1982) for details of methods used.
2. 20 mL of 2.5% ammonium phosphate was added to 10 g of soil. After 24 h, fixed P was measured from P content in the solution.

curves plotting yield against soil-test value for each soil, Olsen P fails to predict sorghum response to P across these four soils. On the other hand, the acid extractants, Bray 2 and Truog, correlate better with dry-matter production and extent of P response.

To eliminate the differential effect of depth of rooting between plant species and soil types, a pot experiment was conducted using soil from fields RCW 8 (Alfisol) and BR 4J (Vertisol). Several crop species were grown in pots containing 1700 cm$^3$ of soil and supplied with a basal application of N and K, to eliminate deficiencies of these elements. Table 3 shows P uptake by shoots at the grain-filling stage for each crop, except sorghum, soybean, pearl millet, and maize on the Alfisol, where plants died within 1 month of sowing. Chickpea grew best on the Vertisol and was second only to pigeonpea on the Alfisol. Thus factors other than depth of rooting must be responsible for the higher uptake of P by chickpea from soils of low P status. The reason for the high P uptake of pigeonpea on Alfisols is discussed by Ae et al. (1991).

Phosphorus-extraction ability of all crops except pigeonpea appears to be better related to the acid soil extractants for available P (Bray 2 and Truog) than to Olsen's alkaline extractant (Tables 2 and 3). It may be noted that in the Alfisol most of the inorganic P is in the iron-bound form (Fe-P), whereas in the Vertisol there is a considerable fraction of calcium-bound P (Ca-P) (Table 2). Thus the results so far suggest that roots of crops other than pigeonpea are acidifying the soil to release P from Ca-P (Marschner and Römheld 1983), which is much more abundant in the Vertisol.

## Soil pH and Phosphorus Solubility

To examine the relationship between pH and form of P in the soil, we compared the solubility of calcium phosphate ($CaHPO_4$), aluminum phosphate ($AlPO_4$), and iron phosphate ($FePO_4$) over a wide pH range in solution. Figure 2 shows that acidification markedly increases the solubility of $CaHPO_4$ but does not alter the very low solubility of $AlPO_4$ and $FePO_4$. When P was extracted from the same Alfisol and Vertisol used in pot experiments at various pH levels in buffer solutions, the Vertisol showed a pattern similar to that of $CaHPO_4$ (Fig. 3). However, in the Alfisol, solubilization of P was only slightly enhanced at low pH. These data suggest that Vertisols can release more P for plant uptake than Alfisols if they are acidified, even though P fixation is greater in Vertisols than Alfisols.

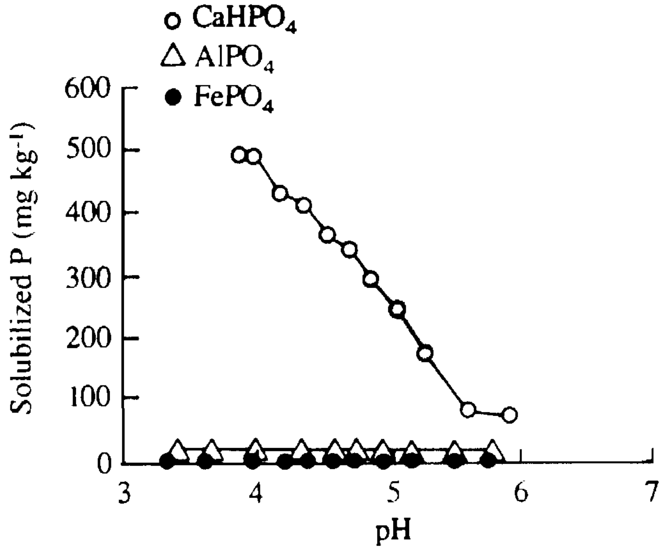

**Figure 2. Effect of pH on the solubility of calcium phosphate ($CaHPO_4$), aluminum phosphate ($AlPO_4$,) and iron phosphate ($FePO_4$).**

## Acidification of the Rhizosphere

We then examined the ability of different crop species to acidify the rhizosphere. Various soil fractions associated with the rhizosphere were taken, as illustrated

**Table 3. Shoot phosphorus contents (mg pot$^{-1}$) of several crop species at the grain-filling stage after growth in potted Alfisol (RCW 8) and Vertisol (BR 4J) without phosphorus fertilizer in a greenhouse.**

| Soil | Chickpea | Pigeonpea | Sorghum | Soybean | Pearl millet | Maize |
|---|---|---|---|---|---|---|
| Alfisol | 4.73 | 5.72 | 0.59[1] | 1.40[1] | 0.64[1] | 0.51[1] |
| Vertisol | 7.79 | 2.34 | 3.91 | 6.53 | 5.38 | 6.13 |
| SE | ±0.77 | ±0.82 | ±0.39 | ±0.20 | ±0.34 | ±0.25 |

1. Plants died 1 month after sowing.

in Figure 4. Crop species (sorghum, maize, soybean, pearl millet, chickpea, and pigeonpea) were grown in pots, using soil from fields RCW 8 (Alfisol) and BR 4J (Vertisol), for 2 months, with essential nutrients being supplied by a dilute Arnon's solution. After removal of bulk soil from the pot, roots with attached soil were gently shaken to release loosely attached soil; this was designated rhizosphere soil #1. Then, roots were vigorously shaken to release more tightly attached soil, designated rhizosphere soil #2. Soil remaining on the roots after vigorous shaking was considered rhizoplane-attached soil. These fractions, including the bulk soil, were placed in water at a rate of 10 g 20 mL$^{-1}$ and the pH measured. As Table 4 shows, all crop species acidified the rhizosphere of both soils. In both soils, the pH of the rhizoplane-attached soil was often more than 1.5 units lower than in the bulk soil. However, because of the dilution factor, these data would underestimate pH in the soil solution of the rhizosphere.

To estimate rhizosphere pH more accurately, we used an agar plate method. Roots of 10-day-old seedlings were placed on agar plates containing 1 mM CaSO$_4$ and one of the following pH indicators:

- bromcresol purple (pH 5.2 purple - pH 6.8 yellow)
- bromcresol green (pH 3.8 yellow - pH 5.4 blue)
- bromphenol blue (pH 3.0 yellow - pH 4.6 blue)
- thimol blue (pH 1.2 yellow - pH 2.8 red).

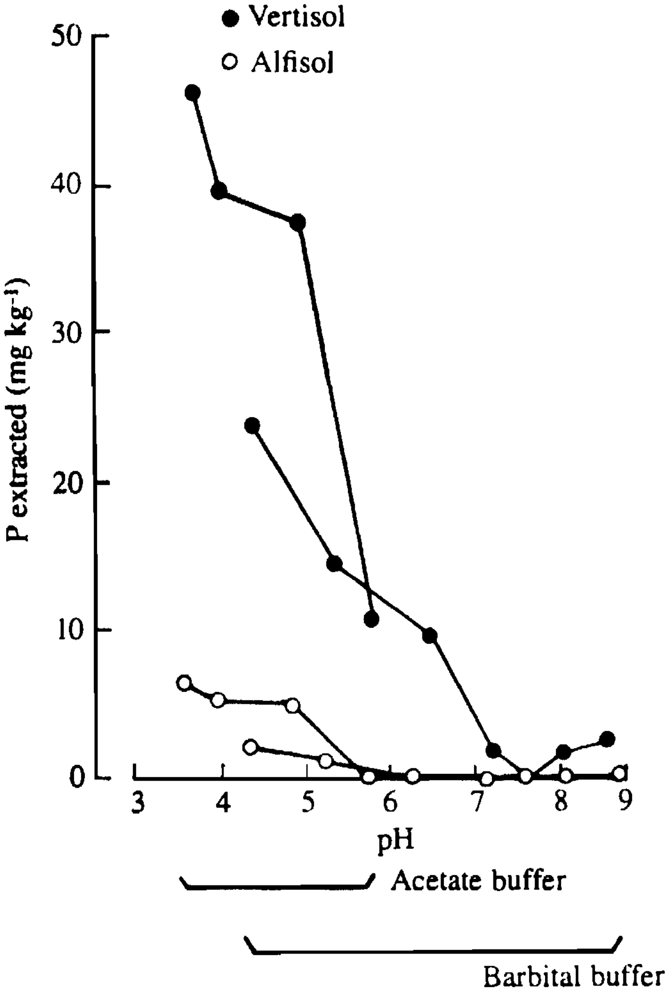

**Figure 3. Extraction of P by buffer solutions at various pH levels from an Alfisol and a Vertisol used in a pot experiment at ICRISAT Center.**

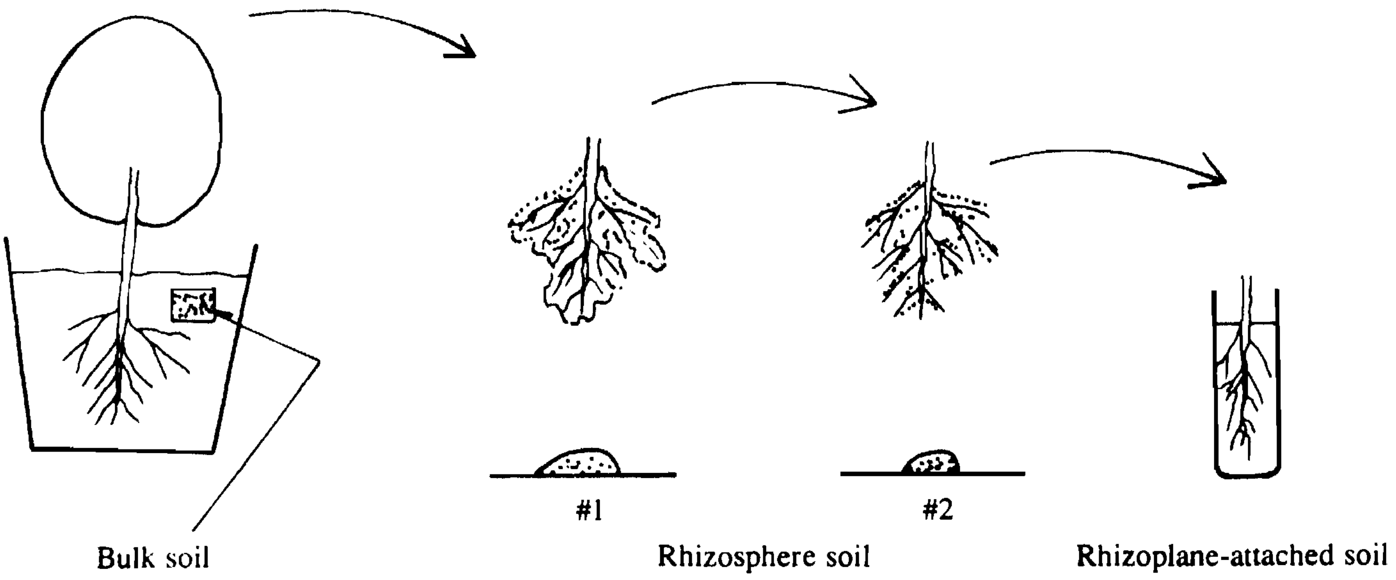

**Figure 4. Method of fractionation of rhizosphere and rhizoplane soil.**

Table 4. pH of bulk, rhizosphere (#2), and rhizoplane-attached soil of crop species grown for 2 months in pots containing an Alfisol or a Vertisol.

| Crop | Soil | pH<br>Bulk soil | <br>Rhizosphere soil | <br>Rhizoplane-attached soil | SE |
|---|---|---|---|---|---|
| Pigeonpea | | | | | |
| | Alfisol | 8.46 | 7.14 | 6.82 | ±0.20 |
| | Vertisol | 9.27 | 8.13 | 7.60 | ±0.18 |
| Chickpea | | | | | |
| | Alfisol | 8.44 | 7.13 | 6.68 | ±0.20 |
| | Vertisol | 9.20 | 8.17 | 7.51 | ±0.18 |
| Soybean | | | | | |
| | Alfisol | 8.87 | 6.81 | 6.29 | ±0.30 |
| | Vertisol | 9.24 | 8.20 | 7.53 | ±0.18 |
| Sorghum | | | | | |
| | Alfisol | 8.59 | 7.66 | 7.22 | ±0.15 |
| | Vertisol | 9.17 | 8.44 | 7.99 | ±0.13 |
| Pearl millet | | | | | |
| | Alfisol | 8.73 | 7.57 | 6.82 | ±0.20 |
| | Vertisol | 9.06 | 8.65 | 7.77 | ±0.13 |
| Maize | | | | | |
| | Alfisol | 8.79 | 7.19 | 6.99 | ±0.22 |
| | Vertisol | 9.19 | 8.50 | 7.76 | ±0.15 |

The agar plate was adjusted to pH 6.5. All crops—chickpea, pigeonpea, sorghum, maize, soybean, and pearl millet—changed the color of bromcresol purple and bromcresol green, but did not detectably change the color of the other two indicators. Thus rhizoplane pH appeared to be in the range of 3.6-4.8.

The color-changed area affected by root exudates was estimated by a grid method comparing color-changed area (A) with root area (B) on the agar plate. Thus A/B indicates the amount of acid secretion per unit area of roots. Table 5 shows that chickpea secretes two to four times as much acid as the cereals and more than the other legumes. Gas chromatographic analysis of the root exudates from the different crops showed that citric acid was the major component exuded and that chickpea exuded the most

Table 5. Color change with pH indicator bromcresol green[1] caused by root exudates of various crop species on an agar plate.

| Crop species | Area of color changed (=A) (mm$^2$) | Area of roots (=B) (mm$^2$) | A/B |
|---|---|---|---|
| Sorghum | 144 (±36.8)[2] | 1240 (±108) | 0.12 (±0.02) |
| Pigeonpea | 104 (±11.6) | 1112 (±40) | 0.09 (±0.01) |
| Chickpea | 548 (±89.2) | 2084 (±192) | 0.26 (±0.02) |
| Soybean | 256 (±18.8) | 1848(±300) | 0.15 (±0.03) |
| Pearl millet | 56 (±10.8) | 1072 (±228) | 0.06 (±0.01) |
| Groundnut | 516 (±45.2) | 2792 (±48) | 0.19 (±0.02) |
| Maize | 280 (±31.6) | 2160 (±288) | 0.13 (±0.01) |

1. pH 3.8 - 5.4 (yellow - blue)
2. Standard errors in parentheses.

(Table 6). The greater acid secretion from chickpea roots would imply that a greater volume of rhizosphere soil around roots would be acidified in chickpea than in the other crop species.

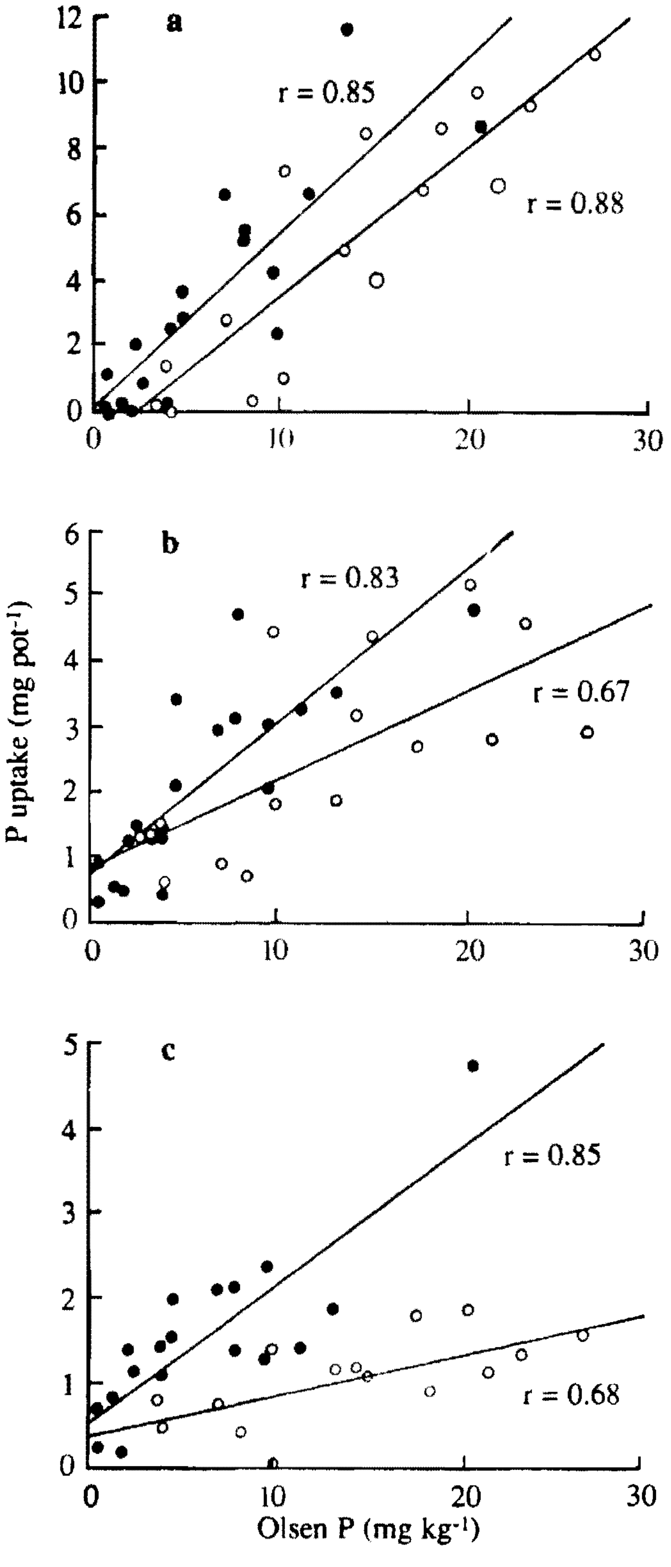

**Figure 5. Relationship between Olsen P and P uptake by (a) sorghum, (b) soybean, and (c) chickpea grown on an Alfisol (○) and a Vertisol (●).**

## Appropriate Soil Tests

In the light of these acidifying effects of root exudates on alkaline soils, we evaluated different extraction

**Table 6. Major organic acids of root exudates[1] from sorghum, pigeonpea, soybean, and chickpea.**

| | Organic acids (mg $g^{-1}$ dry root) | | | |
|---|---|---|---|---|
| Crop | Malonate | Succinate | Citrate | Malate |
| Sorghum | Trace | Trace | 0.045 | 0.008 |
| Pigeonpea | Trace | 0.025 | 0.101 | 0.047 |
| Soybean | 0.324 | 0.046 | 0.481 | 0.078 |
| Chickpea | Trace | 0.054 | 1.292 | 0.025 |

1. Roots of 2-month-old plants grown in sand culture with 5 mg P $kg^{-1}$ were washed in flowing water and exudates collected in 2 mM $CaCl_2$. Collection solution was then eluted through an ion-exchange resin and the acid fractions esterified with methyl alcohol prior to gas chromatographic analysis.

**Table 7. Estimates of pH, electrical conductivity (EC), and phosphorus status (Olsen and Sommers 1982) in Alfisol and Vertisol soil samples.**

| P status | Alfisol (n = 16) | Vertisol (n = 19) |
|---|---|---|
| pH | 6.9 (±0.2)[2] | 8.8 (±0.1) |
| EC (dS $m^{-1}$) | 0.07 (±0.01) | 0.31 (±0.06) |
| P fixation[1] (mg $kg^{-1}$) | 1310 (±160) | 6240 (±300) |
| Total P (mg P $kg^{-1}$) | 164 (±16) | 243 (±20) |
| Inorganic P (mg $kg^{-1}$) | | |
| Ca-P | 26.3 (±5.6) | 82.4 (±6.7) |
| Al-P | 19.3 (±2.7) | 37.2 (±2.4) |
| Fe-P | 69.1 (±5.0) | 68.4 (±5.4) |
| P availability (mg $kg^{-1}$) | | |
| Olsen | 13.5 (±1.8) | 6.0 (±1.2) |
| EDTA-Olsen | 23.3 (±4.4) | 41.9 (±5.0) |
| Ca-Lactate | 15.7 (±3.7) | 20.1 (±3.8) |
| Truog | 29.6 (±5.4) | 60.1 (±6.1) |
| Bray 2 | 23.7 (±4.1) | 29.5 (±3.3) |
| Extraction by buffer (mg $kg^{-1}$) | | |
| pH(3.5-4.1) | 13.3 (±3.2) | 28.8 (±4.3) |
| pH(4.3-4.7) | 10.4 (±3.0) | 19.9 (±3.5) |
| pH(4.9-5.4) | 9.1 (±2.6) | 9.5 (±2.1) |
| pH(6.0-6.6) | 4.7 (±1.4) | 1.5 (±0.5) |

1. 20 mL of 2.5% ammonium phosphate was added to 10 g of soil. After 24 h, fixed P was measured from P content in the solution.
2. Standard errors in parentheses.

methods for available soil P for their applicability to both Alfisols and Vertisols. Soil was collected from 16 sites on Alfisols and 19 sites on Vertisols. The Olsen-P values of these samples ranged from 0.5 to 30 mg $kg^{-1}$ in Alfisols and 0.5 to 25 mg $kg^{-1}$ in Vertisols. Table 7 gives data for the different methods of P extraction, together with pH and electrical conductivity (EC), for these 35 soils. The different crop species were grown in pots containing 1.5 kg of soil of each sample.

For the different soil samples, relationships between P uptake by the plants in pots and Olsen-P values are shown in Figure 5. Olsen-P values for a given level of P uptake were lower in Vertisols than in Alfisols for sorghum, soybean, and chickpea, with the regression lines for the two soils diverging most for chickpea (Fig. 5c). This corresponds with the greater ability of chickpea to exude acid and thus dissolve more Ca-P in Vertisols.

With the acid extractant, Truog, the P uptake for chickpea corresponds better with soil-test values on both soils (Fig. 6a). However, for sorghum, which secretes less acid than chickpea, Truog P overestimates P fertility of Vertisols compared with Alfisols (Fig. 6b).

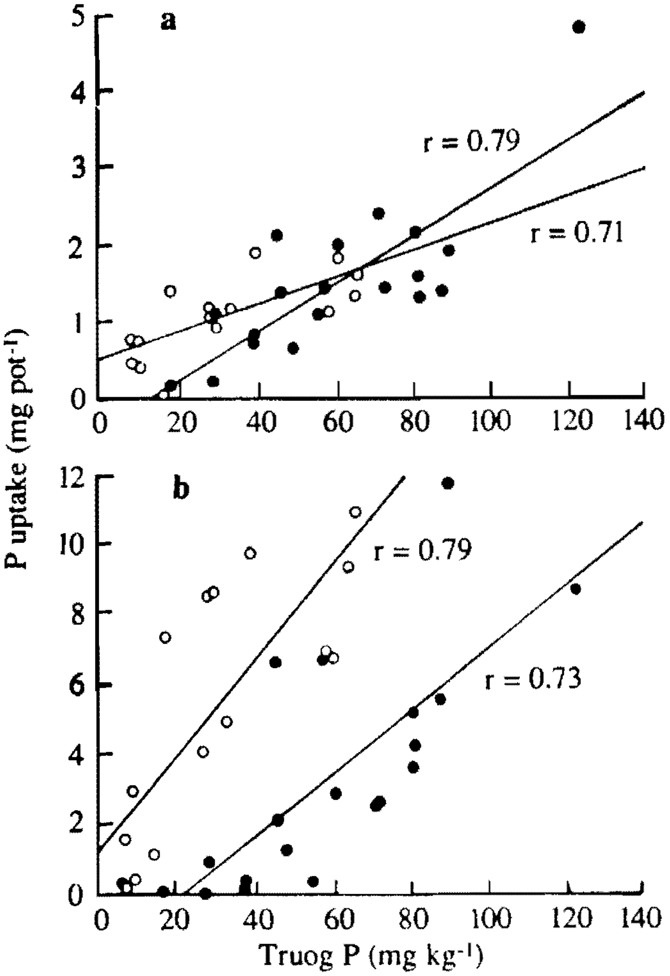

**Figure 6. Relationship between Truog P and P uptake by (a) chickpea and (b) sorghum grown on an Alfisol (○) and a Vertisol (●).**

We tried to model the effect of acid root exudates on soil pH of an Alfisol (RCW 8) and a Vertisol (BR 4J) by titrating soil samples with 0.01 N acetic acid. The titration curves are shown in Figure 7. Only 25 mL of 0.01 N acetic acid is required to lower soil pH to 5.0 in the Alfisol but 70-80 mL is required in the Vertisol. This implies that sorghum, which exudes

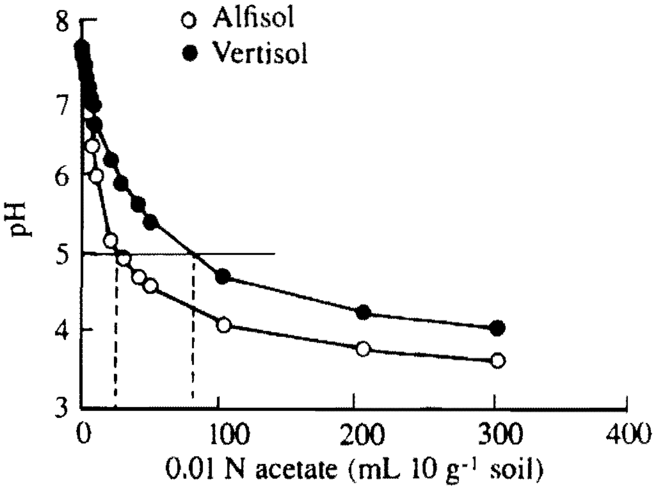

**Figure 7. Effect of 0.01 N acetic acid on soil pH of an Alfisol and a Vertisol.**

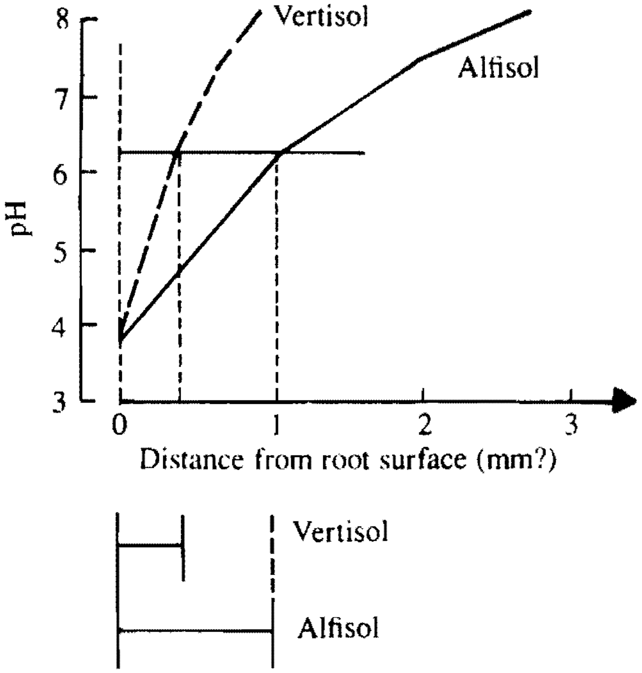

**Figure 8. Model of rhizosphere soil pH.**

relatively less acid than chickpea, has a lower volume of acidified rhizosphere in the Vertisol than in the Alfisol. A model to illustrate changes in rhizosphere pH in relation to distance from the root surface for sorghum or soybean in a Vertisol and an Alfisol is proposed in Figure 8.

Following the model in Figure 8, the volume of rhizosphere soil acidified by sorghum in the Alfisol would be at least twice that in the Vertisol. Therefore, by dividing Truog-P values in Vertisol by 2.5, a better correspondence between soil types can be achieved for sorghum (Fig. 9). When we changed the pH of the Alfisol and Vertisol by adding dilute $H_2SO_4$ or $Ca(OH)_2$, P uptake by sorghum was increased by acidification only on the Vertisol and not affected on the Alfisol (Fig. 10). These results demonstrate that Vertisols have a higher P-fertility potential than Alfisols, even though Vertisols may have lower Olsen-P values and higher P-fixation capacity than Alfisols.

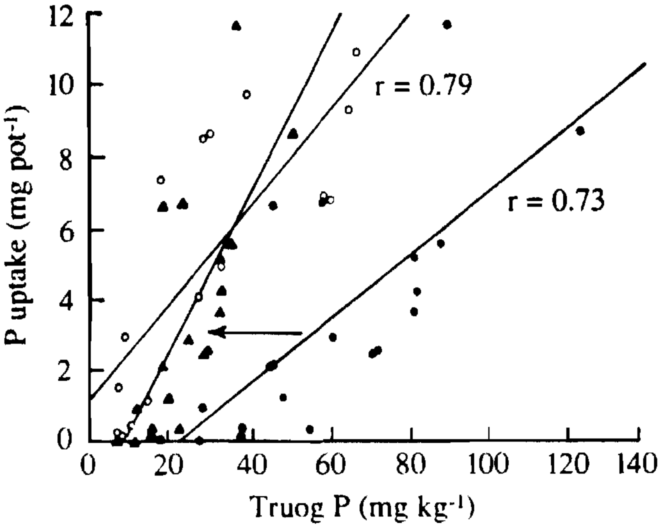

**Figure 9. Relationship between Truog P and P uptake by sorghum grown on an Alfisol and a Vertisol: ○ Alfisol, ● Vertisol, ▲ Vertisol (Truog P × 0.4).**

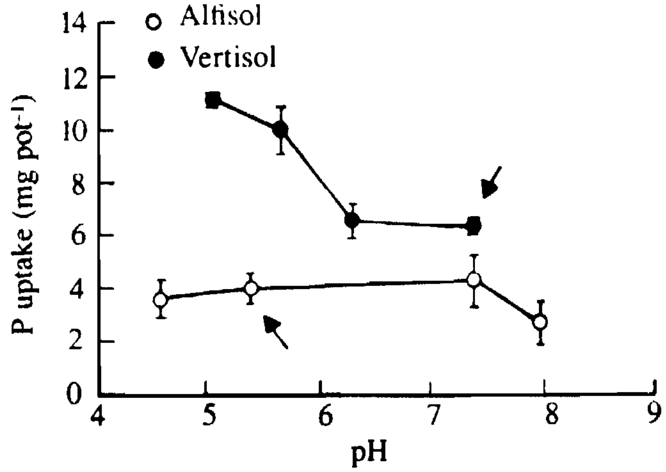

**Figure 10. Effect of soil pH on P uptake by sorghum. Soil pH was modified by adding either dilute $H_2SO_4$ or $Ca(OH)_2$ (→ = Initial pH). Standard errors indicated.**

## Conclusions

- Olsen P cannot be used for simultaneous comparison of P status of Vertisols and Alfisols without separate calibration of yield against soil-test value for each soil type or use of a correction factor.
- Acids secreted from roots of crop plants can readily make available for plant uptake the P from Ca-P, which is much more abundant in Vertisols than in Alfisols.
- Chickpea secretes more acid than soybean, pearl millet, maize, pigeonpea, or sorghum and thus P uptake by chickpea is better simulated across soil types by Truog P.
- For crops exuding less acid than chickpea, Truog P overestimates P availability in Vertisols. A correction factor based on thickness of rhizosphere acidified can overcome this problem.
- In evaluation of P uptake by crop plants, rhizosphere acidification is an important concept.

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# Interpretive Summary of Part 1: Factors Affecting the Availability of Phosphorus in Soils of the Semi-Arid Tropics

F. R. Cox[1]

## Introduction

The preceding papers have evaluated the theoretical and practical aspects of the availability of phosphorus (P) in soils of the semi-arid tropics. These soils are primarily Alfisols and Vertisols, and there are marked differences in P sorption between the two.

The mineralogy of the Alfisols is largely kaolinitic, but the actual composition varies considerably, and most Alfisols contain significant amounts of interlayered minerals. The clays have a relatively small surface area, but have a variable charge that would promote P adsorption, especially at reduced soil pH. The clays are also coated with hematite, which provides a more reactive surface for P sorption. The charge on hematite is affected by pH, but in the range found in the soils of the semi-arid tropics, this is not a major factor affecting P in the soil.

The mineralogy of the clays in Vertisols is primarily smectitic, and there are few other types of clay present. The smectites have a large surface area that would promote P sorption, but, on the other hand, they have a large permanent-charge-based cation-exchange capacity that would repel anions such as phosphate. However, the Vertisols are coated with a silica-alumina gel, with varying amounts of iron (Fe), which does provide a surface for P sorption.

## Factors Affecting Phosphorus Availability

Based on the clay mineralogy of Alfisols and Vertisols, it would appear that there is no factor that would lead to marked P sorption. Both contain surface minerals, and with adequate surface area, there will be significant P sorption. The primary factor affecting sorption, therefore, is the surface area of the soil. As the average texture of Alfisols tends to be sandy, whereas the average texture of Vertisols is clayey, this would indicate that P sorption should normally be greater in Vertisols than Alfisols. This was reported by Ae et al. (1991) in the previous paper. It was also shown by Sahrawat and Warren (1989), who reported that the P buffer capacity for a Vertisol was more than twice that of an Alfisol in peninsular India. This difference reflects effects associated with soil texture.

It should be emphasized that the reaction of P with soil is a surface reaction, and it has been described by a number of adsorption equations. These include, of course, the Langmuir and Freundlich equations, and their use has been reviewed by Sample et al. (1980) and Olsen and Khasawneh (1980). The accepted utility of these equations is a reminder that texture, indicating the surface area of the soil, is a major factor affecting the availability of P in soils, including those in the semi-arid tropics.

Another factor affecting the availability of P in soils of high pH is the presence of free calcium carbonate, or even the presence of higher Ca levels in the soil. In this case, phosphate is affected by the solubility of various calcium phosphate ($CaHPO_4$) compounds and by the presence of free calcium carbonate ($CaCO_3$) surfaces available for sorption reactions. These are important considerations in evaluating the availability of P in most Vertisols.

## Soil Productivity and Phosphorus

In this session it was also pointed out that the productivity of Alfisols and Vertisols differs. Models have been used to describe this difference. One such model

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discussed was the Productivity Index (PI) model (Pierce et al. 1983). It is empirical and simple, being based largely on critical factors such as soil-moisture availability, aeration, bulk density, pH, and salt content. These factors are considered by horizon to the maximum depth of rooting, and their importance in affecting productivity is based on the amount of roots in each horizon.

It was pointed out that fertility variables, especially P availability, could be included in this model. This would mean that an estimate of soil-P availability should be made by horizon. This is stating that an understanding of subsoil P and its contribution to plant nutrition is essential. Subsoil contributions have not been considered previously, but this may explain some of the differences noted by researchers here in India.

During this conference, it was reported that subsoil P was greater in Vertisols than Alfisols. It was also noted that considerable variability exists in the P content of Vertisol subsoils. This may be due to the extreme shrink-swell characteristics of the Vertisols, as they have been referred to as "self-mulching." After the surface has dried, forming large cracks that go quite deep into the soil, surface soil and/or other materials that are higher in P may fall into the crevices. This would cause localized sites of higher P content in the subsoil. This may be the reason for the variability and higher P encountered in the subsoils of Vertisols. It would also indicate the difficulty in accurately assessing the P content of such subsoils.

In the example given of including a P-fertility variable in the PI model, soil-solution P was used as the estimate of P availability. Data from Peaslee and Fox (1978) were presented to show that soil characteristics may not affect the level that is considered sufficient for a given crop. It is likely, however, that with a range in texture, the critical level of solution P would vary (Kamprath and Watson 1980). With finer-textured soils, the quantity factor becomes very large, so the intensity factor exemplified by the solution-P concentration may be smaller. If a soil test is used, its interpretation may also have to be adjusted for texture.

## Appropriate Soil Tests for Phosphorus

An ideal soil test would be one that reflects not only the P intensity and capacity, but also the relationship between them. That relationship is the P buffering capacity—the change in P intensity per unit change in P capacity. The P buffering capacity is largely controlled by the surface area or texture, so that the interpretation of most soil tests for P should be adjusted for texture.

This session showed that changes in soil P due to cropping are highly correlated with soil clay content when the Bray 1 or Mehlich 1 extractants are used for soil tests. With the Olsen extractant, however, clay seems to have less effect, indicating that it somehow adjusts for the P buffering capacity of the soil (Novais and Kamprath 1978). This observation deserves further research, because, if true, the relationship between amounts of P extracted with various reagents would change with the clay content of soils. At present, the relationship among the amounts of P extracted with various reagents is considered similar for all soil conditions except pH. It is known that acid extractants become less effective with increasing pH, and should not be used if any free $CaCO_3$ is present. In fact, the use of any acid extractant would be questionable if the pH is higher than 7, because of the slow rate of dissolution of $CaCO_3$ under basic conditions.

Several mechanisms are involved in P extraction from soils by the reagents used for soil testing. The Olsen extractant, $NaHCO_3$, functions through anion exchange, a mechanism that is effective in acid as well as alkaline soils. For this reason, correlation work with various extractants often indicates that the Olsen extractant is superior, and it is certainly the most universally accepted reagent for extracting P from soils. There also may be more data on critical levels with this extractant than with others.

Ae et al. (1991) reported that crop plants, and particularly chickpea, can considerably lower the pH of the rhizosphere soil in alkaline Vertisols. This would not necessarily negate the use of Olsen's extractant as a soil test in these circumstances, provided that a correlation between plant response and Olsen-P level is still obtained.

There is a lack, however, of data showing the importance of texture, or clay content, in the P soil-test interpretation. Such interpretations must be based on field studies, and one seldom has enough sites varying in clay content to evaluate this effect. In North Carolina, we had the opportunity to study this effect with corn at two sites; one with 40% clay and the other with 10% clay (Cox and Lins 1984). These were long-term residual studies, with a large range of P rates applied once and monitored for extractable soil P over several years. With this system, one can estimate the P sorbed immediately after application, plus that which becomes more occluded over time, or a further, slower reduction in extractable P over time. With this information, it is easy to predict the amount of P fertilizer to be added to achieve a given soil test at a particular point in time.

The range of soil P used in these studies also allowed estimation of the critical P level for a crop. The critical level for the more clayey site was only one-fourth that of the more sandy site. Also, we could predict for each site the amount of P that should be added if the soil test was at any concentration below the critical level, and the rate that should be applied yearly to maintain the critical level. The rate required to maintain the critical level was three times as much for the clayey site as for the more sandy site (Cox et al. 1981).

Further research of this nature has been done with soybean in Brazil. Three soils, with 63, 27, and 12% clay, were used and yields and Mehlich-1-extractable (1:10) soil P measured for about 4 years (Lins et al. 1985). Economic considerations, such as the cost of fertilizer P and the price of the crop, were also included, and the value of their inclusion compared in the analysis of the data. Critical soil-test P levels were also determined by several methods and the results compared. The average critical P levels were 6, 15, and 23 kg P $ha^{-1}$ for soils with clay contents of 63, 27, and 12%, respectively. To maintain the critical levels for another year, 41, 16, and 12 kg P $ha^{-1}$ would have to be applied. Similar results were obtained if economic considerations were not included in this approach, so it seems inclusion of economic considerations did not make a great deal of difference.

Additional research on the subject has been conducted in Brazil. The studies cited above have been continued over additional years, and other locations, soil conditions, and extractants have been evaluated (Lins et al. 1989; Lins and Cox 1989). The soils of that region are Oxisols and most have a kaolinitic mineralogy, but a few have a gibbsitic mineralogy. The results of these studies indicated not only the marked effect of soil texture, but also a difference due to clay mineralogy; the gibbsitic soils behaved differently from the more typical kaolinitic ones. It was apparent that separate calibration studies should be conducted on soils that differ markedly in clay mineralogy.

Similar studies should be conducted in the soils of the semi-arid tropics. Differences are known to exist in P sorption between Alfisols and Vertisols, but whether they are sufficient to affect the interpretation of the P soil-test data is unknown. Also, the effect of texture should be evaluated on these soils. This may be difficult on the Vertisols, since, by definition, they must have more than 30% clay in the control horizon, and there is little difference in texture between the surface and the control horizon.

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# Part 2

# Extraction of Soil Phosphorus by Plant Roots

# The Phosphate Transport System and Its Regulation in Roots

D.T. Clarkson[1] and C. Grignon[2]

## Abstract

*Inorganic orthophosphate ($P_i$) ions enter plant cells against a steep gradient of electrochemical potential. The biochemical mechanism responsible for this transport is unknown at the molecular level but depends on the pH gradient across the plasma membrane (PM) generated by the $H^+$-ATPase. This is because of the energetic coupling of the transport $P_i$ across the PM with transport of protons. The cell walls modify the pH at the membrane surface by restricting the diffusion of $H^+$. The $P_i$ transporter also appears to have an intrinsic sensitivity to pH, its efficiency being increased by the protonation of a group having its pK between 5.5 and 6.5.*

*The influx and net absorption of $P_i$ by roots are modified by the phosphorus (P) status of plants and by the rate of growth, which creates an internal demand for P. In the short term, it has been proposed that the efficiency of the transporters is modulated directly by $P_i$ in the cytoplasm. In the longer term, variations in demand are met by increasing or decreasing the number of transporters in operation. In circumstances where $P_i$ supply exceeds growth requirement, the efflux of $P_i$ from cells becomes an increasingly large proportion of the influx.*

*Phosphate absorption by different parts of the root system is coordinated so that a deficiency in one zone or horizon is compensated for by increased rates of absorption elsewhere. The nature of the signal that brings this about is unknown, but it is possible that the $P_i$ cycling in the phloem, between shoots and roots, may be involved.*

*The relative importance of the properties of the $P_i$ transporter and those relating to root morphology and rhizosphere pH in determining successful P nutrition of field-grown crop plants are assessed in the discussion.*

## Introduction

The solution immediately outside the cells of roots is likely to contain 1 µM phosphate ($P_i$) or less, while in the cytoplasm the concentration will be $10^3$ to $10^4$ times greater. These two solutions are separated by the plasma membrane (PM), which is only about 8 nm thick, and in which is embedded the specialized mechanism responsible for this remarkable concentration of $P_i$. To transport 1 mole of $P_i$ into the interior of a typical root cell, a minimum of 25-40 kJ of energy is required, which is roughly equivalent to the maximum free energy released by the hydrolysis of 1 mole of adenosine triphosphate (ATP) (50-60 kJ $mol^{-1}$). The work thus done in transporting $P_i$ into the cell, and current opinions about the way in which the transporter works, are the subject of the first part of this paper. We use the word opinions advisedly; the molecular details of the transporter are unknown.

From the point of view of mineral nutrition, it is the way in which the transport mechanism is controlled by the plant that may be of wider interest. The intake of $P_i$ can be adjusted, within quite wide limits, to the requirements for phosphorus (P) in growth and

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metabolism. We will argue that this flexibility ensures that plant growth is rarely limited by the ability of roots to absorb $P_i$. It is much more usual for the supply of $P_i$ to the absorbing mechanism to limit uptake (see Amijee et al. 1991). In this regard, the characteristics of the soil are all-important. There are, however, plant responses that can ameliorate the $P_i$ supply from the soil. The morphology of the root system and its relative size, the pH of the rhizosphere soil, and associations with mycorrhizal fungi are all adjustable according to the demand for $P_i$ within the plant.

The mechanism of transport can be discussed in general terms, partly because of our ignorance of its exact nature and partly because it seems unlikely that it will turn out to differ very much between, say, a tropical legume and a temperate cereal plant. The response of the morphological and surface characteristics to P nutrition are likely to be much more specific, and we point to the need for more detailed study in this area.

## Mechanisms of Phosphate Uptake

As indicated above, $P_i$ uptake is active in that it requires an energy source. The ultimate energy source must be a chemical reaction; i.e., the rupture of covalent bonds in molecules such as ATP or reduced substrates produced by photosynthesis or respiration. Two kinds of energetic coupling mechanisms have so far been identified. The so-called primary active transport systems tap these energy sources directly. Thus, in the PM there is an $H^+$-translocating ATPase, which hydrolyzes Mg-ATP. This is a protein with a molecular weight of approximately 110 kDa; there appears to be a large degree of homology in its amino acid sequence in different species and between phylogenetic classes, which indicates its early evolution. In terrestrial plants there is no clear indication that ions other than $H^+$ and $Ca^{2+}$ are transported by primary systems.

### Secondary Active Transport

The other ions are transported by secondary active systems, indirectly coupled to chemical sources of energy. It is highly probable that these mechanisms are provided by proteins with several membrane-spanning sequences. These provide some kind of space or cleft in which ions can be bound at one surface of the membrane and then released at the other after some reorientation of the structure. In these systems there is no enzymatic activity; the transports are driven by the pH gradient and/or the electrical gradient maintained across the membrane by the proton pump (Fig. 1). There is a general consensus that anions are co-transported with $H^+$ (Lüttge and Clarkson 1987), which may be either $H^+$/anion symports, $OH^-$/anion antiports or $HCO_3^-$/anion antiports. This view is based on indirect evidence:

1. Anion absorption is frequently accelerated by lowering the pH of the external solution (Ullrich-Eberius and Ying-Chol 1974; Vange et al. 1974; Lin 1979).
2. From its responses to a variety of metabolic effectors, it seems more dependent on the proton motive force than on the [ATP] in the tissues (Lin and Hanson 1974).
3. In some cases (e.g., $NO_3^-$ uptake), anion uptake is accompanied by alkalinization of the medium (Thibaud and Grignon 1981).
4. In other cases, depolarization of the membrane potential difference (PD) occurs when $P_i$ is added to the external solution. This indicates a net transfer of positive charge into the cytoplasm (Ullrich-Eberius et al. 1981, 1984). However, this electrical effect may be obscured by rapid activation of the $H^+$-pump (Fig. 1) by the acidification of the cytoplasm; this may explain the hyperpolarization seen on the addition of $P_i$ to solutions bathing roots of sunflower *(Helianthus annuus)* and white clover (*Trifolium repens*) (Bowling and Dunlop 1978; Bowling 1983).
5. Finally, no indication of primary active transport has ever been obtained.

Except for the alkalinization of the external solutions, $P_i$ transport into plant cells meets these criteria. Furthermore, the influx is inhibited by mersalyl (Lin and Hanson 1974; Lin 1979), which is known to block mitochondrial $OH^-/P_i$ exchange.

### Extrinsic Binding Proteins

The cells of roots are generally found to have an apparent affinity for $P_i$ ($H_2PO_4^-$) in the micromolar range. It has long been suspected that this high affinity could be due to extracellular proteins resembling the extrinsic binding proteins of bacteria and yeasts

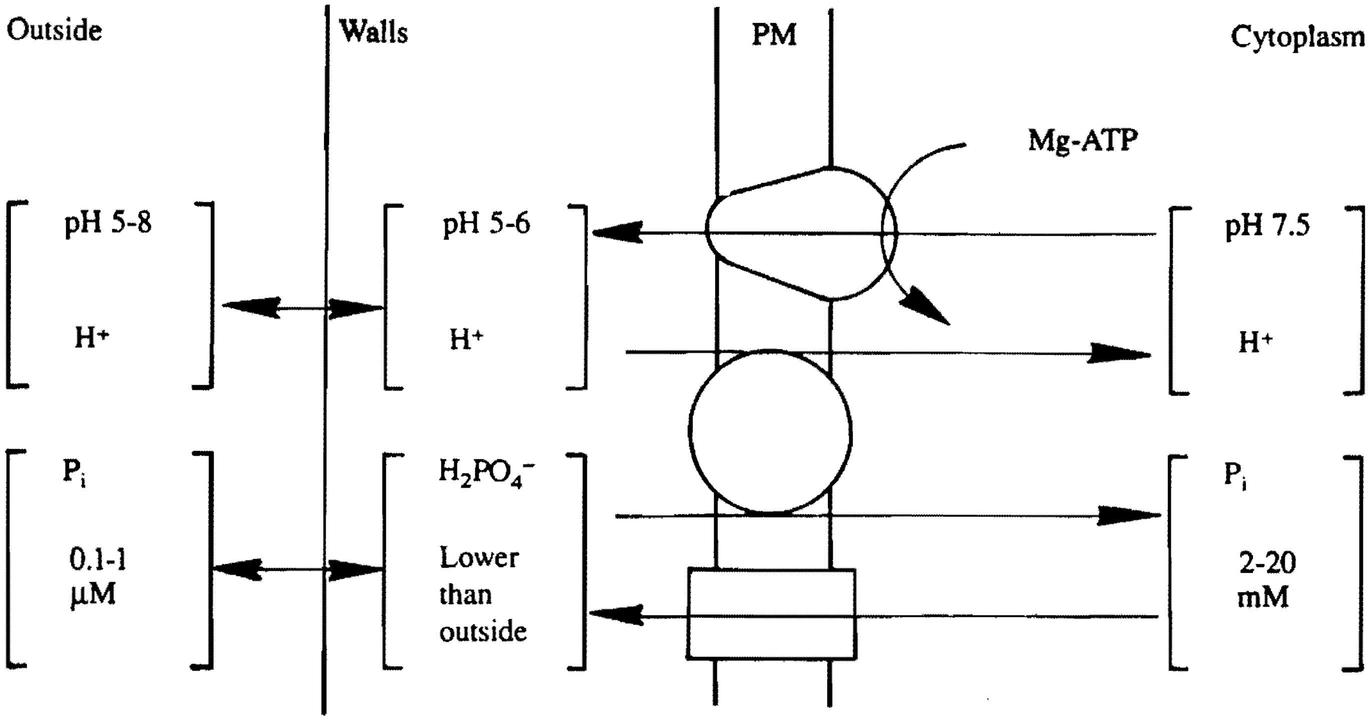

**Figure 1. Current view of the energization of $H_2PO_4^-$ transport across the root cell membrane. The active uptake of $H_2PO_4^-$ is energized by the pH gradient maintained by the ATPase. The cell walls restrict the diffusion of the excreted $H^+$ ions in the medium, and thus may favor their reentry into the cells together with $H_2PO_4^-$. The passive efflux of orthophosphate is probably mediated by another system.**

(e.g., Jeanjean et al. 1981). Popular candidates for this role have been cell-wall acid phosphatases, which are induced by P starvation in parallel with augmented $P_i$-uptake capacity (Lee 1988, and references therein). However, such binding proteins have never been isolated in higher plants. In roots of pea (*Pisum sativum*), osmotic shocks, classically used to extract binding proteins, did not modify the affinity for $P_i$ of either root cells or of their protoplasts; both had similar values for $K_m$ (Lefebvre and Clarkson 1987).

### Influence of pH and Cell-wall Properties on Phosphate Absorption

As indicated above, anion-absorption rates often increase when the external pH is lowered. However, the responses of $^{32}P_i$ influx ($J_{Pi}$) to variations of pH in the external solution are particularly complex, because pH acts on the uptake process at two different levels. First, it determines the concentrations of the various forms of phosphate, according to their pKs and the $[Ca^{2+}]$. Generally, $J_{Pi}$ varies in parallel with the $H_2PO_4^-:HPO_4^{2-}$ ratio in the medium. Although some complications in this relation have been taken to indicate $HPO_4^{2-}$ absorption at high pH (Hagen and Hopkins 1955), it is agreed that $H_2PO_4^-$ is the main transported ion. The effect of pH on $J_{Pi}$, however, is not simply a matter of the $[H_2PO_4^-]$. In roots of corn (*Zea mays*), for example, $J_{Pi}$ decreased between pH 3 and pH 5, even though $[H_2PO_4^-]$ increases in this range, due to the ionization of $H_3PO_4$ (Sentenac and Grignon 1985). Careful analysis of such apparent anomalies led to the conclusion that they were due to differences between the pH at the cell surface and the pH of the bulk solution. The complex shape of the $J_{Pi}$ vs external pH was different from that of $[H_2PO_4^-]$ vs external pH (Fig. 2). When we calculated the $[H_2PO_4^-]$ in the cell walls, using a theoretical model (Sentenac and Grignon 1981), we found a much closer correspondence between $J_{Pi}$ and $[H_2PO_4^-]$. Furthermore, in the range pH 3-5 (in which the $P_i$ transporter has no intrinsic sensitivity to pH: see below), the kinetics of $J_{Pi}$ vs $[H_2PO_4^-]$ in the external medium were pH-dependent, while the relationship between $J_{Pi}$ and $[H_2PO_4^-]$ in the cell wall showed no pH-dependence. This indicates that the observed decrease in $J_{Pi}$ between pH 3 and pH 5 was due to increasing

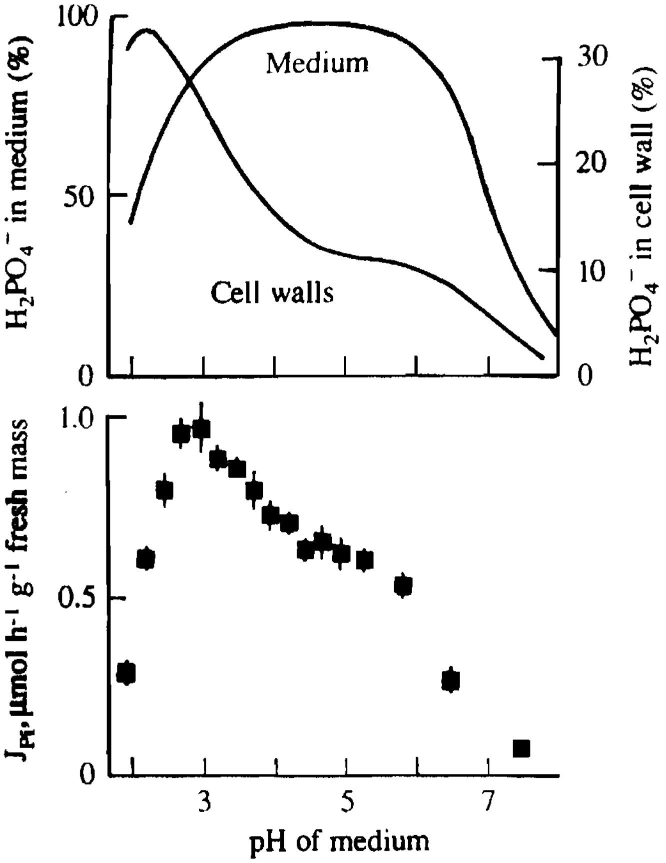

**Figure 2. Effects of the pH on $^{32}P_i$ influx and on the proportion of the $H_2PO_4^-$ form at the cell surface. The upper curves show the percentage of total inorganic P present in the medium, and in the cell walls, as $H_2PO_4^-$. The lower curve was calculated using a theoretical model for ion accumulation at equilibrium in cell walls (Sentenac and Grignon 1981). Subapical segments of 4-day-old corn seedlings. Adapted from Sentenac and Grignon (1985).**

dissociation of uronic acid groups, which lowered the phosphate concentration by electrostatic repulsion.

Another important facet of the cell-wall effect is that the affinity of the transport system for $H_2PO_4^-$ is underestimated when calculated from the $[P_i]$ in the external solution; this is usually a much greater concentration than is present in the wall. When "true" $H_2PO_4^-$ concentrations (calculated in the cell walls) were used, the affinity of the phosphate transporter in corn roots was 5- to 10-fold greater than when apparent external concentrations were used ("true" $K_m$ = 0.25-0.5 µM). Moreover, the value of the apparent affinity (the value usually quoted in published work) depends on all factors that affect electrostatic interactions at the cell surface and thus modify local ionic conditions. This distorts the absorption isotherms, and changes apparent kinetic parameters, even though the intrinsic properties of the $P_i$ transporter are unchanged. This could be shown with isolated root-cell PMs in which the surface potential was modified by variations of ionic strength, pH, or bivalent cation concentration (Gibrat et al. 1985, 1989). In living roots, $Ca^{2+}$ and other polyvalent cations have long been known to stimulate $P_i$ uptake by roots, with an efficiency dependent on their valency (Viets 1944; Tanada 1956; Leggett et al. 1965; Franklin 1969). Since this effect could be obtained after very short pretreatments of roots with the polyvalent cations, it has been attributed to the binding of the cations on the anionic sites at the cell surface. This attenuates the electrostatic repulsion of $H_2PO_4^-$ and thus increases the apparent affinity for this ion (Sentenac 1988). Thus, variations of apparent kinetic parameters of ion transport between species or treatments do not always indicate differences in characteristics of the transporters. They may result from changes in ionic conditions in the cell walls.

### Intrinsic Sensitivity of Phosphate Transporter to pH

The second effect of pH on $P_i$ absorption is exerted directly on the transporter. This was demonstrated in corn roots by measuring $^{32}P$-influx as a function of pH, with the $[P_i]$ calculated to ensure constant $[H_2PO_4^-]$ in the cell walls. In these conditions, the response of $J_{Pi}$ to pH indicated that the efficiency of the transporter varied in parallel with the protonation of a group having its pK near 5.5-6.5. This value suggests that the activating group is the imidazol of a histidyl residue. Indeed, $J_{Pi}$ was shown to be inhibited by a ligand of imidazol (Sentenac and Grignon 1985).

In summary: to function, the $P_i$ transporter must bind both $H_2PO_4^-$ and $H^+$ with $K_m$s near 0.25-0.5 µM and 0.3-4 µM, respectively. Thus, P uptake may be expected to depend on the maintenance of a relatively low value of the soil pH, a parameter that is only partially controllable by the plant. It is worth remembering that the picture described above was obtained in conditions where both $H_2PO_4^-$ and $H^+$ were relatively abundant. What happens to $P_i$ uptake when they are not? Before going further, it is important to understand that $H^+$ accumulated in cell walls by the Donnan effect cannot stimulate $J_{Pi}$ by circumventing a shortage of $H^+$ in the medium. This is simply because accumulation of $H^+$ ions in the Donnan system does not increase their free energy. Furthermore, in the Donnan system $H_2PO_4^-$ is repelled to exactly the same extent as $H^+$ is attracted.

## The Role of the Proton Pump

When the pH of the external solution is increased—i.e., when both [H$^+$] and [$H_2PO_4^-$] become lower—$P_i$ uptake does not cease as might be expected from the H$^+$/$H_2PO_4^-$ symport model. This is because the H$^+$-translocating ATPase in the PM, the proton pump, can acidify the solution in the cell wall close to the membrane surface. It was found that $P_i$ uptake at alkaline pH was strongly inhibited when the proton pump was blocked with vanadate (Thibaud et al. 1988), but that it continued unchanged when a similar treatment was given at acid pH values (Fig. 3). It was concluded that the H$^+$ used for $J_{P_i}$ could come either from the external solution or from the action of the proton pump. The pump causes a shift in the pH of the membrane surface, a fact verified using surface pH probes (Sentenac and Grignon 1987). At pH 8 in the external solution, surface pH was 2 units more acid when the proton pump was activated (Thibaud et al. 1988). This surface accumulation of the excreted H$^+$ results from its restricted diffusion through the walls. Diffusion is accelerated when pH buffers are added to the external solution; although they did not change the external pH, they had the same inhibitory effect on $P_i$ uptake as blocking the proton pump with vanadate. Interestingly, accumulations of $CO_2$ in poorly aerated soils could, because of the formation of a $CO_2/HCO_3^-$ buffering system (Toulon et al. 1989), inhibit $P_i$ uptake by collapsing the surface pH gradient (Fig. 4).

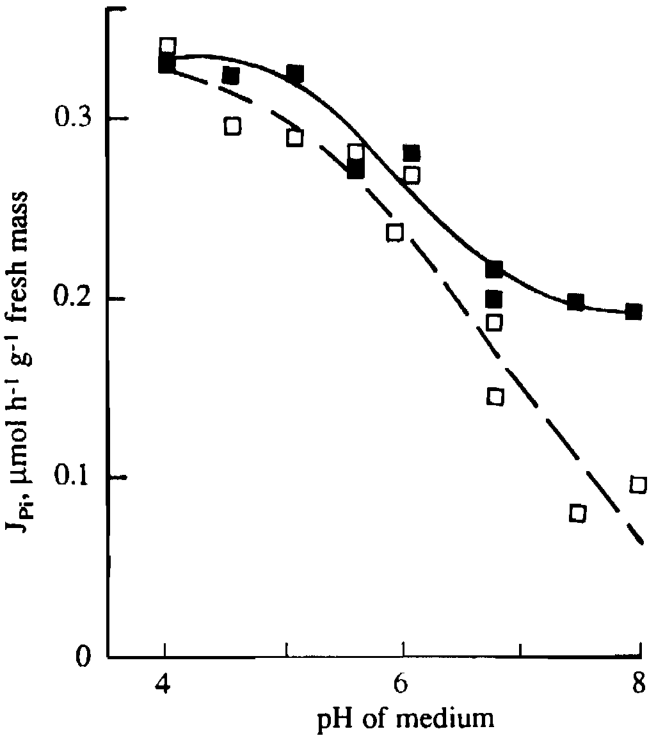

**Figure 3. Effect of the H$^+$-pump activity on $^{32}P_i$ influx. The composition of the media was calculated to ensure a constant concentration of the $H_2PO_4^-$ form (50 µM). This concentration is 100-200 times the $K_m$ of the high-affinity system for $H_2PO_4^-$ uptake. Closed symbols: control, with active H$^+$ excretion. The media were unbuffered, and the pH of each was maintained at the set value with an automatic pH-stat system. Open symbols: the H$^+$-pump was inhibited by 50 µM vanadate, and 5 mM buffers were added to the media. Roots excised from 5-day-old corn seedlings. Adapted from Thibaud et al. (1988).**

These results indicate that the root may maintain the pH at the surface of its cells at relatively low values, compatible with the requirements of anion/H$^+$ cotransports, even if the bulk pH of the medium is unfavorable. Of course, this efflux of H$^+$ needs to be accompanied by net absorption of the nutrient cations. This has implications of two kinds, as it does in the Donnan effect. Firstly, it allows the root to have some control over the ionic environment of the absorption surface. Secondly, it makes the kinetic characteristics of transport systems strongly dependent on all the parameters that influence the rate of net H$^+$ excretion and/or the rate of diffusion of H$^+$ across the walls (i.e., the buffering power of the medium). Thus, valid comparisons of the intrinsic characteristics of $P_i$ transport systems between varieties or species can be made only if experimental conditions ensure that the net H$^+$ transports across the membranes and apoplast are strictly comparable.

## Regulation of Absorption

When plants are grown in flowing culture solutions it is often found that they take up similar amounts of $P_i$ from solutions differing greatly in concentration if they are growing at the same rate. Thus, Breeze and Hopper (1987) found that white clover grew and absorbed $P_i$ at the same rate over a 25-fold range of [$P_i$] once the plants had become equilibrated to their various solutions (Table 1); this was true of plants fed with $NO_3^-$ and of those fixing $N_2$. Evidently, the intake of $P_i$ was related to the rate at which the plants were growing (c.f. $NO_3^-$-fed and $N_2$-fixing plants) and not to the external concentration. We might expect that absorption of $P_i$ by roots growing in more dilute solutions would have been more "costly" in thermodynamic terms than by roots growing in the more concentrated solutions. However, it is necessary to understand a few more details of this experiment before one can see what has gone on. At the outset, all

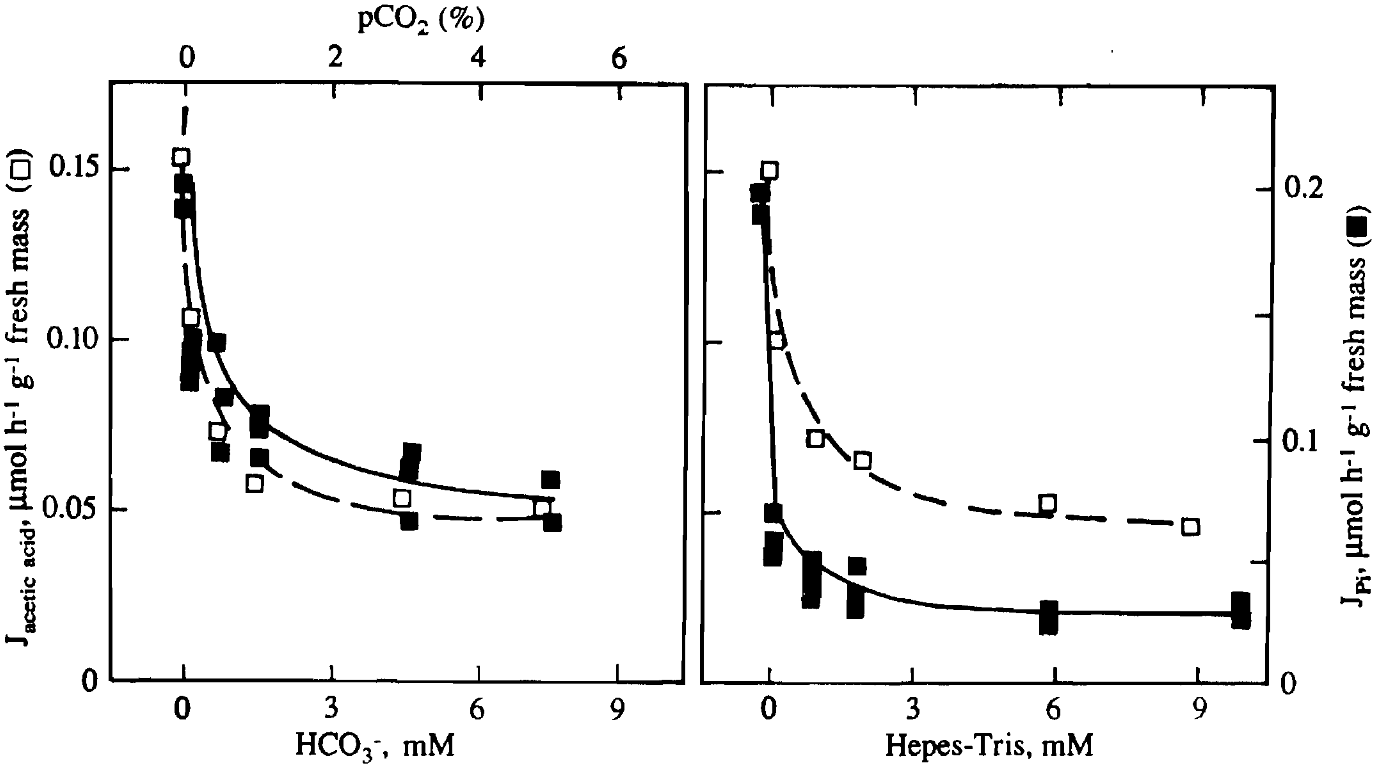

**Figure 4.** Effects of buffers on the surface pH and on $^{32}P_i$ influx in excised corn roots. The influx of ($^{14}$C) acetic acid was shown to be proportional to the concentration of the protonated form. Since the concentration of total acetic acid (50 µM) and the pH (7, maintained with an automatic pH-stat system) were constant, the variations of the acetic acid influx indicate variations of the surface pH. Left: the media were buffered with $HCO_3^-$, using various $CO_2$ partial pressures ($pCO_2$). Right: the medium was bubbled with $CO_2$-free air. Adapted from Toulon et al. (1989).

**Table 1.** Growth and phosphate ($P_i$) uptake over 10 days by *Trifolium repens*. Plants grown in flowing cultures differing in [$P_i$]. (Results from Tables 1 and 2 in Breeze and Hopper 1987).

| Nitrogen source | [$P_i$](µM) | Growth[1] (g culture$^{-1}$)[1] | $P_i$ absorbed (mg culture$^{-1}$) |
|---|---|---|---|
| Nitrate | | | |
| | 0.32 | 10.25 | 40 |
| | 0.64 | 9.57 | 40 |
| | 1.60 | 9.93 | 45 |
| | 8.00 | 9.66 | 45 |
| $N_2$-fixation | | | |
| | 0.32 | 6.98 | 24 |
| | 0.64 | 6.37 | 21 |
| | 1.60 | 5.97 | 27 |
| | 8.00 | 5.89 | 31 |

[1] In the period 14-24 days after treatments were imposed.

of the plants were grown in 0.32 µM $P_i$ for 1 week; the concentrations were then changed. During the first 6 days, the plants in the higher [$P_i$] did take up greater amounts of $P_i$, but by day 15, all of the plants were absorbing at the same rate (Fig. 5). The transport capacity of plants coming into the experiment from the dilute solution was large, but gradually decayed over a 6- to 15-day period when they were kept in more concentrated solution.

Ericsson and Ingestad (1988) approached this subject from a different direction. They supplied $P_i$ to birch (*Betula pendula* Roth.) at a series of rates (a quantity per day rather than a concentration) that were calculated to be either sufficient to sustain the maximum relative growth rate (RGR) or various lower rates. There was a linear correlation between the relative addition rate (RAR) of $P_i$ and the RGR in the range of RGR 0.05-0.24 day$^{-1}$. There was also a linear correlation between the RGR and the percent P in

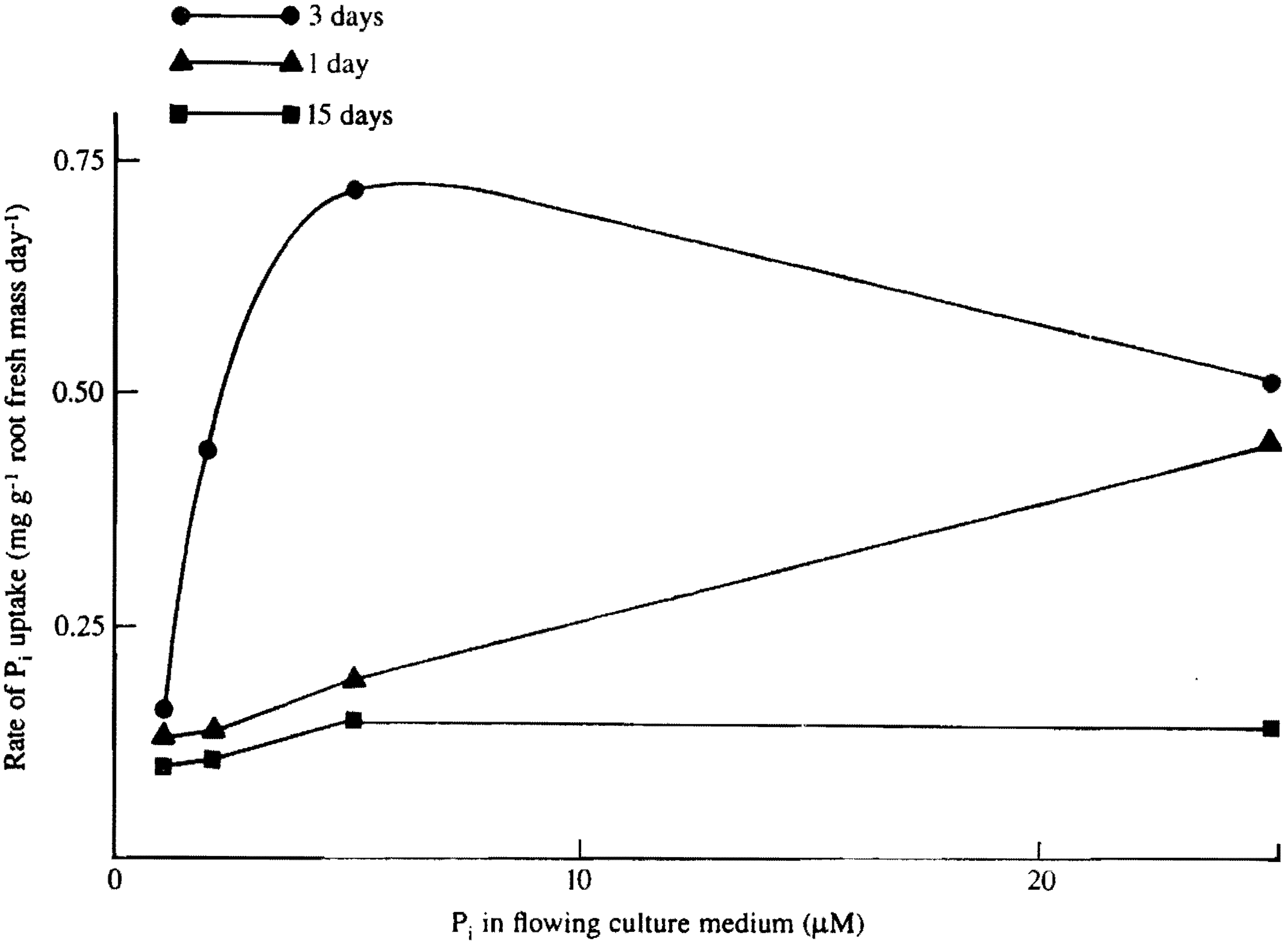

**Figure 5. Changes in the response of the $P_i$ absorption system with time when *Trifolium repens* plants are transferred from a low concentration of $P_i$ to various higher ones (results from Fig. 2 in Breeze and Hopper 1987).**

the fresh tissue of the seedlings. Despite this restriction of growth and the lower tissue-P status, there were no signs of P-deficiency symptoms in the birch seedlings once they had become acclimatized. Saxena (1984) and Chauhan et al. (In press.) noted a similar absence of symptoms of P deficiency in chickpea *(Cicer arietinum)* and pigeonpea (*Cajanus cajan*), respectively, even in situations where growth and development were probably limited by P supply.

From these two examples we might propose that:

1. If $[P_i]_{\text{external}}$ is low, but the supply is infinite, plants will adjust their absorption capacity in an attempt to keep $[P]_{\text{internal}}$ constant.
2. If the P supply is finite and is gradually used up, growth rate will decrease to keep $[P]_{\text{internal}}$ within working limits.

## Transport Capacity and Demand for Phosphorus

We can see how transport capacity can expand when demand increases if we artificially deprive plants of external $P_i$ for some time and then challenge the plants with radioactively labeled $P_i$ ($^{32}P$) to measure influx (Table 2). After 5 days' P deprivation, young plants of the tropical forage legume, siratro (*Macroptilium atropurpureum*), absorbed $P_i$ at three times the rate of the controls (Clarkson et al. 1983). When the P supply was restored to the culture solution, the elevated absorption rate of $P_i$ decayed rather slowly over a period of 4-6 days. For much of this period the rate of P intake exceeded the growth rate, leading to a considerable accumulation of $P_i$ in the leaves (Fig. 6). In some legumes, but not in siratro, such accumulations can lead to the necrosis of leaves (Warren and

**Table 2. Augmentation of $P_i$ influx by P starvation in *Macroptilium atropurpureum* cv Siratro (Data from Table 6 in Clarkson et al. 1983).**

| Time (days) | Phosphate influx (nmol $g^{-1}$ root fresh mass $h^{-1}$)[1] | | Ratio of -P:control |
|---|---|---|---|
| | Control, +P | -P | |
| 0 | 924 (±77) | - | - |
| 2 | 939 (±59) | 2327 (±79) | 2.48 |
| 5 | 572 (±37) | 1806 (±98) | 3.15 |
| | $P_i$ resupplied at the beginning of Day 6 | | |
| 6.3 | 513 (±58) | 1763 (±209) | 3.44 |

1. Results shown with standard errors of mean of 5 replicates.

Benzian 1959; Howell and Bernard 1961; Asher and Loneragan 1967).

How can we explain these changes? It has become clear that there are both short- and longer-term factors that regulate the uptake of $P_i$ (Katz et al. 1986).

## Short-term Changes

In barley (*Hordeum vulgare*) (Lefebvre and Glass 1982) and tomato (*Lycopersicon esculentum*), within a time frame of minutes, the activity of the $P_i$ transporter appears to vary with the $[P_i]$ in the root. An hypothetical explanation of this response is that there are some sites on the cytoplasmic side of the transporter

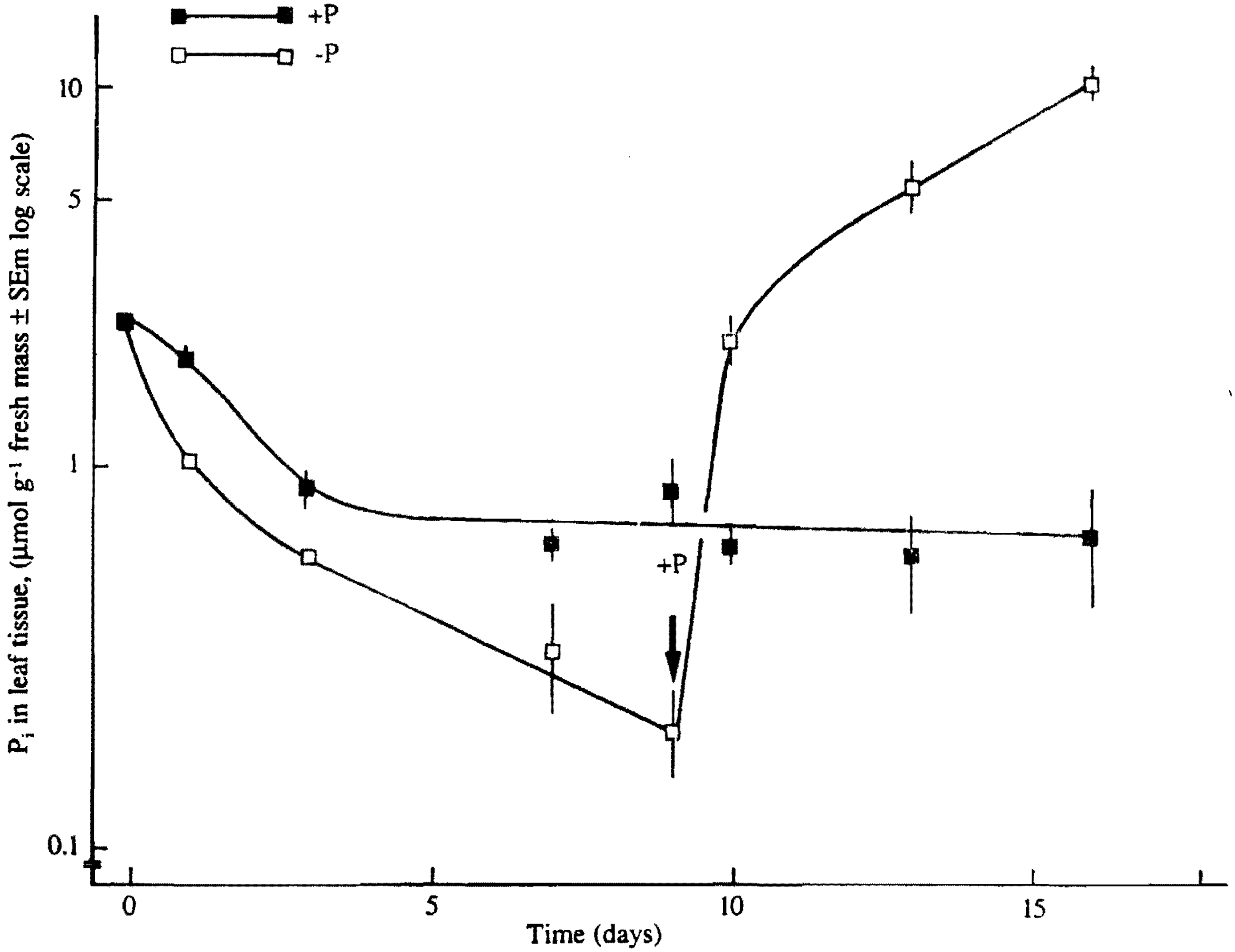

**Figure 6. Effect of deprivation (days 0-9) and resupply (days 9-16) on the concentration of $P_i$ in the fourth trifoliate leaf of siratro (*Macroptilium atropurpureum*). Note that, by day 16, the $[P_i]$ is 20 times higher in the formerly starved plants than in the +P controls. (D.T. Clarkson and P.C. Kerridge, CSIRO Cunningham Laboratory, unpublished results).**

that bind $P_i$ with rather low affinity. It is envisaged that the protein is allosterically regulated. As the cytoplasmic $[P_i]$ rises, these sites become occupied with a consequent reorientation of the protein, which restricts access of the external $P_i$ to binding sites on the outer face of the membrane (see Glass 1983). Transport across the membrane depends on this initial binding.

## Longer-term Changes

The changes in transport activity we considered first (Table 1, Fig. 5) are on a time scale of days rather than minutes. There appear to be two different strategies involved. Where plants are not limited in their growth by the external P supply—i.e., where the transporter is in a fully repressed state—the efflux of $P_i$ rises as the external concentration increases (Cogliatti and Santa Maria 1990). With wheat (*Triticum aestivum*) plants, growing at similar rates in 0.05 and 5 mol $m^{-3}$ $P_i$, the efflux:influx ratio increased from 0.27 to 0.88. Thus the properties of the PM changed in such a way as to prevent potentially harmful accumulations of P within the plant.

When P supply limits plant growth, it is probable that the number of transporters in the membrane increases. If this requires *de novo* transporter synthesis, we must assume that some signal in the cell increases the rate of transcription of the genes or the translation of mRNAs for the transport protein. The nature of this signal is obscure, but it must be highly specific, because only the activity of the $P_i$ transporter varies with P demand (Lee 1982).

## The Search for the Regulator/Signal

The allosteric hypothesis for short-term regulation relies on there being variations in the $[P_i]$ in the cytoplasm close to the transporter. While the chemical analyses of Lefebvre and Glass (1982) appear to support such an explanation, general analysis of root tissue confounds $P_i$ in vacuole and cytoplasm, the former being very much the greater quantity. These compartments can be assessed separately in the living state by nuclear magnetic resonance (NMR) spectroscopy, but the results published to date show that in both young (Lee and Ratcliffe 1983) and mature (Lee et al. 1990) parts of roots, it is the $[P_i]$ in the vacuole which varies with P status, while that in the cytoplasm is strongly buffered. If this is really so, then it is hard to envisage any other phosphorylated compound as the signal, since such compounds will be in a steady state with respect to the resting level of cytoplasmic $P_i$. The only way out of this impasse requires further assumptions about the failure of the NMR technique to measure the physiologically relevant pool of $P_i$ in the cytoplasm. For instance, the technique cannot normally distinguish the separate compartments for $P_i$ within the mitochondria and plastids from those in the ground cytoplasm. With present evidence, it is impossible to say whether or not the allosteric regulation of existing transporters and the synthesis of new ones is responsive to the cytoplasmic $[P_i]$.

## Coordination of Phosphate Absorption within the Root System

One of the most important differences between soil and solution culture relates to the spatial distribution of nutrients. The distribution in the soil may be heterogeneous while that in solution is uniform. The plant may respond to the heterogeneity on several levels. It is well established that roots will proliferate near sites or horizons enriched with N or P, especially if the soil is generally of low nutrient status. This type of response was studied in the laboratory by Drew and Saker (1978), who showed root branching was stimulated in a zone well supplied with phosphate when the remainder of the root system experienced a suboptimal supply of $P_i$.

Even before there has been any morphological response, however, parts of the root system receiving a good P supply can display "compensatory absorption." This phenomenon can be demonstrated in simple experiments, where the root system is divided into portions receiving or lacking a P supply. With plants of potato (*Solanum tuberosum*), $P_i$ was supplied to a single adventitious root axis on rooted shoot cuttings, while the rest of the root system received none (Cogliatti and Clarkson 1983). Uptake of $P_i$ by the single axis was not sufficient to compensate completely for the lack of phosphate elsewhere, but the plants continued to grow. In Table 3, the $[P_i]$ in the shoot was 35% lower in the +P/-P treatment than that in the control plant (+P/+P). In the single root itself, however, the $[P_i]$ was not significantly different from the control and was more than three times higher than that in a plant where the whole of the root system had been deprived of $P_i$. When $^{32}P$-labeled $P_i$ was supplied to these single axes, they absorbed $P_i$ three times as rapidly as the control (+P/+P) and almost as rapidly as the P-starved treatment (-P/-P). The performance of the root was negatively correlated with the

**Table 3. Phosphate absorption by potato plants with roots divided between solutions containing or lacking $P_i$ for 1 week (Data from Table 4 in Cogliatti and Clarkson 1983).**

| Root treatment | | [Phosphorus] | | Uptake rate by single root[1] ($\mu$mol $g^{-1}$ dry mass $day^{-1}$) ($\pm$SEM) | Translocation to shoot | |
|---|---|---|---|---|---|---|
| Single root | Bulk | Single root ($\mu$mol $g^{-1}$) | Shoot | | (%) | ($\mu$mol $g^{-1}$ dry mass $day^{-1}$) |
| +P | +P | 358 | 258 | 320 (± 60) | 57 | 170 |
| +P | -P | 332 | 184 | 900 (± 60) | 70 | 630 |
| -P | +P | 181 | 232 | 540 (± 20) | 44 | 238 |
| -P | -P | 87 | 68 | 1100 (± 60) | 49 | 539 |

1. Measured over 24 h from a solution containing 1 mol $m^{-3}$ $P_i$.

$[P_i]$ in the shoot. A further indication of the controlling influence of the shoot lies in the much higher translocation from the +P/-P roots. Very similar results were found with barley (Drew and Saker 1984).

The coordination of shoot-$P_i$ status with root uptake seems very "sensible," the plant compensating, as far as possible, for localized shortfalls in the external P supply. In soil, it is easy to imagine that $P_i$ absorption may be rather variable over the whole root surface. But plants are not "sensible": they respond only to signals that come from the perturbation of regulating steady states. What, then, is being perturbed in the +P/-P axes in Table 3? Gross analysis of P makes it seem unlikely that the $P_i$ status of the cytoplasm can be very different from that of the controls. It may be, however, that small changes in the concentration in a regulatory pool can be amplified biochemically and have a large effect. The great sensitivity of the PM $H^+$-ATPase to changes in cytoplasmic pH is an example of this. The +P/-P roots also translocate an unusually large proportion of their current $P_i$ intake; the amount of $P_i$ moving across the root and entering the xylem is, therefore, very much greater in plants in this treatment. The radial flow is thus stimulated, implying, perhaps, that the processes that unload the root symplast have also received some message about the parlous state of P nutrition elsewhere in the plant. Perhaps the uptake mechanism responds as a result of this enhanced efflux from the symplast into the xylem vessels.

It is easier to say what the message is not than to be certain what it is. It is not some general metabolic stimulation caused, for example, by increased carbohydrate (CHO) supply in nutrient-stressed roots. Although such changes in CHO are commonly seen (e.g., Chapin et al. 1988b), they would affect the energy supply to all of the transporters, but we see that the effects on $P_i$ uptake are specific for P stress. It is probably not a hormonal message, since, at the present, such effects as abscisic acid and cytokinins have on ion transport are rather general in character (e.g., Chapin et al. 1988a; Parsons et al. 1989). It is possible that the return flow of ions or of some product of their assimilation in the phloem may inform the roots about the nutrient status of the shoot (Cooper and Clarkson 1989; Clarkson and Saker 1990) but further work is needed to clarify this matter.

## The Relative Importance of Aspects of Phosphate Transport

In both the short and longer term, there are marked changes in the capacity ($V_{max}$) of the transport system for $P_i$ and sometimes there can be changes in the affinity of the system ($K_m$) as well. It follows that little useful information can be gained by measuring kinetic parameters in a single set of conditions. To gain insight into the potentialities of the system, it is necessary to describe a response surface for which the coordinates might be $[P_i]_{external}$, influx, and time over which the plant is exposed to a given concentration. From what has been discussed earlier, one would expect much of this surface to be flat (a plateau), the kinetic parameters being adjusted continuously to meet the requirement created by growth. In a study where both the elements of time and changing root morphology were taken into account, it was evident that the $V_{max}$ of $P_i$ transport per unit root surface decreased in the period 26-41 days after sowing in all 4 species examined, the decrease being in the order pigeonpea > chickpea > soybean >>maize (Itoh 1987). The relative size of the root system (total plant mass:root-surface area) increased in this period; the relative responses were in a similar sequence, chickpea > pigeonpea > soybean >> maize. Thus the capacity of the system in these plants was governed largely by the relative size of the root surface.

The increase in the capacity for $P_i$ transport when demand is high results in rates of uptake that greatly exceed any probable growth rate of the plant. Because this high rate of uptake is sustained for some time after the P status of P-deprived plants has returned to normal levels, the plant can quickly find itself faced with toxic quantities of $P_i$ in its tissues (e.g., Cogliatti and Clarkson 1983; Clarkson et al. 1983). By experiment, we find that an influx of about 0.5 $\mu$mol $P_i$ $g^{-1}$ root fresh mass $hour^{-1}$ will keep the [P] constant in barley plants growing at a rate of 0.2 $day^{-1}$. This rate can be expanded to about 2.5 $\mu$mol $P_i$ $g^{-1}$ root $hour^{-1}$ when demand is high in P-deprived plants; thus while growing normally, barley uses only 20% of its transport capacity. Selection or manipulation of plants to achieve higher maximum rates of phosphate uptake is likely to result only in a larger proportion of that capacity being unused.

Similar considerations apply to other nutrients. Sulfate-uptake capacity is repressed by about 90% when siratro (Clarkson et al. 1983) or barley (Clarkson and Saker 1989) are grown without S limitation. Nitrate-uptake capacity is expressed to only about 25% of maximum in barley where the N supply is adequate (Lee and Drew 1986). We conclude that if plant growth was being restricted by the internal supply of $P_i$, there is plenty of scope for increased absorption, if the nutrient is available to the root surface.

Other papers in this volume will discuss the factors which are of practical importance in P nutrition. By "practical" one usually means some aspect of the system that can be manipulated to advantage. Even when plants were grown with what appears to have been an abundant P supply in the soil, the factors that had the greatest influence on the uptake of P by maize were those related to the size and geometry of the root system (Silberbush and Barber 1983). In this respect, the role of vesicular-arbuscular mycorrhizae can be very important, especially in P-deficient soils. The modification of rhizosphere pH, by legumes in particular, seems to play a very important role in solubilizing otherwise unavailable P. The "proteoid" roots of lupin (*Lupinus albus*) have been shown to dissolve $CaHPO_4$ granules suspended in the agar across which roots were growing (Gardner et al. 1981). Chickpea roots, even when nonnodulated and given $NO_3^-$, changed the pH of rhizosphere soil from pH 6.0 to 4.5 (Marschner and Römheld 1983). The fixation of $N_2$ by nodules leads to additional acidification of the rhizosphere. The chickpea crop does not usually respond to P fertilization, even on soils of low P status, if soil moisture levels remain adequate (Saxena 1984), but there are marked differences in the susceptibility of varieties to Fe-deficiency chlorosis in calcareous soils (Saxena 1984; Saxena and Sheldrake 1980). Since "efficient" Fe nutrition usually involves rhizosphere acidification, there may be some differences in P nutrition as well. Pigeonpea is also relatively efficient at absorbing P from soils of low P status in comparison with cereal crop plants (Sheldrake 1984). Again, the striking difference with nonlegumes probably lies in the rhizosphere acidification rather than the root morphology or intrinsic differences in the nature of $P_i$ transport. The quantitative significance of acidification emerged from a study by Grinsted et al. (1982), who, working with rapeseed (*Brassica napus*), showed that P desorption in the rhizosphere increased 10-fold during a decrease in pH from 6.5 to 4.2. In this species, P deficiency actually promotes rhizosphere acidification.

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# Modeling Phosphorus Uptake and Utilization by Plants

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## *Abstract*

*The uptake processes of phosphorus (P) from soil are complicated by the fact that it is a highly immobile element, and transport through soil to the root surface is often a rate-limiting step. The difficulties are enhanced by the dependence of the diffusion coefficient upon the soil type, P concentration, and soil moisture content. A model for P uptake from soil is therefore basically a diffusion model for an irregularly distributed sink in a medium of variable diffusion coefficients. The dynamic nature of the process, in that the root system is constantly growing and developing, also has to be taken into account. Finally, there are modifications of the root that have a strong bearing on its ability to take up P from the soil. These include uptake by root hairs, local pH changes in the rhizosphere, effect of root exudates, and vesicular-arbuscular mycorrhizal (VAM) associations.*

*The approach towards a model of P uptake must therefore be gradual, with steadily increasing levels of sophistication and complications being introduced. The earliest models were for artificial arrangements using planar geometry. Other models dealt essentially with single roots, in that they ignored any interaction between roots. More complex models that included the growth of the whole plant were later developed. This work showed that in many soil conditions, particularly when the plant was P-deficient, the restriction on uptake lay almost entirely upon P supply and transport in the soil, and not with the root uptake properties. The success of some simple models is surprising, when the real complications in the rhizosphere processes are considered.*

## Introduction

Over the past three decades, nutrient-uptake studies, in particular those of phosphorus (P) uptake, have addressed the real processes taking place, drawing attention to the fact that transport of elements through the soil is important, and can be a rate-limiting step in the uptake process. This approach has led to extensive work on diffusion and mass flow through the soil, as outlined in the book by Nye and Tinker (1977). At the same time, there has been a change towards regarding the plant or the crop as a dynamic system, in which conditions change as growth progresses. Accordingly, the modeling of P uptake has to deal simultaneously with: first, complex and changing soil conditions; second, a growing and extending root system; and finally, a changing plant demand. Each of these has its complications, and it is perhaps not surprising that total success has yet to be achieved.

In this paper, we shall cover some aspects of P chemistry in the soil with regard to its transport to the root, move on to P absorption by the root, then present an overview of the P-uptake models, and finally, discuss some of the other effects that are also important in P uptake but have not been incorporated into the existing models.

## Soil Phosphorus Equilibria and Transport

There have been some excellent reviews published on this subject by Khasawneh et al. (1980), White

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(1980), Barber (1984), and Wild (1988). Also, several papers in this volume describe aspects of P chemistry in the soil. Despite this, the dynamics of P, particularly with regard to plant growth, are still not fully understood. The reason for this is the complexity of soil-P chemistry and the fact that it can be altered by plant roots. Many soil types contain substantial quantities of both organic and inorganic P, but only a small fraction of it is present in the soil solution as phosphate ions and available to plant roots at any one time. Although the soil contains considerable quantities of organic P, this cannot be utilized by plants until it has been mineralized by enzymatic hydrolysis. This process is generally too slow to make any immediate contribution to the P nutrition of plants. Inorganic phosphate ions are present in the soil solution at concentrations of the order of $10^{-6}$ M, and even in well-fertilized agricultural soils, concentrations rarely exceed $10^{-5}$ M. Greater concentrations can be found, but only immediately after fertilization on light sandy soils. The reason for the low P concentrations in the soil solution is that phosphate ions are strongly adsorbed on to soil mineral surfaces, and they form sparingly soluble compounds with calcium (Ca), iron (Fe), and aluminum (Al).

Phosphate is strongly adsorbed on many soil constituents, such as the clays (Sanchez and Uehara 1980). The relationship between adsorbed P and that in solution (i.e., the adsorption isotherm) is usually curvilinear, indicating that the slope or buffer power varies with the concentration. It is further complicated by the fact that the desorption isotherm of the same soil could be very different from the adsorption isotherm. This causes difficulty in interpreting and predicting effects of changes in any soil property. However, for the purpose of modeling P uptake, it is best to assume that there is a single desorption isotherm that is constant in a uniform soil, unless one is to model different parts of the soil separately. Such an assumption is an oversimplification, but at present it is difficult to overcome this.

Transport of nutrients in soil is generally accepted to be by mass flow and diffusion. Other hypotheses, such as interception of nutrients by growing roots (Barber 1962), are untenable. Mass flow is defined as "the movement of ions to the root by the convective flow of water to the root surface." It is dependent upon the transpiration rate and the concentration of the element in solution. As the concentration of P in soil solution is very low, especially in the less fertile soils commonly found in semi-arid environments, the significance of P contributed by mass flow is negligible. Therefore, a great deal of attention has been given to describing and modeling diffusion, and in fact, the majority of P-uptake models are diffusion models with slight modifications. Diffusion is defined as "the movement of ions by random, kinetic motion of molecules." It results in a net movement of ionic compounds from a location of high concentration to one of low concentration. Basically, all diffusion is assumed to occur in the solution phase, and the diffusion coefficient (D) is defined by Fick's First Law [Flux = –D (dC/dx)]. In a complex medium such as soil, D can be expressed as (Nye and Tinker 1977):

$$D = D_l \, \theta \, f_l \, (dC_l/dC) \qquad (1)$$

where $D_l$ is the diffusion coefficient of P in water; $\theta$ is the volumetric soil water content, i.e., fraction of soil volume occupied by water, which determines the cross-sectional area through which P can diffuse; $f_l$ is the impedance factor, which accounts for the tortuosity in the diffusive pathway; $dC_l/dC$ is the inverse of the slope of the desorption isotherm (the slope of the desorption isotherm, i.e., $dC/dC_l$ being the buffer power (b)); $C_l$ is the concentration of P in soil solution, and C is the total concentration of diffusible P in the soil (diffusible within the time-scale under consideration). To avoid complications, an averaged diffusion coefficient is used in most cases. The buffer power may range from 10 to 1000 for P, $D_l$, is about $10^{-5}$ cm$^2$ s$^{-1}$, and in a moist sandy soil, $\theta f_l$ is approximately $10^{-1}$. Consequently, the diffusion coefficient for P is likely to be in the range $10^{-7}$ to $10^{-9}$ cm$^2$ s$^{-1}$. Given the latter value, the root-mean-square displacement of the phosphate ion is about 0.1 mm day$^{-1}$, compared with 10 mm day$^{-1}$ for a highly mobile ion such as nitrate.

## Phosphorus Absorption by the Root

A continuing problem in modeling root activity concerns the "active fraction" of a root system, for it used to be thought that uptake was confined to the root tips. Hence the assumption with regard to modeling uptake of any nutrient is that the uptake process is equal over all parts of the root system. The data of Clarkson (1981) would indicate that at least in some plants, P can be taken up over a considerable length of root behind the root tip. In young plants, where the root increases in length exponentially with time, giving roughly a constant ratio of young to old roots, the average root age may not vary greatly, and therefore, under these conditions, it is probably safe to regard all roots as equivalent. However, it is still far from clear whether absorption properties differ with the type of root of varying anatomy, e.g., seminal or nodal axis, first- or second-order laterals, etc. Presumably, in the absence of any evidence to the contrary, they will continue to be considered equivalent, the only difference being in their diameters. Also, in some situations, adverse physicochemical conditions may render parts of a root system ineffective.

The strength of the root system as a sink can be defined in terms of the relationship between the concentration of P at the root and the rate at which uptake occurs. Numerous studies in solution culture have established this relationship and have identified critical concentrations for maximum growth (e.g., Asher and Loneragan 1967). At very low concentrations, the absorption rate per unit area, i.e., the flux into roots (F), is linearly related to concentration at the root surface; i.e., the concentration in the external medium in a well-stirred solution culture. The proportionality constant has been termed the root absorption coefficient ($\alpha = F/C_l$) by Nye and Tinker (1977). These authors coined a further term, the root demand coefficient ($\alpha r_0$), where $r_0$ is the root radius. At concentrations commonly found in arable soils, the relationship between flux and concentration becomes asymptotic, and P uptake by plant roots is best described by a Michaelis-Menten (M-M) type relationship,

$$F = (F_{max} / K_m + C_l)\, C_l \qquad (2)$$

where $F_{max}$ is the maximum flux achieved, and $K_m$ is the concentration at which half $F_{max}$ is achieved. $C_l$, as before, is the P concentration in soil solution. A modified version of this relationship (Claassen and Barber 1976) incorporates a term, "E," the rate of efflux from the root. A later version (Nielsen and Barber 1978) includes the term "$C_{min}$", which they defined as the concentration in solution below which net uptake ceases.

Relationships of this type are a central feature of many supply-uptake models, in which they act as a link between supply and demand. However, there is an emerging awareness that the M-M constants, i.e., $F_{max}$ and $K_m$, depend upon many plant demand factors. They have been shown to vary with the growing conditions of light and temperature (Barber 1984), with plant age (Jungk and Barber 1975), root-to-shoot ratio (Barber 1985), and nutrient status of the plant (Claassen and Barber 1977). Again, averaged values can be used to accommodate this variation. The most recent version of the M-M relationship for potassium put forward by Glass and Siddiqui (1984) incorporates the internal concentration in the plant as well as a relationship between $F_{max}$ and $K_m$ and concentration in the root. Their model is complicated, but it is a welcome attempt to incorporate a feedback mechanism from the plant as a regulator of flux into roots.

Another disadvantage of using the M-M relationship is that the flux parameters depend markedly upon the method of measurement. For example, very different values of $F_{max}$ and $K_m$ have been obtained by the depletion and rapid-flow techniques (Wild et al. 1979; Mullins and Edwards 1989). It is only in the latter case that the essential conditions are met: first, that the concentration at the root surface is constant and a known value, and second, that the plant grows in equilibrium with this value. It is interesting to note that maximum growth can be sustained by submicromolar concentrations (Loneragan and Asher 1967), provided the solution is replenished at a sufficiently rapid rate, indicating the importance of nutrient-supply rate as opposed to concentration in solution per se.

## Nutrient Supply-Uptake Models

### Development of Models

There have been several excellent review articles and books on modeling nutrient uptake from soil over the last 20 years, notably by Olsen and Kemper (1968), Barley (1970), Nye and Tinker (1977), Barber (1984), Willingen and van Noordwijk (1987), and more recently by Rendig and Taylor (1989) and Jungk and Claassen (1989). Bray (1954) first recognized the importance of nutrient mobility in soil as an integral part of the uptake process. Barber (1962) subsequently made calculations comparing the importance of mass flow, diffusion, and root interception for bringing nutrients to the roots. These initial papers were to provide the basis for the mathematical treatments of nutrient transport to roots that were to follow.

The simplest system to model is the radial diffusion of ions to a cylindrical sink, that is the root, in an infinite medium. The change in concentration around the root with time is given by

$$dC/dt = (1/r)\,(d/dr)\,(r\,D\,(dC/dr)) \qquad (3)$$

where r is the radial distance from the axis of the cylinder. Under steady-state conditions where D, the diffusion coefficient, is constant (Crank 1975), the flux into a unit of root length (the "inflow", I) is given by

$$I = 2\pi D \, \Delta C / \ln (r/r_o) \qquad (4)$$

where $r_o$ is the root radius. In terms of solution concentrations, for which the diffusion coefficient in equation 4 can be substituted by equation 1 to give

$$I = 2\pi D_l \, \theta \, f_l \, \Delta C_l / \ln (r/r_o) \qquad (5),$$

Baldwin et al. (1973) performed the steady-state calculation for a finite medium. In their calculations, a finite boundary condition was introduced to allow for uptake by competing roots in a root system. This was achieved by allowing each root to exploit a concentric cylinder of soil, so that for a regular, parallel array of roots, the mean half-distance between roots (x) is equal to $1/\sqrt{\pi L_v}$, where $L_v$ is the rooting density (cm root $cm^{-3}$ soil). No nutrients are allowed to cross the boundary at x, so that $dC/dr = 0$ at $r = x$ and $t > 0$. Generally roots can be considered as noncompeting if $x > \sqrt{Dt}$ (Nye and Tinker 1977). A further refinement was the expression of the concentration gradient between the root surface and the soil in terms of an average value for the whole soil medium. This is an extremely practical approach, as this concentration can be measured by extracting the soil solution. When $x >> r_o$, equation 5 reduces to

$$I = 2\pi D_l \, \theta \, f_l \, \Delta C_l / \ln (x/1.65 \, r_o) \qquad (6)$$

Equation 6 is very useful for calculating potential nutrient-supply rates by diffusion and has been used by Burns (1980) and applied to crops by Barraclough (1986, 1987, 1989a, 1989b). As an example of its use pertinent to the present objectives, potential diffusive supply rates for P under a range of soil types and conditions are given in Table 1. "Wet," "moist," and "dry" soils correspond to θ (the volumetric moisture content) values of 0.4, 0.3, and 0.2, respectively, and for "light," "medium," and "heavy" soils, $f_l$ (the impedance factor) was assumed to be equal to θ, 3θ/4, and θ/2, respectively (Nye 1979). The root radius was assumed to be 0.015 cm (a typical value for soybean) and the soil temperature 25°C.

Barber (1978) reported a maximum P-uptake rate for soybean of 0.62 kg $ha^{-1}$ $day^{-1}$. With a rooting density of 1 cm $cm^{-3}$ on a medium, moist soil, a concentration difference of 97 μM P in soil solution would be required to sustain this uptake by diffusive supply. The measured P uptake of the topsoil was in fact 74 μM, so that uptake from the subsoil was necessary to account for the observed crop uptake. In theory, it would be possible to make an approximate prediction of uptake with time by applying the steady-state equation in successive time steps (Nye and Tinker 1977). More realistically, the transport equation can be solved analytically for the transient situation (non-steady-state) when a linear boundary condition at the root surface applies (e.g., $F = \alpha C_l$) and D is constant.

**Table 1. Potential diffusive supply rates of phosphorus (kg $ha^{-1}$ $day^{-1}$ μM $P^{-1}$ in solution) to plant roots under various soil conditions.**[1]

| Soil type | $L_v$ (cm $cm^{-3}$) | Wet $\theta = 0.4$ | Moist $\theta = 0.3$ | Dry $\theta = 0.2$ |
|---|---|---|---|---|
| Light | 1 | 0.0153 | 0.0086 | 0.0039 |
| $f_l = \theta$ | 3 | 0.0555 | 0.0312 | 0.0139 |
|  | 5 | 0.1036 | 0.0582 | 0.0259 |
| Medium | 1 | 0.0115 | 0.0064 | 0.0030 |
| $f_l = 3\theta/4$ | 3 | 0.0417 | 0.0234 | 0.0105 |
|  | 5 | 0.0776 | 0.0437 | 0.0195 |
| Heavy | 1 | 0.0077 | 0.0044 | 0.0019 |
| $f_l = \theta/2$ | 3 | 0.0278 | 0.0156 | 0.0070 |
|  | 5 | 0.0519 | 0.0292 | 0.0130 |

1. $r_o$ = 0.015 cm, T = 25°C; θ = volumetric soil water content; $f_l$ = impedance factor; $L_l$ = rooting density.

In Table 2, we summarize nutrient supply-uptake models over the last 30 years. Bouldin (1961) and subsequently Olsen et al. (1962) and Passioura (1963) used an analytical solution for transient-state diffusion through an infinite medium. Olsen et al. (1962) included the soil buffer power and also tested constant flux and constant concentration (at the root) boundary conditions. These solutions were applied to plant uptake situations by Olsen and Watanabe (1970), and also by Brewster and Tinker (1970). Generally, analytical solutions of transport equations are only possible for simple, planar geometry (see Nye 1966a), or for cylindrical geometry with simple boundary conditions, such as a constant root absorbing power (Bouldin 1961) or a constant flux into roots (Olsen et al. 1962).

Transport equations for more complicated geometries and conditions can be solved rapidly by numerical analysis on computers (Passioura and Frère 1967; Nye and Marriott 1969). Essentially, these early "numerical" models were used to investigate the principles of nutrient transport to roots, the interplay of

**Table 2. Thirty years of nutrient supply-uptake models.**

| Year | Authors | Model |
|---|---|---|
| 1961 | Bouldin | Diffusion, transient-state, single nongrowing root, $\alpha$ constant, infinite medium, analytical solution |
| 1962 | Olsen et al. | As Bouldin + soil buffer |
| 1963 | Passioura | As Bouldin + single growing root |
| 1966a | Nye | Diffusion, transient-state, planar geometry, analytical solution |
| 1966b | Nye | As Olsen + equivalent cylinder model for root hairs |
| 1967 | Lewis and Quirk | Diffusion, transient-state, exponential decrease in $C_l$ at root surface with time, infinite medium, numerical solution |
| 1967 | Passioura and Frère | Mass flow and diffusion, transient-state, infinite medium, numerical solution |
| 1969 | Nye and Marriott | Mass flow and diffusion, transient-state, single root, M-M, infinite medium, numerical solution |
| 1970 | Barley | Mass flow and diffusion, transient-state, root competition, $\alpha$ constant, irregular parallel roots, numerical solution |
| 1971 | Sanders et al. | Electrical analogue |
| 1973 | Baldwin et al. | Mass flow and diffusion, steady-state, root competition |
| 1975 | Nye et al. | Whole-plant model, diffusive supply according to Baldwin et al. |
| 1976 | Claassen and Barber | As Nye and Marriott + uptake by complete root system, E |
| 1976 | Bhat et al. | As Nye and Marriott + sink term for root hairs calculated according to Baldwin et al. |
| 1978 | Nielsen and Barber | As Claassen and Barber + $C_{min}$ |
| 1979 | Noordwijk and van Willigen | Diffusion, constant P-uptake rate |
| 1981 | Barber and Cushman | As Claassen and Barber + root competition |
| 1983b | Itoh and Barber | As Barber and Cushman + root hairs according to Bhat et al. |
| 1986 | Claassen et al. | As Nye and Marriott + root competition |
| 1987 | Willigen and van Noordwijk | Diffusion, incomplete root-soil contact |
| 1989 | Bouldin | Multi-ion uptake |

supply and demand, and to predict concentration profiles around absorbing roots. Claassen and Barber (1976) incorporated a subroutine for root growth into their model, although this was omitted from a subsequent version "in the interests of user flexibility" (Claassen et al. 1986). Barber and Cushman (1981) also included root growth (linear or exponential) and a boundary condition to accommodate root competition, essentially the zero transfer boundary used by Baldwin et al. (1973). By including root length, predicted fluxes per unit of root could be converted into whole-plant uptakes, thereby providing an opportunity to test such models against measured plant uptakes. This basic theme has been further modified or extended by other workers; van Noordwijk and Willigen (1979) used a constant rate of P uptake by a crop in conjunction with the transport equation 3 to predict for how long a particular rooting density in soils of given P fertility could sustain this uptake rate, and later went on to develop a model for effects of incomplete root-soil contact upon uptake (Willigen and van Noordwijk 1987).

One of the most elaborate versions of the supply-uptake model was put forward by Nye et al. (1975). These authors constructed a whole-plant P-nutrition model. The pivotal feature of this was the percent P concentration in the shoot. This determined the plant growth rate via the net assimilation rate, the ratio of leaf area to shoot mass, and the partitioning of dry matter between roots and shoots. Below ground, P was transported to the root by diffusion, and the percent P was allowed to modify the root absorbing power, the fineness of the root system, and the partitioning of P between root and shoot. Such an approach could be modified to include P uptake in models describing crop growth.

The contribution to P uptake by the root hairs was first incorporated into a model by Bhat et al. (1976), who modified the diffusion equation to include uptake by hairs in successive radial zones around the central root axis. Later, Itoh and Barber modeled the effect of root hairs on P uptake by six plant species of differing root-hair morphology. In the first instance (Itoh and Barber 1983a), they used the Barber-Cushman model, in which total uptake was calculated by adding that due to root hairs and that due to roots alone, and subtracting that arising from areas of overlapping supply. This gave good agreement between observed and predicted uptake values. From their data, they concluded that, to be effective under their experimental conditions, root hairs needed to exceed 0.3 mm in length. However an attempt to include root hairs into the basic transport equation proved to be less successful, with predicted uptake being overestimated by up to 100% (Itoh and Barber 1983b).

All of the modeling efforts to date have concentrated on the uptake of one nutrient at a time. Recently, Bouldin (1989) has developed a multi-ion uptake model. The novel feature of this model, other than its complexity, is that it provides for the maintenance of electroneutrality in the soil, soil solution, and plant during uptake, an essential requirement for this being the presence of $CO_2$. Soil reactions, transport, and uptake are treated in consecutive time steps. The model requires over 20 soil and plant parameters, and so far has not been validated experimentally. The value of such models is doubtful in practice, although they can be very illuminating in sensitivity analyses.

## Validation of Models

Models are readily validated under uniform conditions, but validations have met with varying degrees of success, depending upon how far these conditions have been stretched. A major problem is that many of the soil and plant parameters change with P concentration and time. While this presents no problems in the modeling, it is rarely practicable, or even possible, to measure these changes in order to provide an unequivocal validation of the model. As mentioned earlier, it has become accepted practice to use mean values for model parameters, yet clearly, these will not always prove adequate.

A further problem concerns the assumption that roots have a regular, parallel distribution. However, the difficulties of modeling a "realistic" root system are formidable. As yet, there is no analytical solution of the diffusion equation for a system consisting of two parallel roots, let alone irregular, nonparallel arrays, which may also have nodules. A regular distribution is favored in homogeneous soils, since the roots will branch and grow into unexploited zones, whereas in a non-uniform soil, roots will tend to proliferate in favorable zones. The problem of irregular but parallel arrays has been tackled by assigning polygons of irregular cross-section to each root and converting them to equivalent cylinders (Barley 1970; Willigen and van Noordwijk 1987) and by considering uptake as arising from a series of cylinders of different radii. Barley (1970) found very small differences in uptake between regular and irregular arrays by his method, although Baldwin et al. (1972) suggested that this may have been due to how roots were located within each polygon. These authors simulated competing root systems with an electrical analogue and showed that differences in uptake between regular and random distributions in uniform soil could be as much as 20%. A high degree of "clumping," caused by impenetrable soil clods for example, was likely to restrict nutrient uptake far more.

The existing models have confirmed that nutrients reach the roots by diffusion and mass flow and that earlier unlikely concepts of root interception (Barber 1962) and contact exchange (Jenny and Overstreet 1939) are unnecessary. However, the success in predicting P concentration profiles around single, isolated roots (Bhat and Nye 1974) has not been matched with similar success in predicting P uptake by whole plants. Brewster et al. tested the whole-plant model for P uptake developed by Nye et al. (1975) in pot-grown onions (1975) and rape (1976). Five levels of soil P were tested and the model was found to be successful at the intermediate P levels only. Predicted uptake was less than observed at the lowest P level, especially for rape, which was explained by the root-induced solubilization of P rather than by root hairs.

The discrepancy at the highest level of P was ascribed to undisturbed soil having a smaller buffer power than that obtained by shaking a soil with a large excess of solution (the method used). This could be due to new surfaces being generated by vigorous shaking, or equilibrium times being greater in undisturbed soil.

Barber and his colleagues have carried out many tests of their models. Schenk and Barber (1979a; 1979b) tested the Claassen-Barber model for 17- to 23-day-old maize grown in pots. They found good agreement between observed and predicted values when a single genotype was grown in six soils with initial $C_l$ values in the range of 20 to 120 µM P. In a second experiment, five genotypes were grown in a low-P (7 µM) and a high-P (48 µM) soil. Good agreement was obtained in the high-P soil, but predicted uptake was only 50% of the observed uptake in the low-P soil. In the field, predicted uptake was 67% of the observed for three varieties after 68 days, despite adjustments to the root uptake parameters to account for plant age (Schenk and Barber 1980). Similarly, for field-grown soybeans, Silberbush and Barber (1984) found good agreement between predicted and observed values when initial $C_l$ was 52 µM P, but very poor agreement when initial $C_l$ was 8 µM P.

Accepting that the present models still have many shortcomings, particularly when applied under variable conditions, they are very useful for conducting sensitivity analyses to see which soil and plant parameters have the greatest impact upon nutrient uptake under a given set of conditions. Barber (1984) presents the results of many such analyses in his book. Generally this type of analysis reveals that root length is the most important parameter, followed by soil supply, with root uptake kinetic parameters having very little effect. In a practical extension of this sensitivity work, the models have been used to predict strategies for the optimum placement of P fertilizers (Anghinoni and Barber 1980; Kovar and Barber 1986).

## Other Root Effects upon Phosphorus Uptake

Given reasonable simplifications and assumptions, progress in the modeling of P uptake has been considerable. However, one must bear in mind the importance of the root length in uptake and the fact that this is included as a measured parameter. Root growth provides a driving force for continuing P uptake to match growth rate of the plant. Approximate agreement of the measured and predicted uptake curves in simple simulation is therefore not too difficult to attain if parameters are finely tuned during validation.

In reality, a number of other factors affect P uptake, and few of these have been quantified. The first is root hairs. These extend away from the root surface and are capable of reducing the diffusion pathway near the root surface; i.e., they extend beyond the most intense part of the depletion zone around a root axis. The density, length, and uptake properties of the root hairs are difficult to measure (Ewens and Leigh 1985). In addition, their development can be altered by changing factors in the soil environment. Attempts to include root hairs in modeling of P uptake have not always been successful. More work is needed on the response of root-hair growth to changes in the envi-

It is well known that pH changes in the rhizosphere can vary up to 1 pH unit, mainly due to the imbalance between cations and anions absorbed or secreted by the root (Nye 1986; Römheld and Marschner 1986); release of $H^+$ in exchange for cations, and release of $OH^-$ or $HCO_3^-$ in exchange for anions. Phosphate stress has been shown to stimulate secretion of $H^+$ from roots (Moorby et al. 1988). This would increase the concentration of soil available P, resulting in an increased P uptake by the plant (Hedley et al. 1982). The distance over which the pH change spreads can be predicted reasonably accurately (Nye 1986), though the measurements of all the other changing parameters would prove troublesome. It is almost certain that shifts in pH will change the desorption isotherm of the soil (White 1980); in particular, a decrease in pH may solubilize otherwise unavailable P compounds. The change in P concentration with change in pH is difficult to predict, and results indicate that it could be dependent upon the presence of other elements, e.g., content of exchangeable Al (White 1980). Results of Marschner et al. (1986) show contrasting rhizosphere pH values within a single root system. The observed differences in pH between roots could have a significant effect upon their P absorption. Such changes in rhizosphere pH are complicated and extremely difficult to predict, and no one has satisfactorily included their effect in a P-uptake model.

A further possible effect is that of organic exudates upon P uptake by roots (Uren and Reisenauer 1988), though this is more speculative. There is no doubt that certain compounds are either passively lost or actively secreted into the rhizosphere by the root. These compounds include carbohydrates and organic acids that can stimulate the microbial population, or they could be hydroxy or carboxylic acids that may alter P sorption and perhaps soil pH, affecting the availability of P. The question remains whether the quantities exuded are sufficient, after allowing for degradation by soil microorganisms, to have any significant effect upon P availability. At present these effects are often discounted. More work is clearly necessary for us to understand the complex and changing conditions in the rhizosphere and establish their importance to soil P availability, so that P uptake by the plant can be more reliably predicted.

## Vesicular-Arbuscular Mycorrhizae

It is well known that the most obvious effect on P uptake by plant roots is due to their symbiotic association with vesicular-arbuscular mycorrhizal (VAM) fungi (Harley and Smith 1983). Sanders and Tinker (1971, 1973) found that nonmycorrhizal roots of onion absorbed P at the maximum rate that could be supported by the diffusion process, whereas P uptake (inflow) by mycorrhizal roots was four times greater. They proposed that this increase in P uptake was due to the extension of VAM hyphae beyond the zone of P-depleted soil. Studies using isotopic $^{32}P$ have shown that both nonmycorrhizal and mycorrhizal roots take up P from the same soil pool. However, recently Jurinak et al. (1986) have observed oxalate production by VAM hyphae. If this is a common occurrence in the soil, the fungus alone could have an additional effect by altering the P equilibrium in the soil solution. Bolan et al. (1987) also suggest that there could be a further effect upon the availability of iron phosphates, but it is difficult to find an explanation for their results, and so far no alternative to the original mechanism of Sanders and Tinker (1971) has become accepted.

Considerable progress in analyzing the processes that control the development of VAM infection has been made through the construction of mathematical models. The earliest model was proposed by Tinker (1975), who modeled the growth of the root system in terms of an exponential function with time and assumed that the rate of increase of length of infected root was proportional to the length of root already infected and the length of uninfected root. However, subsequent work (Buwalda et al. 1982a, 1982b) showed that this rate of increase in length of infected root was not affected by increased root density, as would have been expected from the model of Tinker (1975). Smith and Walker (1981) used differential equations to describe the processes of infection in terms of formation of entry points (points at which the fungus enters into the root cortex), and the growth of hyphae along the root interior. Buwalda et al. (1982b) modeled roots that had become primarily infected by passing through a band of inoculum. Their model had two important parameters: "S," which expressed the specific rate of increase of infected root length, and "n," which was the maximum fractional infection attained. When wheat and leeks were raised in soils of increasing P concentration, n was greatly reduced, but S was relatively unaffected. Later, a more mechanistic approach was used (Buwalda et al. 1984), in which progress of infection could be described on the assumptions that: (1) roots were produced at an exponential rate but extended at a constant rate, (2) there was a delay before infection was formed, and (3) infection within the roots extended at a constant rate. Subsequent experiments have tested these assumptions and have generally confirmed them (Amijee et al. 1986, 1989a, 1989b).

Sanders and Sheikh (1983) used a different approach by assuming that the rate of increase of entry points with time was exponential, presumably because the increase in total length of root with time was exponential. They put forward a whole-plant simulation model of a real system, which gave a close agreement between measured and predicted values for growth response due to VAM colonization. However, their model needs to be further tested under a range of environmental conditions. Fitter (1985) has also attempted to model P uptake in mycorrhizal plants, using the basic diffusion equation. His results demonstrate the relative importance of VAM in dry soils, although in such conditions one would expect that the controlling factor was not diffusion, but a reduced plant demand (Nye and Tinker 1977).

None of the above models of VAM colonization has set out systematically to deal with P uptake. Neither has any of the P-uptake models included P absorption by VAM roots; occasionally they are mentioned to explain an unexpected result, e.g., the results of Brewster et al. (1975), which showed marked changes in P uptake of onions accidentally infected by VAM fungus. It is also not surprising that in soils of low P concentration, where VAM colonization is greatest, there is little agreement between predicted and observed P uptake (the predicted value always underestimates the observed value); whereas, in soils of higher P concentration, in which the effects of VAM infection are small, there is good agreement between predicted and observed P uptake. The question therefore arises whether it is possible to include a VAM-infection model in a P-uptake model. In principle, if we were to assume that VAM hyphae behaved in a manner similar to root hairs, it could be possible to include them in P-uptake models, with appropriate modifications for hyphal density, length, and diameter. However, the problems of this could be overwhelming, because there has been no clear evidence to show the active fraction of a VAM root as far as P uptake is concerned. Observations using vital stains (by F. Amijee; M. Jones, personal communication) would suggest that only 10 to 20% of the infected root length is active. Secondly, it would be difficult to determine the soil volume from which P is absorbed by a mycorrhizal root, as measurements to quantify the external hyphae from a unit length of infected root are not easy. Thirdly, it has been assumed that the inflow of P into the root is similar between a nonmycorrhizal and a mycorrhizal part of the same root system; in reality, this is unlikely. Finally, it is well known that P concentration within the plant regulates the extent of VAM colonization, and although the processes have been identified (Amijee 1989; Amijee et al. 1989b), the mechanisms that would explain the cause of these effects are not yet clear. It would be necessary to consider all these factors to include P uptake by VAM roots in a model.

## Conclusion

Nutrient supply-uptake models have confirmed that P essentially reaches the roots by diffusion (Table 2). The models have also successfully predicted P concentration around single roots under controlled conditions. They have met with mixed success in predicting uptake by whole plants and field crops; this may be due as much to the difficulties of obtaining the correct values for the model parameters as to the models themselves. The statement made more than 10 years ago by Nye (1979) would still appear to be valid for modeling P uptake today: "It is possible to predict uptake for solutes by uniformly growing plants in a well-defined environment from homogeneous soils provided they have well-defined buffer powers. Root hairs, mycorrhizae, buffer powers, solubilization of sparingly soluble nutrients by root-induced pH changes or exudation of chelating agents, make the prediction of uptake of ions maintained at very low concentrations very difficult." In fact, the success of some of the simple models is surprising, when the real complications in the rhizosphere processes are considered.

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# Mugineic Acids as Examples of Root Exudates Which Play an Important Role in Nutrient Uptake by Plant Roots

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## *Abstract*

*Although it is recognized that plants may obtain sparingly soluble nutrient elements from soils through the solubilizing action of some components of root exudates, present knowledge about the chemical identity of such components is still limited. This paper deals with an iron (Fe) acquisition system in graminaceous species (now generally called Strategy II), in which certain species of ferric-specific ligands, phytosiderophores, play a central role.*

*The function of phytosiderophores is to extract Fe(III) from soil and transfer it into root cells via the matching transport system. All such ligands so far known are novel amino acids analogous to mugineic acid (MA), and are collectively called the mugineic acid-family phytosiderophores (MAs). MAs can be classed as potent sequestrants for soil Fe(III). When added to calcareous, high-pH soils, MAs exhibited far higher Fe(III) extraction efficiency than other ligands such as deferri-ferrioxamine B (FOB), ethylenediaminetetraacetic acid (EDTA), diethylenetriaminepentaacetic acid (DTPA), and ethylenediaminedi-o-hydroxyphenylacetic acid (EDDHA).*

*In general, the release of MAs by the roots of Fe-efficient grasses is greatly enhanced by Fe deficiency, suggesting that the primary factor responsible for the Fe efficiency of grasses may be the ability of their roots to synthesize and secrete MAs under Fe stress. There is, in fact, a good correlation between the degree of Fe efficiency of several crop species and their ability to secrete MAs under Fe stress: both of these traits are in the order barley > wheat, rye > oats > maize > sorghum > rice.*

*There is substantial evidence that, with the onset of Fe deficiency, synthesis and accumulation of MAs in barley roots rapidly increases. MAs thus accumulated are then secreted collectively through a special transport system, which operates periodically every morning. This "MA secretory transport system" has been characterized in some detail. Since many soils in arid and semi-arid regions are calcareous and high in pH, genetic improvement of Fe efficiency of crop plants may be of practical importance in dryland farming. Closer examination of Strategy II, especially of the MAs biosynthetic apparatus in grass roots, may lead to solving Fe-deficiency problems in crop plants. Further, understanding of this mechanism may improve understanding of similar mechanisms affecting other plant nutrients.*

## Introduction

Among the long-standing considerations in plant nutrition research is the role of root exudates in nutrient uptake by plant roots. In many studies of this question, attention has been directed to the effect of exudates on microbial activities in the rhizosphere, which in turn influence nutrient uptake in diverse ways (Nicholas 1965; Rovira 1979; Curl and Truelove 1987). For example, free-living microorganisms in root environments have been shown to compete with plant roots for available nutrients (Barber and Lough-

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man 1967), to produce siderophores (Powell and Szaniszlo 1982; Hemming 1986) and other chelating agents (Duff et al. 1963; Moghimi et al. 1978a, 1978b), and to liberate various metabolites capable of affecting root development and function (Curl and Truelove 1987, pp. 185-187). These microbial processes appear to be much enhanced by continuous supply of organic materials from living roots. Nonetheless, it is difficult to assess to what extent these complicated (and largely uncontrolled) processes actually contribute to nutrient uptake under natural field conditions, and they do not usually seem to be major factors in plant mineral nutrition (Russell 1977).

Another important way in which root exudates can contribute to nutrient uptake by plant roots is that they include special components capable of mobilizing sparingly soluble nutrients in soils. Among such components so far noted are various chelating, reducing, and acidifying (i.e., proton and organic acids) substances and hydrolytic enzymes, such as phosphatase (Amann and Amberger 1989). Increased release of one or more of these substances by the roots of a plant under deficiency of a particular nutrient, which normally tends to be in an insoluble state in the soil, might be considered as an indication of the presence of a self-controlling uptake system for that particular nutrient element. As will be discussed later, the existence of such uptake systems specifically involved in the process of iron (Fe) acquisition from aerobic soils has been substantiated in a wide range of plant species.

Although present knowledge on the direct effect of root exudates on phosphorus (P) nutrition is still limited and fragmentary, several lines of experimental evidence suggest its potential importance. Increased release of phosphatases from the roots under P deficiency appears to be a common phenomenon among higher plants. According to Tadano and Sakai (1991), all of the nine plant species they tested responded to P deficiency by significantly increasing liberation of acid phosphatase, the rate of the increase ranging from 50% (azuki bean) to 2000% (lupin). Gardner et al. (1983) found that the roots of lupin (*Lupinus albus* L.), a species efficient in P utilization, excreted a large amount of citric acid during growth on a P-deficient rooting medium. On the other hand, Ae et al. (1990) showed that the capability of pigeonpea to grow well on Alfisols (soils containing Fe-bound P as the major P source for plants) may be interpreted in terms of $Fe_3PO_4$-solubilizing activity of certain components of their root exudates, namely piscidic acid and its *p*-O-methyl derivative.

The foregoing selected papers seem to suggest the possibility that there might be many instances where some components of root exudates participate in regulatory control of P uptake by plant roots, especially from soils with low P availability; however, available data are not yet sufficient to substantiate this possibility.

In recent years, the study of the Fe acquisition system in graminaceous plants, in which mugineic acids (MAs), a group of natural chelators released from the roots, play a central part, has progressed considerably. The purpose of this paper is to outline the constitution and operation of this Fe acquisition system, with special emphasis on the efficiency of MAs in Fe extraction from selected soils.

Iron ranks as one of the most abundant metal elements in the earth's crust, along with aluminum (Al) and calcium (Ca). However, in well-aerated soils it is virtually insoluble, because ferric oxides provide solid-phase control of Fe solubility. According to Lindsay (1984), the minimum solubility of ferric oxides occurs in the pH range of 7.4 to 8.5, where calcareous soils are strongly buffered by a large amount of calcium carbonate ($CaCO_3$) deposition. It seems natural, therefore, that the majority of terrestrial plants, especially those that inhabit regions with calcareous, high-pH soils, had to evolve a powerful Fe acquisition system, by which they could overcome the problem of Fe deficiency. Interestingly, two separate Fe acquisition systems, one for dicotyledons and one for grasses, have been identified to date in angiosperms.

## The Iron Acquisition System in Dicotyledons (Strategy I)

Intensive study of the system operative in dicotyledons, now generally called Strategy I, was triggered by the pioneering work of Brown et al. (1961), who first noted the characteristic "Fe stress response" appearing in the roots of Fe-efficient dicotyledonous plants. Thus, this system was fairly well characterized before the end of the 1970s.

Briefly, Strategy I is comprised of two integral parts, an Fe(III)-reducing enzyme system and a potent proton extruding pump, which are both located on the plasma membrane of morphologically specialized root epidermal cells and become operative in response to Fe deficiency (see recent reviews by Bienfait 1987 and Römheld 1987). Along with the above functions, Fe-stressed dicotyledonous roots often liberate phenolic compounds, such as caffeic acid

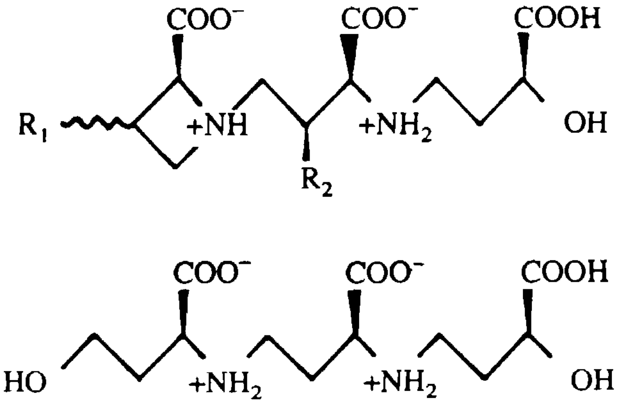
(Olsen et al. 1982), though the functional significance of these compounds is still debated (Bienfait 1987). Strategy I is now believed to be omnipresent in all families of angiosperms, except Gramineae (Römheld 1987), which exhibit no distinct Fe-stress response as found in dicotyledons.

## The Iron Acquisition System in Grasses (Strategy II)

It was not until the discovery of MA and analogous natural chelators by our research group (Takagi 1976; Takemoto et al. 1978; Fushiya et al. 1980; Nomoto et al. 1981; Takagi et al. 1984) that the existence of a grass-type iron acquisition system, or Strategy II, became known. Although this system is confined to the plants belonging to Gramineae (Takagi et al. 1984; Römheld 1987), it is evidently of great agronomic importance, as Gramineae include many major crops, such as wheat, rice, maize, and barley. Some of the grasses (e.g., rice, sorghum, maize, and sugarcane) are Fe-inefficient, and Fe deficiency in these crops is a serious problem in regions that have calcareous soils.

The distinctive feature of the grass-type system is its strong resemblance to the high-affinity microbial Fe assimilation system, in which siderophores play a central role. According to Neilands (1981a), siderophores are defined as low-molecular-weight (500-1000 Daltons), virtually ferric-specific, ligands, the biosynthesis of which is carefully regulated by Fe and the function of which is to supply Fe to the cell via the matching transport system. Much the same is true of the grass-type system, except that it uses its inherent Fe(III) ligands of exceptionally small molecular size (300-340 Daltons). All of these ligands so far discovered are novel amino acids analogous to MA, and are collectively called "mugineic acid-family phytosiderophores" (MAs) (Fig. 1). Despite their relatively small molecular size, MAs have a strong affinity for Fe(III) and provide octahedral ferric complexes (Fe(III)-MAs) of high stability, the putative formation constant of which is in the order of $10^{32}$ (Murakami et al. 1989).

It can be safely said that the role of MAs in the grass-type system is to extract Fe(III) from aerobic soils and to carry it into the root cells through a transport system specific for Fe(III)-MAs. This, in turn, implies that Fe uptake of grasses is a direct function of the amount of Fe(III)-MA complexes formed at the root-soil interface, and that any failure of Fe(III)-MA formation in the rhizosphere will cause the plants to develop Fe-deficiency chlorosis. In harmony with this concept, secretion of MAs by the roots of Fe-efficient grass species is greatly enhanced in response to Fe deficiency (Takagi 1976; Takagi et al. 1984), suggesting that the primary factor responsible for the Fe efficiency of grasses is the ability of their roots to increase the synthesis and secretion of MAs in response to Fe stress. There is in fact a good correlation between the degree of Fe efficiency of major cereal crops and the ability of their roots to liberate MAs under Fe deficiency, both of these traits being in the order: barley > wheat, rye > oats > maize > sorghum > rice (Marschner et al. 1986; Kawai et al. 1988b). When stressed for Fe, the roots of barley often secrete as much as 15 mg of MAs per gram of dry root per day (Takagi et al. 1984). This amount roughly corresponds to 10, 100, and 500 times the amount of MAs released by Fe-stressed maize, sorghum, and rice roots, respectively (Kawai et al.



$R_1 = H$, $R_2 = OH$, Mugineic acid (MA)
$R_1 = R_2 = H$, 2'-deoxymugineic acid (DMA)
$R_1 = R_2 = OH$, 3-hydroxymugineic acid (HMA) or 3-epi-hydroxymugineic acid (epi-HMA)

Avenic acid (AvA)

**Figure 1. Mugineic acid-family phytosiderophores (MAs).**

1988b), and this seems sufficient to account for the outstanding Fe efficiency of barley, a crop species originating from southwestern Asia, where calcareous soils predominate (Takahashi 1955).

The most impressive phenomenon in the excretion of MAs by Fe-stressed barley roots is its characteristic diurnal variation. Under natural day-night regimes, the excretion occurs quite regularly within a specific period (3-5 h) in the morning of each day (Takagi et al. 1984). Recent studies in our laboratory (Takagi et al. unpublished data) revealed that with the onset of Fe deficiency, synthesis of MAs in barley roots is accelerated remarkably, to cause a rapid and large accumulation in the roots. Most of the MAs thus accumulated are then secreted collectively through a special transport system, which operates periodically every morning. It was disclosed also that this "MA-secretory transport system" is highly dependent on metabolic energy, that the MAs liberation by this system is attended by symport of equimolar $K^+$, and that its operation time is under the control of an endogenous circadian clock. Hence, the MAs liberation by Fe-stressed barley roots is evidently a distinct phenomenon, which falls into the category of true "secretion." The periodic operation of the MA-secretory system may be taken as an ingenious strategy of grasses for minimizing loss of secreted MAs by microbial degradation in the rhizosphere and by outflow into the bulk soil (Takagi et al. 1988).

With regard to the biosynthetic pathway of MAs in barley roots, there is substantial evidence that L-methionine (Met) must be in close proximity to the final step of MAs synthesis (Mori and Nishizawa 1987). Based on the examination of $^{13}$C-NMR spectra of MA and 2'-deoxymugineic acid (DMA) isolated from the secretions of Fe-stressed barley roots fed with L-[1-$^{13}$C]Met, Kawai et al. (1988a) proposed that MAs may be synthesized through the sequential conjugation of three 2-aminobutyrate moieties of Met. On the one hand, Shojima et al. (1989) developed a cell-free system of barley root tips which, in the presence of adenosine triphosphate (ATP), could convert Met to nicotianamine, the putative immediate precursor of DMA. More recently, this same cell-free preparation was shown to convert Met to DMA when supplemented with nicotinamide adenine dinucleotide-reduced (NADH) and an amino-group acceptor, such as 2-oxoglutarate (Shojima et al. 1990). Thus, the conversion of Met to MAs follows the sequence: Met → S-adenosylmethionine → (polymerization of 2-aminobutyrate moieties) → nicotianamine → DMA → MA → epi-hydroxymugineic acid (epi-HMA).

However, the roots of barley under Fe stress normally contain negligible amounts of Met, and the metabolic route involved in the production of quantities of Met required for maintaining an enhanced rate of MAs synthesis still remains to be studied.

To sum up, grasses are obviously conditioned to secure the requisite Fe by means of autonomous production (synthesis-secretion) of MAs in the roots. In other words, they are obliged to secrete sufficient MAs to form the requisite amount of Fe(III)-MAs complexes in the rhizosphere soil during the plant growth period. Since the formation of Fe(III)-MAs may be strongly affected by chemical and physical properties of the soil environment, it seems desirable to collect information about the efficiency of Fe extraction by MAs from soils with various properties. This problem is dealt with in the following section.

Mugineic acids are one of the smallest molecules among known ligands of biological origin which form a Fe(III) complex of octahedral structure (Nomoto et al. 1987). These MAs have a much simpler structure—and thus appear less effective—than the various siderophores of microorganisms. Actually, the Fe(III)-complexing constant of MA is reported to be 18.1 (Sugiura et al. 1981), which is much lower than that of siderophores of microbial origin (ca. 30, Neilands 1981b). Therefore, the question arises as to how effectively these "mini-siderophores" can solubilize sparingly soluble ferric iron in the soil.

In order to answer this question, the solubilizing efficiency (amount of Fe solubilized by a mole of

**Table 1. Characteristics of chelators used to solubilize iron from soil. (Reprinted from Takagi et al. (1988) p. 645, by courtesy of Marcel Dekker Inc.)**

| Chelator | Molecular weight (Dalton) | Fe (III) complex-forming constant |
|---|---|---|
| Ethylenediaminetetraacetic acid (EDTA) | 292 | 25.1 |
| Diethylenetriaminepentaacetic acid (DTPA) | 393 | 28.1 |
| Ethylenediaminedi-*o*-hydroxyphenylacetic acid (EDDHA) | 360 | 39.0 |
| Deferri-ferrioxamine B (FOB) methanesulfonate salt (®Desferal; Ciba-Geigy Co.) | 657 | 30.6 |
| Mugineic acid (MA) | 321 | 18.1 |
| 2'-deoxymugineic acid (DMA) | 305 | - |

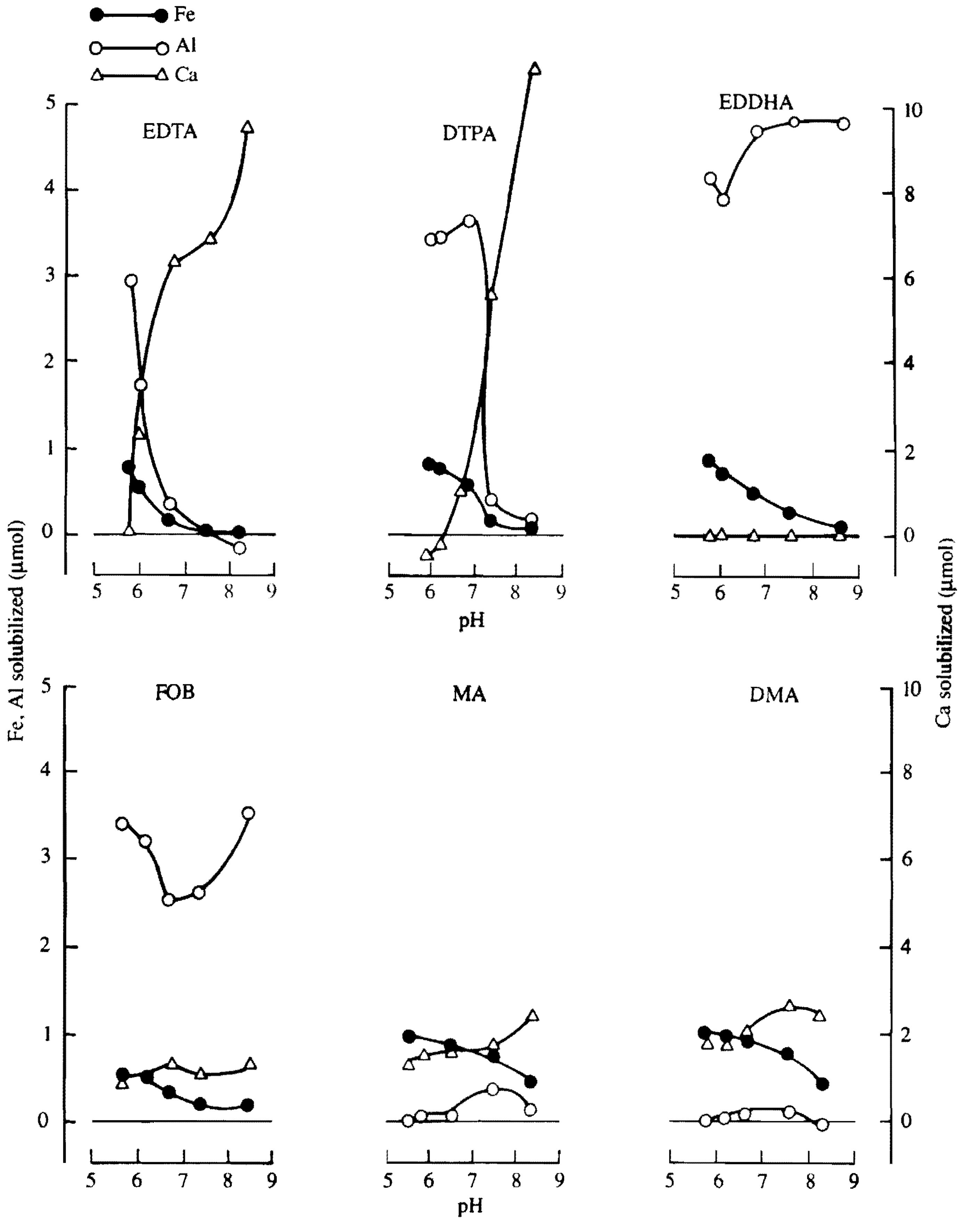


Figure 2. Effect of soil pH on the ability of chelators to solubilize iron (Fe), aluminum (Al), and calcium (Ca) (μmol metal per 5 μmol chelator; soil:solution = 1:20, 30°C; 3 h shaking). EDTA = ethylenediaminetetraacetic acid; DTPA = diethylenetriaminepentaacetic acid; EDDHA = ethylenediaminedi-*o*-hydroxyphenylacetic acid; FOB = deferri-ferrioxamine B; MA = mugineic acid; DMA = 2'deoxymugineic acid. (Courtesy of Marcel Dekker Inc.)

ligand molecule) of purified MA was investigated, in comparison with that of some natural and synthetic chelators (see Table 1). The deferri-ferrioxamine B (FOB) referred to in Table 1 is one of the siderophores produced by actinomycetes.

### Effect of Soil pH on Iron-solubilizing Efficiency

First, Ando soil (pH = 5.7, total carbon content = 9%) at five levels of pH, adjusted by addition of lime, was used, and the solubilizing ability of the chelators for iron and other polyvalents tested. A 20-mL solution of each chelator (5 μmol per 20 mL) was added to 1 g of soil (air-dried and sieved) and shaken for 3 h at 30°C and centrifuged. The supernatant was passed through a 0.1 μm millipore filter and the content of Fe and other metals measured by atomic absorption spectrophotometry.

Unexpectedly, of the six chelators used, two MAs—MA and DMA—showed the highest solubilization of Fe (Fig. 2). Their solubilizing efficiency declined to a lesser extent at higher pH levels than that of the other chelators. In other words, they had relatively higher solubilizing efficiency at high pH.

For example, at a soil pH of 7.3, the amount of Fe solubilized by MA or DMA was three to four times more than that by ethylenediaminedi-*o*-hydroxyphenylacetic acid (EDDHA) or FOB. These results were assumed to be due to much lower affinity of MA and DMA for Al and Ca in soil. Thus, these MAs may have very high Fe-solubilizing efficiency in soil because they are not bound to other polyvalent metals, such as Al or Ca, which exist in large amounts in the soil, along with Fe. The results shown in Figure 2 support this assumption. Although ethylenediaminetetraacetic acid (EDTA) and diethylenetriamine pentaacetic acid (DTPA) solubilized more Ca in the higher pH range, and FOB more Al, MA and DMA solubilized none, or very small amounts, of these metals. Besides Fe, MA also solubilized copper (Cu) and zinc (Zn) (Fig. 3), but the

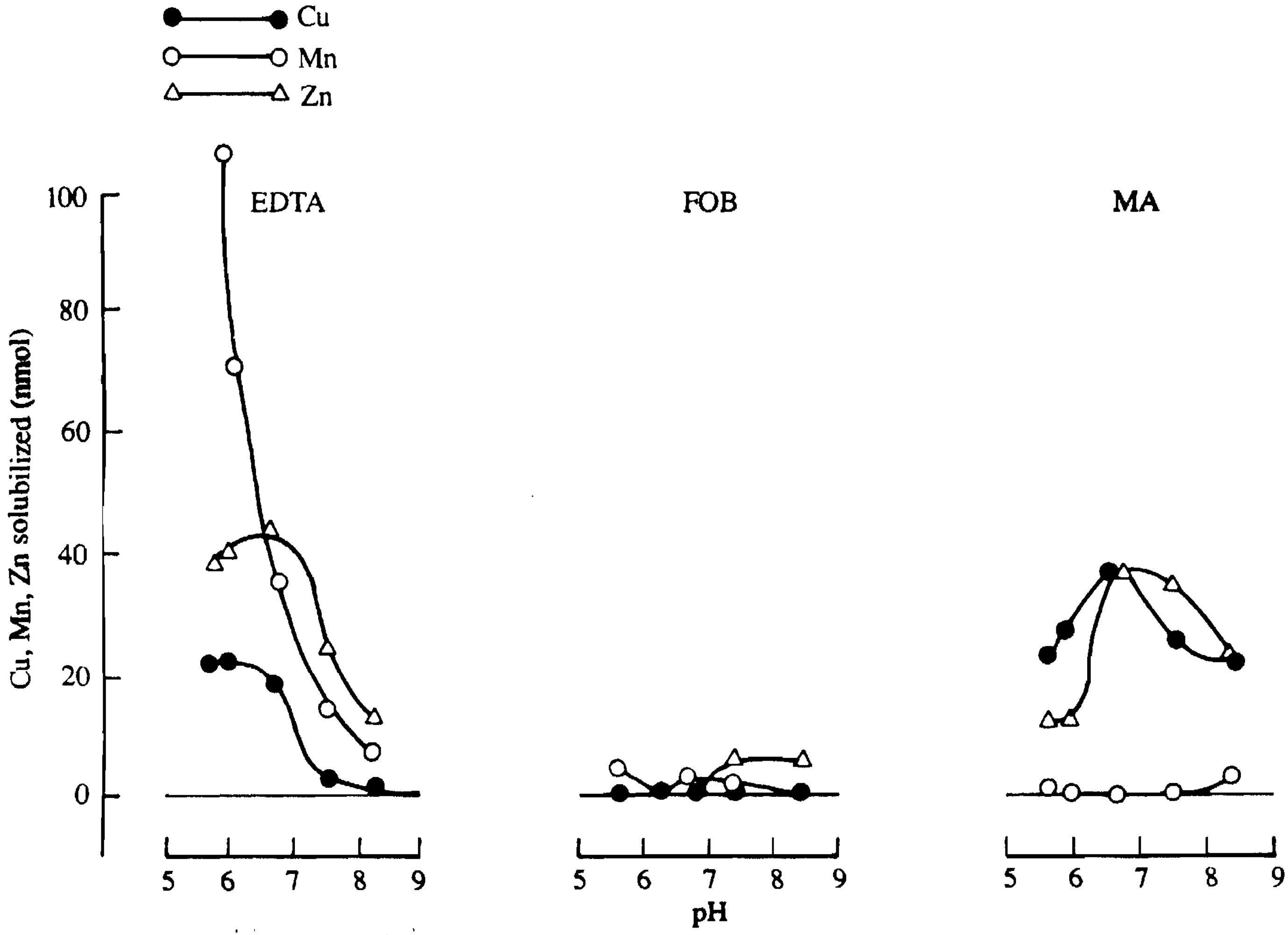


**Figure 3.** Effect of soil pH on the ability of chelators to solubilize copper (Cu), manganese (Mn), and zinc (Zn). (See Fig. 2 caption for full names of chelators.) (Courtesy of Marcel Dekker Inc.)

amount of these two metals is very low in the soils used and their possible interference with Fe solubilization can be ignored.

### Effect of Aluminum and Calcium on the Solubilization of Iron from Ferric Hydroxide Gel

The assumption that there is less interference of Al and Ca with the Fe-solubilizing ability of MAs was further confirmed by the following experiment. Ferric hydroxide gel suspension (50 mM Fe) was prepared by neutralizing ferric chloride solution by slowly adding sodium hydroxide. Then, three kinds of ferric gel suspensions of pH 4-8 were prepared by adding 15 mL acetic acid-barbital buffer (30 mM), and either 1 mL of (1) calcium chloride, (2) aluminum hydroxide (both 50 mM), or (3) distilled water, to 1 mL of the prepared ferric gel suspension. Then 1 mL of EDTA-2Na, FOB, or MA, at 5 mM, was added to the suspension, which was shaken for 3 h at 30° C, and then the concentration of Fe in the liquid phase was measured as described previously.

The results obtained (Fig. 4) showed that the solubilization of Fe from ferric hydroxide by EDTA is strongly inhibited by Ca or Al. The amount of Fe solubilized in the presence of Ca or Al decreased markedly as the pH of the solution increased, which implies that the ability of EDTA to solubilize Fe is lost in soil of high pH, because EDTA would bind with Ca; FOB behaved like EDTA in relation to Al.

However, MA showed far lower affinity than EDTA or FOB for Al and Ca: the amount of Fe solubilized by MA was reduced by only 50% in the presence of Al and was not affected by the presence of Ca. This difference in affinity for Al and Ca explains the far higher Fe-solubilizing efficiency of MAs in soils of high pH.

Figure 4 also shows that the Fe-solubilizing ability of MA from Fe(III) gel in the absence of Al or Ca was about half that of EDTA or FOB. This phenomenon was earlier assumed to be due to a relatively low affinity of MA for Fe(III) or to the difference in reaction time, but now experiments have shown that it is mainly due to adsorption of MA by ferric hydroxide gel. The same adsorption occurs in Ando soil to a

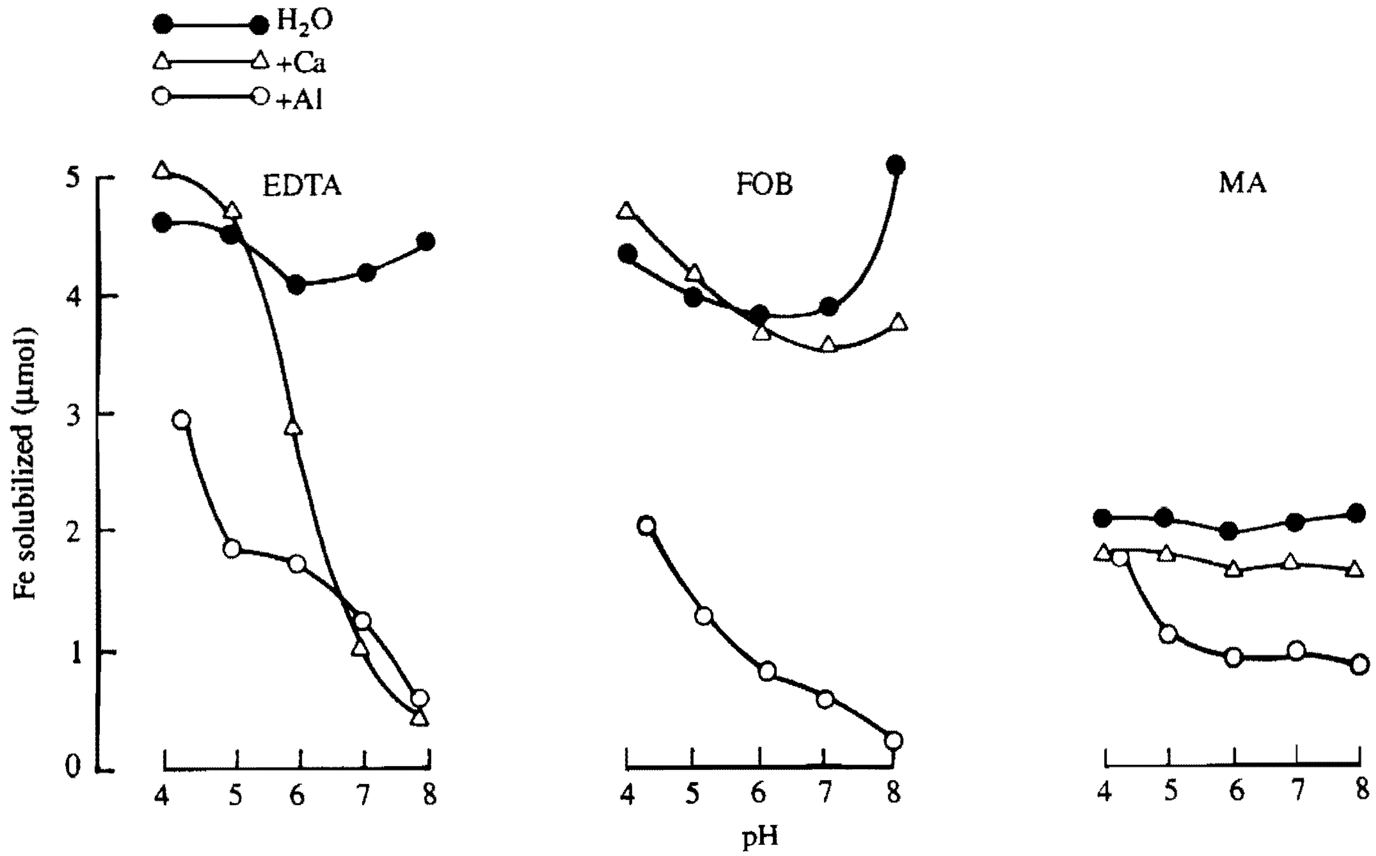


**Figure 4. Effect of calcium (Ca) and aluminum (Al) on the ability of chelators to solubilize iron (Fe) from ferric hydroxide gel. (See Fig. 2 caption for full names of chelators.) (Courtesy of Marcel Dekker Inc.)**

certain extent, but not in calcareous soil, and it is assumed that the amorphous Fe and Al are the main adsorption sites in Ando soil.

### Degradation of Mugineic Acid by Soil Microorganisms

Figure 5 shows the time-course of Fe solubilization when 5 μmol of MA was added to air-dried Ando soil of pH 5.7, according to the method described earlier. The amount of Fe solubilized increased during the first 24 h after addition of MA, but then decreased rapidly. This rapid decrease was assumed to be due to the proliferation of soil microorganisms which consume or degrade MAs, because it was completely inhibited by the addition of thymol, an antimicrobial agent, to the reaction solution. Mugineic acids are amino acids and would therefore be attacked by rhizosphere microorganisms as soon as they are exuded from roots. Figure 5 shows that degradation of MA in the soil did not begin until 24 h after addition, probably because air-dried soil was used in this experiment. However, in the actual rhizosphere of barley, exuded MA may be more rapidly degraded.

Figures 6 and 7 show the time course of Fe solubilization when 1.4 μmol of MA was added to the rhizosphere and nonrhizosphere soil of barley grown in pots and to bare (nonplanted) soil. The pH of the soil used was 5.4 and 7.7 (adjusted by the addition of lime). The results showed that the degradation rate of the added MA was in the order of rhizosphere soil > nonrhizosphere soil > bare soil, suggesting that the rhizosphere of barley is the active site for the MAs-degrading microorganisms. It was also of interest that the MA in the soil of higher pH (Fig. 7) decomposed more slowly than in the soil of lower pH (Fig. 6).

Several factors should be considered in evaluating the rate of Fe solubilization from soil by MAs. These include: (1) binding of MAs to heavy metals other than Fe, (2) adsorption of MAs to soil particles, (3) leaching of MAs beyond the rhizosphere, and (4) degradation of MAs by microorganisms in the rhizosphere.

The last factor is particularly important. Watanabe and Wada (1989) identified six strains of MAs-degrading bacteria from barley roots grown under Fe-deficient conditions and suggested that these bacteria existed on the root surface. The MAs are exuded regularly in the morning from barley roots. How long do these exuded MAs stay in the rhizosphere to fulfill the function of solubilizing Fe? As a model experiment to answer this question, 5 μmol of MA was added at 24-h intervals to air-dried Ando soil adjusted

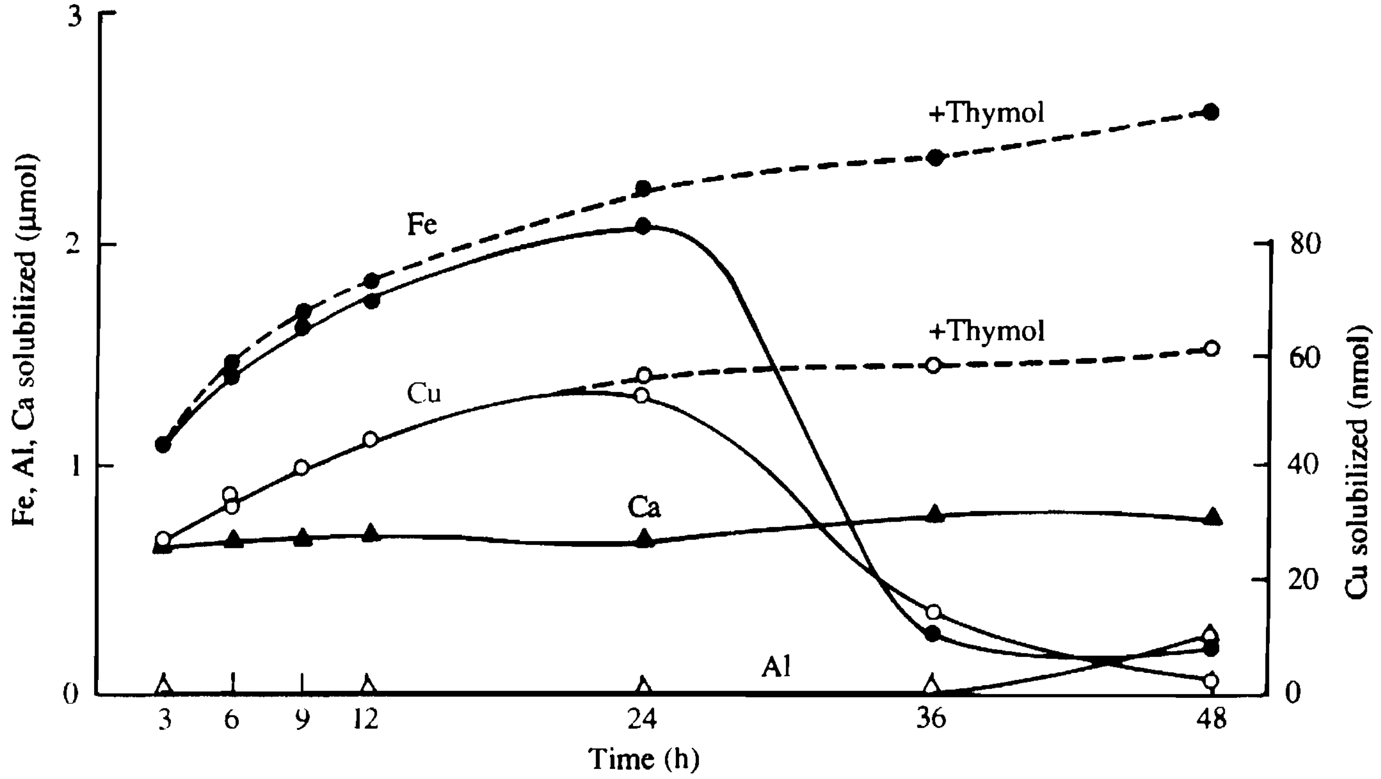


Figure 5. Time course of solubilization of soil metals by mugineic acid and the effect of thymol on solubility. (Courtesy of Marcel Dekker Inc.)

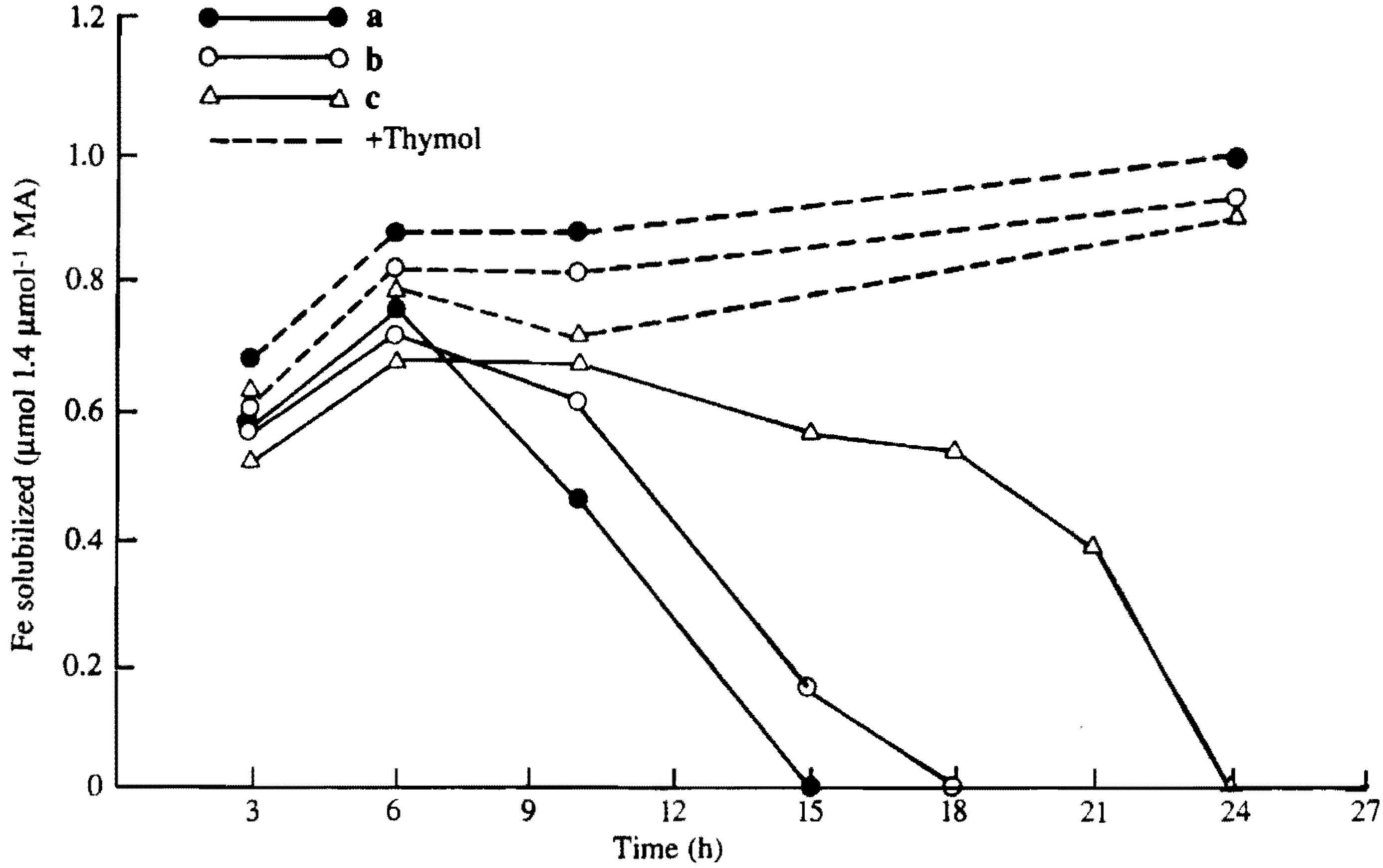


**Figure 6. Time course of iron (Fe) solubilization by mugineic acid (MA) (soil pH = 5.4): (a) in the rhizosphere soil of barley (some roots included); (b) in the nonrhizosphere soil of barley; (c) in bare soil.**

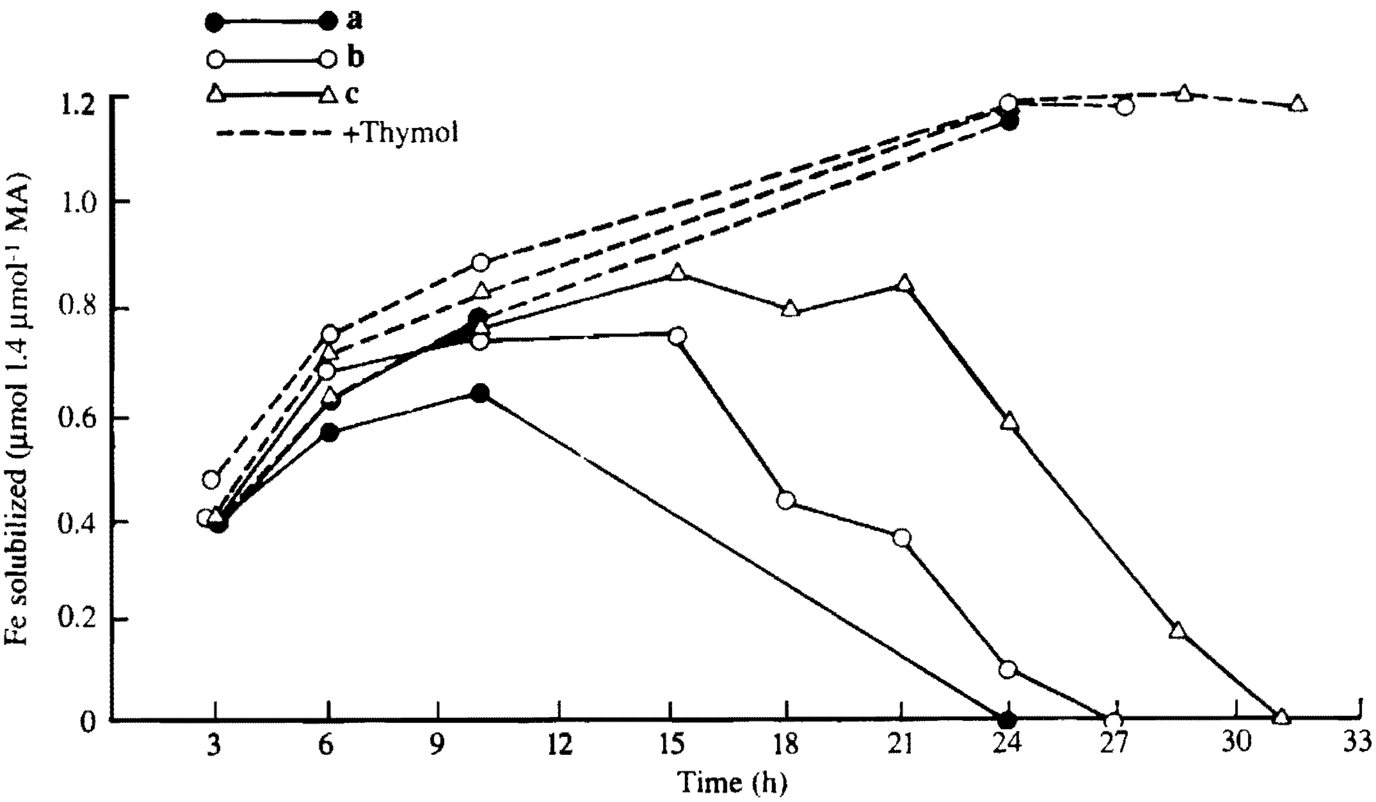


**Figure 7. Time course of iron (Fe) solubilization by mugineic acid (MA) (soil pH = 7.7): (a) in the rhizosphere soil of barley (some roots included); (b) in the nonrhizosphere soil of barley; (c) in bare soil.**

to pH 5.6 and 8.1 with lime, and the time-course of the Fe solubilization was investigated under a constant temperature of 30° C (Fig. 8). These data show that MA decomposed more rapidly at later intervals, and at the third interval, most of the MA disappeared within 4-6 h after addition. It is presumed that MA added initially induced multiplication of MAs-degrading microorganisms, and thus MA added at later intervals decomposed more rapidly.

If we apply these data to the actual rhizosphere of barley, MAs are likely to remain in the rhizosphere for only a few hours after their exudation, and only the Fe solubilized in that limited time can be absorbed by roots. Therefore, it can be argued that the ability of MAs to solubilize Fe should be evaluated in terms of the amount solubilized within that limited time. Furthermore, the conditions (temperature, time, concentration of MAs, soil moisture, etc.) under which the Fe-solubilizing ability is investigated for the evaluation, should be the same as in the actual rhizosphere. These investigations still need to be done.

These results strongly suggest that the activity of bacteria causes a big loss of MAs exuded from roots. Against this, as a possible measure taken by the plant, the regular exudation of MAs mentioned previously is used as a skilful means to avoid the attack by microorganisms on MAs in the rhizosphere and leads to the effective solubilization and absorption of Fe by roots. The regular excretion of MAs always takes place in the morning, because the MAs are then less likely to be leached from the rhizosphere.

## Efficiency of Mugineic Acid in Solubilizing Iron in Calcareous Soils

Calcareous soils with neutral or alkaline pH and deficient in available Fe are widely distributed in arid and semi-arid regions (Vose 1982). Generally, these soils contain up to 60% of free $CaCO_3$ and are strongly buffered to the pH range 7.4-8.5 (Lindsay and Norvell 1978; Lindsay 1984). This is where solubility of inorganic Fe is lowest and the reactivity of Fe is lowest, and thus represents the soil from which plants and microorganisms absorb Fe with the most difficulty. Therefore, the ability of MAs to act as phytosiderophores is most critically evaluated from their Fe-solubilizing efficiency in soil of this kind. Since it was difficult to obtain calcareous soil in Japan, Ando soil made alkaline by lime was used in our previous experiments. But recently we were able to obtain calcareous soils from the midwestern USA, and the Fe-solubilizing efficiency of MAs in these soils was investigated in comparison with FOB and DTPA.

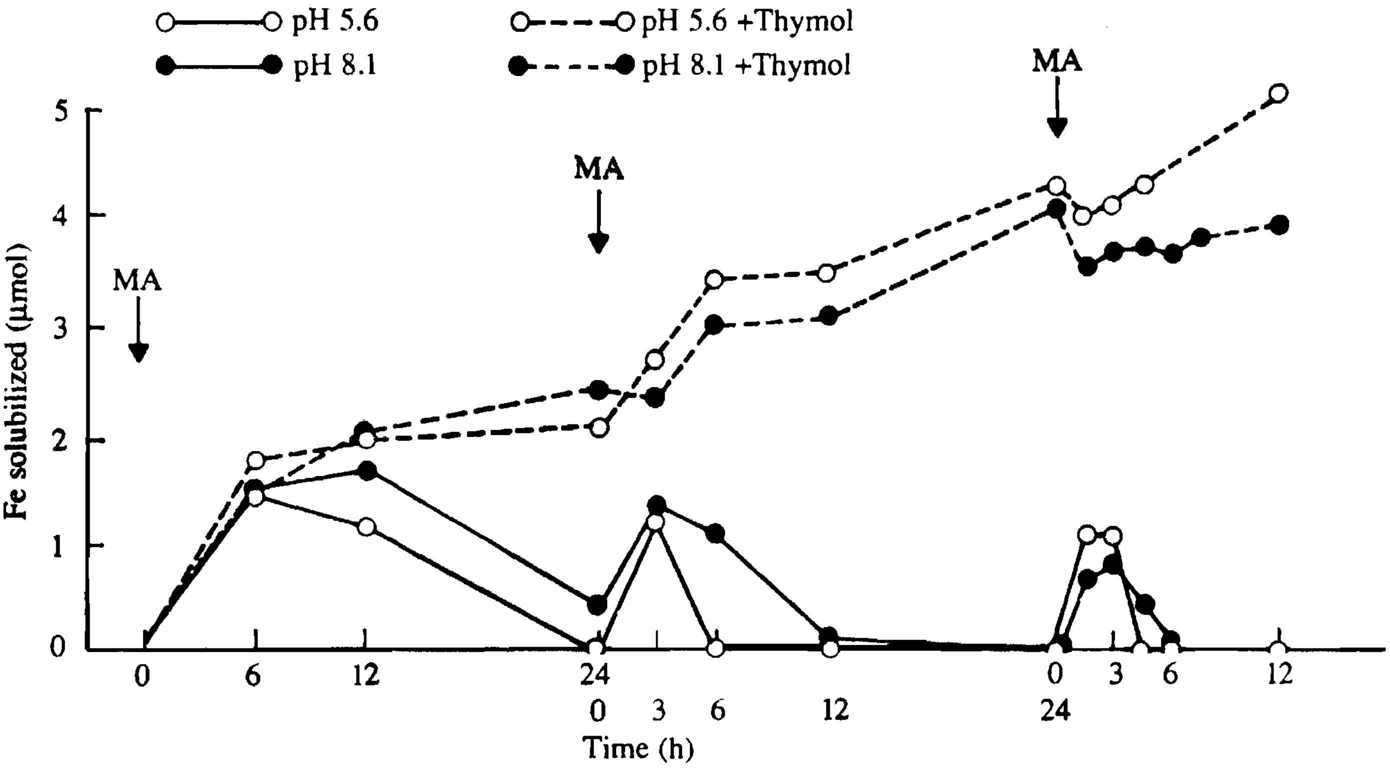


**Figure 8. Time course of soil iron (Fe) solubilization when mugineic acid (MA) was added at 24-h intervals.**

Figure 9 shows the relationship between the amount of MA added and the amount of Fe solubilized from a lime-amended Ando soil and two calcareous soils collected in the U.S. states of Utah (UT-2) and New Mexico (NM-2), with pH($H_2O$) of 8.1 and 8.5, respectively. Iron solubilization from the naturally calcareous soils was much more difficult than from Ando soil amended with lime; for example, the efficiency of the Fe solubilization when 1 $\mu$mol of MA was added (100 × $\mu$mol-Fe/$\mu$mol-MA) was around 70% in the Ando soil, 30% in UT-2, and only 13% in NM-2. However, these results do not mean that the ability of MA to solubilize Fe from calcareous soils is less than that of synthetic chelators or siderophores of microbial origin. On the contrary, MA had higher Fe-solubilizing efficiency than FOB or DTPA when these compounds were added to UT-2 and NM-2 soils (Fig. 10). Interestingly, the solubilizing efficiency of MA at low concentrations (< 1 $\mu$mol $g^{-1}$ dry soil) is much higher than that of the other chelators. For example, the amount of Fe solubilized 20 h after the addition of MA (0.5 $\mu$mol) to NM-2 soil was three times more than that solubilized by DTPA and seven times more than that by FOB (Fig. 10b). This figure also shows that 5 $\mu$mol of DTPA or FOB is needed to solubilize the same amount of Fe solubilized by 0.5 $\mu$mol of MA (i.e., 0.12 $\mu$mol Fe).

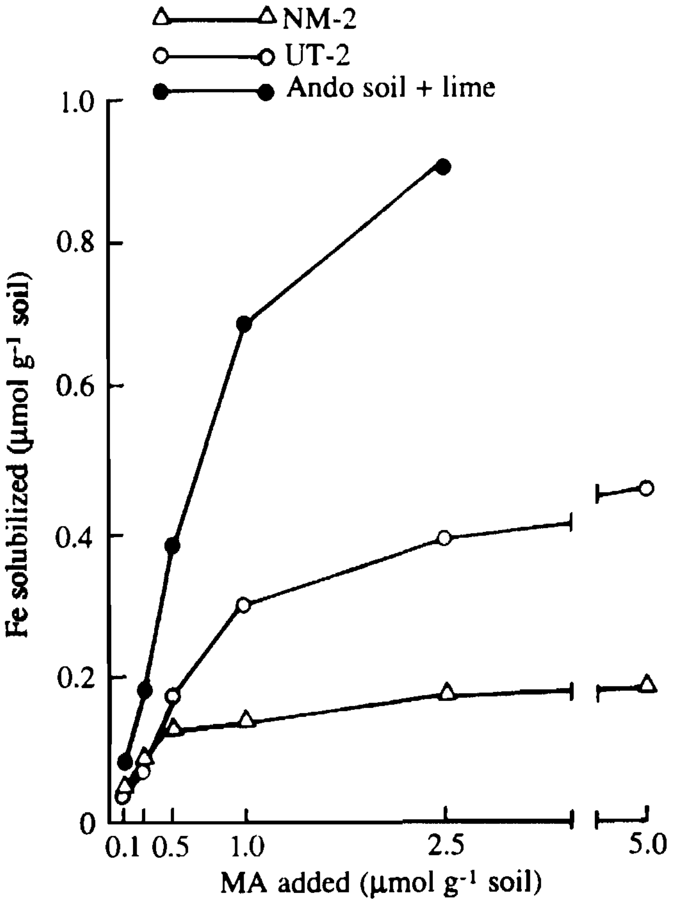


**Figure 9. Relationship between mugineic acid (MA) added and iron (Fe) solubilized by MA from two calcareous soils (UT-2 and NM-2) and Ando soil amended with lime (pH = 7.7). Incubation for 20 h at 25° C.**

The reason why MA is able to solubilize Fe from calcareous soil so effectively is, as already mentioned, the special Fe(III) complex-forming characteristic of MA, which is not easily inhibited by major polyvalent metal ions, such as Ca, Al, or Mn. Therefore, in principle, for graminaceous crops it is not adequate to use a soil test for available Fe involving a chelator other than MAs (c.f., the widely used "DTPA soil test," Lindsay and Norvell 1978). It is suggested that a soil test using MAs to assess the availability of Fe to graminaceous crops should be developed. Interestingly, MA solubilized P from $FePO_4$ but not from $AlPO_4$ while FOB did mobilize P from both of these insoluble salts (S. Kamei and S. Takagi, Iwate University, unpublished data).

Recently, we confirmed that the three representative phytosiderophores, MA, DMA, and epi-HMA had almost the same efficiency in solubilizing Fe in the calcareous soil UT-2 (S. Takagi et al., unpublished data). The metal complex-forming constants of these three MAs are similar (Murakami et al. 1989): they form a $[Fe(III)_{LH-1}]$ type of Fe(III) complex, which is accompanied by the dissociation of a proton at the terminal hydroxyl, at a pH greater than 3. The formation constants ($\log K_{ML-1}$) of the Fe(III) complexes are around 33 for these MAs (Murakami et al. 1989). These values are much higher than the previously known formation constant of Fe(III)-MA ($\log K = 18.1$) (Sugiura et al. 1981) and are comparable to those of many siderophores of microbial origin.

Neilands (1981b) mentioned in his review on siderophores that a molecular size of at least 600 Daltons is necessary to form a stable Fe(III) complex of octahedral structure, which is adapted to the high affinity transport system of microbial cells. However, MAs can form Fe (III) complexes as stable as other siderophores, even though they are relatively small molecules; MAs also have remarkable complexing characteristics, as described above. These points reveal that the MAs are compact and efficient siderophores that have evolved in graminaceous plants, these plants themselves being well advanced in the evolutionary process. This evolution has taken place by the plants developing a precise understanding of their growth medium, the soil. The extent to which such evolution has occurred to enhance the ability of

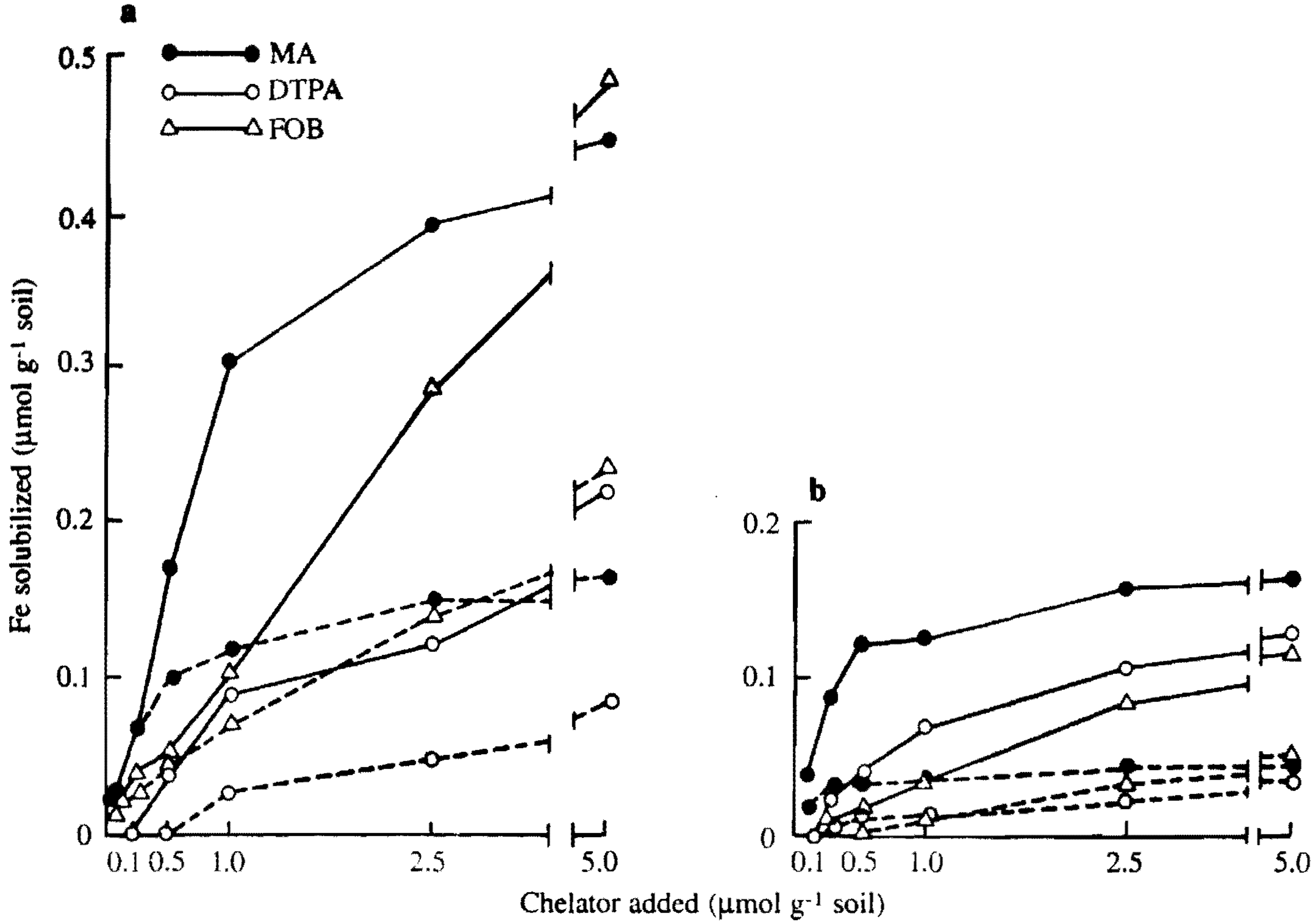


**Figure 10. Ability of three chelators (see Fig. 2 caption for full names) to solubilize iron (Fe) from the calcareous soils (a) UT-2 and (b) NM-2; (- - -) 3 h incubation; (—) 20 h incubation.**

plants to absorb and regulate other nutrients from growth media with unfavorable levels of that nutrient is yet to be adequately explored. Strategy II for Fe uptake provides an example of what may be occurring for other nutrients, albeit by the operation of different mechanisms, such as proposed by Ae et al. (1991a, b).

## Acknowledgments

Table 1 and Figures 2, 3, 4, and 5 in this paper are reprinted from Takagi et al. (1988), pages 645-649, courtesy Marcel Dekker, Inc. Figures 6,7,8,9, and 10 use reproduced from Takagi (1990), pages 36-41, courtesy Hakuyushia, Inc.

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# Phosphorus Uptake Mechanisms of Pigeonpea Grown in Alfisols and Vertisols

N. Ae,[1] J. Arihara,[2] and K. Okada[3]

## Abstract

*In India, pigeonpea [*Cajanus cajan *(L.) Millsp.] has been traditionally grown as an intercrop, mainly with cereals such as sorghum and pearl millet, under low-input conditions. Response of pigeonpea to phosphorus (P) application is generally lower than that of other crops, even in soils with low P fertility. This has been attributed to its root distribution to deeper soil layers than roots of other crops, its strong mycorrhizal associations, and its particular mechanisms of absorbing P. In this study, the lower P response of pigeonpea could not be attributed to the first two factors. However, pigeonpea was shown to be more efficient in utilizing iron-bound phosphorus (Fe-P) than several other crop species (sorghum, maize, pearl millet, groundnut, and soybean).*

*Analysis of root exudates revealed large amounts of citric acid in pigeonpea, but this organic acid was also present in the other species examined and thus did not explain the differential ability of species to utilize Fe-P. The active fractions of root exudates peculiar to pigeonpea were identified as (*p*-hydroxybenzyl) tartaric acid (piscidic acid) and (*p*-methoxybenzyl) tartaric acid. It is thought that the hydroxyl and carboxyl groups of the tartarate portion chelate* $Fe^{3+}$*, thus releasing P from Fe-P.*

*These results suggest that pigeonpea can increase the available P pool of cropping systems in which it is grown by accessing Fe-P to a greater extent than other crop species can. These findings have particular relevance to low-P Alfisols in which Fe-P is the dominant form of soil P, and explains a particular advantage of pigeonpea-based cropping systems in these soils.*

## Introduction

Phosphorus (P) is normally the most limiting nutrient for growth of leguminous crops in tropical and subtropical regions. This is particularly so for soils with high contents of iron (Fe) or aluminum (Al) oxides where P is strongly bound and thus is less available for uptake by crop plants. Pigeonpea [*Cajanus cajan* (L.) Millsp.] has been widely cultivated on the Indian subcontinent since ancient times, as an intercrop with cereals and other crop species. Many field experiments have shown that response of pigeonpea to P is low, in comparison with the response of other crops and in soils of low apparent available P status (ICRISAT 1981; Johansen, 1990). Possible reasons for this include an extensive rooting habit, strong mycorrhizal development, and a special ability of pigeonpea to extract soil P not normally available to other crop plants. In this chapter, we investigate the mechanisms by which pigeonpea extracts P from soils of low apparent available P status.

In the semi-arid tropics (SAT), Alfisols and Ver-

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tisols are major soil types (El-Swaify and Caldwell 1991), and studies were conducted on representative examples of these soils at ICRISAT Center. The electrical conductivity (EC), pH, and P status of soils typical of those used for experimentation are shown in Table 1. In Alfisols, most of the P is associated with iron (Fe-P); in Vertisols, although Fe-P is the largest fraction, there is also a large fraction of calcium-bound P (Ca-P). Phosphorus can be solubilized from the Ca-P fraction by acidification of the rhizosphere, as a result of excretion of organic acids and $H^+$ from roots (Moghimi et al. 1978; Marschner and Römheld 1983; Ae et al. 1988, 1991).

**Table 1. Electrical conductivity (EC), pH, and various estimations of phosphorus contents (Olsen and Sommers 1982) of a typical Alfisol and Vertisol in which pot and field experiments were conducted (ICRISAT Center).**

| Form of P | Alfisol | Vertisol |
|---|---|---|
| EC (mS $cm^{-1}$) | 0.04 | 0.11 |
| pH ($H_2O$) | 6.0 | 8.1 |
| P estimate (mg $kg^{-1}$) | | |
| Total | 122 | 153 |
| Ca-P | 3.8 | 52.8 |
| Al-P | 8.1 | 18.1 |
| Fe-P | 51.3 | 77.4 |
| Olsen | 4.1 | 0.7 |
| EDTA-Olsen | 6.0 | 18.0 |
| Bray 1 | 3.9 | 0.5 |
| Bray 2 | 6.0 | 20.2 |
| Truog | 7.6 | 48.3 |
| Ca-lactate | 2.3 | 10.8 |

## Comparative Phosphorus Response of Pigeonpea

To confirm the response of pigeonpea to fertilizer P application in comparison with sorghum response, a rainfed experiment was conducted in an Alfisol and a Vertisol field in the 1987 rainy season. Phosphorus was applied as single superphosphate. Nitrogen (N) at 120 kg N $ha^{-1}$ was applied to sorghum, but no N was applied to pigeonpea, as it formed nodules with native *Rhizobium* spp on these soils. Dry-matter production, P uptake, and grain yield of sorghum without P application were higher on the Vertisol than on the Alfisol (Fig. 1). Conversely, however, these parameters for pigeonpea were higher on the Alfisol than on the Vertisol. The response of sorghum to P application was much greater on the Alfisol than on the Vertisol, but this was not the case for pigeonpea (Fig. 1).

The greater P uptake without P fertilizer addition and the lower P response of pigeonpea compared with sorghum on the Alfisol could perhaps be explained by the deeper root penetration of pigeonpea and the consequent access to P from a greater soil volume (Arihara et al. 1991). To test this hypothesis, a pot experiment was conducted, using the same soils as in the field experiments, wherein soil volume was limited and plants were grown under controlled and otherwise nonlimiting conditions in a greenhouse. This experiment has been described by Ae et al. (1991, in this volume), and the data for shoot P content in the absence of P fertilizer are shown in their Table 3. On the Alfisol, only pigeonpea and chickpea could survive until the grain-filling stage; all other species died within a month. Pigeonpea took up more P than chickpea on the Alfisol (5.7 vs 4.7 mg $pot^{-1}$). On the Vertisol, all crops survived and grew but pigeonpea absorbed less P than the other crops. These results essentially parallel the field results and thus suggest that differences in root morphology do not account for the differences in P response between pigeonpea and sorghum.

## Utilization of Fe-P

The fact that pigeonpea performed better on the Alfisol than on the Vertisol and also better than the other three crops on the Alfisol suggests that it is better able to access the large Fe-P fraction in the Alfisol (see Table 1). To test the ability of pigeonpea to utilize Fe-P, a pot experiment was conducted to compare calcium phosphate ($CaHPO_4$), aluminum phosphate ($AlPO_4$), and iron phosphate ($FePO_4$) as P sources. A sand-vermiculite mix was used as the growth medium, and a complete nutrient solution with one of the three P sources applied. Water solubilities of the P sources were 44 mg P $kg^{-1}$ for $CaHPO_4$, 5.1 mg $kg^{-1}$ for $AlPO_4$, and 2.9 mg $kg^{-1}$ for $FePO_4$ at pH 7 in the sand-vermiculite medium.

Figure 2 shows P uptake by six crop species from these P sources, measured on plants harvested just prior to flowering. Pigeonpea could take up 2.5-7.0 times more P from $FePO_4$ than the other crops at a level of 80 mg P $kg^{-1}$. This confirms that pigeonpea can solubilize P from $FePO_4$ much better than the other crops can. Pigeonpea could take up P from $FePO_4$ and $CaHPO_4$ to the same extent, but to a lesser extent from $AlPO_4$. Sorghum and the other crop species could absorb P much better from $CaHPO_4$ than from either $AlPO_4$ or $FePO_4$ (Fig. 2). These results indicate a unique ability of pigeonpea to solubilize Fe-P. Ability to solubilize P from Al-P or Fe-P has also been claimed for other plant species, such as *Eucalyptus* spp (Mullette et al. 1974) and *Brassica napus* (Bekele et al. 1983).

As it is known that pigeonpea is strongly mycorrhizal (Manjunath and Bagyaraj 1984), it is necessary to ascertain whether vesicular-arbuscular mycorrhizal (VAM) associations contribute to the different P responses of pigeonpea and sorghum in these soils. A pot experiment was conducted using steam-sterilized Alfisol and Vertisol, with and without VAM inoculation. A mixture of five types of VAM (*Glomus constrictum*, *G. fasciculatum*, *G. epigeum*, *G. monosporum*, and *Acaulospora morrowae*), was applied to the 2.5 kg of soil in each pot. There were also P treatments of 0, 9, 22, 43, and 86 mg $kg^{-1}$.

Growth of pigeonpea was markedly stimulated by VAM on both soils with no applied P (Table 2). Sorghum growth was stimulated only on the Vertisol. On the Alfisol, sorghum failed to survive with or without VAM inoculation. This shows that VAM acts not by dissolving relatively nonavailable forms of P, such as Fe-P, but by allowing more efficient uptake of P that

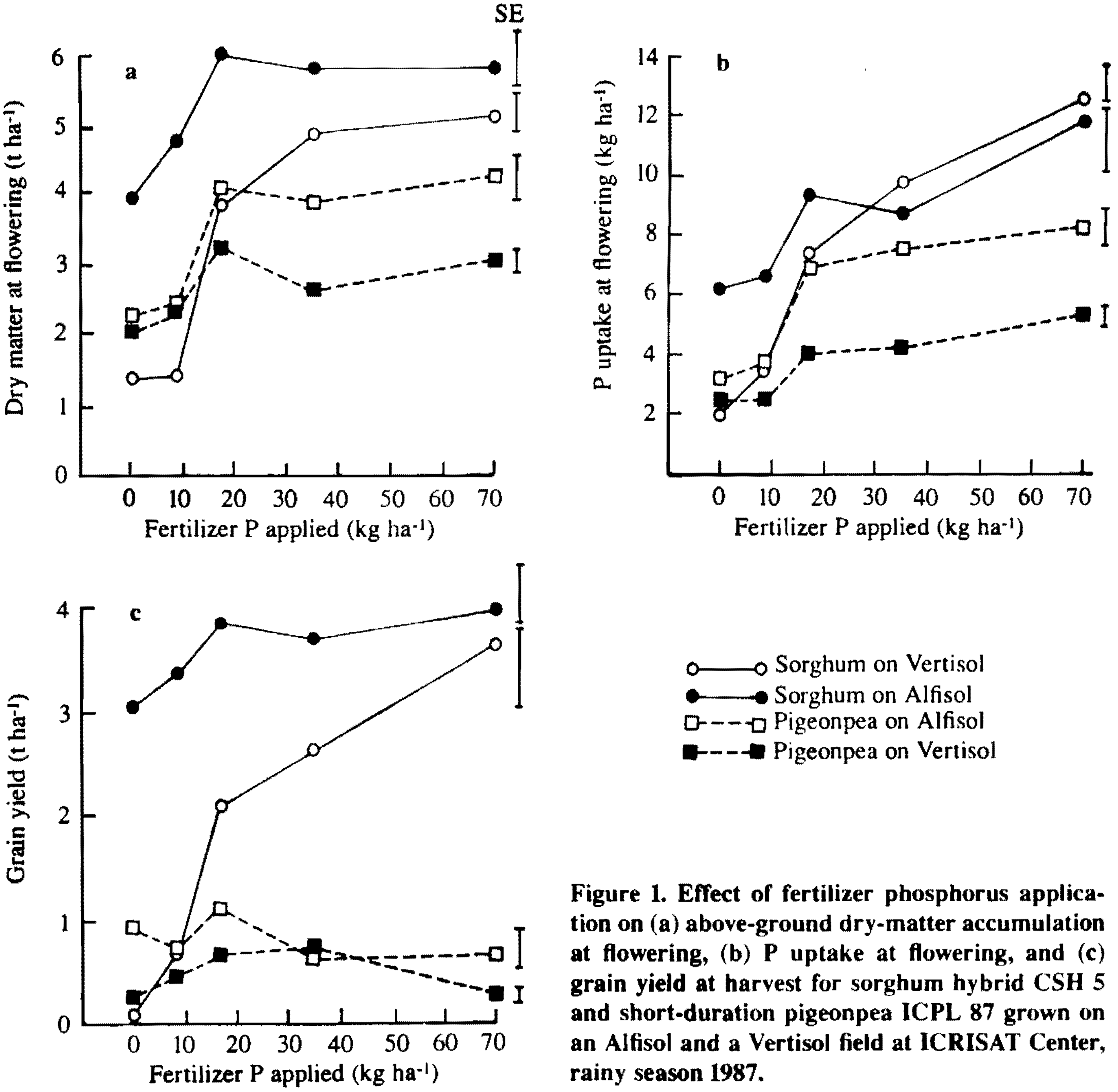


**Figure 1. Effect of fertilizer phosphorus application on (a) above-ground dry-matter accumulation at flowering, (b) P uptake at flowering, and (c) grain yield at harvest for sorghum hybrid CSH 5 and short-duration pigeonpea ICPL 87 grown on an Alfisol and a Vertisol field at ICRISAT Center, rainy season 1987.**

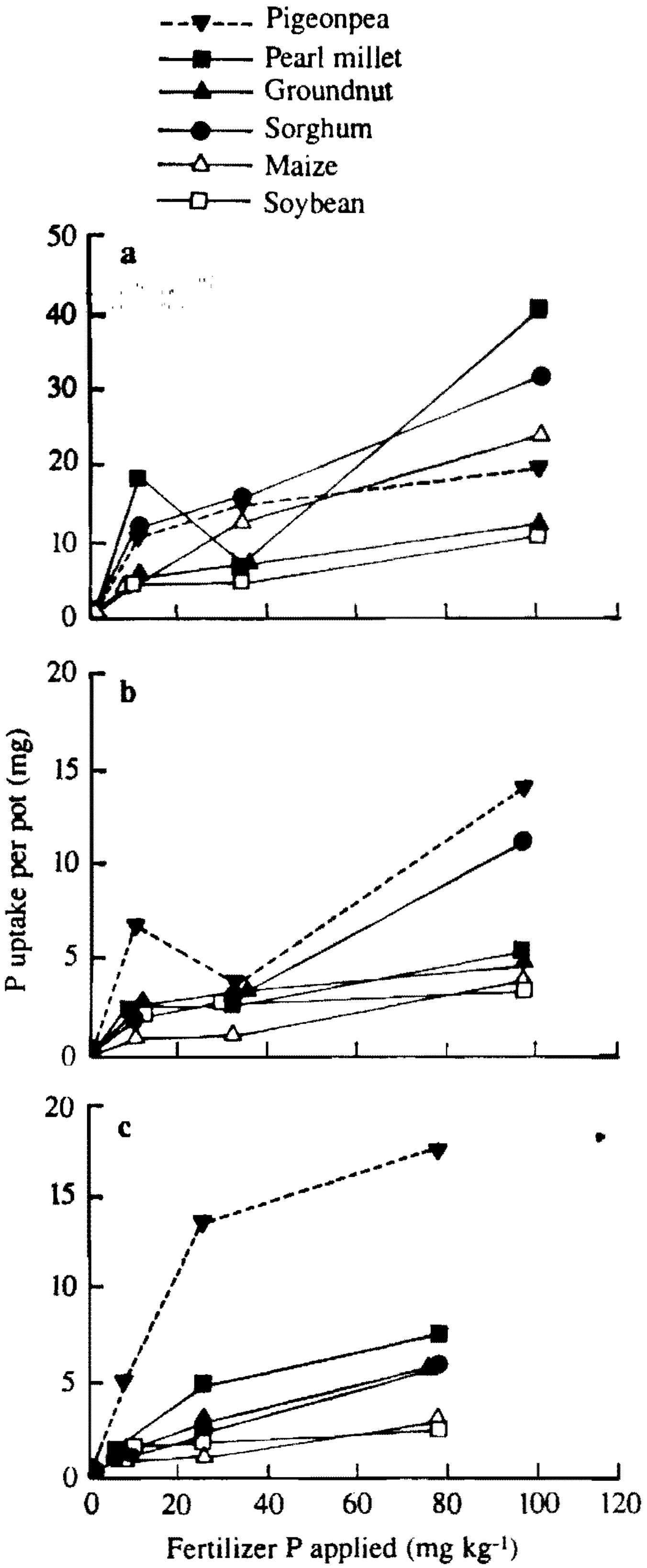


**Figure 2. Effect of different sources of applied phosphorus (a) calcium phosphate ($CaHPO_4$), (b) aluminum phosphate ($AlPO_4$), and (c) iron phosphate ($FePO_4$) on P uptake of various crops just prior to flowering in a sand-culture experiment. SE = ±2.91, for comparing means (n = 3) for each crop at the same combination of P source and P level.**

is already in a soluble form. This mode of action of VAM has been previously described (Mosse 1981). Therefore, the ability to solubilize Fe-P in Alfisols appears to be an inherent characteristic of pigeonpea.

## Root Exudates

Gardner et al. (1983) and Gardner and Boundy (1983) proposed that, for the P-uptake mechanism of lupin, citric acid exuded from the roots formed high molecular-weight complexes with Fe-P, causing P to be released on reduction of $Fe^{3+}$ to $Fe^{2+}$. We collected the root exudates of pigeonpea, sorghum, soybean, and chickpea grown in sand culture at a low P level (5 mg $kg^{-1}$) for 2 months. The major organic acids identified after gas chromatographic analysis are given in Table 6 of Ae et al. (1991, in this volume). Citric acid was a major component of root exudates of all species tested, with pigeonpea exuding much less citric acid than soybean or chickpea but more than sorghum. Pigeonpea also exuded less malonate, succinate, and malate than soybean. Thus the citric acid mechanism proposed by Gardner and coworkers would not explain the particular advantage shown by pigeonpea in solubilizing Fe-P.

Root exudates were collected from pigeonpea grown in low-P sand culture, as described above. The exudates in the 2 mM calcium chloride ($CaCl_2$) collection solution were separated into anionic (acid), cationic, and neutral fractions by ion-exchange resin chromatography. The acid fraction was twice as active as the cationic fraction in dissolving $FePO_4$ and the neutral fraction was inactive. Comparison of gas chromatograms (GC) of the acid fraction of root exudates from sorghum, soybean, and pigeonpea showed peaks at 23-24 min retention time peculiar to pigeonpea. Over various runs, the height of these peaks was inversely proportional to the height of citric acid peaks. Subsequent GC-mass spectrometer (MS) and nuclear magnetic resonance (NMR) analysis identified molecular weight and chemical structure of the compounds associated with peaks peculiar to pigeonpea (Ae et al. 1990). They were (*p*-hydroxybenzyl) tartaric acid and (*p*-methoxybenzyl) tartaric acid. The former compound is named piscidic acid and is one of the chemical constituents of hypnotic and narcotic drugs that have long been extracted from the bark of the Jamaica dogwood tree (*Piscidia erythrina* L.) (Freer and Clover 1901; Bridge et al. 1948). However, these substances have not been previously considered in relation to the P-absorption ability of roots.

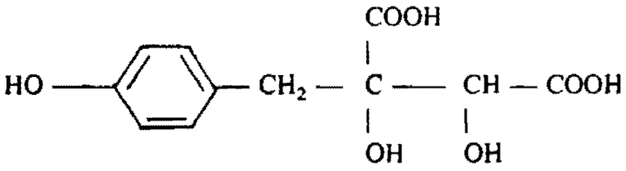
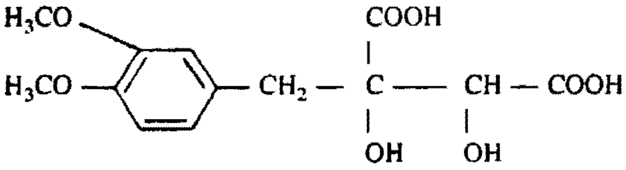
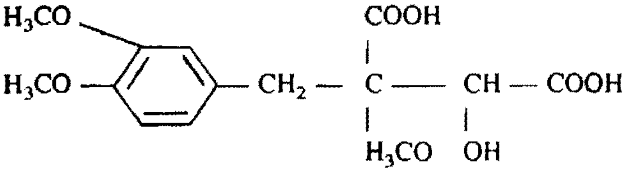
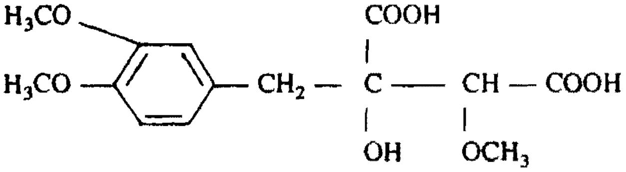
**Table 2. Effect of vesicular-arbuscular mycorrhizal (VAM) inoculation on the growth of pigeonpea and sorghum in sterilized soils without applied phosphorus. Values are means ± standard error; n = 5.**

| Crop | Soil | Dry-matter production (g pot$^{-1}$) -VAM | Dry-matter production (g pot$^{-1}$) +VAM |
|---|---|---|---|
| **Pigeonpea** | | | |
| | Vertisol | 0.36 ±0.08 (0)[1] | 13.46 ±0.23 (38.4 ±5.1) |
| | Alfisol | 0.36 ±0.08 (0) | 11.18 ±1.61 (20.2 ±2.9) |
| **Sorghum** | | | |
| | Vertisol | 0.30 ±0.05 (0) | 16.61 ±3.28 (34.9 ±6.9) |
| | Alfisol | 0.10 ±0.04 (0) | 0.09 ±0.03 (17.8 ±4.9) |

1. Values in parentheses indicate percentage of VAM-infected roots.

In order to understand the mode of action of piscidic acid in releasing P from Fe-P, we prepared piscidic acid from *Narcissus pocticus* bulbs (Bridge et al. 1948) and also synthesized some derivatives of fukiic acid (Sakamura et al.1973) which have absolute configurations similar to that of piscidic acid (Yoshihara et al. 1974). The ability of these organic acids to release P from $FePO_4$ was tested at pH 4.5, a pH to be

**Table 3. Chemical structure of piscidic acid and its derivatives and their effects on phosphorus release from ferric phosphate ($FePO_4$).**

| Chemical | Formula | Released P (µg P mL$^{-1}$)[1] |
|---|---|---|
| Control (water) | | 1.48 |
| Piscidic acid |  | 4.37 |
| Dimethyl fukiic acid |  | 4.44 |
| Trimethyl fukiic acid (a) |  | 3.27 |
| Trimethyl fukiic acid (b) |  | 3.23 |
| SE | | ±0.40 |

1. Piscidic acid and its derivatives were dissolved in 0.2 mM acetate buffer (pH 4.5) with 5.0 mg of $FePO_4$ per 1.0 mL solution. The concentration of these chemicals was adjusted to 2.5 mM. After shaking, P content in supernatant was measured.

expected in the rhizosphere (Table 3). Piscidic acid and dimethyl fukiic acid have similar P-releasing ability; the trimethyl fukiic acids have a lower P-releasing ability. These results suggest that the alcohol and carboxyl groups of the tartarate portion of piscidic acid are involved in chelation of $Fe^{3+}$, and thus in the release of P. Further studies are required to determine the actual method of P release and the amounts of piscidic acid and related compounds released at different stages of pigeonpea growth.

Despite the apparent specific effect of piscidic acid in releasing P from Fe-P, we cannot exclude the role of other organic acids in solubilizing sparingly soluble inorganic P in the soil. For example, citrate is well known for its capacity to desorb phosphate from sesquioxide surfaces by anion exchange (Parfitt 1979). Marschner (1986) proposed a combination of mechanisms involving both desorption and chelation that could explain the effect of citrate in mobilizing P from Fe-P or Al-P. The major organic acid in root exudates of chickpea, pigeonpea, soybean, and sorghum, is citric acid (Table 6 of Ae et al. 1991, in this volume). Apart from pigeonpea, only chickpea appeared able to utilize Fe-P in an Alfisol of low P availability (Table 3 of Ae et al. 1991, in this volume), as the other crop species could not survive on this soil because of the severe P deficiency. The survival of chickpea could be attributed to the ability of its roots to exude 2.5 times more citric acid than soybean roots and 25 times more than sorghum roots (Table 6 of Ae et al. 1991, in this volume).

The citric acid in root exudates of pigeonpea could therefore have a role in solubilizing P from both Fe-P and Ca-P, as described by Ae et al. (1991). It may then be expected that pigeonpea would be particularly advantaged in extracting P from Vertisols of low available P levels due to the abundance of both Fe-P and Ca-P in this soil type (Table 1) and the specific action of at least two of the components of its root exudates in mobilizing P (piscidic acid acting on Fe-P and citric acid acting on Ca-P and Fe-P). However, growth and P uptake of pigeonpea is always less on Vertisols than on Alfisols in both field (Fig. 1) and pot studies (Table 3 of Ae et al. 1991, in this volume). We attribute the general poorer growth of pigeonpea on Vertisols not so much to P limitation as to the adverse effects of lowered soil aeration (Okada et al. 1991); even in pot studies, the Vertisol maintained at field capacity restricts the growth of pigeonpea as compared with lighter-textured soils (C. Johansen, ICRISAT, personal communication).

Piscidic acid is a phenolic acid like *p*-hydroxybenzoic acid (Börner 1958), ferulic acid, and *p*-coumaric acid (Börner 1955, 1956), and these phenolic acids are considered to be toxic and contribute to "soil sickness." It would be potentially detrimental for the piscidic acid-Fe complex to remain in the rhizosphere, because of such toxicity as well as the possibility of excess Fe uptake into roots, which would result in precipitation of P in plant cells. By contrast, citric acid is not toxic, and the citrate-Fe complex is thought to be a common mode of entry of Fe into the root (Marschner 1986).

It was indeed found that chickpea, which secretes more citrate than other crop species, has a higher Fe concentration than the other species tested (Table 4). The Fe concentration in pigeonpea is the lowest of the legumes tested and is also lower than that in maize. The Fe:P ratio, which indicates the degree of exclusion of Fe in relation to P uptake, is also lowest for pigeonpea (Table 4). These results suggest that the piscidic acid-Fe complex is indeed excluded from the rhizosphere so as to allow unimpeded uptake of solubilized phosphate ions at the root surface. The proposed mechanism is illustrated in Figure 3, and is similar to Mechanism III of Marschner (1986). However, further studies are needed to confirm this hypothesis.

**Table 4. Concentrations (mean ± standard error) of phosphorus (P) and iron (Fe), and Fe:P ratio, in shoots of crop species at the grain-filling stage grown on Alfisol of low P status. Values are means for the P application rates of 0, 9, 22, 44 and 87 mg $kg^{-1}$. Same experiment as described by Ae et al. (1991) where the P-uptake data at 0 mg P $kg^{-1}$ are given in their Table 3.**

| | Concentration | | |
|---|---|---|---|
| Crop | P(%) | Fe (mg $kg^{-1}$) | Fe:P ratio |
| Chickpea | 0.28 (±0.04) | 453 (±35) | 0.190 (±0.046) |
| Pigeonpea | 0.27 (±0.03) | 259 (±15) | 0.101 (±0.014) |
| Sorghum | 0.14 (±0.02) | 168 (±17) | 0.129 (±0.016) |
| Soybean | 0.19 (±0.03) | 410 (±123) | 0.292 (±0.149) |
| Pearl millet | 0.12 ±0.03) | 167 (±23) | 0.159 (±0.031) |
| Maize | 0.13 (±0.02) | 274 (±65) | 0.235 (±0.062) |

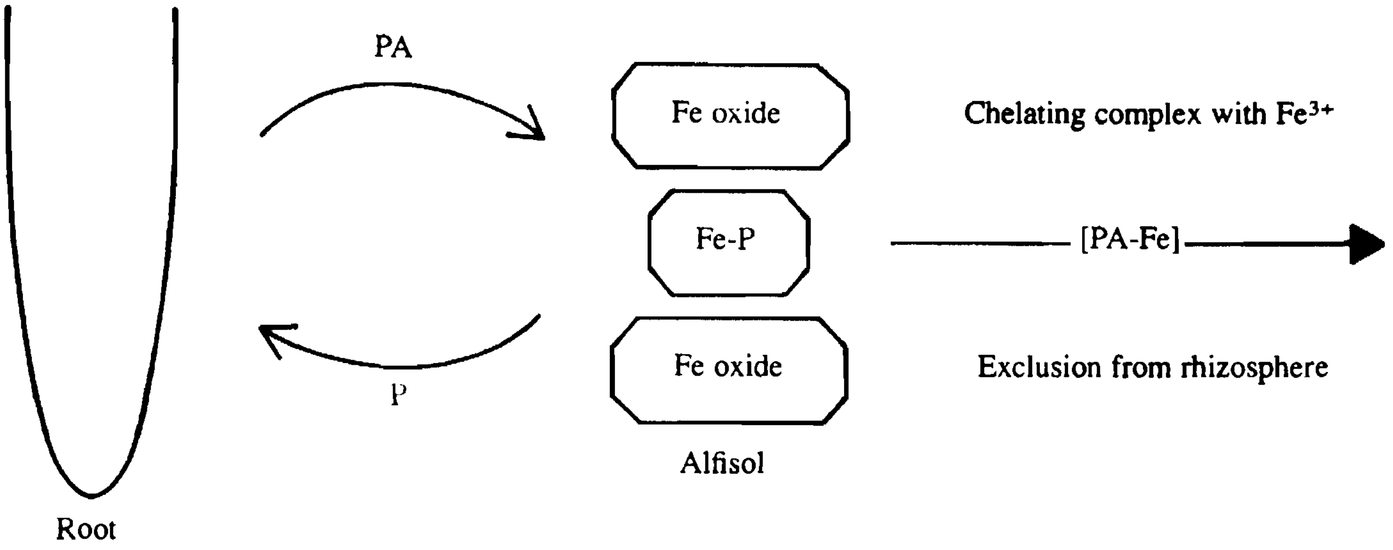


**Figure 3. Postulated P-uptake mechanism in pigeonpea involving piscidic acid (PA).**

## Conclusions

The apparent ability of pigeonpea to utilize Fe-P, which is only sparingly available to other crop species, has important implications for cropping systems under low-input agriculture in the SAT. As a first consideration, one of the reasons for the demonstrated ability of pigeonpea to grow and yield well in soils of low available P status and without P fertilizer application appears to be its ability to tap Fe-P by means of its unique root exudates. Secondly, it may be considered that growing pigeonpea would increase the available P pool of the entire cropping system. Pigeonpea can convert Fe-P into an available form of P much better than other crop species can. Consequently, succeeding crops in the rotation may access such P from the residues or former rhizosphere soil of pigeonpea. Thirdly, pigeonpea is mostly cultivated as an intercrop with companion crops such as sorghum. Thus, particularly in Alfisols, pigeonpea is less likely to compete with companion crops for scarce resources of available P, such as soil Ca-P or fertilizer P, because of its ability to utilize Fe-P which is only sparingly available to other species. Evidence for this is presented by Arihara et al. (1991, in this volume).

In view of the probable increasing cost and scarcity of soluble P fertilizers, especially for resource-poor farmers in marginal environments, a search for pigeonpea genotypes or other crop species with high efficiency of use of relatively insoluble P sources would seem worthwhile. However, a prerequisite to this endeavor would be bet'er quantification of the effects of particular root exudates under field conditions.

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# Interpretive Summary of Part 2: Extraction of Soil Phosphorus by Plant Roots

N. Claassen[1]

## Introduction

The first part of this book deals with phosphorus (P) in soil and its chemical behavior in relation to its availability to plants. This second part concentrates on plant factors, specifically, on the root and its role in P acquisition from soil.

## The System: Its Components and Functioning

The system we are concerned with consists of the root surrounded by soil. The supply of P to the root depends on soil properties such as P content, chemical form of P compounds, and the mobility of this P in soil. These properties constitute the P availability of a soil. The amount of P a plant can extract from this available P depends on its root length and on morphological and physiological properties of the root. These plant properties comprise the acquisition capacity of the plant. In the following I will describe the components of the system and its functioning, including the interaction among the components.

### The Root

In the process of P transfer from the soil to the plant, the root functions as the absorbing organ, as a sink. The root may also enhance this process by changing the chemical environment in the rhizosphere and thereby making P more available.

The properties of the root related to the absorption of P were treated in depth and detail by Clarkson and Grignon (1991). Reviewing the literature, they concluded that P uptake or transfer from the outside of the plasma membrane into the cell is facilitated by a secondary active transport system. The biochemical mechanism for this transport system is not known at the molecular level. Clarkson and Grignon have also described several properties of the transport system and how it reacts to proton concentration.

Two factors of the transport system seem of practical interest for the nutrition of crops, i.e., its very low $K_m$ (Michaelis constant) value and the regulation of its uptake capacity according to the P supply in the external solution. This is shown in Figure 1 for soybean grown in flowing nutrient solution of various P concentrations. While the $K_m$ value was similar for all treatments (1.0-1.7 μmol P $L^{-1}$) the maximum influx

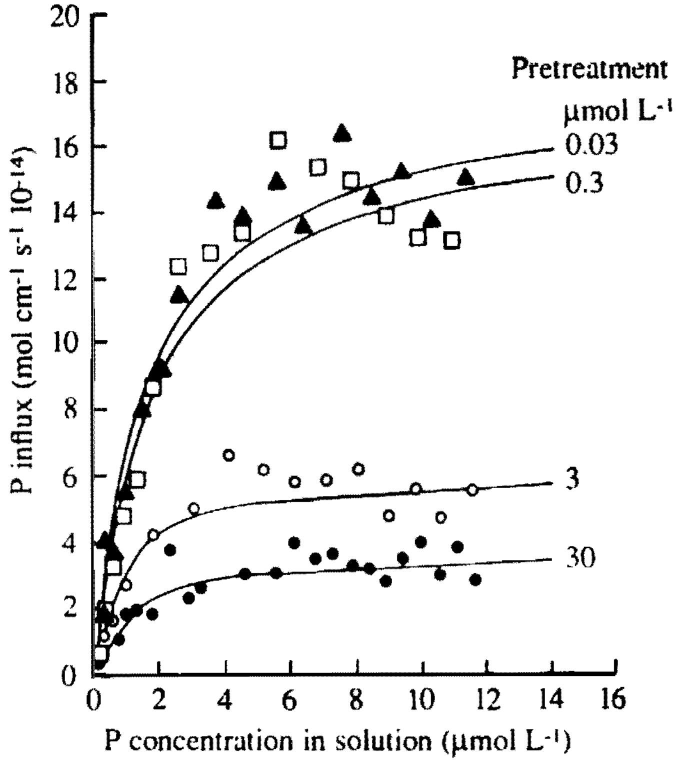

**Figure 1. Phosphorus-uptake isotherms for soybean grown in flowing nutrient solution of various P concentrations (pretreatment) (Jungk et al. 1990).**

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($I_{max}$) increased from $3.7 \times 10^{-14}$ to $17.6 \times 10^{-14}$ mol $cm^{-1}$ $s^{-1}$ when the P concentration during pretreatment was reduced from 30 to 0.03 μmol $L^{-1}$. The $K_m$ value observed in this experiment is somewhat higher than that reported by Clarkson and Grignon for the transporter itself. This is because the experiment was conducted with intact roots, where the plasma membrane is separated from the nutrient solution by the cell wall.

The increased $I_{max}$ at low external P concentration is probably due to an increased synthesis of P transporters in the plasma membrane. This is an adaptation that enables plants to obtain enough P even at very low concentrations.

The properties of the transporter described above lead Clarkson and Grignon to the very important conclusion that "this flexibility ensures that plant growth is rarely limited by the ability of roots to absorb $P_i$ (inorganic P). It is much more usual for the supply of $P_i$ to the absorbing mechanism to be limiting uptake." The P nutrition of crops will therefore mainly depend on the capacity of the soil to supply P to the root surface. This aspect will be treated later.

The root not only acts as a sink for P but may also change the chemical and biochemical environment of the rhizosphere (the soil surrounding the root). It is well known that roots change the pH of the soil, secrete reducing or chelating substances, and increase the activity of soil microorganisms. By these processes, roots affect the availability of soil nutrients.

Takagi (1991) showed the elaborate system that grasses have developed to acquire iron (Fe) from sparingly soluble compounds. With Fe deficiency, the roots of grasses enhance the release of ferric-specific ligands, called phytosiderophores, which have been identified as amino acids analogous to mugineic acid. These phytosiderophores, after being released, have the function of forming very stable Fe(III) complexes which are then carried back into root cells via a matching transport system.

Chemical mobilization of P has been postulated many times. This process may be of great significance for the P nutrition of crops, as Figure 2 illustrates. There, P uptake of sugarbeet was measured in the field, on the one hand, and calculated by a model that did not include chemical mobilization by the root, on the other. Calculations were performed with a model based on the principles discussed by Amijee et al. (1991), but which included root hairs. The difference between measured and calculated P uptake may therefore be attributed to chemical mobilization of P. As can be seen at low soil-solution concentrations of P, up to 75% of P uptake may be chemically mobilized by the roots of sugarbeet.

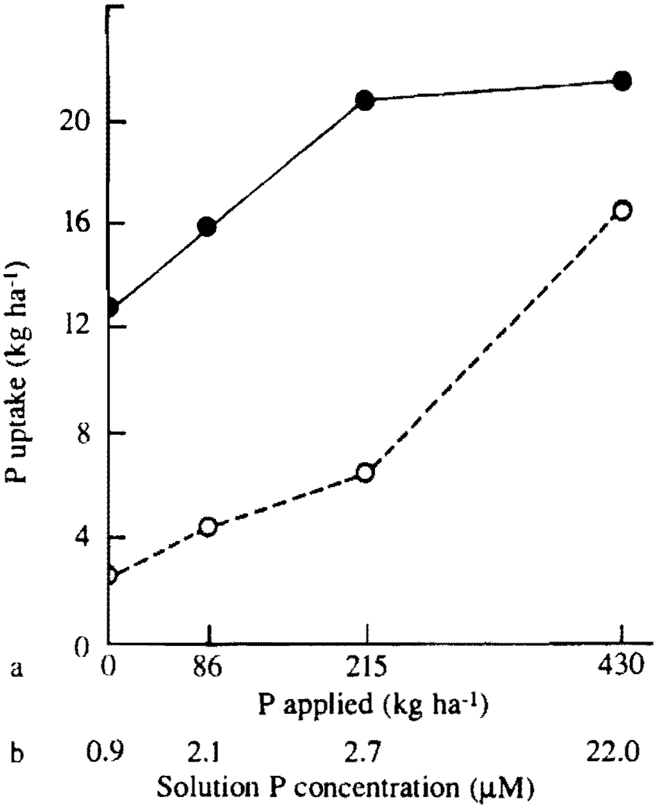

**Figure 2. Phosphate uptake by sugarbeet in July at different (a) P fertilizer rates and (b) solution concentrations. ● = measured, ○ = calculated by a simulation model including root hairs (Claassen 1990).**

The significance of P mobilization for the P nutrition of pigeonpea on an Alfisol was also shown by ICRISAT (1989). While sorghum showed almost no growth and chickpea only 50% of its maximum yield on a nonfertilized soil, pigeonpea attained full yield on the same soil. This high yield potential of pigeonpea was attributed to its capability to solubilize Fe-P, which is the main P fraction of the Alfisol used.

Several mechanisms have been proposed for P mobilization by plant roots. but the exact functioning, as shown before for Fe, is not yet known.

Phosphorus mobilization has often been attributed to root-induced pH changes in the rhizosphere, as shown in Figure 3 (Gahoonia 1987). The observed decrease of pH in the rhizosphere due to ammonium-N ($NH_4$-N) application, even so little as 10 mg N 100 $g^{-1}$ soil, is associated with a large depletion of P at the root surface. When, in another experiment, the soil was acidified artificially with $H_2SO_4$, P depletion at the root surface was also increased, but to a much smaller extent, indicating that factors other than pH also influenced P mobilization of $NH_4$-fed plants.

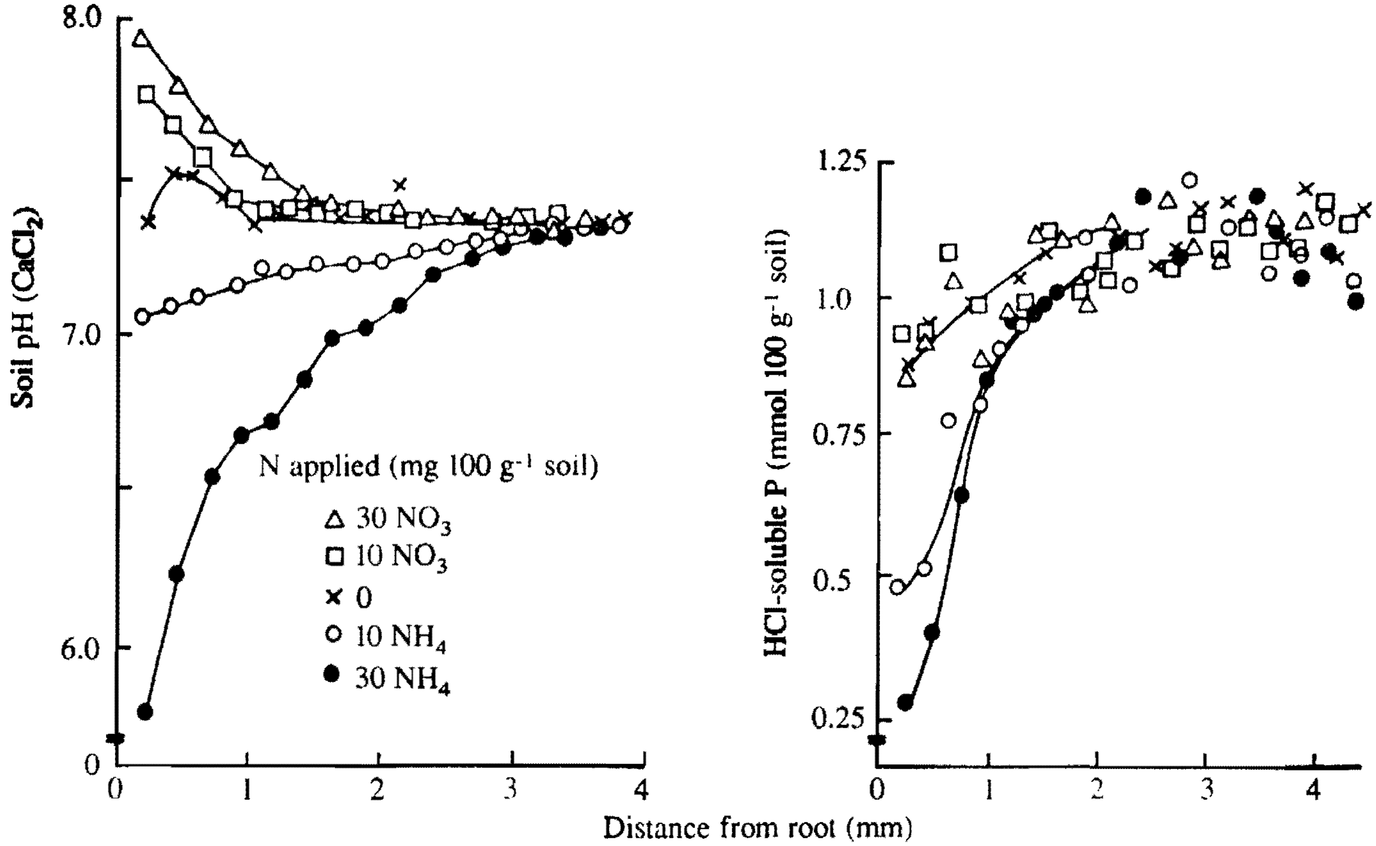

**Figure 3. Soil pH changes and P depletion in the rhizosphere of 10-day-old ryegrass as influenced by ammonium-N ($NH_4$) and nitrate-N ($NO_3$) nutrition (silt loam soil formed from loess) (Gahoonia 1987).**

These findings are in accordance with those of Gardner et al. (1983), who concluded that P mobilization of white lupin is not so much based on the decrease in rhizosphere pH as caused by the secretion of citrate. They proposed that citrate would form a polymer with Fe and P, increasing P concentration in soil solution and thereby its transport to the root.

Equally interesting are the findings of Ae et al. (1991). They found that pigeonpea grows better than sorghum, soybean, or maize on an Alfisol where P is mainly in the form of Fe-P. This difference did not show up on a Vertisol containing a much greater proportion of Ca-P. When grown in sand culture with $FePO_4$ or $CaH_2PO_4$ as a P source, pigeonpea utilized both forms of P equally efficiently, while the other species hardly grew with $FePO_4$. After a detailed and elaborate study of root exudates, Ae and his coworkers were able to identify piscidic acid as the substance responsible for the mobilization of Fe-P by pigeonpea. When piscidic acid is added to sparingly soluble $FePO_4$ it increases P solution concentration.

Research is needed to assess the mode of action of piscidic acid in the soil/root system: its release by pigeonpea roots and factors affecting it, how P solubilized by piscidic acid is utilized by the plant, whether it is released at the surface of the plasma membrane before uptake or is taken up as a complex, as was shown for Fe bound by phytosiderophores (Takagi 1991).

The P-uptake capacity of a root system depends not only on physiological properties of the root, as previously discussed, but also on morphological properties, such as root radius and root hairs, and on the length of the root system. Another distinct feature related to P uptake by crops is the symbiosis with mycorrhizal fungi, which is treated in Part 3.

The P nutrition of a crop depends on the capabilities of its root system. This obvious statement emphasizes, however, the necessity of quantifying those root properties, including the root-growth pattern, in order to be able to understand the P nutrition of a crop.

## The Soil

Clarkson and Grignon reached the conclusion that even very low P concentrations hardly limit growth, because plants adjust their uptake system to the P concentration. Therefore, soil-grown plants will show P deficiency because of an insufficient P supply to the root surface rather than because of a low concentration in soil solution itself.

The total amount of P in soils is usually large. Even those soils described by Ae et al., which were deficient in P for plant growth, contained 122 and 153 mg P $kg^{-1}$; i.e., about 400 to 600 kg P $ha^{-1}$ in the plow layer. The low availability of this P is because of the low P concentration in soil solution, which limits P transport to the root surface.

For P transport in soil, diffusion rather than mass flow is the mechanism of major significance. The flux by diffusion, F, is given by

$$F = -D\, dC/dx \tag{1}$$

where D is the diffusion coefficient in soil and dC/dx the concentration gradient (see also Amijee et al.). Since P movement in soil is only in the liquid phase, we can write

$$D = D_l\, \theta\, f_l (dC_l/dC) \tag{2}$$

where $D_l$ is the diffusion coefficient of P in water; $\theta$ is the volumetric soil water content, which determines the cross-sectional area through which P can diffuse; $f_l$ is the impedance or tortuosity factor, which, for a given soil, increases with $\theta$; $C_l$ is the P concentration in soil solution; C is the P concentration in soil participating in the diffusion process; $dC_l/dC$ is the slope of the desorption curve, its inverse being the buffer power, b.

Two important consequences follow from the fact that P only diffuses in the liquid phase. First, the concentration gradient driving the flux by diffusion is that in the soil solution; a low soil solution concentration means a small concentration gradient. The transport to the root, and thereby P uptake, can only be increased by increasing P concentration in soil solution. This, as was already seen, happens when pigeonpea secretes piscidic acid. Second, soil water content has a dominant effect on D and therefore on the transport to the root (Equations 1 and 2). This is of major significance for the semi-arid tropics, where the soil water regime may vary from waterlogging to permanent wilting point in the course of a growing season.

Other chemical aspects of P in soil that are relevant to its availability to plants were, in part, treated together with P mobilization by plants, but mainly in the papers in Part 1.

## Soil × Plant Interactions

The uptake of P by the plant is the result of the interaction of the plant with the soil. Some of these processes were treated in describing chemical mobilization of P by the plant. On the other hand, processes involved in P uptake by the root from soil solution and P transport in soil were treated separately. In reality, however, they proceed at the same time; furthermore, they influence each other.

One way to describe and study this complex system is by mathematical simulation models. To do this, the processes involved and the factors affecting them must be known, and a mathematical description of them given, as shown in Equations 1 and 2 and the Michaelis-Menten formalism for ion influx into roots (see also Amijee et al. 1991, in this volume).

Amijee et al. presented a thorough review of the models on nutrient uptake, starting with the prototypes from the 1960s. They showed the structure of the models, the assumptions and simplifications made as well as their limitations. Most models consider the root only as a sink; neither chemical mobilization through root exudates nor root hairs are normally included. In some cases, results calculated with those models agreed with observed data. In other cases, mainly at low P levels in soil, observed P uptake was higher than that calculated. This suggests that root hairs or chemical mobilization are operative. Thus it is possible to use these models to assess the significance of root hairs or P mobilization by roots.

Simulation models are also useful for assessing the significance of soil and plant parameters by means of sensitivity analysis. They show that, of the soil parameters, soil-solution P concentration is the one that most influences P uptake by a crop, followed by soil water content, $\theta$. Of the plant parameters, root length is of major importance, but the parameters of Michaelis-Menten kinetics may also be significant, especially if P uptake is by root hairs or mycorrhizal hyphae. Because of their small radius, soil-solution concentration is not much decreased at the absorbing surface of hyphae (Barber 1984; Claassen 1989).

Another soil × plant interaction is that of soil water content and P uptake. This interaction is complex. The effect of soil water on P transport in soil has already been treated. But, on the one hand, low soil water content reduces root growth (Pearson 1966) and, on the other, promotes root-hair growth (Mackay and Barber 1987) and root-exudate production (Nambiar 1976). The outcome of these opposing effects is difficult to predict. More detailed investigations are therefore required on this aspect, particularly for the semi-arid tropics, where soil water content may vary considerably during the growth period.

## Research Requirements

An aim of research at ICRISAT is to improve management practices through a better knowledge of the dynamic soil-plant system; i.e., of its components and their interactions. Knowing the way a system functions enables the formulation of management practices that will help improve the P nutrition of plants.

### Necessary Measurements and Procedures

To understand the processes and factors involved in P uptake from soil, some of the measurements should be taken repeatedly during the crop growing season:

- root and shoot development;
- P uptake and P influx into the root (mol P $cm^{-1}$ root $s^{-1}$);
- root exudates;
- root properties, such as root length, root radius, and root hairs;
- soil parameters during the growing season, such as soil water content, soil-solution P concentration, and labile P.

Furthermore, models should be used to test whether the system is understood and/or to make predictions on the behavior of the system. The models that could be used have been presented by Amijee et al., but less complex models may also have a role. For example, to test whether root competition is likely, the extension of the P-depletion zone, $\Delta r$, can be estimated by

$$\Delta r = \sqrt{2Dt} \qquad (3)$$

where D is the diffusion coefficient of P in soil and t is time of diffusion, which may be equated to time of uptake of a root segment.

### Topics of Special Interest

Some of the topics that need further investigation have already been referred to in the description of the soil-plant system. They will be restated here together with other topics.

Soil moisture is a dominant growth factor in the semi-arid tropics; therefore, research should be done on:

**Effects of soil water and sequential soil drying on P uptake in different soil types.** Important and necessary measurements should be root-length development and P influx (mol $cm^{-1}$ $s^{-1}$), among others.

**The mechanism of chemical P mobilization.** Since chemical mobilization of P by crops, especially by pigeonpea, is a vital process in P acquisition, further research is needed on the mechanism of chemical P mobilization. The utilization of soil P by plants depends on its chemical nature. For example, pigeonpea mobilizes Fe-P, which is a useful way to obtain P from an Alfisol. Vertisols have more Ca-P than Alfisols, but still have relatively large amounts of Fe-P. The extent to which this Fe-P is accessed by pigeonpea is not clear. Therefore, more research is needed on chemical characterization of soil P and relative availability of the different P components to crop species. Can other species, growing together or in sequence with pigeonpea profit from the P mobilized by pigeonpea? If so, what are the mechanisms?

**Methods of P application and its timing in a crop rotation.** Pigeonpea has been shown to utilize $FePO_4$ very efficiently. However, although iron phosphate ore reserves are relatively large (McClellan and Gremillion 1980), they have not been used as a fertilizer source. Therefore investigations are needed into the possibility of using $FePO_4$ as a P fertilizer for field-grown pigeonpea. In the same project, it should be investigated whether the P obtained by pigeonpea from $FePO_4$ and returned to the soil by crop residues is then available to other crops.

The proposed topics are by no means exhaustive and should be looked at as a part of a future research approach.

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# Part 3

# Improving the Phosphorus Nutrition of Grain Legumes in the Semi-Arid Tropics

# Possibilities for Manipulating Mycorrhizal Associations in Crops

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### *Abstract*

*Vesicular-arbuscular mycorrhizae (VAM) occur in the roots of most crops and are known to play an important role in crop growth. Legumes are quite responsive to VAM, especially in soils with low available phosphorus (P) levels. Possible approaches to manipulating VAM associations may be (1) inoculation with selected VAM fungi, (2) selection of plant genotypes that are conducive to colonization by efficient VAM fungi, and (3) establishment of a soil environment that favors increased VAM number and activity. This chapter evaluates the feasibility of each of these possible approaches, using appropriate examples from the literature and from our experience.*

*Manipulating VAM associations through inoculation is not feasible on a field scale unless pure VAM fungi can be grown in large quantities by standard microbiological techniques. There is also increasing evidence that the magnitude of VAM activity differs among plant genotypes, and numerous studies have indicated that VAM fungal status can be altered by soil management. Our experience in exploiting the VAM fungus along with the use of rock phosphate in West Africa has revealed the possibility of improving crop production in low-P soils, using rock phosphate as a P fertilizer.*

## Introduction

Vesicular-arbuscular mycorrhizae (VAM) occur in the roots of most crop species, and VAM fungi are known to be ubiquitous in agricultural soils. The VAM fungus is an important component of the rhizosphere and creates a mutually beneficial root-fungus association, which has been extensively documented in recent years (e.g., Hayman 1974; Mosse 1980). It is well established that VAM infection can markedly improve plant growth in soils where nutrient concentrations are suboptimal. Of all the nutrients, P is the one most studied in relation to VAM, because improved growth by VAM infection is most often correlated with P uptake by the plant. Thus the extent of VAM benefit is often assessed in terms of improved P uptake rather than of increased biomass production.

It would be most beneficial if VAM associations could be manipulated and utilized to increase crop production in areas where fertilizer availability is limited. Possible approaches to manipulating VAM fungi associated with annual crops may be (1) inoculation with selected VAM fungi, (2) selection of plant genotypes that preferentially favor colonization by efficient VAM fungi, and (3) establishment of soil environments more conducive to proliferation of VAM fungi in the rhizosphere and their enhanced symbiotic function.

We assess each of these approaches here by reviewing the literature and by drawing on our experience in using VAM in West Africa. The first approach is discussed at length, as inoculation with VAM fungi in the field is often considered a feasible way of manipulating the VAM-crop association. This review is

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not exhaustive; it is limited to examples that are relevant to evaluating the possible approaches to manipulating VAM associations.

## Possible Approaches to Manipulating VAM

### Inoculation with Selected VAM Fungi

Four important requirements must be met for successful VAM inoculation. The introduced VAM fungi should:

1. show a certain degree of specificity or preference for the host plant;
2. compete with the indigenous fungi;
3. outnumber indigenous VAM fungi at infection sites on roots; and
4. be more efficient than indigenous fungi in enhancing plant growth.

Each requirement will be assessed by citing relevant examples in the literature.

## Specific or Preferential Association

All mycorrhizal plant species seem to form symbioses with any of the endophyte species, unlike the *Rhizobium*-legume symbiosis, which is far more specific. However, some degree of preferential association has been reported. For example, spore production by *Glomus monosporum* was found to be higher in association with clover (*Trifolium pratense*) and grapevine (*Vitis vinifera*) than with meadow grass (*Poa pratensis*) and onion (*Allium cepa*) (Giovannetti et al. 1988). Van Nuffelen and Schenck (1984) found that certain VAM species had higher spore germination, hyphal root penetration, and root colonization on soybean than other VAM species did. Wilson (1984a) found that three VAM fungi differed in their infectivity on subterranean clover (*Trifolium subterraneum*). These findings support the view that preferential association can be used to select host-VAM fungi combinations that give the greatest VAM colonization for improving plant growth.

## Competition between Introduced and Indigenous VAM Fungi

The introduced VAM fungi must not only survive a multitude of abiotic and biotic stresses, but also compete with indigenous VAM fungi for successful establishment. As indigenous VAM fungi are better adapted to particular soils, they are more likely to be competitive than introduced VAM fungi. For example, in one study, native VAM fungi were more competitive in infecting the roots first, and more extensively colonizing them, compared with the introduced VAM fungus (Saiz and Arines 1988). On the other hand, there are some reports in which an introduced VAM fungus enhanced plant growth even in the presence of indigenous VAM fungi. Hall (1984) assessed the effects of inoculating white clover with selected strains of VAM fungi in fields containing the normal complement of indigenous VAM fungi. In all of his experiments, there were significant responses to an inoculum of *Gigaspora margarita*, *Glomus mosseae*, or *Glomus macrocarpum*, or a mixed inoculum of *Glomus pallidum* and *Glomus tenue*.

Wilson and Trinick (1983) used the term "aggressiveness" in describing the competitive abilities of VAM fungi. An aggressive fungus is one that can maintain infectivity in a mixed inoculum. There are several features of VAM fungi that enable them to compete against each other. Early spore germination and infection, high infectivity, and rapid and extensive infection will be advantageous, enabling an introduced VAM fungus to establish even in the presence of indigenous VAM fungi. Wilson (1984b) found that *Gigaspora decipiens* was more aggressive than *Glomus fasciculatum* and *G. tenue* and was able to exclude the other two fungi, but it had low infectivity. The aggressiveness of *G. decipiens* was partly attributed to it being an early colonizer.

VAM inoculation responses need not necessarily be due to the ability of introduced VAM fungi to exclude indigenous VAM fungi. Introduced and indigenous VAM fungi can also cooperate synergistically (Barea et al. 1980). Inoculation with *G. mosseae* improved plant growth, plant nutritional status, and nodulation of the legume, *Medicago sativa*, grown in nonsterilized soil. The introduced VAM fungus established well and formed mixed infections with indigenous VAM fungi in establishing the host-fungus association.

## Inoculum Density and Rate and Extent of VAM Infection

Rapid and extensive infection is an important factor in determining both the effectiveness of a VAM fungus in increasing plant growth, and its ability to compete with other fungi for infection (Wilson 1984a). Formation of primary infection points is therefore important, and their number is known to be controlled by inoculum level, more specifically, by inoculum density, that is, the number of propagules $g^{-1}$ of soil. Many inoculation trials have been conducted with unknown quantities of inoculum or inoculum concentrations based on spore number. However, the spore number alone does not determine the number of infection sites or the extent of infection. The number of propagules available for infection is more relevant to the measurement of infectivity or root colonization. Haas and Krikun (1985) investigated the relationship of root colonization with inoculum density. Root colonization by VAM fungus was correlated with inoculum density, which in turn was correlated with the height and mass parameters measured in bell pepper (*Capsicum annuum* L.) seedlings.

As inoculum density is an important parameter in assessing the quality of inoculum, it is useful to compare fungi at similar inoculum densities for selecting fungal species with high infectivity and high rates of infection development. Wilson (1984a) demonstrated that the infectivity and rate of infection development of *G. fasciculatum* were greater than those of *G. decipiens*.

## Efficiency of VAM Fungus

An introduced VAM fungus that can compete with indigenous VAM fungi and initiate infection is not necessarily successful; it should also be efficient in enhancing plant growth. This efficiency is difficult to measure, because enhanced plant growth results from the combined effects of the fungus and many processes in infected plant and in the soil. In general, the efficiency of the VAM is measured by comparing the growth of plants inoculated with various VAM species and strains.

The responsiveness to VAM inoculation differed with plant species, VAM species, and even with isolates of the same species (e.g., Clarke and Mosse 1981; Daft 1983; Van Nuffelen and Schenck 1984; Jensen 1984). In the strict sense, comparison of efficiency should be made with known inoculum density. As discussed earlier, Haas and Krikun (1985) tested isolates of *G. macrocarpum*, at known numbers of propagules, for their efficiency in enhancing plant growth of bell pepper. Efficiency varied considerably, both among *G. macrocarpum* isolates collected from different soils and among isolates collected from the same soil. From these studies, it seems evident that efficient VAM for particular host-plant species are available and that it is possible to select the most appropriate fungi for an inoculation program.

### Selection of Plant Genotypes More Responsive to Indigenous VAM

Although the extent of root colonization and responsiveness to VAM fungi are known to differ from one plant species to another, much less is known about the differences among genotypes within a plant species. Heckman and Angle (1987) examined 15 soybean cultivars for colonization by a heterogeneous field population of VAM fungi at two P levels and found that colonization varied significantly with cultivar. Addition of P to the soil reduced colonization, but there was no cultivar × P interaction. Krishna et al. (1985) found that root colonization by indigenous VAM fungi differed among 30 pearl millet genotypes. In another experiment, with two male-sterile lines, restorer lines, and their derived crosses, Krishna et al. (1985) also found that root colonization differed significantly among pearl millet genotypes, suggesting that the trait for VAM colonization is heritable.

Because genotypes within a plant species show different levels of root colonization by indigenous VAM fungi, an important consideration is whether the level of colonization can be used as a selection criterion for responsiveness of plant growth to VAM fungi. However, VAM infection is not always beneficial to the host plant; it can be parasitic under poor light and temperature conditions (Hayman 1983). Azcon and Ocampo (1981) found that variation among wheat cultivars in root colonization by *G. mosseae* was not correlated with growth response. On the contrary, Wilson (1984a) proposed that the extent of infection is an important factor in determining the effectiveness of VAM fungi in increasing plant growth. In pearl millet, total mycorrhizal root length and percentage colonization were correlated with total root length, shoot and total dry matter, and total P uptake (Krishna et al. 1985).

At present, no conclusive and clear relationship is apparent between the levels of mycorrhizal infection and plant responsiveness to VAM fungi. As Hayman

(1983) stressed, the VAM association system must be regarded as consisting of the plant, the fungal endophyte, soil components, and the interaction of all these. Therefore, variation among genotypes in VAM colonization should be considered as the combined effect of an interaction among genotype, VAM species or strain, and soil environment.

It is likely that genotypes whose roots are more colonized by VAM fungi are more subject to beneficial or parasitic effects. This suggests that it is possible to use the degree of VAM colonization or the mycorrhizal root length as an indicator of the level to which VAM associations can be manipulated.

### Agronomic Practices Influencing VAM Fungal Association

Various physical, chemical, and biological factors affect the VAM association system. Light and temperature are known to affect plant-VAM balance (Hayman 1974; Son and Smith 1988). Soil pH is also an important factor affecting VAM symbioses (Hayman and Tavares 1985; Skipper and Smith 1979). Since VAM fungi and rhizobacteria coexist in agricultural lands and both microorganisms affect plant growth, their interactions can easily be visualized (Meyer and Linderman 1986). However, light, temperature, pH, and microbiological components can be manipulated only to a limited extent in the field. On the other hand, it is much easier to alter the soil environment of agricultural land by changing (1) cropping pattern, (2) nutrient status, and (3) cultivation method.

## Cropping Pattern

Since crop species differ in their associations with VAM fungi, it is expected that cropping sequence and pattern modify VAM status in the soil. Black and Tinker (1979) measured the root colonization and spore numbers of VAM fungi with different crop rotations of barley, kale, and fallow. Kale is known to be nonmycorrhizal. Spore numbers and subsequent infections of a barley crop were the largest following barley; both kale and fallow breaks reduced spore population and infection similarly. However, Ocampo and Hayman (1981) observed the reverse; they found in pot experiments that the amount of VAM infection was not depressed in soil previously cropped with a nonmycorrhizal crop—indeed, the early establishment of VAM infection in host crops was stimulated by nonmycorrhizal crops. Harinikumar and Bagyaraj (1989) showed that cropping with groundnut resulted in higher VAM colonization, sporulation, and infective propagules in the soil than cropping with cowpea and finger millet, and these effects were carried over to the next season when sunflower was grown. They speculated that the taproot system and absence of root hairs in groundnut may be the reason for the enhanced mycorrhizal propagules in the soils cropped with groundnut. These contradictory observations cannot be conclusively explained, but a generally supported inference is that in crop rotations that include nonmycorrhizal plants or plants that develop weak VAM associations, infection may be reduced in subsequent crops.

Studies on effects of crop rotation indicate that inclusion of appropriate crop species can selectively improve soil VAM status, although it is difficult to predict which crop species are most likely to stimulate VAM development. One suggestion is that plants with coarse roots and few root hairs are more VAM-dependent, whereas plants with fine root hairs are less dependent (Mosse 1980). In general, the legumes belong to the former group. However, it should be recognized that the choice of a particular crop for a cropping system involves many factors that can influence VAM status: land preparation, fertilizer application, and time of sowing.

## Soil Nutrient Status

The extent to which VAM fungi improve plant growth depends on plant-available P status of the soil. The beneficial effect of VAM fungi is reduced or eliminated when readily available P is supplied in sufficient quantity. Because P ions have low mobility in the soil, VAM can increase P uptake in soils of moderate or low P status, as the VAM hyphae tap soluble P beyond the P-depletion zone around the root surface (Hayman 1983). Moderate rates of P fertilization do not necessarily depress VAM infection. For example, in pot experiments, two isolates of *G. clarum* showed different efficiency in increasing growth and VAM colonization of soybean, but both isolates showed the highest VAM colonization in plants supplemented with a low level of P (Louis and Lim 1988). The same response to P has been found in ladino clover infected by *Acaulospora louis* (Wilson 1988). The length of hyphae of *G. fasciculatum* was also maximum in subterranean clover fertilized with a low level of P (Abbott et al. 1984). In general, the results from field studies have shown P application to depress VAM infection, perhaps because higher P levels were applied in the field than those used in pot experiments. However, increased root infection with increasing P application has also been observed. For example, cassava roots showed increased infection by *Glomus manitrotis* with increasing P application up to 200 kg P $ha^{-1}$, although infection by other VAM fungi decreased with increasing P application (Sieverding and Howeler 1985). Clark and Mosse (1981) compared indigenous and introduced VAM fungi in their response to P application (82.6 kg P $ha^{-1}$) and found that in barley roots, added P depressed infection by indigenous VAM more than it depressed infection by the introduced VAM fungus.

The level of P fertilizer at which VAM development and activity are best enhanced depends on: the levels of P available to both plant and VAM in the soil, the host plant, the VAM species, and the soil environment. It should be noted that P levels adequate for growth of the host plant are not usually those suited for VAM development and activity. However, considering that P is essential for both the host plant and the VAM fungus, it is obvious that a certain level of available soil P should be ensured for the crop to derive maximum benefit from VAM associations.

A further question is whether sparingly soluble phosphates, such as rock phosphate, can enhance VAM growth. There are numerous reports that mycorrhizal plants can take up P from sparingly soluble phosphate more readily than nonmycorrhizal plants can (Mosse 1980). This is now attributed not to the ability of VAM fungus to dissolve relatively insoluble P but to its capacity to better scavenge the low levels of soluble P in and around rock phosphate particles. Rock phosphate might improve the residual value of applied P in the soil; in addition, it does not reduce the level of VAM infection as soluble P fertilizer does (Barea et al. 1980).

Organic manures have long been known to increase the population and the activity of microorganisms involved in soil fertility. However, information on the effect of organic manures on VAM growth is scarce. The effect of straw on VAM sporulation has been examined in relation to soil tillage (Kruckelmann 1975). Chopped straw applied before tillage over 10 years greatly increased VAM spores in shallow-plowed soil, but did not do so in soil tilled with a rotary hoe or under zero tillage. Harinikumar and Bagyaraj (1989) found that the application of farmyard manure (FYM) at 7.5 t $ha^{-1}$ significantly increased root colonization of VAM and VAM spore numbers in the second season. This effect was carried over even to the third season without further application of FYM. The application of inorganic fertilizer alone at the recommended level (for example, 160 kg N, 33 kg P, and 31 kg K $ha^{-1}$ for maize) reduced VAM infection, but fertilizer application at 50% of the recommended level together with FYM did not reduce VAM root colonization and spore numbers in comparison with the FYM alone treatment. Kruckelmann (1975) has reported that the effect of FYM on mycorrhizal status was not consistent and was influenced by soil type. In a silty clay loam soil at Rothamsted, the most VAM spores were found in the nonmanured plot, whereas in a loamy sand, fewer spores were found in the nonmanured plot. It is likely that organic manure affects VAM growth indirectly, by improving soil conditions, such as water-holding capacity, aggregate formation, and nutrient composition. However, direct effects may also be involved; for instance, *G. mossae* and *G. caledonium* were shown to survive and grow saprophytically as hyphae in organic matter (Warner 1984).

## Tillage

Soil disturbance changes physical, chemical, and biological properties of the soil, and thus affects root growth and distribution. Consequently, tillage practices may affect the root-VAM association. Excessive secondary tillage and traffic reduced the colonization of common bean (*Phaseolus vulgaris*) root by VAM (Mulligan et al. 1985). An inverse relationship was found between VAM colonization in common bean and bulk density of the clay. The suggested mechanisms are that compacted soils limit root growth and root length, and therefore reduce the frequency with which roots encounter VAM spores. The decrease in VAM colonization in compacted soils may also result from reduced soil aeration. Although lowered oxygen ($O_2$) concentration may not be the sole cause of decreased VAM infection, it greatly influences the activity of VAM fungi. Saif (1983) found that the effect of soil $O_2$ was more pronounced in mycorrhizal plants than in nonmycorrhizal plants. The VAM fungi differed in their response to different $O_2$ levels, but increasing levels of $O_2$ increased the growth of all mycorrhizal plants in the same way, with an optimum $O_2$ concentration of 16%. Saif (1983) concluded that, to derive the greatest benefits from mycorrhizal associations, it is essential to maintain soil aeration at a high level.

The effects of tillage practices on VAM infection have been also studied in relation to P absorption by plants. Evans and Miller (1988) demonstrated that disturbance of a previously zero-tilled soil reduced VAM infection to a degree such that plant P uptake was reduced. Soil disturbance significantly reduced VAM infection in and P uptake by the mycorrhizal plants maize and wheat, but did not reduce P uptake by the nonmycorrhizal plants spinach and rape. Anderson et al. (1987) also made similar observations. Plant P uptake was significantly greater under zero tillage than under conventional tillage, and VAM infection in the surface layer under zero tillage was greater than in any other layer under either zero or conventional tillage. Increased VAM infection in undisturbed soil may be due to the preservation of an intact VAM hyphal network associated with root systems of previous crops. This network can increase infection potential for subsequent crops. Also, higher root density under zero-tillage systems provides more chances for VAM infection, and the greater organic matter in undisturbed soil layers improves VAM development.

## Feasibility of Approaches to Exploiting VAM Associations

We have reviewed above the basic knowledge required to assess the potential for manipulating VAM associations in the field. We now describe our experience in this area, based on experiments conducted at the ICRISAT Sahelian Center at Sadoré, Niger, to help assess the feasibility of adopting possible technologies for field use. One type of experimentation examines whether cultural practices can alter VAM status, and another examines crop response to inoculation with selected VAM.

At Sadoré, VAM spore number was measured in a long-term experiment on the effects of crop residue (pearl millet straw) on the growth of pearl millet. The field has received annually since 1983 four treatments:

1. no treatment (control),
2. fertilizer (30 kg N, 13 kg P, and 25 kg K ha$^{-1}$),
3. straw (2 to 4 t ha$^{-1}$, depending on the previous year's biomass production), and
4. fertilizer plus straw.

The results are summarized in Table 1.

In June, when the plants were at about the three-leaf stage, more spores were found in fertilizer or straw treatments than in the control; the most spores were found in the fertilizer plus straw treatment. In October, just after harvest, spore number in the soil was higher in treatments 3 and 4. Spore number in the rhizosphere in October did not vary with treatment, but infective units of the spores were significantly increased by treatment 4.

We conducted an inoculation trial in two fields at Sadoré: an infertile field, cropped in the previous year with pearl millet and fertilized with 9 kg P ha$^{-1}$, and a virgin field not cropped for at least the past 5 years.

**Table 1. Effect of fertilizer and pearl millet crop residues on vesicular-arbuscular mycorrhizal (VAM) spore numbers, ICRISAT Sahelian Center, Sadoré, Niger, 1988.[1]**

| | Control | Fertilizer | Crop residue | Crop residue + fertilizer | SE |
|---|---|---|---|---|---|
| Grain yield (kg ha$^{-1}$) of pearl millet, 1987 | 56 | 816 | 743 | 1532 | ± 66.0 |
| Endomycorrhizal spores (no. g$^{-1}$ soil) at three-leaf stage, Jul 1988 | 4.3 | 7.3 | 7.4 | 11.7 | ± 0.39 |
| Endomycorrhizal spores (no. g$^{-1}$ soil) at harvest, Oct 1988 | | | | | |
| Bulk soil | 9.5 | 9.5 | 14.0 | 12.9 | ± 0.55 |
| Rhizosphere soil | 17.2 | 15.1 | 15.8 | 13.8 | ± 0.61 |
| | (0.5)[2] | (3.5) | (3.6) | (5.6) | (± 0.64) |

1. Fertilizer applied at 30 kg N, 13 kg P, and 25 kg K ha$^{-1}$; pearl millet straw at 2-4 t ha$^{-1}$.

2. Figures in parentheses are infective VAM units in the rhizosphere.

*Source*: M.J. Daft et al., 1989, University of Dundee, personal communication.

Each field was cropped with groundnut in 1988 under four treatments: (1) control, (2) rock phosphate (17 kg P $ha^{-1}$), (3) inoculation with *G. clarum*, and (4) rock phosphate plus *G. clarum*. Treatment 4 increased dry shoot mass and nodule number in the infertile soil, but had no effect in the virgin soil (Table 2). Overall spore numbers were generally higher in infertile soil. Spore numbers were the highest with rock phosphate plus *G. clarum* in virgin soil, but with *G. clarum* alone in infertile soil.

As discussed earlier, a potential for manipulation of VAM association through inoculation exists if host-VAM fungus features such as specificity, competitiveness, and efficiency are exploited. There are indeed reports on successful inoculation of nonsterilized soils in pots (e.g., Barea et al. 1980, Manjunath and Bagyaraj 1986) and in the field (e.g. Clarke and Mosse 1981; Hall 1984). It may be expected that inoculation responses can be obtained in carefully controlled pot and field experiments conducted by experienced scientists. However, farmers may face practical problems, particularly in selecting appropriate fungi and in using the correct inoculation techniques. It is almost impossible to select the best VAM fungus species for different soil environments by studying the literature. Until widely effective strains of VAM fungus are available, the controlled experiments, such as pot trials, are required to determine specificity, competitiveness, effectiveness, and efficiency of VAM fungus strains against indigenous VAM fungi.

Another immediate problem to be solved is the requirement for large quantities of inoculum. Since the VAM fungi are thought to be obligate symbionts on plant roots, because an artificial medium for independent growth of VAM fungus has not been identified, crops must be inoculated with VAM-infested roots or soil, or with VAM spores sieved from VAM-infested soil. Generally, annual field crops require inoculum rates of several tons per hectare, at least as VAM-infested soil. In our experiment in Niger, sieved spores mixed with local soil were used as inoculum for groundnut. However, the amount of original infested soil used in these trials was about 3 t $ha^{-1}$, as calculated by spore density in our stock culture. These inoculum rates seem impractical for wide utilization of VAM fungi on a field scale. The feasibility of VAM inoculation on a field scale thus depends

**Table 2. Effect of rock phosphate[1] and vesicular-arbuscular mycorrhizal (VAM) inoculation on growth and VAM infection of groundnut, ICRISAT Sahelian Center, Sadoré, Niger, 1988.**

| | Control | Rock phosphate | VAM | Rock phosphate + VAM | SE |
|---|---|---|---|---|---|
| Shoot dry mass (t $ha^{-1}$) | | | | | |
| Virgin soil | 1.81 | 2.13 | 1.70 | 2.34 | ±0.103 |
| Infertile soil | 0.66 | 0.92 | 0.92 | 1.03 | ±0.054 |
| Nodule no. $plant^{-1}$ | | | | | |
| Virgin soil | 190 | 278 | 199 | 295 | ±9.2 |
| Infertile soil | 87 | 87 | 104 | 156 | ±9.5 |
| Grain yield (t $ha^{-1}$) | | | | | |
| Virgin soil | 1.13 | 1.26 | 1.19 | 1.32 | ±0.350 |
| Infertile soil | 0.32 | 0.50 | 0.46 | 0.52 | ±0.372 |
| VAM infection (%) | | | | | |
| Virgin soil | 49 | 54 | 52 | 61 | ±1.2 |
| Infertile soil | 56 | 53 | 63 | 67 | ±2.9 |
| VAM spores (no. $g^{-1}$ wet soil) | | | | | |
| Virgin soil | 12.6 | 9.0 | 11.5 | 18.5 | ±0.77 |
| Infertile soil | 9.3 | 7.1 | 10.2 | 10.2 | ±0.51 |

1. Rock phosphate applied at 17 kg P $ha^{-1}$.

*Source*: M.J. Daft et al., 1989, University of Dundee, personal communication.

largely on our ability to reduce the bulk of the inoculum to a practical level or to develop a technique to grow large quantities of pure VAM.

An alternative approach is to exploit indigenous VAM fungi by managing plant or soil such that the number and activity of beneficial VAM are increased and the nonbeneficial ones are suppressed. This may be done by selecting or breeding plant genotypes that provide a rhizosphere environment more conducive to establishment and function of indigenous VAM fungi (Hubble 1987). As Hubble notes, "the rhizosphere of particular plant genotypes possesses the characteristics needed to preferentially favor rhizosphere colonization by potentially beneficial indigenous soil microbes. The requisite microbes are already there. A highly favorable environment in the form of a genetically engineered rhizosphere must be provided in order to increase their numbers and activity." The possibility of achieving this on pearl millet has been discussed earlier.

Another approach is to create a soil environment conducive to proliferation and survival of indigenous VAM fungi by using appropriate cultural practices. Soil fertility, particularly P level, affects root colonization of VAM, and soil organic matter and incorporation of crop residues improve VAM status. Rock phosphate also enhanced plant growth and VAM spore numbers, even though it was applied with introduced VAM. This suggests that rock phosphate alone can improve VAM status in soils that have indigenous VAM similar to the VAM inoculated along with rock phosphate. Zero tillage can preserve indigenous VAM. Inclusion of certain crops into a cropping system can increase VAM colonization and sporulation in the associated or following crop. It is highly likely that the influence of soil environment on VAM is mediated by the plant. Therefore, it should be possible to increase VAM function and activity by managing plants and soil simultaneously and thus to increase plant growth and yield.

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# Improving the Mycorrhizal Condition of the Soil through Cultural Practices and Effects on Growth and Phosphorus Uptake by Plants

**J.P. Thompson**[1]

## *Abstract*

*Cropping frequency in semi-arid areas is dictated by rainfall. Clean-fallowing can increase soil water and nitrate for subsequent cropping. However, populations of vesicular-arbuscular mycorrhizal (VAM) fungi decline during fallow because they obligately depend on living plant roots. Crops sown after long periods of fallow have poorly developed mycorrhizal root systems and may suffer from phosphorus (P) or zinc (Zn) deficiencies, a problem known as long-fallow disorder in Australia. Other practices that can deplete VAM populations are fires after clearing of woodlands, waterlogging from seasonal inundation, flood fallow or paddy rice, and land leveling that exposes subsoil. The degrees of P deficiency and growth retardation in a subsequent crop depend on the mycorrhizal dependency of the crop species and on the P status of the soil. Most grain legumes have high mycorrhizal dependency, e.g., 70% for pigeonpea in a Vertisol with 20 mg kg$^{-1}$ bicarbonate-extractable P.*

*Increasing crop frequency improves density of VAM propagules in the soil. Increased frequency can be achieved through "opportunity cropping" or rainy-season cropping. Grain legumes have a special place in intensified cropping systems because they do not require the inputs of nitrogen fertilizers needed by nonlegumes. Although most legume, oilseed, and grain crops build VAM populations, nonhosts such as rapeseed and lupin do not.*

*Management of fallows to reduce the death rate of VAM propagules is also possible by reduced tillage and maintenance of surface residues. Some weed growth or a green manure crop will also build VAM populations but at the expense of soil water reserves.*

## Introduction

The roots of most crop and pasture species can become colonized by naturally occurring symbiotic fungi to form vesicular-arbuscular mycorrhizae (VAM). The fungus obligately depends on living plant roots for essential organic compounds and in return increases the inflow of inorganic phosphorus (P) from the soil to the plant roots. Different crop species depend to varying degrees on adequate colonization of their roots with VAM fungi. Consequently, the inoculum density of VAM fungi in the soil when a crop is sown can be an important factor in determining the P nutritional status of that crop.

Since VAM fungi require living plant roots to complete their life cycle, fungal population densities can be influenced by cropping patterns. The frequency of cropping in the semi-arid tropics is less than in more humid environments, and the general use of P fertilizers is not as well-established as in more intensive agricultural systems. Therefore differences in crop growth attributable to differences in VAM can be quite important in the semi-arid tropics (SAT). This paper will examine important factors and

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agronomic practices that influence VAM fungal populations and are applicable to crop-production systems in the SAT.

## Anatomy of Vesicular-Arbuscular Mycorrhizae

Before considering how populations of VAM may vary, it is well to consider what VAM fungi are. Over 100 species of fungi from 6 genera can form VAM (Hall 1984). All are phycomycetous, their hyphae usually without cross-walls. They produce thick-walled resting spores, or chlamydospores, in soil, and classifications of the genera and species are based largely on spore morphology. Despite the large number of VAM fungal species, there is little host specificity, and a single fungal strain can colonize any host species from a wide range of plant families. There is more evidence of different edaphic requirements, in particular, soil pH (Mosse 1973).

The spores are about 50-500 µm in diameter, depending on the fungal species, and so are among the largest of all fungi. If a spore germinates in soil, it is capable of limited hyphal growth before it contacts a plant root. The hyphae usually form a small infection cushion or appressorium on the root surface, then penetrate the epidermis and grow between the cells within the root cortex.

Arbuscules, similar to haustoria of some pathogenic fungi, are produced in cortical cells on hyphal branches from the intercellular hyphae. A side-branch hypha penetrates the cell wall, invaginates the plasmalemma, and forms branches of successively smaller diameter to finally become less than 1 µm. Thus a structure is formed with a very large surface of intimate contact between the fungus and the living plant cell (Brown and King 1982). Typically, a cortical cell contains one arbuscule, which occupies a considerable proportion of the cell volume; e.g., about 35% in wheat (*Triticum aestivum* L.), oats (*Avena sativa* L.), and maize (*Zea mays* L.), increasing by about tenfold the surface area:volume ratio of the host protoplast (Alexander et al. 1988).

The hyphae from the cortex grow out into the soil beyond the root-hair and P-depletion zone and can take up phosphate several centimeters from the root surface (Rhodes and Gerdemann 1975). Phosphate is polymerized into polyphosphate granules and transported by cytoplasmic streaming through the fungal hyphae to the arbuscules, where exchange with the host takes place (Cooper 1984).

As the plant matures, and particularly at low P levels (Thompson 1986), vesicles form within the cortex. Vesicles are terminal swellings of the hyphae, spherical or ellipsoidal in shape and similar in size to extraradical spores. Vesicles probably function as storage organs, as they contain lipid droplets and may prolong the viability of the fungus in the root as the latter senesces. Chlamydospores are produced on the external hyphae in the soil as the mycorrhiza matures. Spore production is possibly stimulated by physiological changes in the host plant as an annual crop matures or the tops of a mature perennial plant are pruned (Ferguson and Woodhead 1982).

## Host Range

Although about 85% of plant species are hosts for VAM, some families have a very low proportion of mycorrhizal species. Newman and Reddell (1987) gave the percentage of mycorrhizal species among families with agriculturally important crops as: Leguminosae, 90; Compositae, 85; Gramineae, 84; Polygonaceae, 40; Chenopodiaceae, 26; and Cruciferae, 8%. Among agriculturally important cruciferous crops that are nonmycorrhizal are rapeseed (*Brassica napus* L. var. *napus*) (Hirrel et al. 1978) and mustard (*Sinapsis alba* L.) (Fitter and Nichols 1988). The Leguminosae have a high percentage of mycorrhizal species, with lupin (*Lupinus* spp) a notable exception (Trinick 1977). Roots of both rapeseed and lupin contain fungitoxic chemicals that may prevent colonization (Morley and Mosse 1976; Hirrel et al. 1978; Trappe 1987).

Although most crop species can form VAM, they become colonized at varying rates and attain varying levels of root colonization. Thompson and Wildermuth (1989) assessed 37 crop and pasture species in a Vertisol from a wheat field that contained 10 VAM spores $g^{-1}$ soil. The plants were tested as two groups, for predominantly winter-growing and summer-growing species. The percentage of the root length with VAM colonization at flowering of each plant species is given in Table 1. Many of the legumes, including chickpea, had high percent colonization, whereas many of the gramineous species had lower percent colonization. However, some of the species with lower percent colonization had a greater mass of VAM-colonized root than some species with higher percent colonization. The nonhost status of rapeseed and lupin was confirmed.

**Table 1. Host status of summer and winter crop and pasture species for vesicular-arbuscular mycorrhizal (VAM) fungi (Thompson and Wildermuth 1989).**

| Crop | Percent root length with VAM | Crop | Percent root length with VAM |
|---|---|---|---|
| **Summer species** | | | |
| Mung bean | 98.4 | Maize | 45.2 |
| Cluster bean | 84.5 | Lucerne | 31.3 |
| Lablab bean | 75.6 | Wheat | 26.3 |
| Soybean | 64.5 | Buffell grass | 24.1 |
| Cowpea | 61.4 | Green panic | 19.4 |
| Sorghum | 61.3 | White panicum | 18.4 |
| Canary seed | 52.6 | White French millet | 16.7 |
| Sunflower | 49.6 | Rhodes grass | 5.6 |
| Sudan grass | 48.8 | | |
| **Winter species** | | | |
| Wheat | 60.5 | Phalaris grass | 38.9 |
| Chickpea | 59.3 | Linseed | 38.7 |
| Safflower | 59.3 | Woolly-pod vetch | 36.2 |
| Yellow serradella | 58.8 | Snail medic | 35.4 |
| Triticale | 54.7 | Cocksfoot | 32.2 |
| Field pea | 53.3 | Italian ryegrass | 23.1 |
| Canary seed | 47.2 | Lucerne | 18.8 |
| Subterranean clover | 46.9 | Fescue | 6.0 |
| Barley | 45.6 | Perennial ryegrass | 0 |
| Barrel medic | 41.8 | Lupin | 0 |
| Rye | 41.3 | Rapeseed | 0 |
| Oats | 41.1 | | |

## Mycorrhizal Dependency

There is considerable variation in benefits derived by host species from VAM. Some hosts seem almost obligately dependent on VAM for P nutrition and growth, while others seem to derive no benefit except perhaps in the most impoverished soils. In the middle ground are hosts that benefit to varying extents, depending on the P status of the soil. Gerdemann (1975) defined mycorrhizal dependency as "the degree to which a host relies on the mycorrhizal condition to produce maximum growth at a given level of soil fertility." Baylis (1975) drew attention to the relation between root morphology and VAM dependency. Plants with many fine roots and an abundance of long root hairs, typified by ryegrass and termed graminoid by Baylis, can effectively exploit the soil for P without the aid of VAM. At the other extreme are plant species with poorly developed root systems, with thick roots lacking root hairs, typified by *Magnolia*, and termed magnolioid by Baylis. In the middle range are many plant species that benefit to varying degrees, depending on the P status of the soil.

Attempts have been made to quantify mycorrhizal dependency. Menge et al. (1978) calculated a mycorrhizal dependency index as the dry mass of the mycorrhizal plants expressed as a percentage of that of the nonmycorrhizal plants. Plenchette et al. (1983) proposed another index, with values constrained below 100%, termed "relative field mycorrhizal dependency (RFMD)," calculated as:

$$\text{RFMD} = 100 \times (\text{mass of mycorrhizal plant} - \text{mass of nonmycorrhizal plant}) / (\text{mass of mycorrhizal plant})$$

Table 2 shows some results for RFMD that Plenchette et al. (1983) determined by comparing nonmycorrhizal plants in fumigated soil with mycorrhizal plants in unfumigated soil containing 100 mg P $\text{kg}^{-1}$ soil.

**Table 2. Relative field mycorrhizal dependency (RFMD) indexes for some plant species grown in fumigated and nonfumigated soil containing 100 mg P kg$^{-1}$ (after Plenchette et al. 1983).**

| Group | Plant species | Dry mass (g plant$^{-1}$) Fumigated soil | Dry mass (g plant$^{-1}$) Nonfumigated soil | VAM index (%) | RFMD (%) |
|---|---|---|---|---|---|
| I | Carrot | 0.07 | 9.2 | 66 | 99.2 |
| | Garden pea | 1.3 | 40.3 | 89 | 96.7 |
| | Leek | 0.5 | 11.9 | 58 | 95.7 |
| | Kidney bean | 0.7 | 13.3 | 88 | 94.7 |
| | Faba bean | 1.4 | 21.8 | 62 | 93.5 |
| | Sweet corn | 45.5 | 166.5 | 69 | 72.7 |
| | Pepper | 4.1 | 12.1 | 42 | 66.1 |
| | Tomato | 71.2 | 174.6 | 50 | 59.2 |
| | Potato | 107.5 | 185.3 | 44 | 41.9 |
| II | Oats | 208.9 | 170.9 | 79 | 0 |
| | Wheat | 155.5 | 155.6 | 55 | 0 |
| III | Cabbage | 175.6 | 93.3 | 0 | - |
| | Garden beet | 27.1 | 5.6 | 0 | - |

These results illustrate the high mycorrhizal dependency of many legumes, which have coarser and more restricted root systems than many gramineous species (Munns and Mosse 1980).

## Response of Legumes to VAM

Pioneering work by Asai (1944) indicated that nodulation of several legumes by rhizobia depended on their roots being mycorrhizal. There has been much interest in this dual symbiosis of legumes with rhizobia in nitrogen ($N_2$) fixation and with VAM in P uptake, in interactions in plant response, and in possible direct effects, between the two microsymbionts. There have been several reviews on VAM and legumes (Munns and Mosse 1980; Barea and Azcon-Aguilar 1983; Subba Rao and Krishna 1984).

Symbiotic $N_2$-fixation increases plant demand for P, and the most common nutritional disorders in legumes are related to P deficiency (Munns and Mosse 1980). Nodular tissue in legumes may contain up to five times the concentration of P in other plant tissues (Subba Rao and Krishna 1984), and nitrogenase activity has a high P demand, with about 21 mol ATP converted to ADP per mol $N_2$ reduced (Barea and Azcon-Aguilar 1983). Thus VAM improve not only the P nutrition of the legume but also that of the rhizobial bacterioids and the efficiency of $N_2$-fixation. The effects of VAM on $N_2$-fixation and growth of legumes result largely from improved P nutrition (Abbott and Robson 1984), although other mechanisms have been considered. Smith et al. (1979) found the earliest effects of VAM in subterranean clover were to increase root P concentration, nodulation, and nitrogenase activity, these events preceding any increase in P concentration and growth of the tops or of P concentration in nodules. Smith et al. concluded that an increased, steady supply of P from the roots to adjacent developing nodular tissue was the primary benefit from VAM.

Chickpea and pigeonpea response to VAM seems similar to what has been found with other legumes. The effects of dual inoculation with VAM fungi and *Rhizobium* on the P nutrition, $N_2$-fixation and yield of chickpea are illustrated by the results of Subba Rao et al. (1986) shown in Table 3. In a nonsterilized sandy loam soil, inoculation with *Glomus fasciculatum* improved P nutrition, particularly in the presence of 22 kg P ha$^{-1}$ as superphosphate, and increased the nodulation and $N_2$-fixation by native and inoculated strains of rhizobia.

Manjunath and Bagyaraj (1984) studied the response of pigeonpea to factorial combinations of inoculation with *Glomus fasciculatum* and *Rhizobium* and application of P fertilizer (22 kg P ha$^{-1}$) in pots of nonsterilized sandy loam soil of pH 5.6. VAM inoculation substantially increased dry mass of tops and

**Table 3. Effect of vesicular-arbuscular mycorrhizae (VAM) and *Rhizobium* on chickpea in pots of nonsterilized soil supplied with 22 kg P $ha^{-1}$ (Subba Rao et al. 1986). Values are per pot of 4 plants.**

| Inoculation treatment | Nodules | | Shoot mass (g) | Nutrient concentration (g $kg^{-1}$) | | Yield (g) | | Fixed $N_2$ (mg)[1] | |
|---|---|---|---|---|---|---|---|---|---|
| | No. | Mass (g) | | N | P | Grain | Straw | Grain | Straw |
| Nil | 71 | 0.24 | 3.2 | 30 | 2.0 | 6.3 | 8.1 | 119 | 54 |
| VAM | 82 | 0.41 | 3.5 | 30 | 3.5 | 6.2 | 10.1 | 147 | 70 |
| *Rhizobium* | 83 | 0.38 | 3.4 | 33 | 3.3 | 8.0 | 10.9 | 170 | 75 |
| *Rhizobium* + VAM | 89 | 0.47 | 4.9 | 33 | 4.4 | 9.3 | 11.5 | 184 | 87 |
| SE | ±1 | ±0.02 | ±0.1 | ±1.4 | ±0.2 | ±0.4 | ±1.0 | ±5 | ±6 |

1. Fixed $N_2$ determined by isotope dilution with addition of 20 kg N $ha^{-1}$ as$NH_4$-N.

their content of P and N (Table 4). Best responses in all three parameters were obtained from the combination of VAM inoculation, P application, and *Rhizobium* inoculation. Wellings et al. (In press.) assessed growth of pigeonpea in a steam-sterilized Vertisol containing 20 mg $kg^{-1}$ bicarbonate-extractable P (Colwell method) and more than 100 mg $kg^{-1}$ acid-extractable P. Inoculation with the VAM fungus *Glomus mosseae* substantially improved the P nutrition and growth and, to a lesser degree, the zinc (Zn) nutrition, of pigeonpea (Table 5).

## Effect of VAM on Phosphorus Response Curves

Abbott and Robson (1984) strongly recommended comparing mycorrhizal and nonmycorrhizal plants over a range of applied P rates so that full response curves could be obtained. This has the advantage of allowing two comparisons between mycorrhizal and nonmycorrhizal plants, that is, a vertical comparison of the yield increase at any given P level and a horizontal comparison of the savings in applied P to achieve a particular yield. Also, establishing the complete response curve permits assessment of whether other plant responses are direct results of VAM colonization or mediated via improved P nutrition. Abbott and Robson fitted Mitscherlich equations to both mycorrhizal and nonmycorrhizal treatments of the form $Y = A - Be^{-cx}$, where Y is dry mass of shoots at any particular rate of P(x), A is maximum dry mass under the experimental conditions, B is a constant for a particular soil-plant combination reflecting the responsiveness of the soil, and c is the curvature or Mitscherlich constant. Comparison of these parame-

**Table 4. Response of pigeonpea at 50 days after sowing to phosphorus (P) and dual inoculation with vesicular-arbuscular mycorrhizae (VAM) and *Rhizobium* (Manjunath and Bagyaraj 1984).**

| Treatment | | | Shoot dry mass (g $plant^{-1}$) | Nutrient content of shoots (mg $plant^{-1}$) | |
|---|---|---|---|---|---|
| P (kg $ha^{-1}$) | VAM | *Rhizobium* | | N | P |
| 0 | 0 | 0 | 1.7 | 49.9 | 3.3 |
| 0 | 0 | + | 1.9 | 54.1 | 3.3 |
| 0 | + | 0 | 3.9 | 119.9 | 4.5 |
| 0 | + | + | 4.9 | 131.6 | 6.9 |
| 22 | 0 | 0 | 4.5 | 87.6 | 8.9 |
| 22 | 0 | + | 5.2 | 168.9 | 11.0 |
| 22 | + | 0 | 5.6 | 169.2 | 12.5 |
| 22 | + | + | 6.6 | 200.4 | 14.5 |
| SE | | | ±0.7 | ±19.6 | ±1.3 |

**Table 5. Response of pigeonpea to vesicular-arbuscular mycorrhizal (VAM) inoculation in a sterilized Vertisol (Wellings et al., in press).**

| Treatment | Root length with VAM (%) | Dry mass (g plant$^{-1}$) |  | Nutrient concentration (g kg$^{-1}$) |  |  |  |
|---|---|---|---|---|---|---|---|
|  |  | Shoot | Root | P | Zn | N | P/Zn |
| Nil | 0[1] (0) | 0.34 | 0.34 | 0.5 | 0.013 | 34 | 38 |
| +VAM | 36.6[1] (35.6) | 1.11 | 0.62 | 1.6 | 0.017 | 25 | 100 |
| SE | ±1.9 | ±0.05 | ±0.03 | ±0.05 | ±0.0006 | ±0.8 | ± 4 |

[1] Arcsin √% transformation with equivalent mean in parentheses.

ters of the curves for nonmycorrhizal and mycorrhizal plants is the most complete way to assess the value of VAM with respect to P.

Bolan and Robson (1983) found that subterranean clover (*Trifolium subterraneum* L.), when grown in a lateritic subsoil without VAM, did not respond to superphosphate below a threshold value of about 70 mg P kg$^{-1}$ soil, giving a sigmoidal rather than a Mitscherlich response curve. In contrast, mycorrhizal clover or ryegrass, irrespective of VAM colonization, responded to all rates of P from about 10 to 150 mg P kg$^{-1}$ soil in a normal Mitscherlich-type response. The sigmoidal response of nonmycorrhizal clover could be induced in surface soil by increasing its P sorption by the addition of iron hydroxide. Inoculation with the VAM fungus, *Glomus fasciculatum*, eliminated the threshold at all rates of iron hydroxide additions.

The sigmoidal response curve is therefore a phenomenon of a mycorrhiza-dependent plant species growing without VAM in a soil of high P-sorption capacity. A similar sigmoidal response curve was obtained by Bell et al. (1989) when groundnut (*Arachis hypogaea* L.) was grown without VAM in an Oxisol, a ferruginous red soil of high P-sorption capacity. Here a threshold of about 60 kg P ha$^{-1}$ was indicated (Fig. 1). These are extremely important effects to rec-

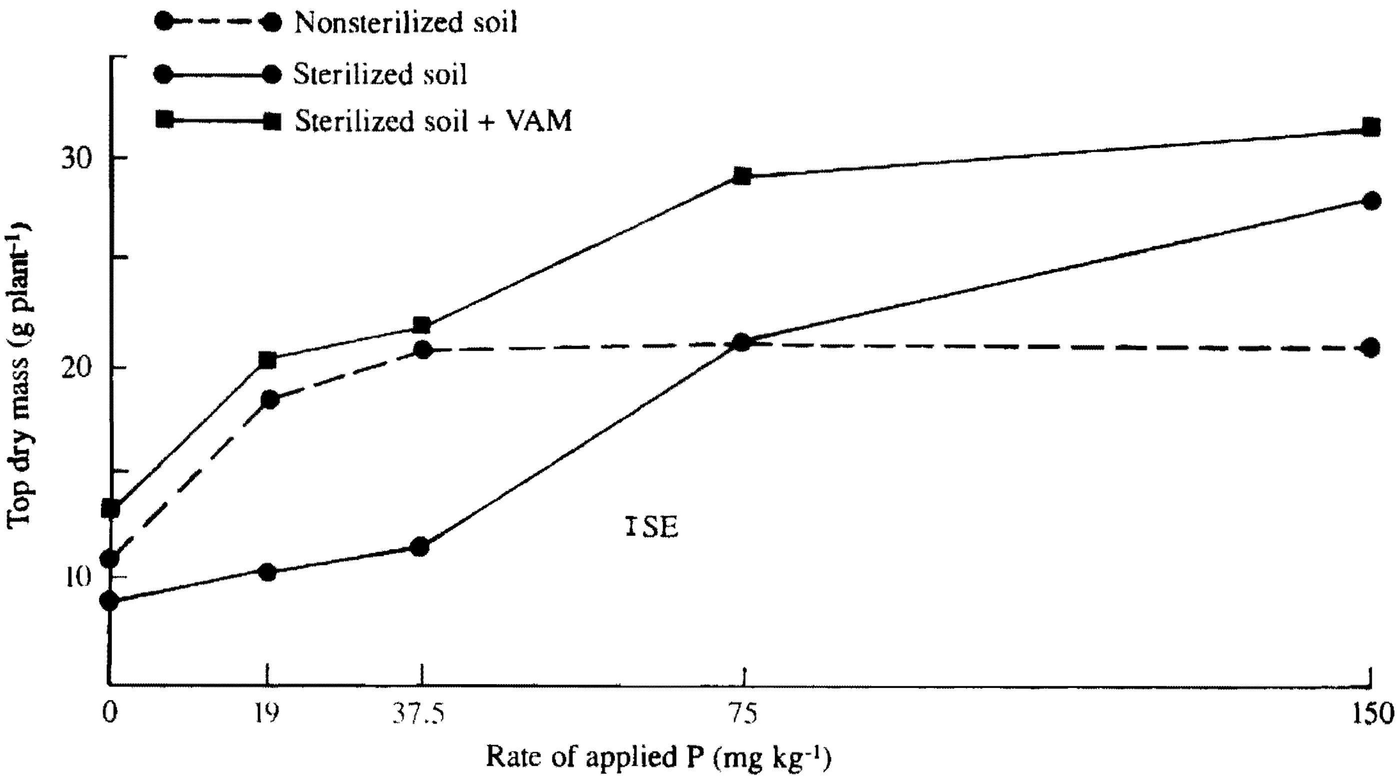

**Figure 1. Effect of vesicular-arbuscular mycorrhizae (VAM) on response of groundnut to rate of P fertilizer in an Oxisol. (From Bell et al. 1989.)**

ognize, for where VAM have been severely depleted in high P-fixing soils, it is possible to misdiagnose an acute P deficiency by a lack of response to P fertilizer applied at normal rates. Normal rates of P derived from calibrations for crops with the normal VAM may be grossly inadequate for crops with very poor VAM.

The work of Yost and Fox (1979) clearly showed the value of VAM to a number of highly mycorrhiza-dependent crops growing in a soil with large amounts of sorbed P of low availability. They established, by prior fertilization of an Oxisol, a range of soil-solution concentrations from 0.003 to 1.6 mg P L$^{-1}$ and grew a number of crops in fumigated (nonmycorrhizal) and unfumigated (mycorrhizal) treatments. The levels of soil P at which fumigation ceased to make a difference in plant P concentration of different species were: soybean 0.1, cowpea 0.2, onion 0.8, *Leucaena leucocephala* 1.6, *Stylosanthes hamata* 1.6, and cassava more than 1.6 mg P L$^{-1}$.

Bolan et al. (1984) showed that mycorrhizal roots of subterranean clover and extractants of sodium bicarbonate ($NaHCO_3$) and calcium chloride ($CaCl_2$) accessed sorbed P, but nonmycorrhizal clover roots did not. Because $^{32}P$ added to soil exchanged with P already sorbed on iron hydroxide, there was no difference in specific activity between mycorrhizal and nonmycorrhizal plants. These authors therefore considered that the lack of difference in specific activity obtained in several previous studies does not eliminate the possibility that mycorrhizal plants can obtain forms of P that are unavailable to nonmycorrhizal plants.

The fact that the mycorrhizal condition of the soil can strongly influence the P nutrition of mycorrhiza-dependent plant species raises the question of whether the VAM status could be used to predict fertilizer P requirements. The work of Stribley et al. (1980) with leeks in a greenhouse experiment showed that correlation between growth and bicarbonate-extractable P was clearly improved with control over VAM status. Unfortunately, work to assess the value of quantitatively determining VAM status for prediction of P requirements has not been extended to the field.

Another aspect of mycorrhizal studies in relation to nutrition arises where nonmycorrhizal plants suffer not only from P deficiency but also from Zn deficiency. This has arisen in crops grown on Australian Vertisols. Examples of the synergistic response in linseed are given in Table 6. The nonmycorrhizal plants do not respond to either element applied alone but respond synergistically to the combination of P and Zn. In contrast, the mycorrhizal plants are capable of near-maximum growth without application of either element. Extending the concept of rate response to this interactive situation between P, Zn, and VAM inoculum density requires large factorial experiments.

**Table 6. Effects of vesicular-arbuscular mycorrhizae (VAM), and Zn and P fertilizers on whole-plant and seed yield of linseed (g pot$^{-1}$ of 4 plants) (J.P. Thompson, unpublished data).**

| Soil sterilization | VAM inoculation | Fertilizer application | | | |
|---|---|---|---|---|---|
| | | Nil | Zn | P | P+Zn |
| Whole plant mass | | | | | |
| - | - | 17.9 | 23.0 | 13.9 | 25.6 |
| + | - | 0.8 | 2.1 | 1.5 | 25.4 |
| + | + | 25.5 | 32.3 | 24.5 | 32.3 |
| SE | | | ±1.1 | | |
| Seed yield | | | | | |
| - | - | 5.7 | 8.5 | 5.1 | 10.0 |
| + | - | 0.1 | 0.3 | 0.1 | 8.0 |
| + | + | 9.5 | 12.7 | 8.1 | 11.2 |
| SE | | | ±0.5 | | |

## Factors Affecting VAM Colonization

### Fallowing

Since VAM fungi obligately depend on living plant roots for continued growth and multiplication, it follows that clean fallowing with thorough weed control will reduce VAM propagule density in the soil. Evidence for this was initially obtained from England. Salt (1977) found that VAM colonization of wheat was poorer after fallow than after faba bean (*Vicia faba*). Black and Tinker (1977) found that the number of VAM spores and subsequent colonization of a barley crop were lower after fallow than after barley. VAM spore number mL$^{-1}$ soil solution fell from 29 to 18 after 1 year of fallow and then to 4 after 2 years.

Inoculation with VAM was used to demonstrate plant growth responses to VAM in fallow fields. Potatoes grown after fallow yielded 20% more when inoculated with soil from a barley field containing a greater density of VAM spores (Black and Tinker 1977). Inoculation with VAM from pot cultures increased the growth of onions, lucerne, and barley in a long fallow field (Owusu-Bennoah and Mosse 1979).

Although these results demonstrate the effect of fallow on VAM, fallow duration is usually short in England and fertilizer inputs are high. However, where fertilizer use is minimal, as on Vertisols of the eastern grain belt of Australia, a crop problem known as long-fallow disorder has been recognized since the 1940s (Hart 1962). Recently, Thompson (1987) showed that this resulted from depleted VAM propagules and poor colonization of crops after fallowing.

Long fallows in this environment arise in various ways. Temperatures allow cropping at any time of the year, but the rainfall quantity (500-900 mm) and variablity allow an average of only one crop per year. Winter crops are grown from May to November and summer crops from October to March. Sequences of winter crops or summer crops are interspersed by a 6-month fallow period, which is termed normal or short fallow. Switching between summer and winter crop sequences can result in long fallows of 11-14 months. If rainfall permits, sequences can be switched by double-cropping, resulting in little (<2 months) to no fallow period. Double-cropping in response to rainfall rather than in a planned rotation is termed opportunity cropping. Longer fallows of 18 months occur if a crop is missed in a winter or summer sequence through failure of planting rains, and even longer fallows can occasionally occur through successive failures.

Better crop growth is usually expected after weed-free fallowing from increased soil water and nitrate and from reduction in weeds and pathogens. However, a significant proportion of crops grow worse after long fallows than after normal fallows or double crops. This long-fallow disorder affects a wide range of crop species to various degrees, with linseed being one of the most sensitive crops (Hart 1962). Crops following long fallow can be considerably improved by P and Zn fertilizers (Leslie 1969). Thompson (1987) sampled paired plantings of crops from Queensland farms, one crop on long fallow exhibiting the disorder, with poor growth and symptoms of P or Zn deficiency, and the other on short fallow, with better growth and no symptoms. Invariably, the plants following long fallow had lower percent colonization of the roots with VAM fungi and up to 80% reduction in midseason top growth. Some examples for the winter crops chickpea and wheat and the summer crop sorghum are given in Table 7. Similar results and field observations indicate that the problem affects other crops, including linseed, barley, sunflower, soybean, navybean, and pigeonpea. Differences in VAM colonization were sometimes less apparent in older crops, because the percent VAM colonization increases with time, giving some alleviation of the disorder.

In replicated field trials, the effects of fallow duration and intensity of prior cropping with a number of winter and summer crops on the density of VAM spores in the soil and on subsequent VAM colonization and growth of linseed have been investigated (J.P Thompson, unpublished data). Figure 2 shows the increase in VAM spore population when sorghum is grown in fallow soil and the distribution of spores in a Vertisol profile; VAM spores are most concentrated in the topsoil and their number diminishes with depth. The difference between cropped and fallow soil is greatest in the topsoil and is still apparent at 120-cm depth in this deep black soil.

Linseed has proved one of the crops most sensitive to long-fallow disorder and has been much used as a test plant in agronomic and VAM research on the problem. The effect of fallow duration on density of VAM spores and on root colonization and growth of linseed is given in Table 8. The long (18-month) fallow resulted in far fewer VAM spores in the soil prior to sowing, and in poorer VAM colonization and growth of linseed without P fertilizer. At a subsequent stage in this experiment, maize was grown after

**Table 7. Effect of fallow duration on percent colonization by vesicular-arbuscular mycorrhizae (VAM) and crop growth on Vertisols in Queensland, Australia. (Thompson, 1987; Thompson, unpublished data).**

| Crop and fallow duration[1] | Crop age (weeks) | Root length with VAM (%) | Shoot dry mass (g plant$^{-1}$) |
|---|---|---|---|
| Wheat | | | |
| Long | 5 | 14.8[2] | 0.10 |
| Short | 5 | 47.8[2] | 0.55 |
| Sorghum | | | |
| Long | 4 | 1.6 (±1.0)[3] | 0.2 (±0.01) |
| Short | 4 | 25.0 (±3.9) | 1.4 (±0.2) |
| Sorghum | | | |
| Long | 8 | 2.5 (±1.2) | 11.9 (±2.1) |
| Short | 8 | 31.9 (±1.7) | 57.8 (±8.5) |
| Chickpea | | | |
| Long | 12 | 17.5 (±6.8) | 0.5 (±0.1) |
| Short | 12 | 72.7 (±5.9) | 2.9 (±0.2) |

1. Long = 14 months; short = 6 months.
2. Single composite of 18 plants.
3. Standard error (n = 3) in parentheses.

**Table 8. Effect of fallow duration on number of vasicular-arbuscular mycorrhizal (VAM) spores, VAM-colonized root, and growth of linseed with and without fertilizer (J.P. Thompson, unpublished data, Mt. Maria, Queensland, Australia 1984).**

| Fallow duration (months) | VAM spores (no. $g^{-1}$ soil) Soil depth 0-15 cm | VAM spores (no. $g^{-1}$ soil) Soil depth 15-30 cm | Root length with VAM at 77 days (%) 0-15 cm depth | Shoot mass (mg $plant^{-1}$) -P | Shoot mass (mg $plant^{-1}$) +P |
|---|---|---|---|---|---|
| 18 | 16.1 | 11.5 | 21.4 | 111 | 277 |
| 6 | 45.9 | 23.0 | 53.7 | 163 | 209 |
| 2 | 54.2 | 31.3 | 44.1 | 167 | 216 |
| SE | ±2.2 | | ±2.1 | ±6.9 | |

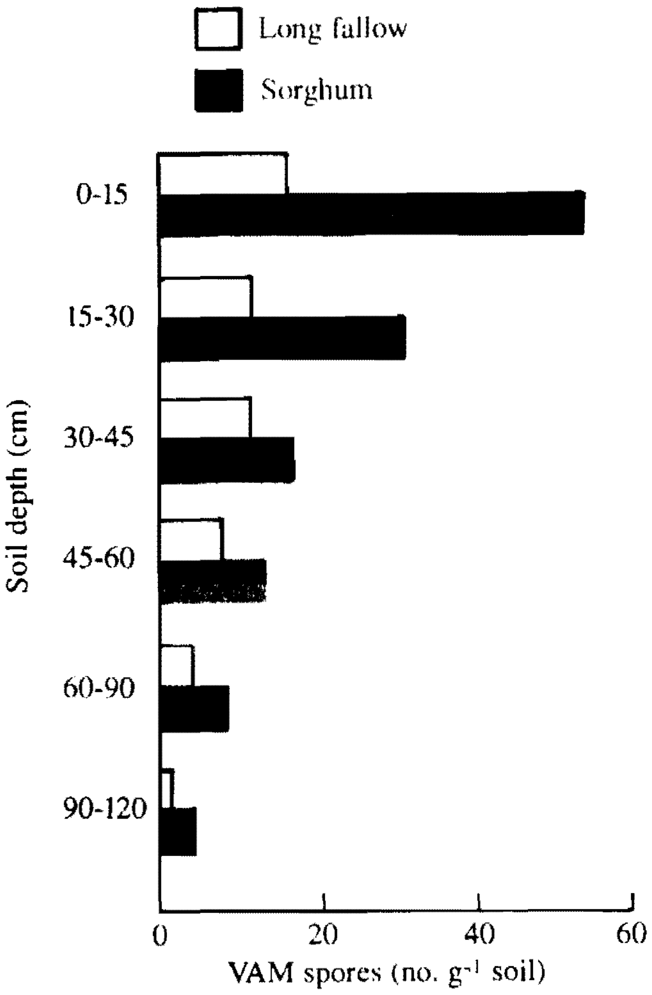

**Figure 2. Effect of fallow and cropping with sorghum on soil-profile distribution of vesicular-arbuscular mycorrhizal (VAM) spores in a Vertisol, Mt. Maria, Queensland, Australia, 1984. (Fallow = 22 months after a wheat crop and sorghum = 6 months after sorghum) (J.P. Thompson, unpublished data.)**

fallow lengths of 6, 11, and 21 months (Table 9). Once more, the longer the fallow, the fewer the VAM spores before sowing, the lower the percent VAM colonization of maize roots, the lower the grain yield, and the more responsive the yield to P and Zn fertilizer.

## Overcoming Long-fallow Disorder through Cropping

Clearly, VAM propagules decline in soil on fallowing; conversely, they increase during cropping. Recently, the value of various crop species in breaking a very long fallow of 6 years on a Vertisol was examined at Mt. Maria on the Darling Downs of Queensland (J.P. Thompson, unpublished data). The area had been kept weed-free as far as possible since 1983 through cultivation with tyned implements and herbicide (glyphosate) as required. A set of winter crops was grown from June to December 1988 and a set of summer crops from October 1988 to April 1989. VAM spores were counted after the various treatments in late May, and linseed was sown in early June. Percent colonization of the roots of linseed was determined at 41 days, and dry mass of the tops at 61 days. Very large differences were obtained in the growth of the linseed in 1989, with exceptionally poor growth after the fallow and after the nonhost rapeseed (Fig. 3). Of the winter crops grown in 1988, chickpea resulted in the best growth of linseed in 1989, with wheat the best of the other crops (Fig. 3). Linseed growth was generally better when the crop was grown directly after the summer crops (double-cropping)

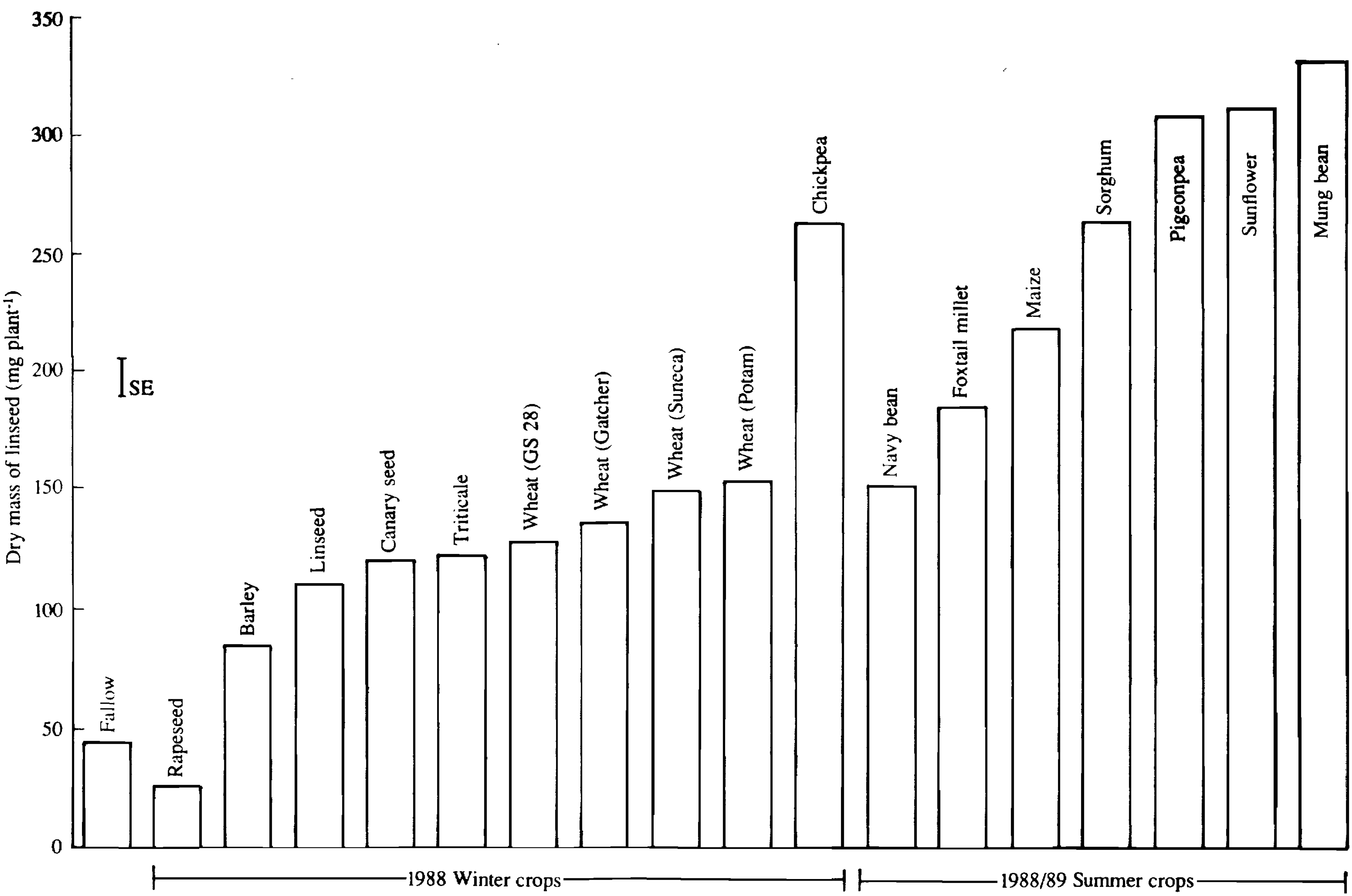

**Figure 3. Effect of prior cropping in 1988/89 with a range of winter and summer crops to overcome long-fallow disorder in linseed, grown in 1989. (J.P. Thompson, unpublished data.)**

**Table 9. Effect of fallow duration on number of vesicular-arbuscular mycorrhizal (VAM) spores, VAM-colonized root, and grain yield of maize with and without P and Zn fertilizer (J.P. Thompson, unpublished data, Mt. Maria, Queensland, Australia 1984).**

| Fallow duration (months) | VAM spores (no. g$^{-1}$ soil) |  | Root length with VAM at 51 days (%) |  | Yield (kg ha$^{-1}$) |  |
|---|---|---|---|---|---|---|
|  | Soil depth |  | Soil depth |  |  |  |
|  | 0-15 cm | 15-30 cm | 0-15 cm | 15-30 cm | -P and Zn | +P and Zn |
| 21 | 14.2 | 9.1 | 34.3 | 21.9 | 2865 | 4937 |
| 11 | 26.5 | 16.5 | 33.8 | 35.1 | 3625 | 3632 |
| 6 | 44.3 | 22.6 | 53.4 | 45.1 | 5162 | 4704 |
| SE | ±2.2 |  | ±2.0 |  | ±433 |  |

than after the winter crops with a normal fallow of 6 months (Fig. 3). In this purely agricultural system of annual cropping and fallow, the number of VAM spores in the soil before a crop is sown appears to be a good predictor of subsequent VAM colonization of the roots and growth of a mycorrhiza-dependent crop. There was an asymptotic relationship between percent VAM colonization of the linseed roots and the number of residual spores in the soil from the various precrop treatments (Fig. 4). The dry mass of the plants at 68 days was linearly related to the percent colonization of the roots at 41 days (Fig. 5) and

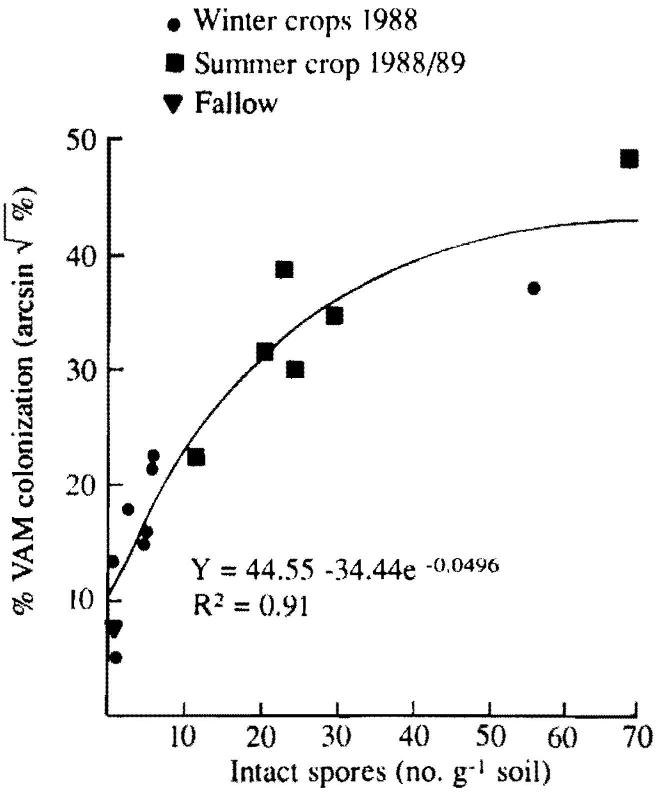

**Figure 4. Relation between percent colonization by vesicular-arbuscular mycorrhizae (VAM) of linseed at 41 days and the number of VAM spores in the topsoil before sowing, Mt. Maria, Queensland, Australia, 1989. (J.P. Thompson, unpublished data.)**

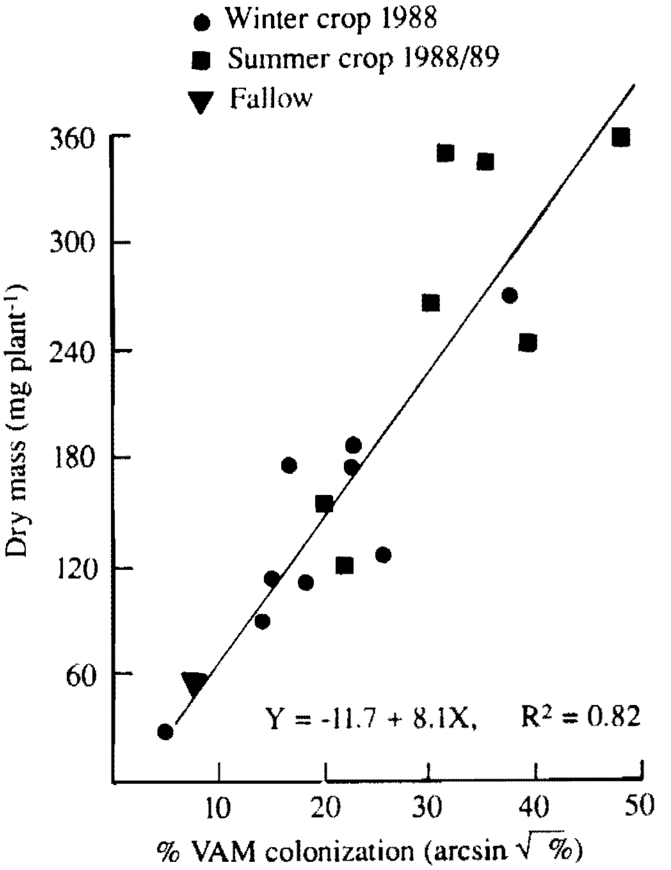

**Figure 5. Relation between dry mass of linseed plants at 68 days and percent mycorrhizal colonization at 41 days. Each point represents a different winter or summer crop in the previous year. (J.P. Thompson, unpublished data.)**

asymptotically related to the number of spores in the soil presowing (Fig. 6).

Although rapeseed grows well in long fallow soil, its effects on mycorrhiza-dependent crops that follow should always be considered. Fields of cotton have grown poorly on Vertisols after rapeseed, the cotton roots having only half as much VAM colonization as after wheat (Thompson et al. 1989). At Bangalore in India, similar results were obtained on an Oxisol where a 1-year fallow reduced the number of VAM propagules by 40%, and the growing of the non-mycorrhizal crop, mustard, reduced them by 13% (Harinikumar and Bagyaraj 1988).

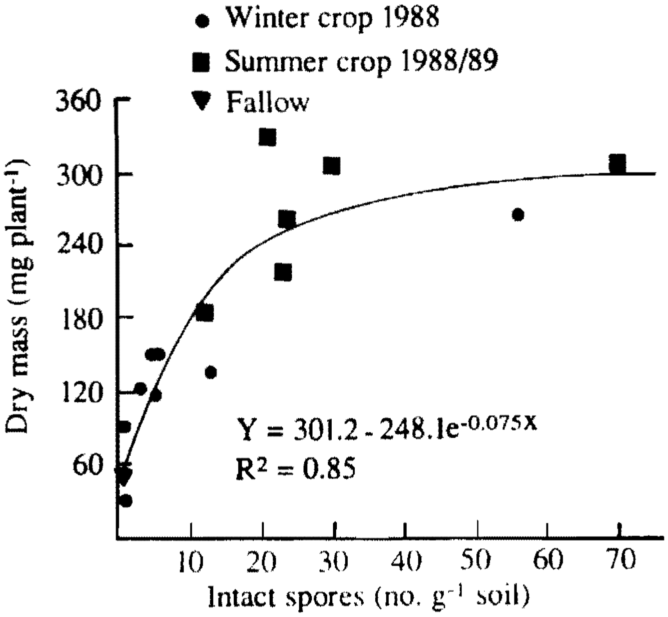

**Figure 6. Relation between dry mass of linseed plants at 68 days and number of vesicular-arbuscular mycorrhizal (VAM) spores in the topsoil before sowing. Each point represents a different winter or summer crop in the previous year. (J.P. Thompson, unpublished data).**

## Survival of VAM Propagules in Fallow

VAM propagules can be chlamydospores, colonized root pieces, and extraradical hyphae. The relative longevity of these various propagules in fallows and factors causing their demise are not fully understood. Chlamydospores by their very structure seem best adapted for survival and can remain viable for several years in stored dry soil, whereas roots remain infective for only a few weeks (Mosse 1963). However, Tommerup and Abbott (1981) found that root pieces colonized by *Glomus fasciculatum*, *G. monosporum*, and *Gigaspora calospora* were infective after 6 months' storage in dry soil, with new hyphae growing from the original hyphae in the dead root cortex to colonize clover roots. However, root pieces colonized by *Acaulospora laevis* and *Glomus caledonium* were noninfective when treated in the same manner. Variation in vesicle formation may account for variation in effectiveness of root inoculum between experiments. Biermann and Linderman (1983) found that the presence of intraradical vesicles greatly improved the infectivity of roots as inoculum. Root pieces colonized by *Gigaspora* species that do not produce intraradical vesicles were noninfective.

Tommerup (1985) found quiescent spores of several VAM fungi were prevented from germinating in soils under crops and pastures and in pot cultures by water-soluble, heat-labile compounds. During fallow, this mechanism should diminish, permitting spore germination and eventual loss of infectivity. The decline of VAM in fallow could well be influenced by repeated wetting and drying cycles, with propagules germinating under moist conditions to eventually die when stressed before they encounter living roots. Multiple germination of spores (Koske 1981) or retention of infectivity of germinated spores for up to 4 months (Tommerup 1984) would delay but not prevent the decline.

In addition, there is a range of microorganisms that parasitize and antagonize VAM and meso- and macro-organisms that consume VAM spores. Ross and Daniels (1982) suggested that such organisms could account for the lower densities of spores in natural systems than can be achieved in pot cultures with sterilized soil free of hyperparasites. Although such inimical organisms would be present under crops, where they could also limit VAM effectiveness, their activity in the absence of VAM replenishment during fallow would contribute to a decline in VAM propagules.

### Long-term Crop Rotation

Clearly, the density of propagules in soil depends primarily on the growth of previous crops. The cumulative effects of long-term cropping may differ from short-term effects. Kruckelmann (1975) compared the effects of 16 years of monoculture of six crops in Germany with 2-year rotations of the same crop alternated with oats. The greatest number of VAM spores was present with wheat monoculture and decreased in the order wheat > oats > rye > maize > sugarbeet > potato. High numbers of spores in wheat fields have been confirmed in several other studies. Sugarbeet is a nonmycorrhizal crop, and a low spore count is expected. Although potato is a host, its poor ability to build VAM populations has been confirmed in results from Israel (Z. Frank, Volcani Institute, personal communication). Probably the sparse root system of potato and the high inputs of fertilizers, including P, usually applied to potato account for the result. Alternating a crop with oats tended to bring VAM populations to the mean of that obtained with the particular crop and oats in monoculture.

The possibility that continued cropping with different crop species may select different species of VAM fungi was examined by Schenck and Kinloch (1980). They followed annual root colonization and spores of VAM fungi for six crops grown in monoculture for 6 years on a newly cleared woodland site in Florida, USA. The highest number of spores was associated with soybean and the lowest number with the native woodland. The greatest number of VAM species was associated with sorghum. Certain species were more numerous around certain crops: *Gigaspora margarita*, *G. gregaria*, *G. gigantea* in soybean; *Glomus fasciculatum* and *G. clarum* in bahia grass; and *Acaulospora* spp in cotton and groundnut. Generally, *Glomus* spp were recovered in greatest number from around monocotyledonous crops. Differences in rhizosphere pH among plant species may select fungal species with different pH optima.

It appears that annual cropping favors VAM spore production more than native perennial vegetation. Mosse and Bowen (1968) and Hayman and Stovold (1979) also found more spores in Australian wheat and other agricultural fields than in adjacent natural grasssland-bush soils. Nonetheless, the percentage of the roots colonized tended to decrease substantially from 1972 to 1973 in four crops studied in monoculture by Schenck and Kinloch (1980) and then to increase from 1973 to 1976. VAM propagules other than spores, such as colonized roots and free hyphae from the cleared woodland, were probably effective inocula in the first year. Strains dependent on such propagules possibly declined on cropping, to be replaced by better-adapted, sporing strains.

Strzemska (1975) assessed VAM in 20 legume species at defined growth stages for 3 years in the field in Poland. He found a continuous series, ranging from consistently well-colonized species, such as serradella (*Ornithopus sativus* L.), red clover (*Trifolium pratense* L.), common vetch (*Vicia sativa* L.), faba bean (*Vicia faba* L. var *minor*), and field pea (*Pisum arvense* L.), to poorly colonized ones, such as common bean (*Phaseolus vulgaris* L.), black medic (*Medicago lupulina* L.), fenugreek (*Trigonella foenumgraecum* L.), greater birdsfoot trefoil (*Lotus uliginosus* Schk.), and melilot (*Melilotus albus* Desr.). Such data provide valuable comparisons between plant species but care should be taken where only one cultivar has been examined. For example, Mosse and Thompson (1984) found in single-endophyte tests with *G. mosseae* and *G. fasciculatum* inoculated on common bean that the improved variety Canadian Wonder had poor colonization (3-8% of root length) but the unimproved variety Jamapa had excellent colonization (60-80%).

## Soil Disturbance

The effects of severe soil disturbance in reducing VAM infectivity have been studied in relation to topsoil treatment in strip-mining operations (e.g., Allen and Allen 1980). Evidence is now accumulating to show that the soil disturbance of normal agricultural tillage operations may also reduce VAM infectivity. When assessed by serial plantings of test rows of linseed in experiments in Queensland, Australia, long-fallow disorder was found to be induced more rapidly if the fallow was tilled than if it was left untilled (Leslie and Whitehouse 1966). In a 10-year experiment in Germany, Kruckelmann (1975) found that severe tillage (rotary hoeing) reduced the number of VAM spores compared with zero tillage, but shallow plowing increased them. Addition of chopped straw increased the number of spores in the shallow-plowed treatment even further. However, Smith (1978) found similar total numbers of VAM spores in the soil profile of tilled and zero-tilled plots of continuous wheat in Western Australia, although the zero-tilled plots had more spores in the top 8 cm of the profile and the tilled plots had more in the 8-15 cm layer. Yocom et al. (1984) found poorer colonization of winter wheat in the field after cultivated fallow than after zero-tilled fallow. Bioassay of mycorrhizal infection potential in disturbed soil samples from the field plots showed similar trends, but with both fallow treatments considerably below the potential of uncultivated grassland.

Recently, Miller and coworkers in Canada have stressed the effects of tillage in reducing VAM infectivity and P and Zn uptake by maize, caused by disruption of a VAM hyphal network in the soil. Evans and Miller (1988) removed undisturbed cores in plastic cylinders from long-term (>9 years) zero-tilled plots and produced disturbed treatments by removing the soil from the core, disrupting aggregates to pass a 0.5-cm sieve, and repacking the soil in the cylinders. Three weeks after germinated maize seeds were sown, the VAM colonization of the roots was determined and relative P nutrition was expressed by the ratio of shoot P to available soil P. The results show that VAM colonization intensity was reduced to about one-quarter and P uptake to half by this relatively mild disturbance treatment. Similar effects were obtained with mycorrhizal wheat, but not with spinach (*Spinacea oleracea* L.) or rapeseed, both nonhosts of VAM fungi.

Fairchild and Miller (1988) determined how soon differences between undisturbed and disturbed soil develop. Starting with disturbed soil in plastic cylinders, they grew maize for 3 weeks; harvested the tops; disturbed and repacked one set of cylinders, leaving another set undisturbed; and replanted. They repeated the procedure through three 3-week cycles. There was a rapid increase in VAM colonization and P absorption (Fig. 7) by maize over the three growth cycles when this initially disturbed soil was left undisturbed. Effects on VAM colonization and P nutrition were apparent as early as 14 days after sowing in the third cycle, although a difference in dry matter was not apparent until 21 days, indicating the sequence of cause and effect.

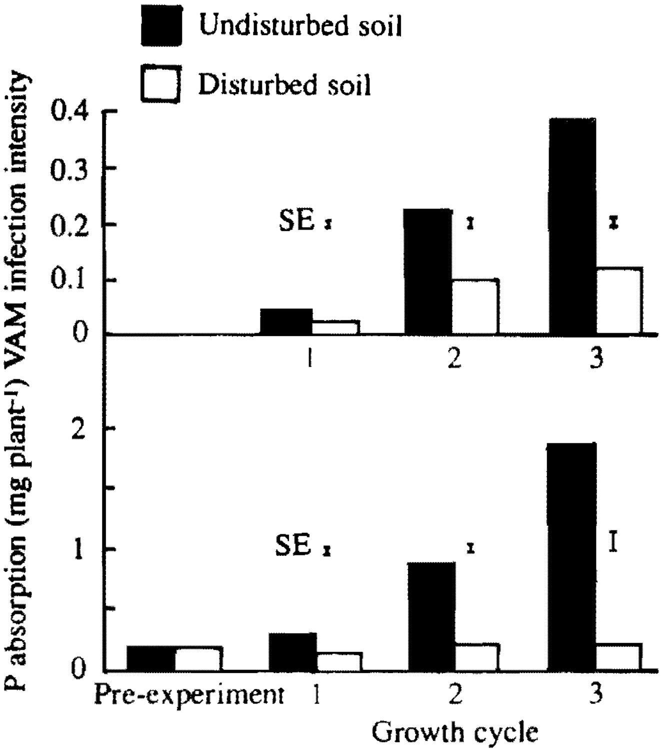

**Figure 7. Effect of soil disturbance on vesicular-arbuscular mycorrhizal (VAM) infection and P uptake of maize over successive 3-week cycles of growth. At the end of each cycle, the maize was harvested and the soil disturbed again before replanting. (From Fairchild and Miller 1988.)**

Evidence for the importance of the preexisting hyphal network in colonizing seedlings in undisturbed soil has come from work of Jasper et al. (1989a, 1989b) and Evans and Miller (1989). Their results with split-plot techniques, using nylon mesh to allow hyphae but not roots to pass between compartments, have shown that the hyphal network remains highly infective even when detached from plant roots, but loses infectivity when the soil is disturbed. The hyphal network retained its infectivity for at least 36 days in dry soil, tolerated drying to as low as -21 MPa (Jasper et al. 1989b), and remained viable after roots had died.

Clearly, avoidance of soil disturbance is one way to assist early VAM colonization of crops and improve early P nutrition. The chlamydospores of VAM fungi are structurally better for longer-term survival and tolerance of adverse conditions than VAM hyphae, but hyphae may establish an effective symbiosis sooner. Evans and Miller (1989) suggest that an infective mycorrhizal network in undisturbed soil may well be able to conduct P from the soil as soon as it is effectively linked to the seedling roots. This would provide earlier benefits to the crop than colonization from spores and the longer time needed for an external hyphal network to be produced after internal colonization of the roots. This is of much practical importance in achieving early colonization and better early P nutrition in crops. The work of Jasper et al. (1989b) raises the question of how long a network of VAM hyphae can remain infective if the soil is left undisturbed. From the experiments of Evans and Miller (1988) it seems that the fungal hyphae remained infective for 7-8 months after plant death, through periods when the soil was partly frozen. Warner and Mosse (1980) and Tommerup and Abbott (1981) also provided evidence of similar longevity of hyphae not connected to roots. If the hyphal network from a previous crop is valuable to a succeeding crop for early VAM colonization and P uptake, then the agronomic management of hyphal networks between successive crops is of much practical significance and worthy of more research.

## Heating and Fire

VAM fungi are not particularly tolerant of heat. Thompson (1989) determined the effect of moist heat on a Vertisol that had grown successive sorghum crops and contained many VAM spores and colonized root pieces. Heating the soil for 30 min at 50°C substantially decreased early colonization of wheat and at 60°C, effectively eliminated it. In parts of the tropics, bare topsoil may well reach these temperatures and become depleted in VAM. Poor growth of soybean occurring on bare soils in the Northern Territory of Australia could in part result from temperature effects on VAM (T. Price, Northern Territory Department of Industries and Development, personal communication). Retention of surface residues to reduce soil temperature would be desirable under these conditions.

Where woodland is cleared and burned before growing crops, heating of the soil may cause reduction in VAM populations and poor crop growth. When open woodland on an infertile Alfisol in the Northern Territory is cleared, pushed into windrows, and burned, maize grows poorly where the timber has been burned. In this situation, there is poorer VAM colonization of the maize roots in the windrow position than in the rest of the field (Thiagalingam et al. 1988).

## Fungicides

Other factors during crop growth can directly affect the VAM fungi detrimentally. A clear example is soil treatment with fungicides, reviewed by Menge (1982). Fumigation of the soil with broad-spectrum agents such as methyl bromide and methyl isothiocyanate can effectively eliminate VAM, resulting in poor growth of mycorrhiza-dependent crops. Although field fumigation is an unlikely farm practice in the SAT, it is a valuable research tool to investigate effects of VAM in the field. There have also been several reports of toxicity by soil- or seed-applied fungicides, such as the nonsystemic fungicide PCNB and the systemic fungicides benomyl and triademifon. Possible inimical effects on VAM from use of these fungicides should be kept in mind.

## Fertilizers

Hayman (1982) stated that changes in soil fertility due to amendment with mineral fertilizers or organic matter can markedly influence VAM in terms of root colonization and number of spores. He indicated that there is some evidence that organic matter additions lead to better mycorrhizal development and considerable information on the negative effects of N fertilizer on mycorrhizal formation. He cited experiments from England on a heavy clay soil at Rothamsted and a sandy soil at Woburn to show that N applied as ammonium nitrate markedly decreased VAM colonization of wheat and spore numbers. He cited contrary results from Germany that showed increases in spore number with N fertilizer and suggested the variation may reflect differences in basic soil fertility. It is also possible that the acidifying effect of ammoniacal N fertilizers may be more detrimental to some VAM fungi (Thompson 1986) in more acid or less well-buffered soils than in other soils.

Although results from Rothamsted indicated that P fertilizers reduced VAM less frequently than did N (Hayman 1982), there have been many other studies showing that high concentrations of phosphatic fertilizers can reduce the intensity of VAM colonization. Most of these studies have been in pots, and more work at field rates of P usage would be desirable. In one of the most recent studies, Amijee et al. (1989) assessed the colonization of leek (*Allium porrum* L.) roots with *G. mosseae* growing at six concentrations of Olsen P, ranging from 22 to 344 mg $kg^{-1}$ soil. Addition of P increased the initiation of main roots and lateral roots, thereby increasing root available for colonization. Consequently, the total length of colonized root increased with increasing P up to 150 mg $kg^{-1}$ soil. When P exceeded 140 mg $kg^{-1}$, the rate of extension of fungal colonization fronts was about halved, and the percentage of root length colonized fell from a maximum of 21% with 75 mg to 7.7% with 208 mg P $kg^{-1}$. Detailed analysis of the nature of the colonization at 10-day intervals suggested that formation of secondary entry points was probably the rate-limiting step in the colonization of the roots, and its rate was reduced by added P. It is considered that the reduction in entry-point formation is due to a physiological response in the host to increasing P supply rather than a direct effect of P on the extraradical phase of the fungus. Earlier, Ratnayake et al. (1978) had suggested the physiological control in citrus was a reduction in organic root exudation at high P levels. Similarly, Jasper et al. (1979) concluded for subterranean clover that higher P concentrations in the plant resulted in lower soluble carbohydrate concentrations in the roots and exudates and a lower frequency of entry points.

Although VAM inhibition by high rates of P has been demonstrated many times in greenhouse experiments, it is still difficult to extrapolate to the field (Hayman 1975). Hayman found for a clay soil at Rothamsted that field crops usually had most VAM colonization without P fertilizer but most spore numbers at intermediate rates of P (total of 330 kg P ha-¹ applied as superphosphate over 12 years). This, of course, is a high rate of application in many parts of the world. Changing the rate of superphosphate application for 10 years (from 0 to 224 kg ha-¹ year-¹) in a sandy loam soil that had received 150 kg ha-¹ year-¹ for the previous 15 years did not cause changes in the abundance or types of VAM spores or in their ability to colonize clover and improve its growth (Porter et al. 1978). It is difficult to generalize, because of differences in native soil fertility, differential response of different plant species, and changes in populations of VAM species or strains with changing fertility. Thompson (1986) used multiple regression to relate VAM colonization of wheat and maize in sand culture to root concentrations of N and P. Under these conditions, the level of colonization was increased by root N but decreased by root P. Hepper (1983) also found VAM colonization of lettuce roots increased with higher N concentrations and lower P concentrations in the roots.

Hayman (1975) reviewed early literature, which indicated that organic manures often enhanced VAM development more than mineral fertilizers or no fertilizer. Farmyard manure favored arbuscular development in citrus roots, and humus offset the reduction in VAM colonization of alpine plants under low light intensity.

Wellings et al. (In press.) grew pigeonpea with factorial treatments of inoculation with *G. mosseae*, inoculation with the fungal pathogen, *Phytophthora drechsleri*, and P (0, 10, and 50 mg kg-¹) and Zn (0 and 15 mg kg-¹) fertilizers. They found that VAM colonization, P nutrition, and growth of pigeonpea responded to inoculum of *P. drechsleri*, which failed to infect (Fig. 8), suggesting a response to the organic matter of the inoculum. Further research is warranted on the effects of organic matter in promoting VAM colonization and VAM-mediated plant responses. It would be desirable to identify whether the responses are a direct stimulation by an organic supply to the extraradical hyphae of the fungus with essential connections to the root cortex or due to the P content of the organic matter, possibly in a "slow-release" form.

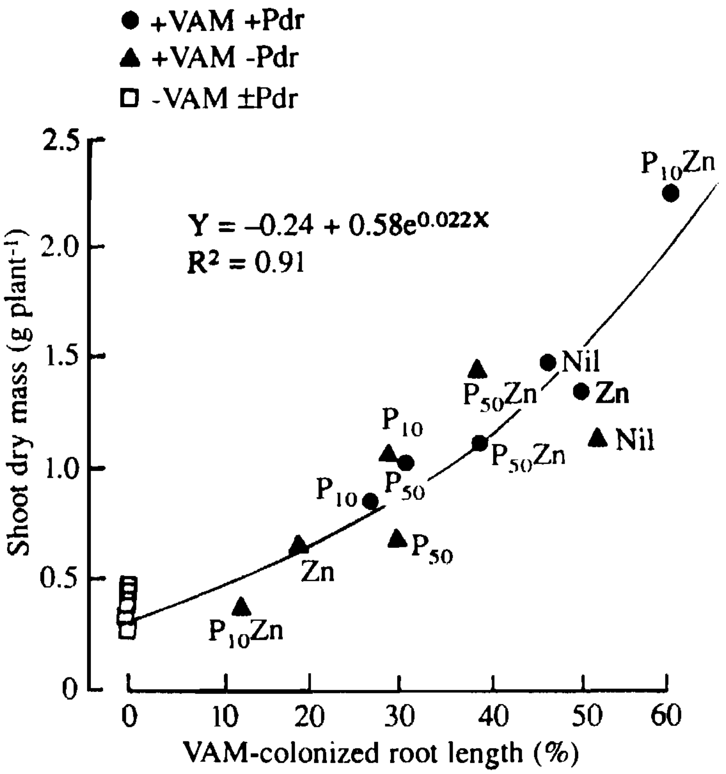

**Figure 8. Relation between shoot dry mass and percent colonization of pigeonpea by vesicular-arbuscular mycorrhizae (VAM), with different treatments involving VAM inoculation, *Phytophthora drechsleri* inoculation (Pdr), and P and Zn fertilizers in a sterilized Vertisol. The inoculum of *P. drechsleri* did not infect the plants or cause disease. (From Wellings et al., in press.)**

## Waterlogging

VAM fungi are aerobic organisms. If culture pots become waterlogged, development of the fungus is poor or nonexistent. Likewise, although VAM fungi are very widely distributed in natural plant communities, they are rare in very wet soils (Hayman 1982). It seems highly probable that certain agricultural practices that result in soil waterlogging are detrimental to VAM fungal populations. There are several reports of poor growth of upland crops following paddy rice, with increased responses to P fertilizers (Brandon and Mikkelsen 1979; Muirhead 1981). The problem is seen to be one of crystalline iron oxides in the soil dissolving under the anaerobic conditions of rice culture, with reoxidation when the field is drained to amorphous iron oxides with higher P-sorption capacity than the crystalline iron oxides of the soil before flooding (Willett 1979; Muirhead 1981). It is possible that depletion of VAM propagules also contributes to the problem. Ilag et al. (1987) used a most-probable-number bioassay of VAM propagules in some rice-based cropping systems in the Philippines. Propagules decreased with increasing period of submergence of the rice and were fewer in a rice-rice cropping pattern than in a rice-maize-mung bean pattern. Propagules increased on weeds during fallow periods after the rice and reached a peak at maturity of the upland crops, but plummeted when the soil was plowed and harrowed. Therefore P deficiency in upland crops following paddy rice is probably due to the combination of higher P adsorption by iron oxides and lower VAM propagule density. These are the very conditions under which Bolan and Robson (1983) found that mycorrhiza-dependent crops exhibit sigmoidal responses to applied P. In this regard, Kuo and Huang (1982) found that VAM inoculation of soybean following paddy rice increased grain yield by 21%, whereas P fertilizer at 60 kg ha$^{-1}$ increased yield by only 14%.

The *haveli* system of fallowing in India, by which water is deliberately ponded in bunded fields during the rainy season to be stored for dry-season cropping, might also deplete VAM populations and increase P sorption when the field is drained. The possibility of a depletion in VAM for chickpea growth following *haveli* fallow should be considered. There is much interest in crop rotations of chickpea and pigeonpea with rice and wheat (Wallis and Byth 1987). It is likely that mycorrhizal colonization of these legumes should be of the order: after wheat > after upland rice > after paddy rice. Avoidance of unnecessary tillage before the leguminous crops would also substantially aid their early VAM colonization.

## Conclusions

The best way to improve the mycorrhizal condition of the soil is through cropping with mycorrhizal host crops, which include cereals, legumes, and oilseeds. To avoid problems, it is best not to sow mycorrhiza-dependent crops, which include chickpea and pigeonpea, in VAM-depleted situations. Depletion of VAM inoculum potential can arise during weed-free fallowing, growth of nonhost crops such as mustard and rapeseed, severe soil disturbance in tillage operations, waterlogging in paddy rice and flood fallowing, severe fires, and topsoil stripping. Therefore intensifying cropping is beneficial for VAM. In semi-arid areas, the frequency of cropping will be dictated by available water, and avenues to improve this through reduced tillage and residue retention should be pursued. Intensification of cropping also places demands on soil nitrate supply, and replacement through fertilizer or legumes is essential. Here the possibility of grain legumes such as chickpea and pigeonpea being self-sufficient for N allows economic intensification of cropping, and any prospect of improved N supply for a following cereal crop is a bonus. Not only will chickpea and pigeonpea benefit from the VAM inoculum residual from a previous host crop but they themselves are excellent providers of VAM inoculum for a following mycorrhiza-dependent crop species.

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# Soil Aeration Status of Alfisols and Vertisols as a Limiting Factor for Growth of Pigeonpea

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## Abstract

*In the semi-arid tropics (SAT), rainfall events in the rainy season can be intense and cause waterlogging and aeration problems in soils of high clay content. Pigeonpea is particularly sensitive to temporary waterlogging, and this has been considered one of the major constraints to its growth in peninsular India. However, there have been few studies on the aeration status of soils in the SAT.*

*From 1987 to 1989, the change in oxygen concentrations in the soil atmosphere was investigated as an index of soil aeration. After heavy rainfall events, the oxygen concentration at 15-cm depth fell to lower than 10%, and it took several days to recover. Even in Alfisols, oxygen concentration decreased to levels comparable to Vertisols.*

*Root respiration was inhibited at oxygen concentrations below 10%, and that of nodules below 20%. It was concluded that oxygen deficiency created in the soil was the factor limiting pigeonpea growth.*

*As a measure to improve soil aeration, the effect of ridging on the aeration status of soils and on the growth of pigeonpea and sorghum was investigated. Better aeration was maintained, to deeper soil layers, in a ridge-and-furrow system—with ridges spaced at 75 cm—than on flatbeds. Sorghum growth was not affected, but pigeonpea growth was better with the ridge-and-furrow system, especially on an Alfisol with poor physical properties. There were indications that better soil aeration at early growth stages facilitated deeper root penetration and permitted plants to cope better with terminal drought stress.*

## Introduction

The semi-arid tropics (SAT) are usually characterized by their long dry seasons and erratic rainfall patterns. However, rainfall events can be intense, resulting in temporary waterlogging or even complete flooding of fields. Pigeonpea [*Cajanus cajan* (L.) Millsp.] is particularly susceptible to waterlogging (Chauhan 1987). In peninsular India, pigeonpea has been traditionally grown as an intercrop with sorghum [*Sorghum bicolor* (L.) Moench] or other crops during the rainy season. In this case, pigeonpea starts to flower at the end of the rainy season and sets pods in the postrainy season. But the problem of waterlogging has become acute with the introduction of short-duration pigeonpea, which completes most of its growth stages within the rainy season.

In the rainy season of 1986, a fertilizer trial for pigeonpea and sorghum was conducted in two Vertisol and two Alfisol fields at ICRISAT Center. Figure 1 shows the total dry matter of both crops at the flowering stage. The growth of sorghum on the low-

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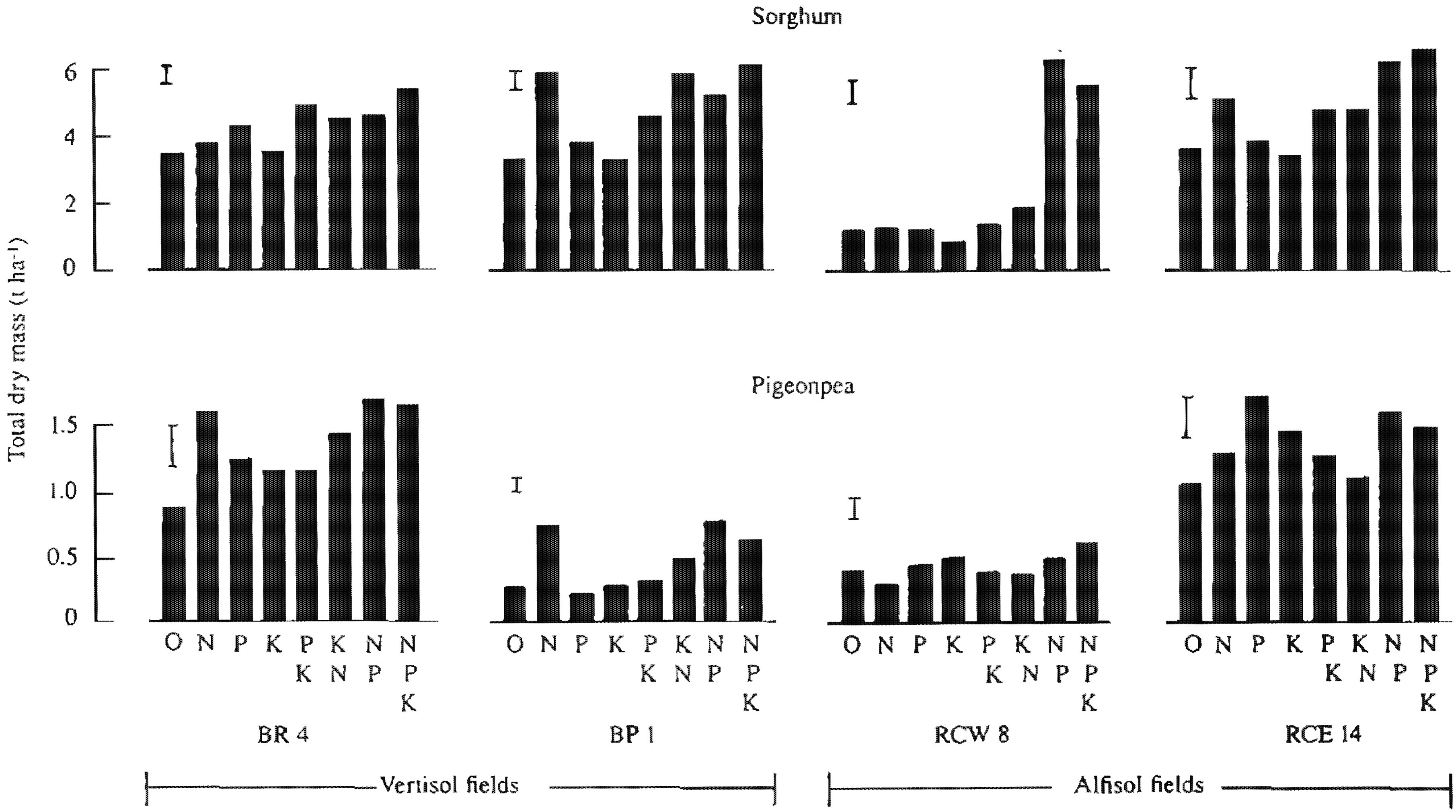

**Figure 1.** Effect of nitrogen (N), phosphorus (P), and potassium (K) application (150 kg N, 65 kg P, 125 kg K $ha^{-1}$) on the above-ground dry matter of sorghum and pigeonpea at 63 days after sowing (DAS) on 29 Aug 1986 on Vertisols and Alfisols at ICRISAT Center, rainy season 1986. Standard errors indicated.

fertility Alfisol field RCW 8 was less than that on the other three fields. But with the application of both nitrogen (N) and phosphorus (P), the growth of sorghum was maintained well in every field.

However, the growth of pigeonpea was severely restricted in fields BP 1 (Vertisol) and RCW 8 (Alfisol), and the application of N, P, and potassium (K) did not improve it. From the observation that the water stayed longer in these fields after rains, it was suggested that soil aeration was the main factor limiting pigeonpea growth. Thus, soil physical factors appeared more important than soil chemical factors for pigeonpea growth.

At ICRISAT, we have considered waterlogging a major constraint to pigeonpea cultivation in peninsular India, and screening for waterlogging tolerance in pigeonpea has been in progress since 1978 (Chauhan 1987). However, a basic understanding of the waterlogging syndrome, including soil-aeration status, is lacking for the soils and climatic conditions of the region. For these reasons, we have attempted to quantify the soil-aeration status in the rainy season in ICRISAT fields, mainly by measuring the oxygen concentration in the soil atmosphere as an index of soil aeration.

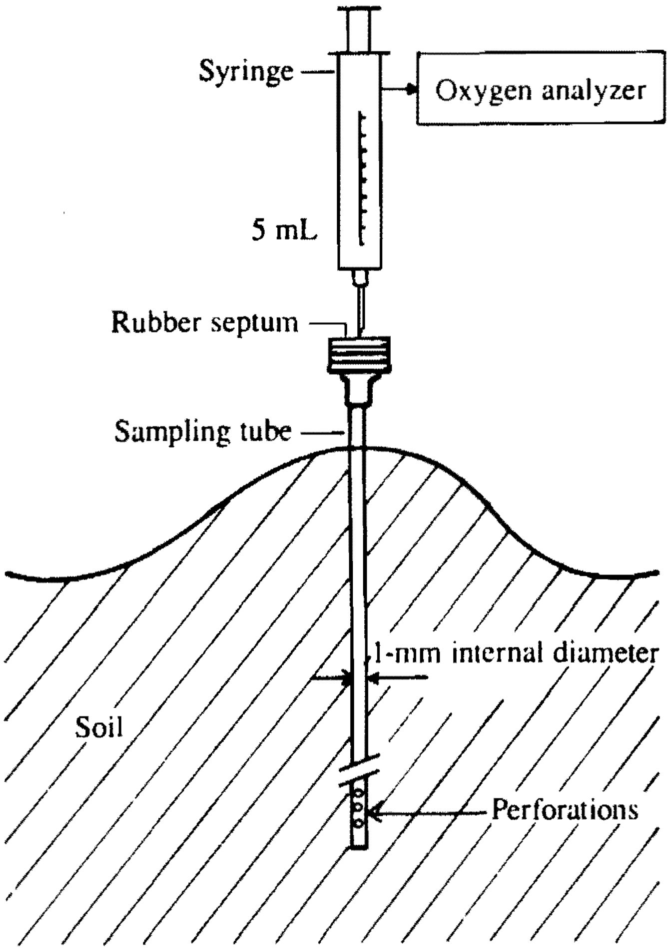

**Figure 2. Apparatus for sampling soil air.**

## Soil Oxygen Concentration

Soil air was sampled at various soil depths using a glass or stainless steel sampling tube (Fig. 2). The air in the pipe was sampled from the rubber septum at the top of the pipe with a plastic syringe, after several days of equilibration. The oxygen concentration of the air in the syringe was measured with an oxygen analyzer (Toray), which uses a solid electrolyte as a detector.

The year 1987 was relatively dry, but in August, rainfall was well distributed and there were heavy downpours at the beginning of each month in September, October, and November. Figure 3 shows the changes in oxygen concentration in the soil at 15- and 30-cm depths in unplanted plots in the four fields that were used for the NPK experiment mentioned earlier. Oxygen concentration decreased gradually during August, but dropped suddenly after the heavy rainfall events at the beginning of September, October, and November. Excess moisture reduces not only oxygen concentration in soil air but also total air space in the soil. Thus the total amount of oxygen (concentration × total air volume) available to plant roots is much lower than the oxygen concentration indicates. Oxygen concentration decreased more in fields BP 1 and RCW 8, where the growth of pigeonpea was worst, than in the other two fields. At the beginning of September, soil air space was filled with water at 30-cm depth for 4 days after the rain stopped in BP 1 and 3 days in RCW 8.

Generally, the problem of soil aeration is considered more serious in Vertisols than in Alfisols, but in our experiment, oxygen concentration in Alfisols was sometimes lower than in Vertisols; for example, in August and October. One explanation may be spatial variability in the amount of rainfall received by different ICRISAT fields, which can be considerable. More likely explanations are:

- after the long dry spell in July and September, the Vertisol could absorb much water by capillary suction and still retain some air space, but the same amount of rainfall brought about excessive free water in the Alfisol and the connections between the air spaces were blocked;

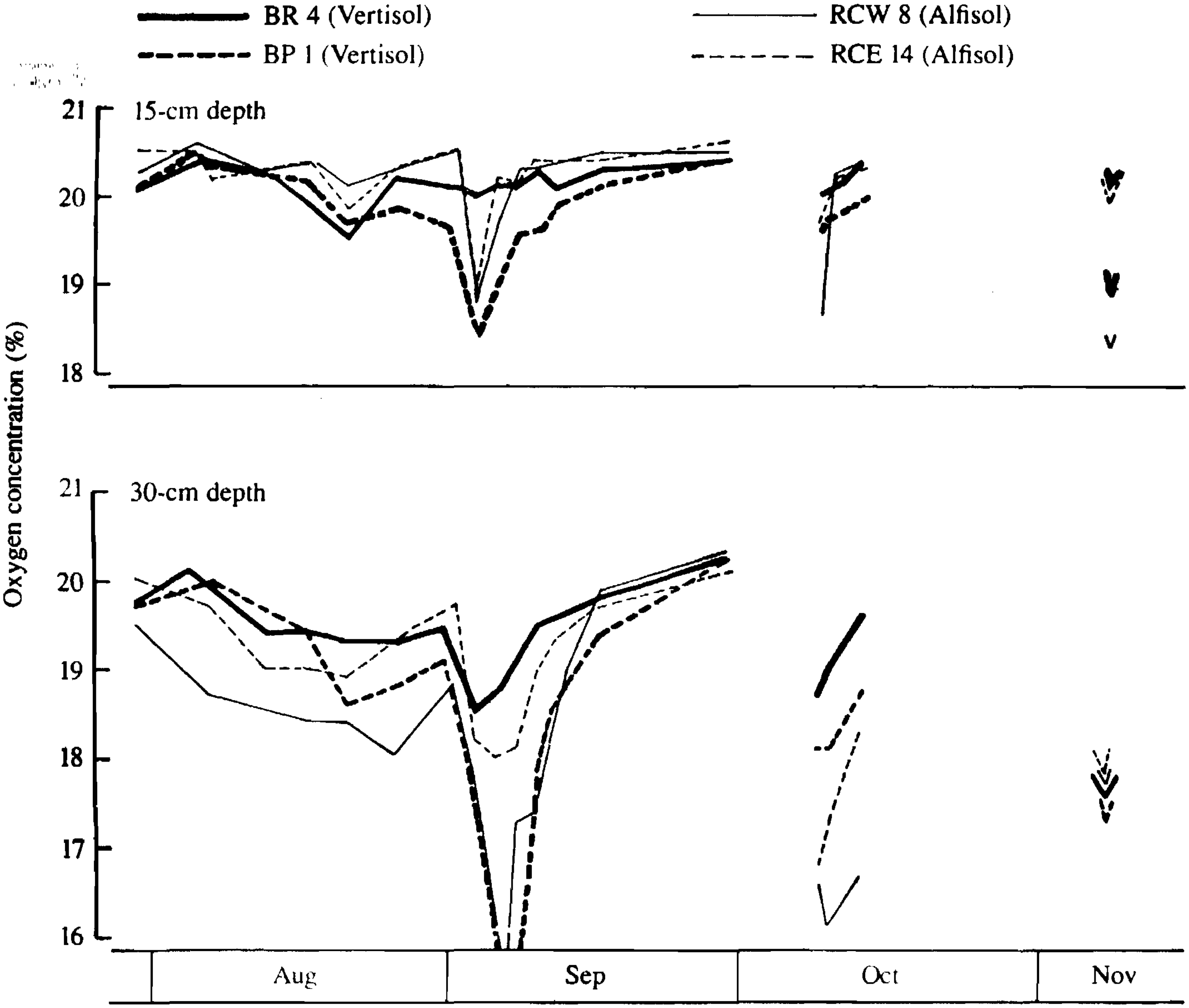

**Figure 3. Changes in oxygen concentration in soil air, ICRISAT Center, 1987. The sharp declines in September, October and November followed heavy rains.**

- a surface crust was formed on the Alfisols, which inhibited oxygen diffusion into the soil.

However, once a soil becomes waterlogged, the condition lasts longer in the Vertisol, because the saturation water conductivity of a Vertisol is much lower than that of an Alfisol (Lal 1986).

In fields BP 1 and RCE 14, after the heavy rains at the beginning of September, October, and November, we found that oxygen concentrations in the rooting zone of pigeonpea dropped sharply: to 10% at 15-cm soil depth and to less than 10% at 30 cm (Fig. 4). Oxygen levels are reduced more in the rooting zone of planted plots than they are in unplanted plots, because of respiration by plant roots and rhizosphere microorganisms. Legume nodules also respire rapidly.

The Vertisols and Alfisols of our experiment are low in organic matter, and microbial respiration in these is largely restricted to the rhizosphere. Therefore the difference in oxygen levels between planted and unplanted plots may be larger in these soils than in soils of higher organic matter content.

The changes in oxygen concentration with soil-moisture status in Vertisols and Alfisols can be summarized as follows:

- The oxygen concentration in the field under rainfed conditions fell to 10% in the plow layer, and even lower in deeper layers, after rainfall

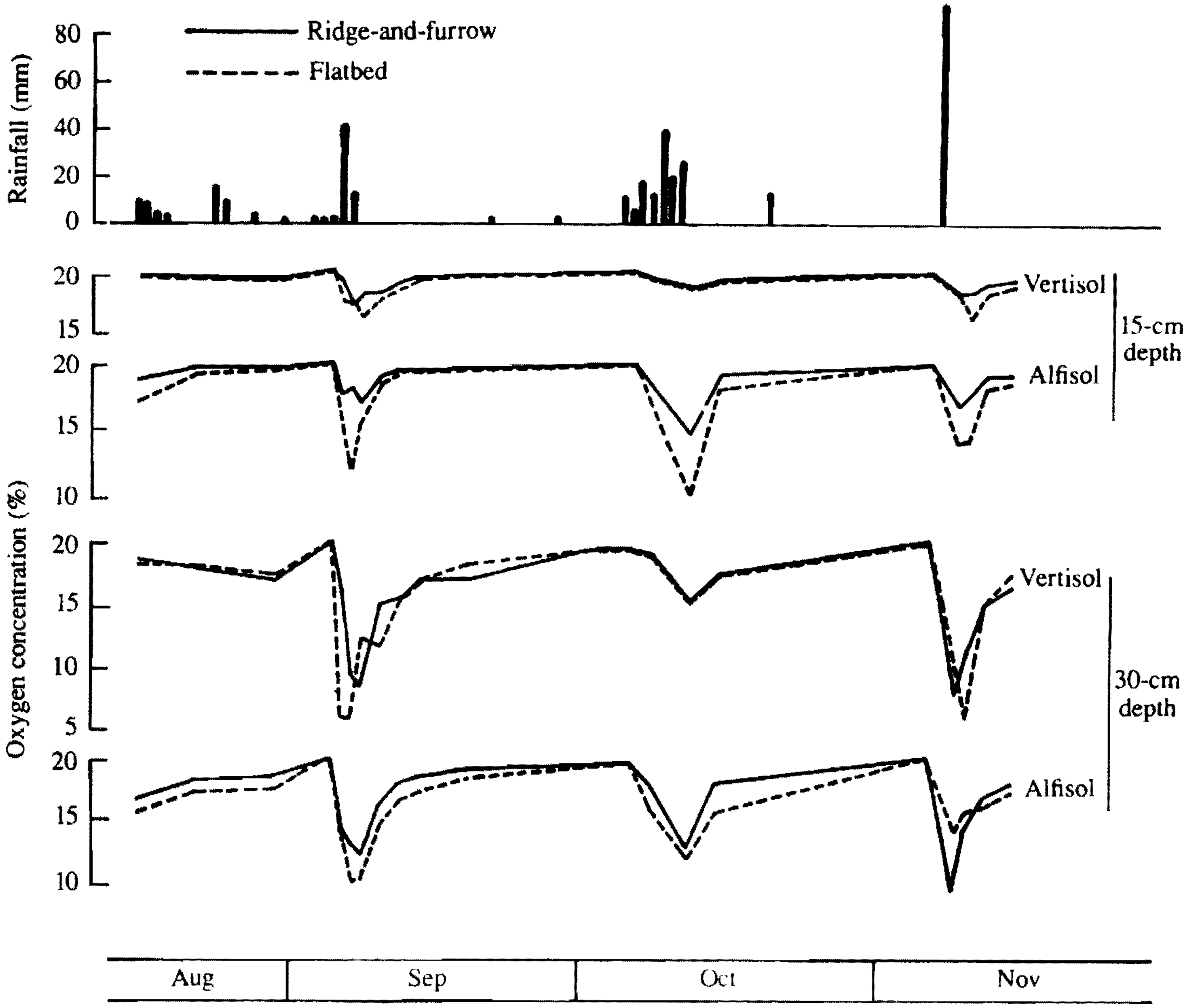

**Figure 4. Oxygen concentration in soil air adjacent to medium-duration (C 11) pigeonpea roots in ridged and flatbed plots in Vertisol (BP 1) and Alfisol (RCE 14) fields, ICRISAT Center, 1987.**

events.

- After heavy rainfall, the aeration status of Alfisols is no better than that of Vertisols.
- The oxygen concentration is lower in the rooting zone than in bulk soil.

## Effect of Oxygen Concentration on Respiration of Roots and Nodules

To determine whether the decrease in soil oxygen concentration actually affects the activity of underground parts of crops, we investigated the effects of oxygen concentration on root and nodule activity. The respiration rate of excised roots of seedlings grown in pots was measured. The plants were grown on Vertisol for 7 or 8 days in a greenhouse; the roots were then washed, the apical 2 cm excised, and its rate of oxygen uptake measured at different oxygen concentrations with a manometer. Root respiration of sorghum began to decrease below 15% oxygen; that of pigeonpea, below 10% (Fig. 5). The growth and function of roots may be adversely affected at oxygen concentrations below 10%, since energy-dependent processes depend on continued aerobic respiration. Thus root growth and energy-dependent nutrient uptake, especially that of P, may be significantly affected at this level of oxygen. Further, other root functions, such as that of producing root exudates that

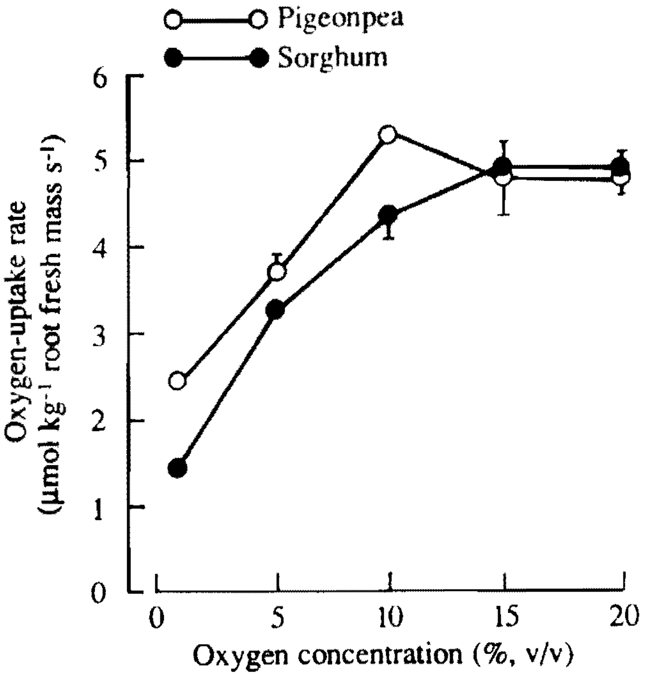

**Figure 5. Effect of oxygen concentration on root respiration of pigeonpea and sorghum. SEs shown only where they exceed the size of the symbol.**

can solubilize otherwise unavailable P (Ae et al. 1991a, 1991b), may also be hampered.

Figure 6 shows the effect of oxygen concentration on nodule respiration of pigeonpea. Using 2-month-old pigeonpea plants, we measured nodule respiration by the same method as that used to measure root respiration. Unlike root respiration, nodule respiration decreased almost linearly from an oxygen concentration of 20%. From this result, it appears that nodule respiration is more susceptible to lowered oxygen concentrations than general root respiration.

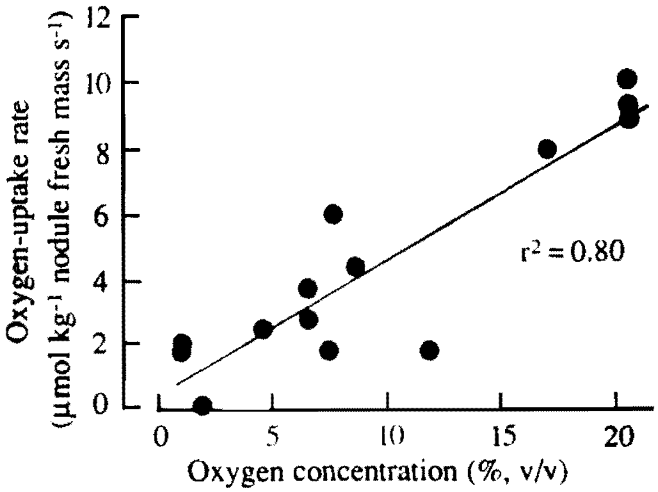

**Figure 6. Effect of oxygen concentration on the nodule respiration of short-duration pigeonpea (ICPL 87).**

Ae and Nishi (1983) found that lowering oxygen concentration from 20 to 10% reduced nodule respiration to some extent in soybean, but the same decrease in external oxygen concentration reduced the $N_2$-fixation rate to a much greater extent (Fig. 7). From these data, it seems likely that the rate of $N_2$-fixation of pigeonpea is also reduced much more than the nodule respiration rate when the oxygen concentration falls below 10%.

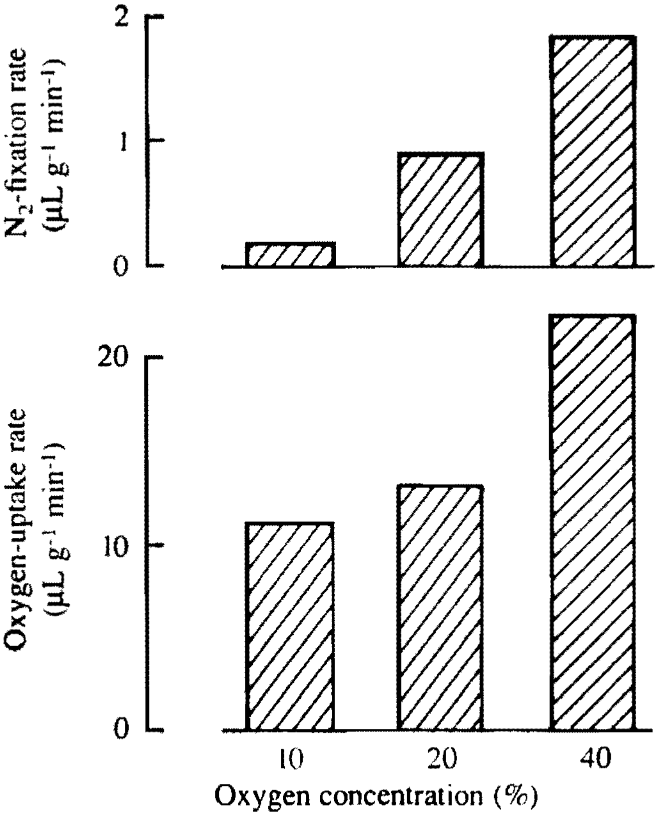

**Figure 7. Effect of oxygen concentration on the nitrogen fixation and respiration of soybean nodules (fresh mass). (From Ae and Nishi 1983.)**

One reason for the relative susceptibility of pigeonpea, as compared with sorghum, to reduced soil aeration is the effect of lowered oxygen concentration on nodule activity. It was shown for red clover that nodulated plants are more susceptible to lowered oxygen concentration in the medium than are ammonium-fed plants (Ferguson and Bond 1954). Another reason is the difference between the two crops in the total oxygen consumption rate of underground parts: at 55 DAS, that of pigeonpea was equal to that of sorghum; at 83 DAS, it exceeded that of sorghum, although the total root mass of pigeonpea was much less than that of sorghum (Fig. 8). This may be attributed, at least partly, to the high respiratory activity of the pigeonpea nodules.

## Effects of Ridging

### Effect of Ridging on Soil Oxygen Concentration

A possible management practice to improve soil aeration is to change the soil surface configuration. ICRISAT has long recognized the importance of maintaining better drainage conditions in Vertisols and has established a technology for doing so, using

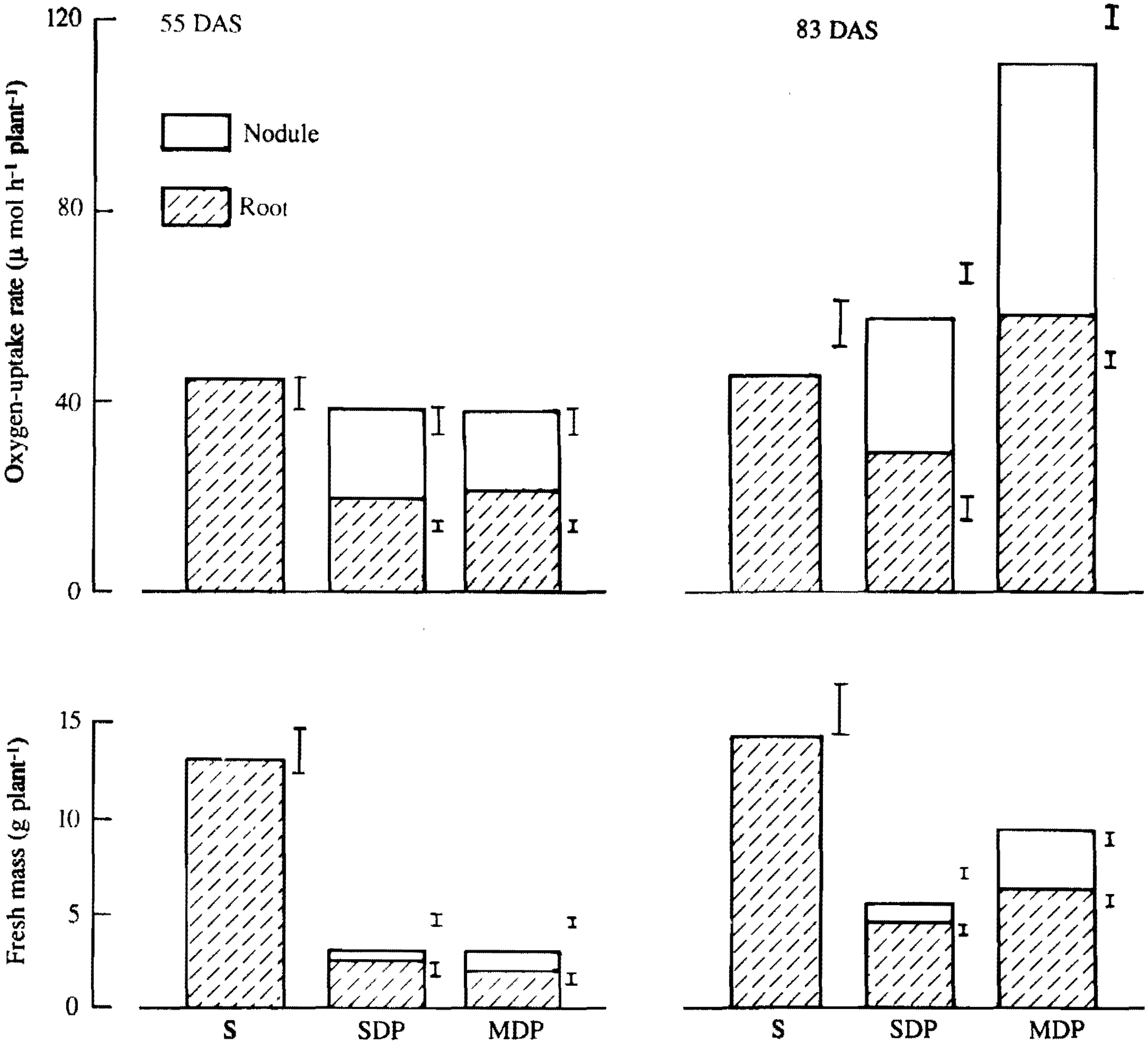

Figure 8. Fresh mass and oxygen-uptake rate of whole underground parts of sorghum (S) and pigeonpea (SDP = short-duration; MDP = medium-duration), at 55 and 83 days after sowing (DAS). SEs for root alone and root + nodule are indicated.

broadbeds and furrows (El-Swaify et al. 1985). But appropriate land configurations for Alfisols remain unclear (El-Swaify et al. 1985, 1987). Evidence has been given that raised land configurations have a disadvantage because they are more subject to erosion (El-Swaify et al. 1985, 1987), but in terms of crop yields, the average yield for several years did not show any marked difference among types of land configuration (Kanwar 1986; El-Swaify et al. 1987). In fact, the results from ICRISAT show that yield advantage or disadvantage differs from year to year and from one crop to another (ICRISAT 1976, 1977, 1980). The possible advantage of a raised land configuration to improve soil-aeration status for the root zone has not been paid sufficient attention, because aeration was not considered a major problem on Alfisols. However, since we determined that it is as important on Alfisols as on Vertisols, we investigated the effect of ridging on soil aeration.

The oxygen concentration at 15-cm depth in the row between plants was investigated in one Vertisol and two Alfisol fields in the 1988 rainy season. The land was plowed and rotavated to a 15-cm depth. A narrow ridge-and-furrow system, with ridges 15 cm high and 75 cm apart, was created for all the plots, and then ridges were flattened by hand in the plots with the flat-on-grade treatment. This year was very wet, and the Vertisol field (BP 1) was completely waterlogged for long periods (Fig. 9). But in some cases, especially early in the rainy season, oxygen concentration remained higher in the ridge-and-furrow system than in the flatbed. The effect of ridging was very clear in the two Alfisol fields also, the oxygen concentration remaining always higher in the ridges than in the flatbed.

Figure 10 shows the distribution of oxygen concentration in an Alfisol field after a rainy day. Higher oxygen concentration was maintained in the rooting zone in the ridge-and-furrow system.

## Effect of Ridging on Crop Growth

The effect of ridging on the growth of sorghum and

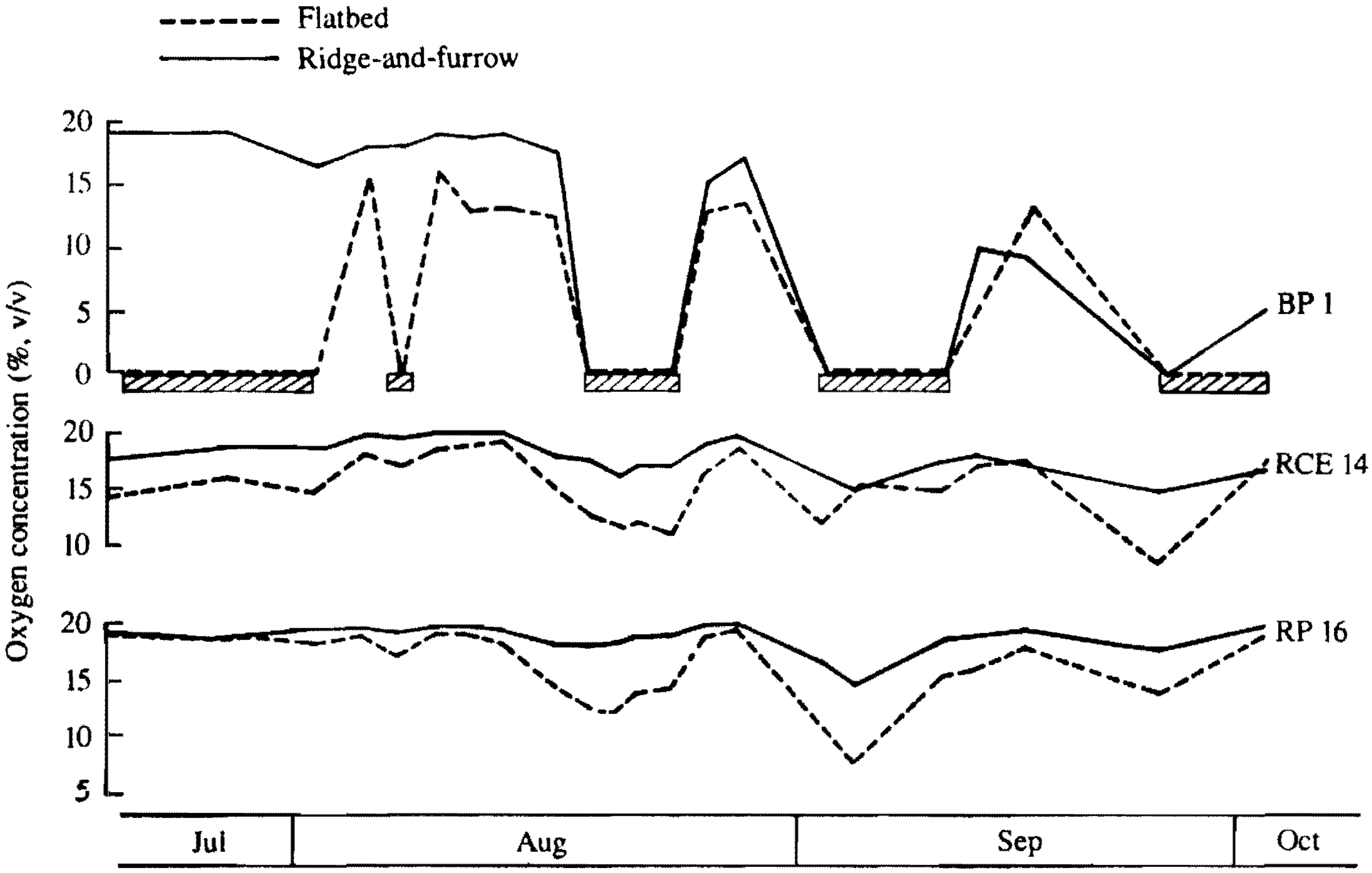

Figure 9. Effect of ridging on oxygen concentration in soil air at 15-cm depth in Vertisol (BP 1) and Alfisol (RCE 14, RP 16) fields in ICRISAT Center, 1988 (▨ indicates water table within 15 cm of the soil surface).

pigeonpea was investigated from 1987 to 1989. Table 1 shows the final total dry matter and grain yield of sorghum. In RCE 14 (Alfisol), ridging reduced growth in 1987, a dry year, because the root zone tended to be drier on ridges. However, in 1988, a wetter year, total dry mass was higher on ridges. In RP 16, an Alfisol field with a better physical structure than RCE 14, with more active clay particles and aggregation, ridging made no difference. In a Vertisol field, where the soil has a high water-holding capacity and drought stress was not a problem in the rainy season, there was no difference in growth in 1987, but in 1988, growth was generally benefited by ridging.

Table 2 shows the effect of ridging on the final total dry matter and grain yield of medium-duration pigeonpea. The ridge-and-furrow configuration was always beneficial for pigeonpea growth and yield. A similar beneficial effect on ridge-planted pigeonpea was also reported by Chowdhury and Bhatia (1971). Being a deep-rooting crop, medium-duration pigeonpea is more tolerant to dry conditions, but is susceptible to wet conditions. In the wetter years of

**Table 1. Effect of ridging on the total and head dry mass of sorghum (CSH 5) at harvest on ICRISAT fields.**

| | | | Dry mass (t ha$^{-1}$) | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Total | | | Head | | |
| Soil type | Field | Year | Flatbed | Ridge-and-furrow | SE | Flatbed | Ridge-and-furrow | SE |
| Alfisol | | | | | | | | |
| | RCE 14 | 1987 | 5.89 | 4.95( 84)[1] | ±0.68 | 1.27 | 1.08( 85) | ±0.20 |
| | | 1988 | 7.98 | 10.21(128) | ±1.27 | 2.58 | 3.13(122) | ±0.66 |
| | RP 16 | 1988 | 11.48 | 11.86(103) | ±1.14 | 4.59 | 4.65(101) | ±0.44 |
| Vertisol | | | | | | | | |
| | BP 1 | 1987 | 7.95 | 7.70( 97) | ±0.67 | 2.58 | 2.42( 94) | ±0.31 |
| | | 1988 | 3.61 | 4.15(115) | ±0.62 | 0.45 | 0.50(112) | ±0.10 |

1. Figures in parentheses show percentage of flatbed values.

**Table 2. Effect of ridging on the total and pod dry mass of medium-duration pigeonpea[1] at harvest on ICRISAT fields.**

| | | | Dry mass (t ha$^{-1}$) | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Total | | | Pod | | |
| Soil | Field | Year | Flatbed | Ridge-and-furrow | SE | Flatbed | Ridge-and-furrow | SE |
| Alfisol | | | | | | | | |
| | RCE 14 | 1987 | 6.09 | 7.23(119)[2] | ±1.01 | 0.36 | 0.57(160) | ±0.42 |
| | | 1988 | 3.27 | 4.33(132) | ±1.16 | 0.83 | 0.99(119) | ±0.59 |
| | | 1989 | 4.05 | 5.30(131) | ±1.67 | 0.65 | 0.92(141) | ±0.44 |
| | RP 16 | 1988 | 7.76 | 9.13(118) | ±0.47 | 2.85 | 3.01(106) | ±0.19 |
| | RCE 24 | 1989 | 6.31 | 6.50(103) | ±0.45 | 0.54 | 0.59(109) | ±0.07 |
| Vertisol | | | | | | | | |
| | BP 1 | 1987 | 5.73 | 6.32(110) | ±0.55 | 1.24 | 1.21( 97) | ±0.40 |
| | | 1988 | 0.71 | 1.27(179) | ±0.42 | 0.13 | 0.32(250) | ±0.07 |
| | BP 2 | 1989 | 6.92 | 6.97(101) | ±0.14 | 1.52 | 1.41( 93) | ±0.20 |

1. Cultivar: C 11 (1987, 1988), ICP 1-6 (1989).
2. Figures in parentheses show percentage of flatbed values.

1988 and 1989, there was a difference in the growth on two types of Alfisols, that is, RCE 14 and RP 16 or RCE 24. The growth was better and the effect of ridging less in RP 16 and RCE 24 fields, which had less tendency to form crusts and higher water infiltration rates than RCE 14. In a Vertisol field also, the effect of ridging was beneficial under conditions that generally suppressed plant growth.

## Possible Mechanisms of Beneficial Effects of Ridging on Pigeonpea Growth

### Emergence

In 1987, there was 117 mm of rain within 1 week after pigeonpea was sown at the beginning of July. The field became excessively wet, and emergence was restricted, especially in the Vertisol field BP 1 and on flatbeds (Table 3). Sorghum had less difficulty than pigeonpea in emerging from a wet soil.

### Root Growth

Root growth was enhanced in the ridge-and-furrow system, and roots grew to deeper layers than in the flatbed system (Table 4), presumably due to the better oxygen conditions in the former system (Fig. 10).

### Mortality Caused by Severe Waterlogging

When the field was excessively wet after heavy rains,

**Table 3. Effect of land configuration on emergence ratio (%)[1] of medium-duration pigeonpea (C 11) and sorghum (CSH 5) in Vertisol (BP 1) and Alfisol (RCE 14) fields, ICRISAT Center, 1987.**

| | BP 1 | | | RCE 14 | | |
|---|---|---|---|---|---|---|
| Crop | Flatbed | Ridge-and-furrow | SE | Flatbed | Ridge-and-furrow | SE |
| Pigeonpea | 59.9 | 95.0 | ±8.8 | 99.1 | 100.0 | ±1.4 |
| Sorghum | 88.3 | 89.9 | ±3.9 | 82.4 | 80.3 | ±3.2 |

1. Estimated at 11 days after sowing (DAS) for BP 1 field and 15 DAS for RCE 14 field.

**Table 4. Effect of ridging on the root distribution of medium-duration pigeonpea (C 11), sampled on 3 Sep 1988 at ICRISAT Center.**

| | Vertisol | | Alfisol | | | |
|---|---|---|---|---|---|---|
| | BP 1 | | RCE 14 | | RP 16 | |
| Depth (cm) | Flatbed | Ridge-and-furrow | Flatbed | Ridge-and-furrow | Flatbed | Ridge-and-furrow |
| | | | Root fresh mass (g plant$^{-1}$) | | | |
| 0- 4 | 1.46 | 2.30 | 7.31 | 12.79 | 10.65 | 8.36 |
| 4- 8 | 0.53 | 1.10 | 2.73 | 6.50 | 7.71 | 5.99 |
| 8-12 | 0.16 | 0.37 | 0.61 | 2.82 | 3.85 | 3.20 |
| 12-16 | 0.04 | 0.07 | 0.16 | 0.77 | 1.96 | 1.74 |
| 16-20 | 0.02 | 0.02 | 0.08 | 0.25 | 1.08 | 0.92 |
| 20-24 | 0.00 | 0.00 | 0.03 | 0.04 | 0.56 | 0.33 |
| 24-28 | 0.00 | 0.00 | 0.01 | 0.03 | 0.28 | 0.15 |
| 28-32 | 0.00 | 0.00 | 0.01 | 0.02 | 0.09 | 0.09 |
| 32-36 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.05 |
| 36-40 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 |
| Total | 2.21 | 3.86 | 10.95 | 23.21 | 26.22 | 20.82 |

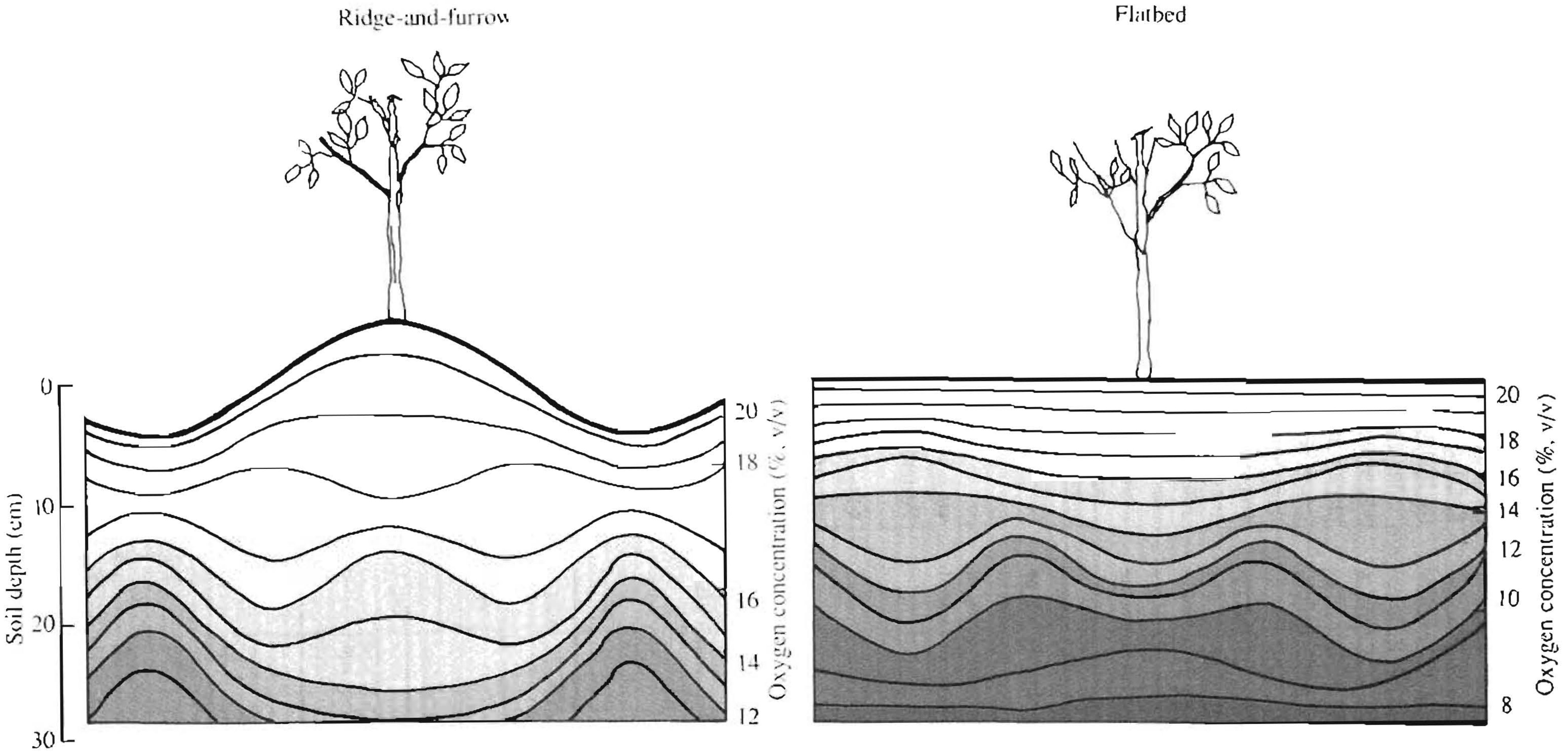

Figure 10. Effect of ridging on oxygen concentration in soil air in an Alfisol field at ICRISAT Center on 27 Sep 1989, after a rainy day.

many plants wilted and died. This is a common phenomenon occurring on both Vertisols and Alfisols in July and August. The wilt is partly attributable to phytophthora blight and partly to unexplained physiological problems. When the root is severely stressed, the respiration rate of epidermal cells is restricted, and the water permeability of these cells, a rate-limiting step to water flux into the root, is lowered. This may in turn result in plant water deficit, wilting, and eventually, death (Russell 1977).

In 1988 and 1989, the survival ratio of young pigeonpea and sorghum plants was counted at the beginning of August, after continuous rainy days (Table 5). Very low survival ratios were observed in some cases, but the survival ratio was always higher in the ridge-and-furrow system. Short-duration pigeonpea (ICPL 87) was generally more susceptible to waterlogging than medium-duration pigeonpea (C 11 or ICP 1-6). This genotypic difference was consistent with results obtained from waterlogging screening at ICRISAT (Y.S. Chauhan, ICRISAT, personal communication).

## Nitrogen Fixation

Pigeonpea leaves became pale green when the fields were excessively wet after heavy rain. This phenomenon was particularly evident around 1 month after sowing, when the plants normally become dependent for their N supply on symbiotic $N_2$-fixation. Nodule formation seemed to be delayed by oxygen deficiency in the wet soil, and nodule function—as reflected in the leaf color—was also affected.

We monitored leaf color with a Minolta Green Meter, which nondestructively measures leaf chlorophyll content. Medium-duration pigeonpea (ICP 1-6) grown on ridges had consistently darker green leaves than that grown on flatbeds (Fig. 11), but short-duration pigeonpea ICPL 87 leaves showed little difference. Thus the two genotypes again showed differences in susceptibility to excess moisture; however, whereas seedling mortality was lower in ICP 1-6 than in ICPL 87, the converse was true of nodule function, which was more impaired in ICP 1-6 than in ICPL 87 under excess moisture and soil oxygen deficiency.

## Water Uptake from Deeper Layers in the Postrainy Season

Ridging benefited the pod-setting of medium-duration pigeonpea (C 11) by maintaining better plant-water relations in the postrainy season. The leaf temperature did not differ much between ridge and flatbed systems at the flowering stage, which corresponded with the end of the rainy season, but it was generally lower for

**Table 5. Effect of ridging on the survival (%) of young pigeonpea and sorghum plants after heavy rain. Measured on 6 Aug 1988 and 10 Aug 1989.**

| | | | Pigeonpea | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Short-duration[1] | | | Medium-duration[2] | | | Sorghum (CSH 6) | | |
| Soil | Field | Year | Flatbed | Ridge-and-furrow | SE | Flatbed | Ridge-and-furrow | SE | Flatbed | Ridge-and-furrow | SE |
| Alfisol | | | | | | | | | | | |
| | RCE 14 | 1988 | 82 | 96 | ± 9 | 98 | 95 | ± 2 | 100 | 100 | 0 |
| | | 1989 | 33 | 70 | ±15 | 71 | 98 | ±16 | 94 | 87 | ±4 |
| | RP 16 | 1988 | 99 | 99 | 0 | 98 | 94 | ± 1 | 100 | 100 | 0 |
| | RCE 24 | 1989 | 92 | 95 | ± 2 | 100 | 100 | ± 2 | 93 | 100 | ±9 |
| Vertisol | | | | | | | | | | | |
| | BP 1 | 1988 | 21 | 32 | ± 5 | 34 | 80 | ± 7 | 100 | 100 | 0 |
| | BP 2 | 1989 | 84 | 89 | ± 3 | 91 | 100 | ± 3 | 100 | 99 | ±3 |

1. Cv ICPL 87.
2. Cv C 11 in 1988; ICP 1-6 in 1989.

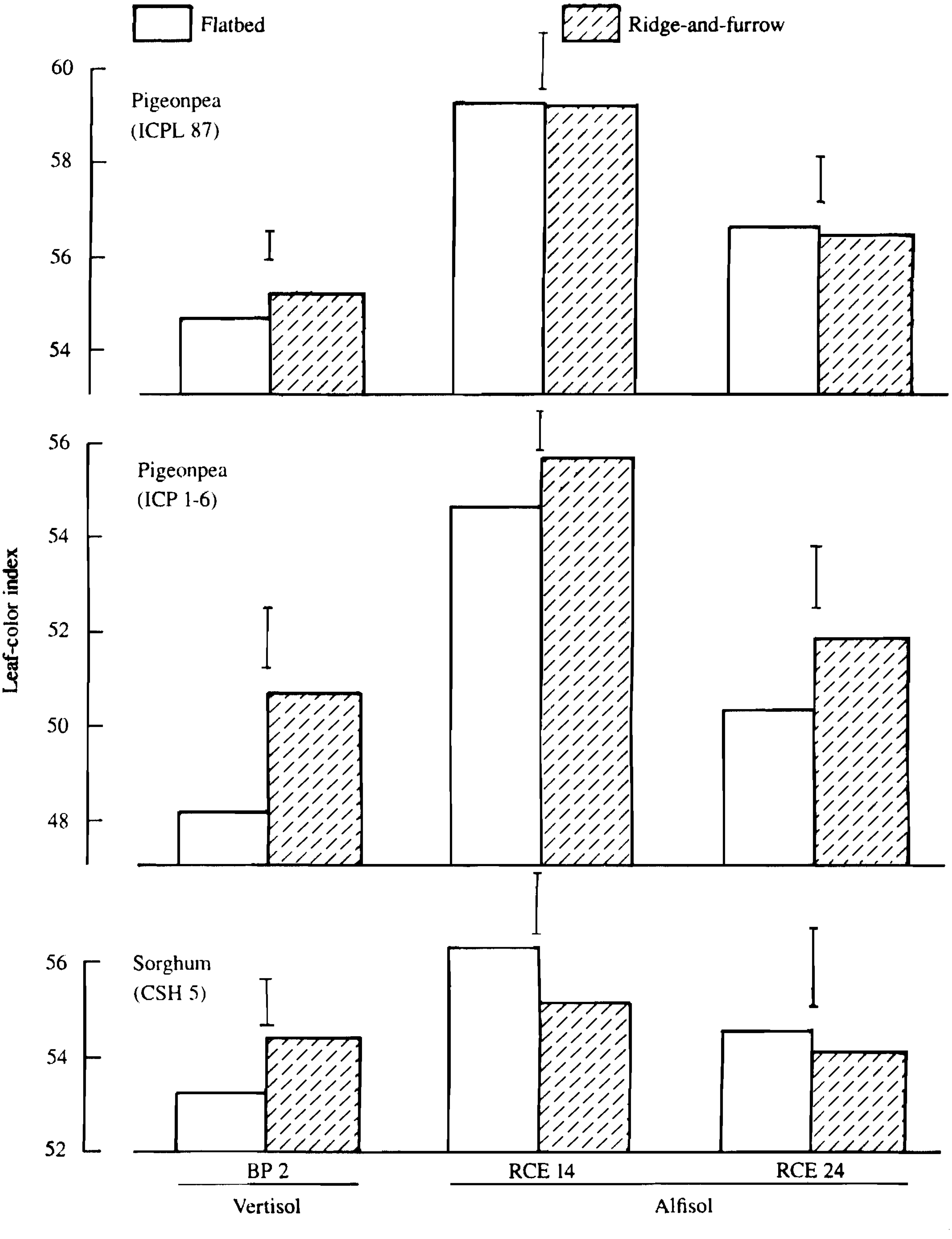

**Figure 11. Effect of ridging on chlorophyll concentration in leaves in short-duration (ICPL 87) and medium-duration (ICP 1-6) pigeonpea and in sorghum (darker green = higher concentration) (23 Aug 1989). Standard errors indicated.**

the ridge-and-furrow system than for the flatbed system at maturity (Fig. 12). Parameters relating to plant-water relations were measured at the stage of pod formation. In 1987, there was little difference in the parameters between the two systems in the Vertisol (Fig. 13). But in the Alfisol, leaves of plants in the ridge-and-furrow system showed higher stomatal conductance, higher water potential, and lower leaf temperature (Fig. 13).

At this time, there was no difference in the soil water content between the two systems, and available soil water existed only in deeper layers of the soil. The root distribution was better and the roots reached deeper layers in the ridge-and-furrow system than in the flatbed (Fig. 14). Therefore, we concluded that the ridge-and-furrow system promoted better distribution of roots, to deeper layers, enabling them to better tap stored soil water and maintain better plant water status from pod-formation to maturity. Deeper root distribution was assumed to be due to better root growth during the rainy season as a result of better aeration in the ridge-and-furrow system.

## Conclusion

The beneficial effect of ridging on pigeonpea plant growth is summarized in Figure 15. The practical implication of this study is that, at least for pigeonpea, the ridge-and-furrow system is more advantageous than the flatbed system on both Vertisols and Alfisols in terms of growth and yield, because the ridge-and-

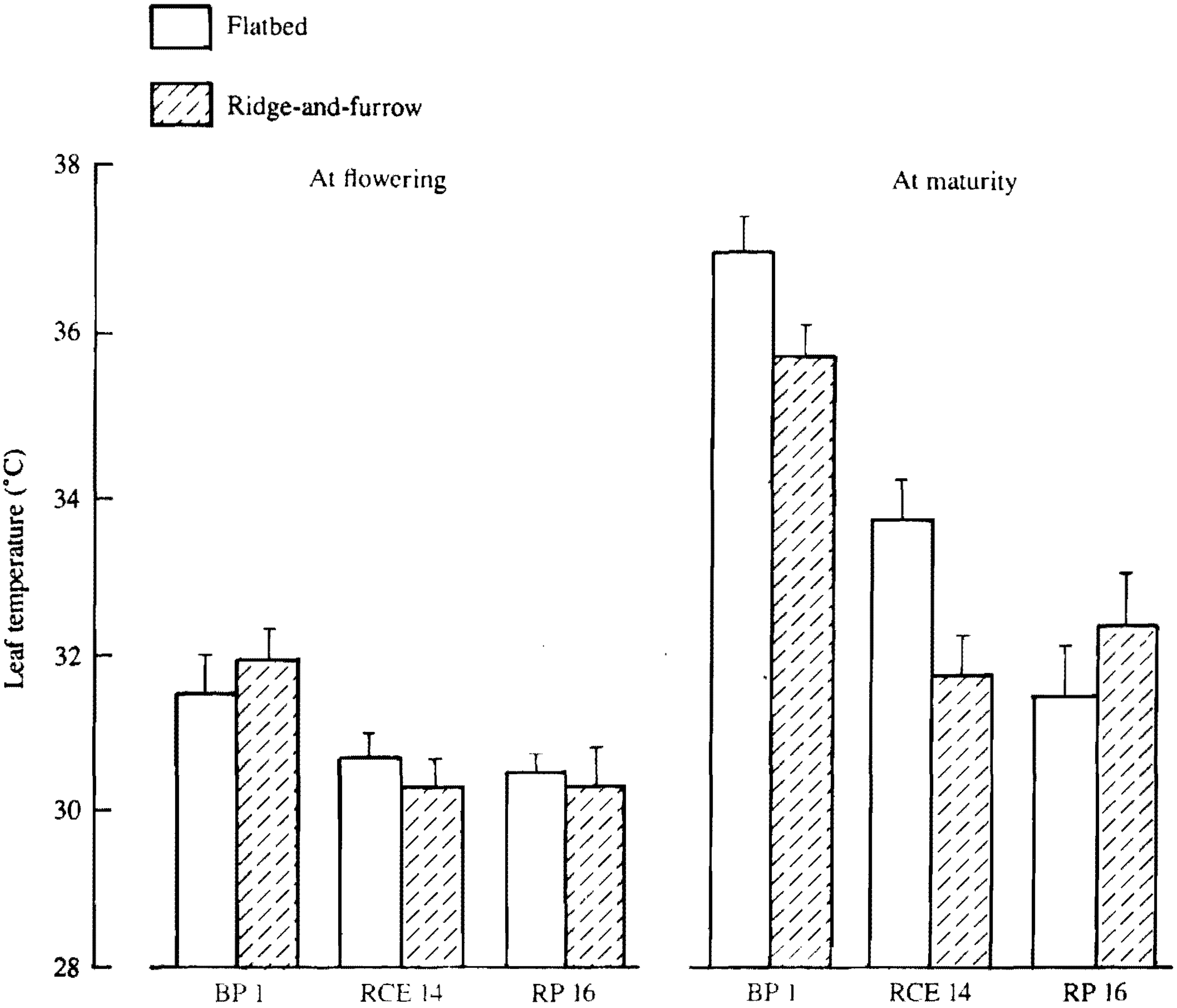

**Figure 12. Effect of ridging on the leaf temperature of medium-duration pigeonpea (C 11). BP 1, Vertisol field; RCE 14 and RP 16, Alfisol fields. Standard errors indicated.**

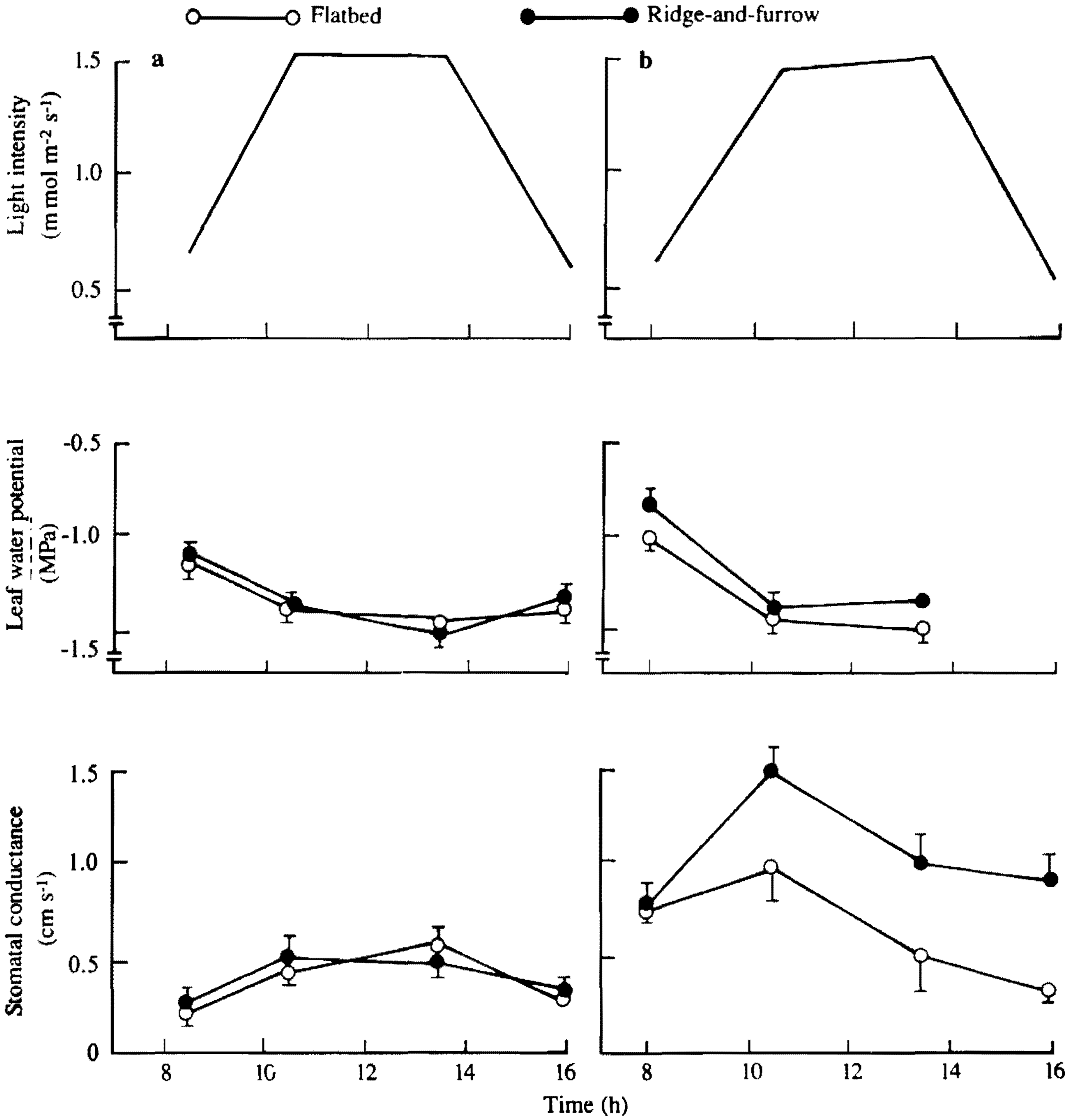

**Figure 13. Effect of ridging on the diurnal changes for leaf water potential and stomatal conductance of pigeonpea (C 11) leaves grown on (a) Vertisol (BP 1, 16 Dec 1987) and (b) Alfisol (RCE 14, 7 Dec 1987) fields. Standard errors indicated, where they exceed symbol size. (From Itoh et al. 1989.)**

furrow system alleviates the stress of anaerobiosis when the soil is too wet. For Alfisols, it was reported that the ridge-and-furrow system has the disadvantage of more soil erosion and runoff (El-Swaify et al. 1985, 1987). The lack of appropriate equipment available to small farmers to make adequate ridges is another problem. But if the plant growth is better on a ridge-and-furrow system, it may in turn lessen soil erosion and runoff, because greater plant cover reduces the impact of raindrops. Runoff is inversely correlated with plant cover (Schreiber and Kincaid 1967). Clearly, further studies on the net effect of different

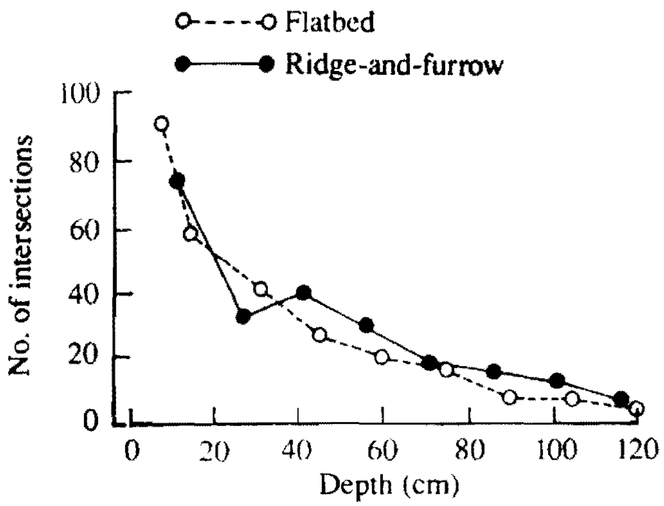

**Figure 14. Root distribution (number of intersections in a 1 × 1 cm grid of 5 × 10 cm area) of medium-duration pigeonpea in an Alfisol at harvest, ICRISAT Center, 17 Mar 1989.**

land configurations in Alfisols (e.g., on the yield and sustainability) are needed.

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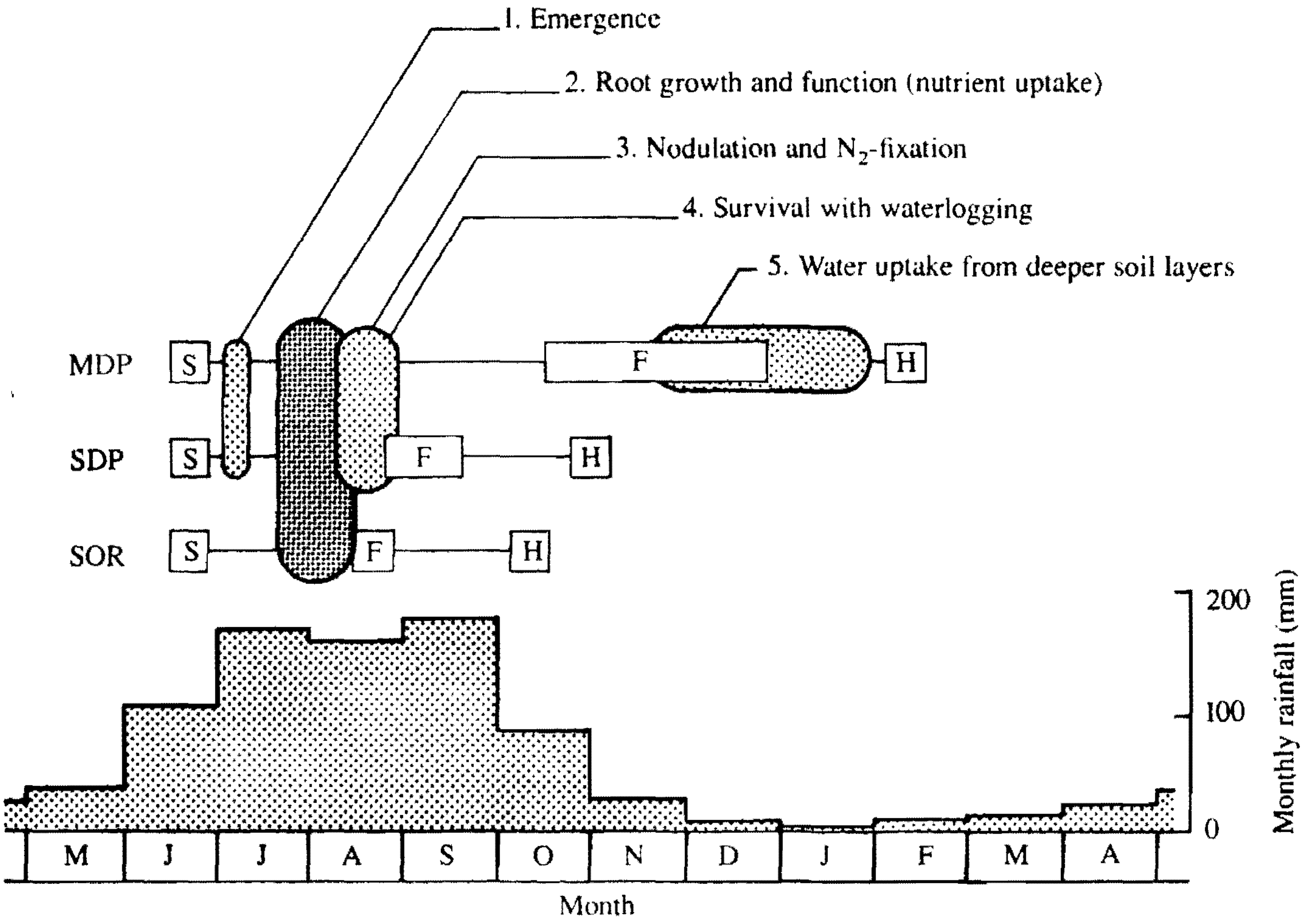

**Figure 15. Summary of the implications of ridging in relation to the phenological development of medium-duration pigeonpea (MDP), short-duration pigeonpea (SDP), and sorghum (SOR). S = sowing, F = flowering, H = harvest.**

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# Improving Responses of Chickpea and Pigeonpea to Phosphorus Application in Vertisols and Alfisols

**J. Arihara[1], N. Ae[2], and K. Okada[3]**

## *Abstract*

*Chickpea and pigeonpea usually do not respond well to phosphorus (P) application in Vertisols and Alfisols of the semi-arid tropics (SAT). Several agronomic studies were conducted to determine the reasons for this.*

*Drilling of P fertilizer is usually recommended for Vertisols and Alfisols in the SAT, to overcome possible problems of P fixation and drying of the surface soil. However, because of difficulties in banding into deeper layers of soil, banding is not always effective. The efficiency of P application methods for chickpea, pigeonpea, and sorghum were compared in both Alfisol and Vertisol fields. Mixing P into the top 15 cm of soil is more effective than shallow banding in increasing dry matter and grain yield of all three crops. This indicates weak P fixation in these soils and the importance of soil moisture level in the fertilized zone for efficiency of fertilizer use.*

*To determine the effect of fertilizer application depth, shallow (5-cm) banding, deep (15-cm) banding, and mixing were compared. Without irrigation, deep banding was most effective in both rainy and postrainy seasons. This is attributed to higher and more stable soil moisture levels at 15-cm depth in both Alfisols and Vertisols. Response of chickpea and pigeonpea to P application rate with different application methods was also determined. For chickpea in Vertisols, deep banding of 10 kg P $ha^{-1}$ was as effective as mixing of 20 kg P $ha^{-1}$.*

*Some physiological constraints to increasing P response in these legumes were recognized. With chickpea grown in peninsular India, the upper limit to yield, which is about 3.5 t $ha^{-1}$, seems to be set by light-utilization characteristics of the crop canopy. Further responses to P above this yield level would require greater light-use efficiency by the canopy.*

*In pigeonpea, P application can sometimes be detrimental to grain yield. In short dry spells on Alfisols, short-duration pigeonpea plants fertilized with P were more susceptible to drought stress than nonfertilized ones. This is because P application encourages greater root proliferation near the soil surface at the expense of deeper rooting. This contrasted with sorghum, where P application did not adversely affect rooting at depth. In short-duration pigeonpea, higher dry-matter production with P application does not always result in higher grain yields. Poor pod-set of pigeonpea after vigorous vegetative growth is the main constraint to increasing grain production with P application.*

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## Introduction

Average grain yields of chickpea and pigeonpea remain below 1 t $ha^{-1}$ in India, the major producer of these two legume crops (Johansen et al. in press). Generally, chickpea and pigeonpea do not show large responses to the application of phosphorus (P) (Tandon 1987), a most important nutrient for the growth of legumes, considering that they can meet most of their nitrogen (N) needs through symbiotic fixation. An understanding of this low responsiveness to P may explain the reasons for the low grain yields usually realized.

A first step in the analysis of this problem is to ascertain whether currently used methods of P application are effective in supplying P to plant roots. If they are not, then studies are needed to determine the most effective method and the rate of P application required to maximize yield. If optimum application methods fail to induce a P response, it is necessary to examine (1) why these legumes perform relatively well in soil of low apparent P fertility without P fertilizer and (2) why there is no marked improvement under well-fertilized conditions. The first aspect is discussed in the first two parts of this book. The second aspect has two components. First, investigation is needed into possible adverse effects of P application on crop growth, as can be observed in pigeonpea growing on Alfisols. Secondly, P-use efficiency of grain production needs to be considered. This is especially relevant to pigeonpea, as grain yield production is often not proportional to the amount of vegetative growth.

## Effective Phosphorus Application Methods for Chickpea and Pigeonpea

For crops grown on Indian soils, drilling of P fertilizer below the soil surface is usually found superior to surface broadcasting with some mixing into the surface soil (Tandon 1987). This is understandable, particularly for situations where fertilizer P is likely to be fixed and where the topsoil is prone to drying out during crop growth. It has been found that deep banding of P fertilizer can be beneficial to both chickpea (e.g., Sharma and Richharia 1962) and pigeonpea (e.g., Pannu and Sawhney 1975) grown under dryland conditions.

### Effect of Placement Method

We tested the effect of shallow banding of P fertilizer at 5-cm depth, the farmers' normal practice, in comparison with mixing of fertilizer in the soil to a depth of 15 cm. Experiments were done on chickpea (cv K 850), pigeonpea (cv C 11), and a sorghum hybrid (CSH 5) in the postrainy season of 1986/87 on a Vertisol and an Alfisol at ICRISAT Center under irrigated and nonirrigated (except for an establishment irrigation) conditions. Phosphorus fertilizer was applied as single superphosphate at a rate of 52 kg P $ha^{-1}$.

On the nonirrigated Vertisol, P application did not significantly affect yields of chickpea or pigeonpea but it did increase grain yield of sorghum, irrespective of application method (Table 1). On the irrigated Vertisol, banding increased grain yield of sorghum

**Table 1. Effect of irrigation and phosphorus application[1] method on grain yield (t $ha^{-1}$) of three crops grown on a Vertisol and an Alfisol at ICRISAT Center, postrainy season 1986/87.**

| | | Vertisol | | | | Alfisol | | | |
|---|---|---|---|---|---|---|---|---|---|
| Crop | Irrigation | Control (no P) | P banded at 5-cm depth | P mixed to 15-cm depth | SE | Control (no P) | P banded at 5-cm depth | P mixed to 15-cm depth | SE |
| Chickpea | - | 1.13 | 0.97 | 1.39 | ±0.24 | 0.09 | 0.07 | 0.06 | ±0.01 |
| Pigeonpea | - | 0.70 | 0.69 | 0.97 | ±0.27 | 0.18 | 0.20 | 0.20 | ±0.06 |
| Sorghum | - | 2.55 | 3.41 | 3.27 | ±0.69 | 0.82 | 0.74 | 0.75 | ±0.19 |
| Chickpea | + | 2.27 | 2.39 | 3.07 | ±0.24 | 0.87 | 0.48 | 0.92 | ±0.13 |
| Pigeonpea | + | 1.19 | 1.39 | 1.83 | ±0.27 | 1.47 | 1.07 | 1.28 | ±0.60 |
| Sorghum | + | 2.61 | 5.42 | 5.78 | ±0.69 | 1.19 | 1.82 | 2.23 | ±0.19 |

1. Phosphorus applied at the rate of 52 kg $ha^{-1}$ as single superphosphate.

only, but mixing significantly increased yield of all three crops (Table 1).

On the nonirrigated Alfisol, neither banding nor mixing improved grain yield of any crop (Table 1). Even on the irrigated Alfisol, P application did not increase yield of chickpea or pigeonpea. However, with irrigation, banding increased sorghum yield slightly (not significantly) and mixing increased it significantly (Table 1).

Overall, application of P by mixing was more effective in increasing grain yield of these crops than banding, which was effective only for sorghum growing on Vertisol. This suggests that P fixation in these soils is not enough to reduce the efficiency of P fertilizer when its contact with the soil is maximized.

The adverse effect of soil drying on the response to P fertilizer was larger for chickpea and pigeonpea than for sorghum. Sorghum grain yield increased with P application on irrigated Alfisols and on Vertisols, irrespective of irrigation. Grain yield of the legumes was increased by P only on the Vertisol where the soil was kept moist throughout the experimental period. The root morphology of these three crops may explain the differences. The crown-root system of sorghum spreads horizontally, near the soil surface, thus facilitating absorption of fertilizer P in both treatments. By contrast, the taproot system of chickpea and pigeonpea, which grows downwards into deeper soil layers, renders them less efficient at absorbing P near the soil surface.

## Effect of Placement Depth

To further investigate the effect of depth of P fertilizer placement on growth of chickpea and pigeonpea, a third treatment—namely, banding at 15 cm—was included. Pigeonpea (cv ICPL 87) was grown on a Vertisol and an Alfisol with and without irrigation in the rainy season of 1987. Phosphorus fertilizer was applied as single superphosphate at a rate of 52 kg P ha$^{-1}$. On the Vertisol, deep banding significantly increased yield of pigeonpea in the absence of irrigation (Fig. 1). With irrigation, neither shallow nor deep banding significantly increased yield over the nonfertilized control, but mixing more than doubled yield. On the Alfisol, there were no treatment effects without irrigation, but with irrigation, grain yield significantly increased in the mixing treatment only, compared with the nonfertilized control (Fig. 2).

An experiment with these P application treatments applied to chickpea (cv K 850) was conducted on Vertisols, with and without irrigation, in the postrainy season of 1988/89. Deep banding appeared beneficial without irrigation and mixing with irrigation, but the differences between application methods were not significant in this case (Fig. 3).

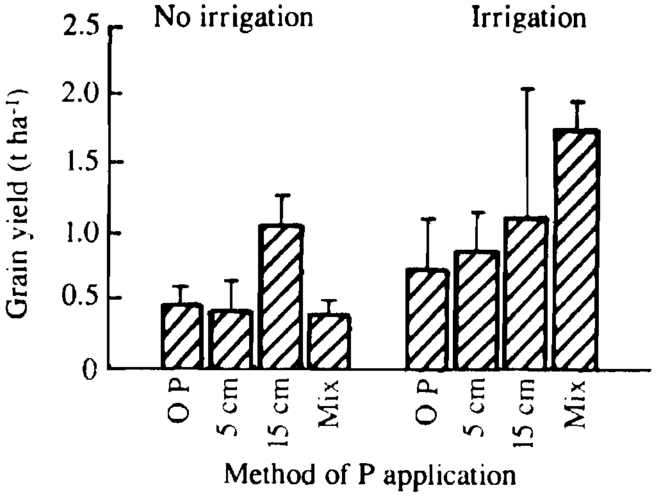

**Figure 1. Effect of P application method on grain yield of short-duration pigeonpea (cv ICPL 87) on a Vertisol, ICRISAT Center, rainy season 1987. 0 P = control (no P applied); 5 cm and 15 cm = banding at 5-cm and 15-cm depths; mix = mixing into soil to 15-cm depth. Standard errors indicated.**

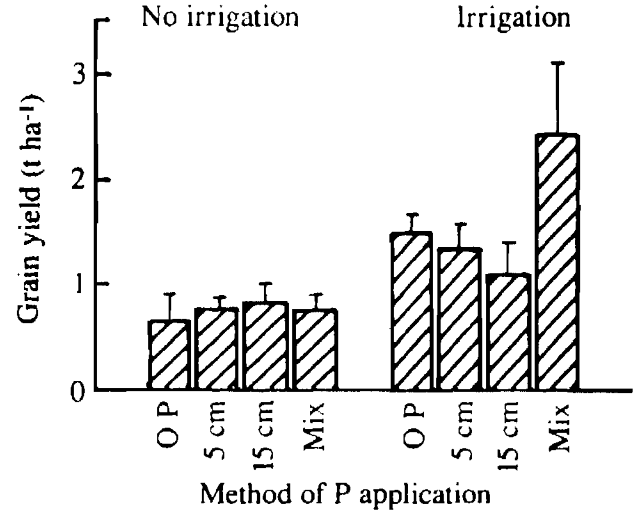

**Figure 2. Effect of P application method (see Fig. 1 for description of methods) on grain yield of short-duration pigeonpea (cv ICPL 87) on an Alfisol, ICRISAT Center, rainy season 1987. Standard errors indicated.**

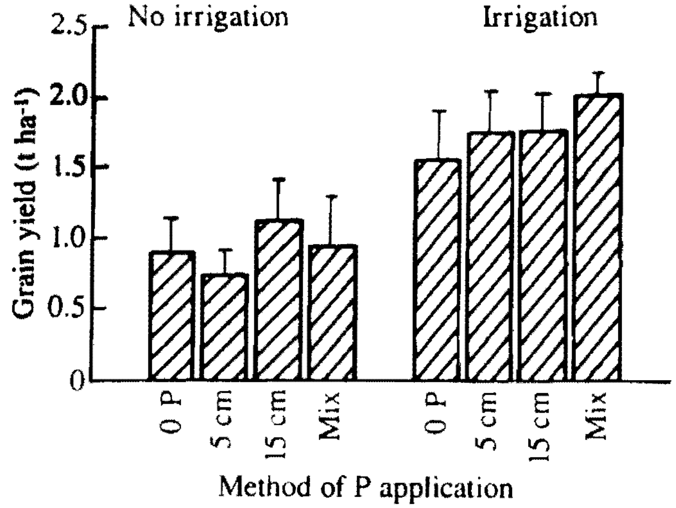

**Figure 3. Effect of P application method (see Fig. 1 for description of methods) on grain yield of chickpea (cv K 850) on a Vertisol, ICRISAT Center, postrainy season 1987/88. Standard errors indicated.**

The P fertilizer was consistently more effective in increasing grain yield, under different situations, with either deep banding or mixing to 15 cm. The soil moisture at 15-cm depth was constantly higher and fluctuated less during the growing season than at 5 cm. Figure 4 illustrates this for pigeonpea grown on Vertisols. Such differences in soil moisture distribution would have contributed to the greater availability of deep-placed P during the growth period.

## Optimum Phosphorus Rate with Different Application Methods

In the previously described P placement studies, only one P application rate was used. This was a high level, chosen to ensure near-maximum growth or yield, but-not so high as to be toxic, as indicated by previous P rate trials (e.g., for pigeonpea, see Fig. 1 of Ae et al. 1991, in this volume). However, the magnitude of differences between P placement methods would be expected to differ at different P rates, especially at suboptimal P levels. Thus we conducted further experiments to compare application methods over a range of P application rates. We grew short-duration pigeonpea (cv ICPL 87) under rainfed conditions in the rainy season of 1989. On the Vertisol, optimum yield was reached at 20 kg P ha$^{-1}$ with deep banding and at 10 kg P ha$^{-1}$ with mixing (Fig. 5). Increasing P application rate in the shallow banding treatment did not significantly improve yield. On the Alfisol, there was no response to P application with any application method (Fig. 5).

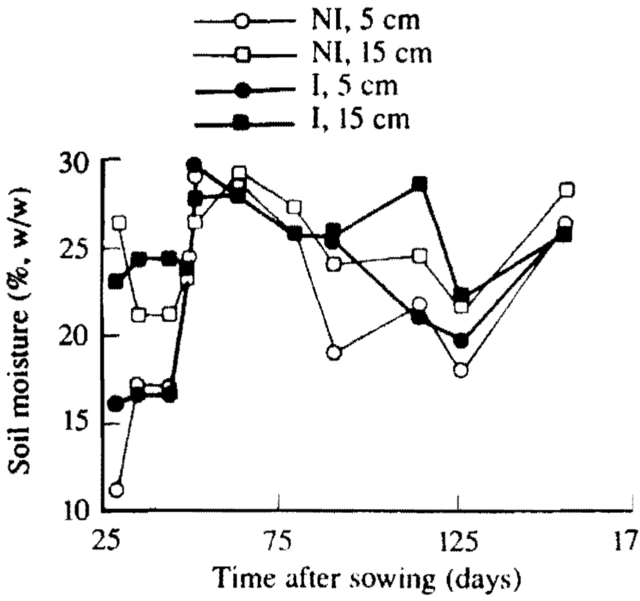

**Figure 4. Changes in soil moisture content at 5- and 15-cm soil depths in irrigated (I) and nonirrigated (NI) treatments for pigeonpea (cv ICPL 87) grown on a Vertisol, ICRISAT Center, rainy season 1987.**

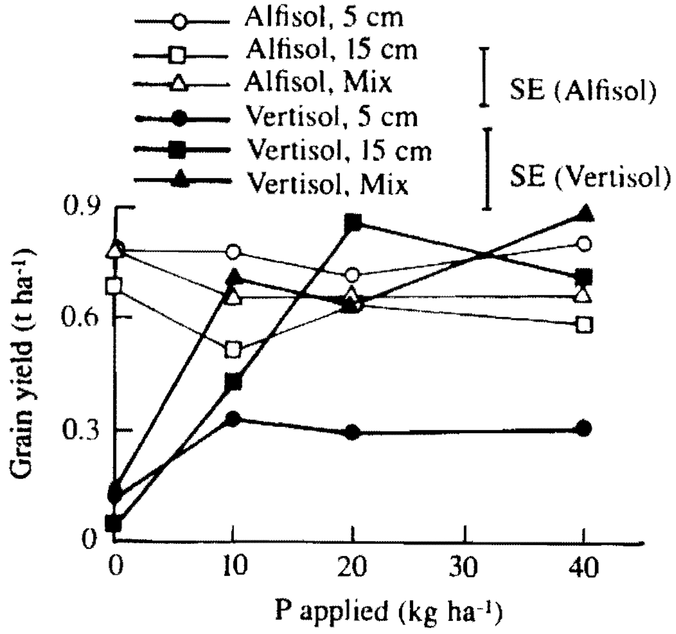

**Figure 5. Phosphorus response of short-duration pigeonpea (cv ICPL 87) with different methods (see Fig. 1 for description) of P application on an Alfisol and on a Vertisol, ICRISAT Center, rainy season 1989.**

For chickpea grown on Vertisols, deep banding always gave the highest yields, both with and without irrigation, and optimum yields were reached at lower P rates than in the mixing treatment (Fig. 6). The optimum P rate with deep banding was about 20 kg P ha$^{-1}$ with irrigation and about 10 kg P ha$^{-1}$ without. Thus the advantage of deep banding in achieving maximum yields at lowest application rates is clearly illustrated for chickpea.

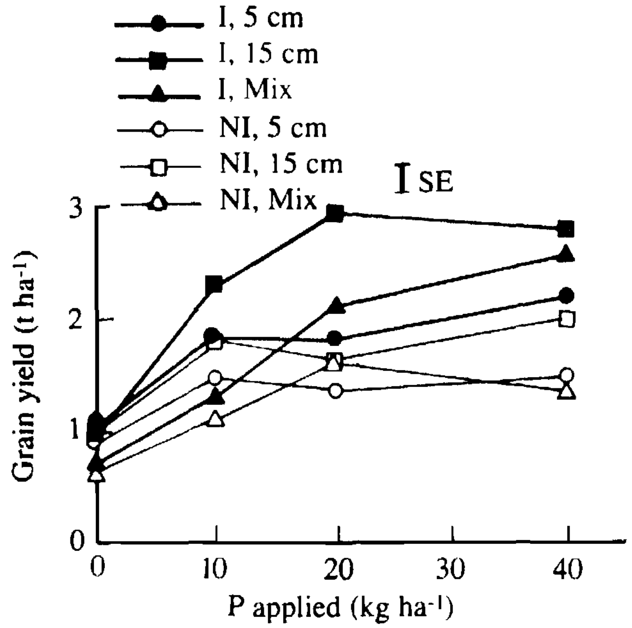

**Figure 6. Phosphorus response of chickpea (cv K 850) with different methods (see Fig. 1 for description) of P application on a Vertisol with (I) and without (NI) irrigation, ICRISAT Center, postrainy season 1988/89.**

These results demonstrate the advantages of deep placement of P fertilizer for chickpea and pigeonpea under semi-arid tropical conditions, with banding rather than mixing more effective, particularly under drier soil conditions. However, the apparent low P-fixing capacity of these soils allows continued availability of P from fertilizer mixed in the top 15 cm of soil, provided adequate soil moisture for root function is available. These results also indicate that P application rate to achieve maximum grain yield is very much influenced by application method and soil moisture status: this needs to be accounted for in formulating fertilizer recommendations for chickpea and pigeonpea.

## Physiological Limits to Increasing Phosphorus Response of Chickpea

The harvest index of chickpea grown in peninsular India is generally high, around 50%, even on irrigated fertile soils. This situation differs from the cool-winter environment of northern India where harvest indices rarely exceed 30% (Saxena and Johansen 1990). The shorter growth duration and more favorable conditions of solar radiation during the grain-filling period in peninsular India may explain this. Thus improvements in chickpea yield in peninsular India are more likely to come from increases in biomass production during a limited growing period than from improving harvest index, which is already very high for a legume crop. Therefore, improvement of soil fertility to maximize biomass formation is an important consideration in peninsular India.

We tried to create nonlimiting soil-fertility conditions for chickpea through treatments involving high levels of N and P application and different tillage designed to improve the rooting medium. An experiment was conducted on a Vertisol given optimum irrigation in the postrainy season of 1988/89. Main-plot treatments comprised discing and deep plowing with discing. Subplot treatments comprised a nonfertilized control, 120 kg N ha$^{-1}$, 52 kg P ha$^{-1}$, and a combined NP treatment. Fertilizers were mixed into the top 15 cm of soil.

By 68 days after sowing (DAS), growth was best with the NP treatment, although a response to P alone was evident (Fig. 7). In the NP treatment, growth was

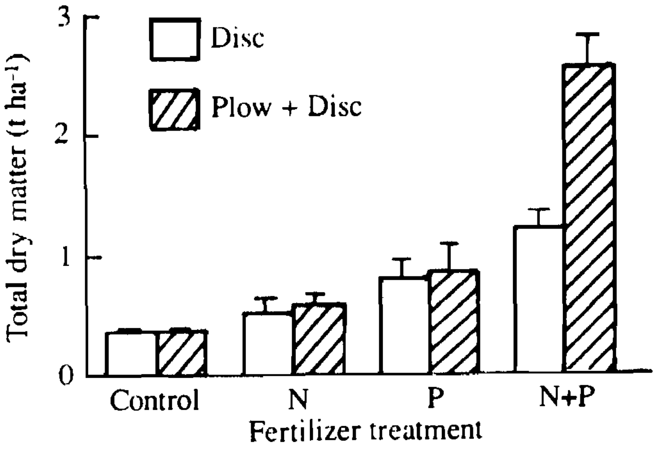

**Figure 7. Effect of tillage treatment and fertilizer application on total dry matter of chickpea (cv K 850) at 68 days after sowing (DAS) on a Vertisol, ICRISAT Center, postrainy season 1988/89. Standard errors indicated.**

much better in deep-plowed plots. However, this pattern of vegetative growth did not translate exactly into grain yield (Fig. 8). The response to P alone was significant, and there was a further yield increase in the NP treatment, indicating a positive interaction between N and P even though the plants were well nodulated. However, deep plowing caused no yield improvement. Thus, yield potential of chickpea in this environment is in the order of 3.5 t ha$^{-1}$, in agreement with the values reported by Saxena and Johansen (1990).

Even though these fertilizer and tillage treatments could markedly stimulate growth (for instance, in the NP, deep-plowed treatment), this did not result in an ultimate yield advantage. The apparent ceiling yield obtained is not likely to be set by limitations of soil fertility but by ability of the crop canopy to utilize light. This was indicated in an experiment where chickpea cultivars with erect (cv K 850) and bushy (cv ICCC 42) growth habits were compared. Treatments of seedbed preparation (flatbed, or ridge-and-furrow) and canopy (tied–i.e., artificially tied up–and natural, i.e., normal development) were also compared (Table 2). In the bushy cultivar particularly, tying up of the canopy reduced the light-extinction coefficient (k), and this was reflected in higher yields.

These data illustrate Liebig's Law of the Minimum, in that P responses can only be expected up to the ceiling yield level, where another factor—in this

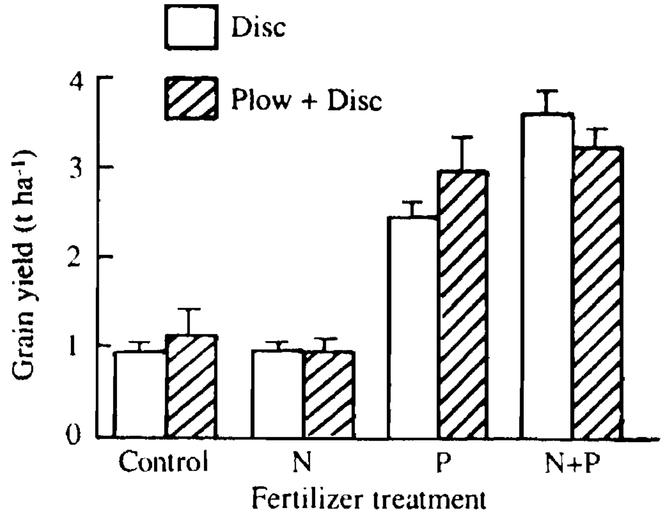

**Figure 8. Effect of tillage treatment and fertilizer application on grain yield of chickpea (cv K 850) on a Vertisol, ICRISAT Center, postrainy season 1988/89. Standard errors indicated.**

**Table 2. Effects of canopy modification[1] on light-extinction coefficient and grain yield of bushy (ICCC 42) and erect (K 850) chickpea genotypes, on a Vertisol at ICRISAT Center, postrainy season 1987/88.**

| | Flatbed | | | Ridge | | |
|---|---|---|---|---|---|---|
| Genotype | Natural | Tied | | Natural | Tied | Mean |
| | | | Canopy light-extinction coefficient (k) | | | |
| ICCC 42 | 1.12 | 0.99 | | 1.20 | 0.82 | 1.03 |
| K 850 | 1.00 | 0.98 | | 1.14 | 0.91 | 1.03 |
| **SE** | | | ±0.13 | | | ±0.07 |
| **Mean** | 1.06 | 1.02 | | 1.17 | 0.86 | 1.03 |
| SE | | | ±0.09 | | | |
| CV (%) | | | 22 | | | |
| | | | Grain yield (t ha$^{-1}$) | | | |
| ICCC 42 | 2.80 | 3.12 | | 2.46 | 3.54 | 2.98 |
| K 850 | 3.16 | 3.09 | | 2.69 | 3.17 | 3.03 |
| **SE** | | | ±0.27 | | | ±0.13 |
| **Mean** | 2.98 | 3.11 | | 2.58 | 3.36 | 3.01 |
| SE | | | ±0.19 | | | |
| CV (%) | | | 18 | | | |

1. Natural = not modified; tied = canopy tied up to increase light penetration.

case, light utilization—sets the limit to yield formation. Thus, if erect chickpea genotypes with better light-utilization characteristics and yield potentials exceeding 3.5 t ha$^{-1}$ can be bred, greater P requirements and consequently, P responses may be expected in high-yield environments.

## Physiological Limits to Increasing Phosphorus Response of Pigeonpea

### Below-ground Effects

We have found that application of P can sometimes adversely affect the growth of pigeonpea. This was clearly apparent in a P application experiment conducted in the rainy season of 1986. On a Vertisol, total dry-matter production of ICPL 87 increased with application of 52 kg P ha$^{-1}$ throughout growth. On an Alfisol, however, total dry-matter production was superior with P application only until the end of the rainy season, to about 80 DAS (Fig. 9). Thereafter, the dry matter of the fertilized pigeonpea failed to increase, but that of the nonfertilized pigeonpea continued increasing. The severe terminal drought stress observed on fertilized pigeonpea in this experiment suggested an adverse effect of P application on root development.

To confirm this hypothesis, the effect of P application on the root distribution of pigeonpea (ICPL 87) and sorghum (CSH 5) was observed in Alfisol and Vertisol fields in the rainy season of 1989. Application of 52 kg P ha$^{-1}$ mixed into the top 15 cm of soil promoted root development of sorghum in the upper soil profile of both the Alfisol and the Vertisol (Fig. 10). The root system of pigeonpea tended to become shallower in the Alfisol (Fig. 11). In the Vertisol, P application enhanced root growth near the surface, but had no consistent effect at greater depths (Fig. 11). Thus, on the Alfisol only, the relatively lower root development of pigeonpea below 40 cm in the P-fertilized treatment would thus make it more prone to drought stress on drying of the topsoil.

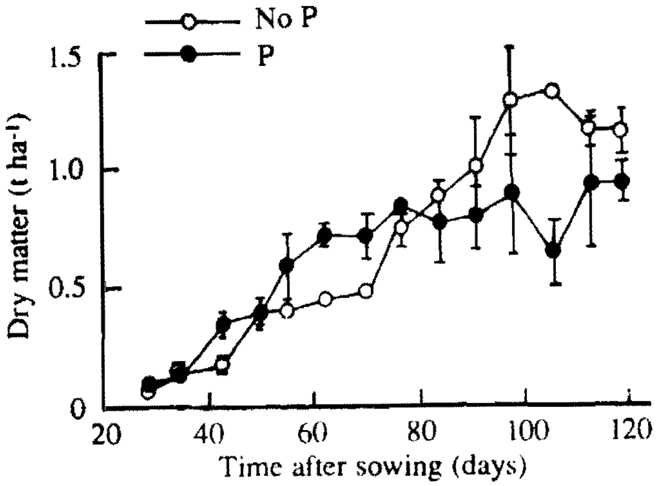

**Figure 9. Effect of application of 52 kg P ha$^{-1}$ on dry-matter accumulation of short-duration pigeonpea (cv ICPL 87) grown on an Alfisol, ICRISAT Center, rainy season 1986. Standard errors indicated where they exceed symbol size.**

Further investigations of effects of P application on root development were made for plants grown in 90-cm-long tube pots filled with an Alfisol of low P status. Application of P increased crown-root formation in sorghum and generally increased the size of

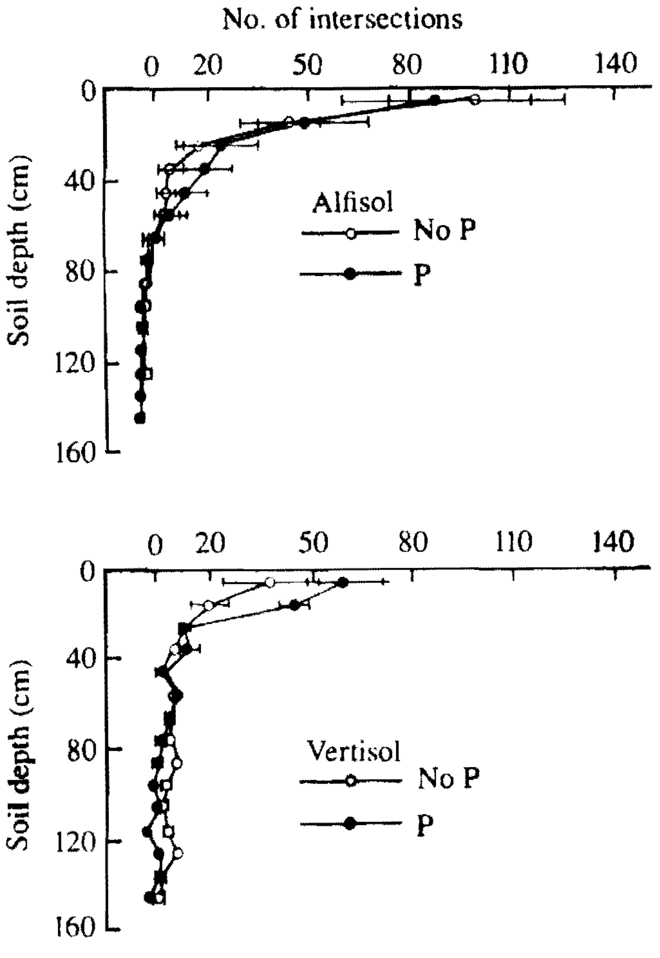

**Figure 10. Effect of application of 52 kg P ha$^{-1}$ on root development (number of intersections in a 5 × 5 cm grid) of sorghum (CSH 5) in an Alfisol and a Vertisol field, ICRISAT Center, rainy season 1988. Standard errors indicated where they exceed symbol size.**

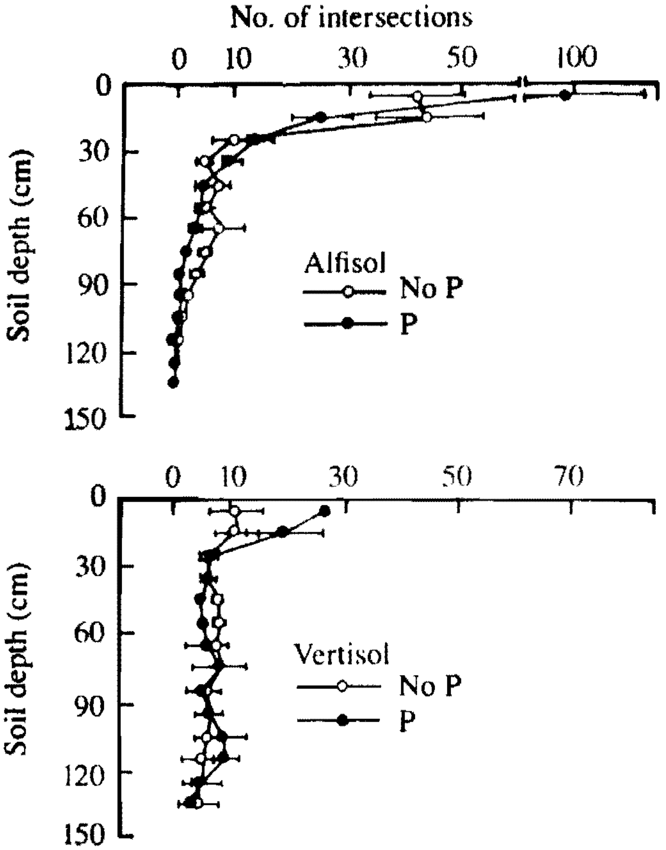

**Figure 11. Effect of application of 52 kg P ha$^{-1}$ on root development (number of intersections in a 5 × 5 cm grid) of short-duration pigeonpea (ICPL 87) in an Alfisol and a Vertisol field, ICRISAT Center, rainy season 1988. Standard errors indicated where they exceed symbol size.**

the root system. In pigeonpea, P application increased numbers of secondary and tertiary roots but decreased the length of the taproot. These results were consistent with field observations and explain how P fertilization interacts with drought stress in pigeonpea.

## Above-ground Effects

Pigeonpea of all durations is notorious for its low and widely fluctuating harvest index (Sheldrake 1984). It often decreases with an increase in biomass production, which may be promoted by P application. Thus a key to improving P-use efficiency in pigeonpea would be to raise the harvest index.

We also conducted a yield-maximization study with short-duration pigeonpea (ICPL 87) on a Vertisol, in the rainy season of 1989; N, P, and tillage treatments were similar to those described for chickpea. We also included a canopy-modification treatment, by tying up branches to allow greater light penetration. Although there was a significant P response, we could not further increase yield by improving light penetration (Fig. 12), as we could for chickpea. This suggested that overall solar radiation was too low for canopy modification to make much difference.

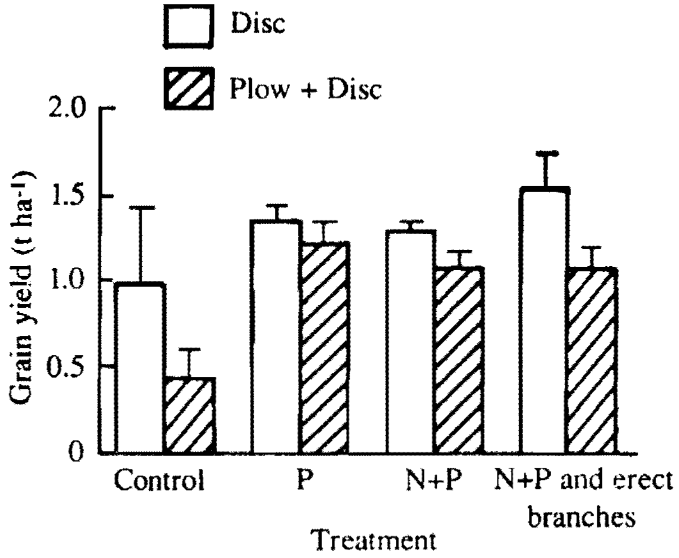

**Figure 12. Effect of tillage treatment, fertilizer application (120 kg N, 52 kg P ha$^{-1}$) and canopy modification on grain yield of short-duration pigeonpea (ICPL 87) in a Vertisol field, ICRISAT Center, rainy season 1989. Standard errors indicated.**

As Figure 13 shows, the flowering and reproductive growth period of short-duration pigeonpea (Aug-

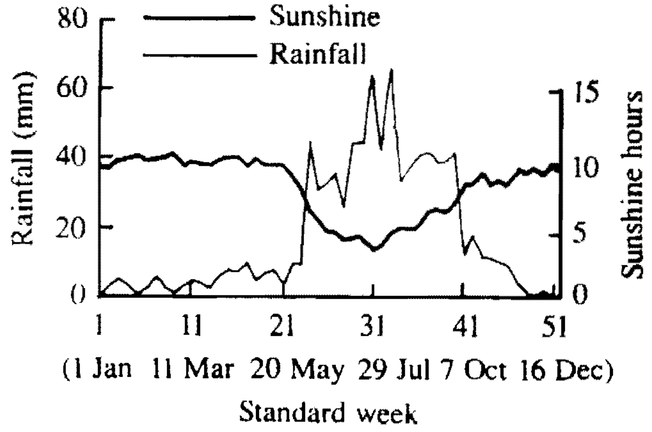

**Figure 13. Long-term average pattern of rainfall and sunshine hours at ICRISAT Center (1974-88).**

Sep) coincides with the rainy season and periods of lowest solar radiation. It is suggested that the limitation of photosynthates during this period may be responsible for the flower abortion and poor pod-set in short-duration pigeonpea. In this respect, medium-duration pigeonpea may have an advantage, in that flowering and pod-set occurs after the rainy season, when solar radiation is higher.

However, the environmental factors governing flower and pod-set in pigeonpea are yet to be clarified (see Sheldrake 1984). It does not seem possible to improve the predictability of fertilizer P-use efficiency of pigeonpea until we have greater understanding of, and control over, pod-set.

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# Interpretive Summary of Part 3: Improving the Phosphorus Nutrition of Grain Legumes in the Semi-Arid Tropics

A.D. Robson[1]

## Introduction

There are at least four approaches to increasing the efficiency of use of soil and fertilizer phosphate. First, species and genotypes can be selected that have a greater capacity to obtain phosphate from the soil or a greater capacity to utilize phosphate for maximizing grain yield within the plant. Second, the symbiosis between plants and vesicular-arbuscular mycorrhizal (VAM) fungi can be manipulated to maximize phosphate uptake from soil. Third, removal of chemical and physical limitations to root growth or activity can enable greater uptake of phosphate. Fourth, the uptake of fertilizer phosphate can be increased by changing either the placement or form of the fertilizer applied. In this summary, I will consider the potential for increasing phosphate uptake and utilization by all but the first approach.

## Vesicular-Arbuscular Mycorrhizae

The potential for manipulating the mycorrhizal symbiosis to increase phosphate uptake either by soil management or inoculation depends upon the extent and timing of mycorrhiza formation, the nature of the plant roots, and perhaps the form of phosphate in the soil. With existing knowledge, we are not able to (1) identify sites where the symbiosis is operating suboptimally, (2) quantify the benefits that would result from increasing the rate and extent of colonization of roots by effective fungi, or (3) identify the most efficient method for managing the fungi either by modifying agronomic practice or by inoculation. What further research is required to answer these questions?

### Estimating Benefits

First there is a need to develop quantitative approaches to estimate the benefits of the symbiosis in particular situations. To achieve this, there is a need for an understanding of (1) the extent to which phosphorus (P) deficiency limits plant growth, (2) the extent of mycorrhiza formation expected, and (3) the effects of agronomic practices on the formation and functioning of the symbiosis.

The potential benefit from the symbiosis is best estimated by comparisons of the amounts of applied phosphate required for nonmycorrhizal plants to achieve the same growth as mycorrhizal plants (Fig. 1; Abbott and Robson 1991a). To estimate this benefit, it is necessary to compare the response to phosphate for mycorrhizal and nonmycorrhizal plants, using several levels of applied phosphate. Comparison of the growth of mycorrhizal and nonmycorrhizal plants at a particular phosphate level is less valuable, because the response will decrease with increasing P supply (Abbott and Robson 1984).

The potential benefit will depend upon the plant species (Yost and Fox 1979) and perhaps the genotype within species. The suggestion of Baylis (1970) that plants with fibrous root systems and long root hairs are probably less dependent on VAM than those with coarse roots and sparse root hairs appears to be generally valid, but there have been no quantitative relationships established between measurable properties of roots and potential benefit from VAM. The growth of both pigeonpea and chickpea can be substantially increased by increasing the extent of colonization of roots by mycorrhizal fungi (Thompson 1991). The extent to which genotypes of pigeonpea and chickpea differ in the potential benefit of the mycorrhizal sym-

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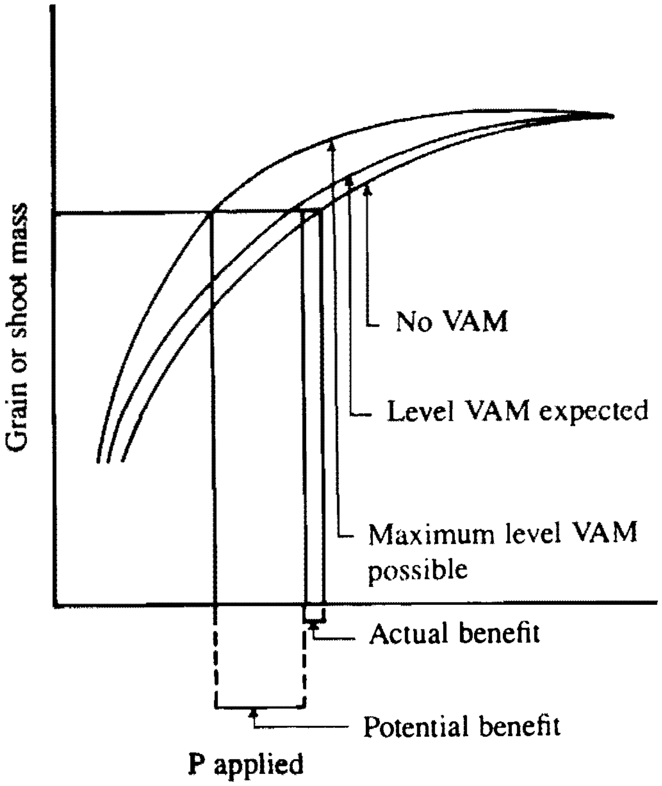

**Figure 1. Potential and actual benefits of the mycorrhizal symbiosis (modified after Abbott and Robson 1991a).**

biosis has not been adequately investigated. Genotypes can differ in their requirements for P when nonmycorrhizal, associated with differences in maximum growth rate; in their ability to take up P; or in the utilization of P in the plant. Hence comparisons of potential benefit from VAM among genotypes should be made using several levels of applied P.

The potential benefit may also depend upon the forms of phosphate in the soil. For subterranean clover, potential benefit was greatest for crystalline iron phosphate, least for potassium phosphate, and intermediate for colloidal iron phosphate (Bolan et al. 1987). It would also be expected that potential benefit would increase as the capacity of the soil to adsorb P increased. However, there is no satisfactory experimental data to support this hypothesis. Additionally, there is a need to establish quantitatively the nature of the relationship between potential benefit and adsorption capacity. In relation to forms of phosphate, it would be worthwhile to examine the interaction between VAM and the solubilization of insoluble P by compounds produced by plant roots.

The actual or current benefit that plants derive from the mycorrhizal symbiosis will depend very much on the rate and extent of colonization of plant roots by VAM fungi. These occur in almost every soil, but abundance and species diversity differ among soils (Abbott and Robson 1991b). In a soil where the resident VAM fungi infect rapidly and extensively, there would be little difference between actual and potential benefit. However, the quantitative nature of the relationship between benefit and the rate and extent of mycorrhiza formation has not been satisfactorily established for field-grown plants. In several studies, generally with young plants, there has been a linear relationship between percentage of root length colonized and shoot mass (e.g., Fig. 5 in Thompson 1991). In some other studies, generally with older plants, there has been little relationship between plant growth and the extent of root colonization (e.g., Owusu-Bennoah and Mosse 1979). One reason for this is that there may have been differences in the rate of mycorrhiza formation.

A major difficulty is in predicting mycorrhizal development for particular situations. Mycorrhiza formation in the field is not well correlated with numbers of either spores or infective propagules (Abbott and Robson 1991a). We have found reasonable relationships between the extent of colonization of roots in plants grown for 3 weeks in a greenhouse and the extent of colonization in field-grown plants (L.K. Abbott, A.D. Robson, and M.A. Scheltema, unpublished data). At some sites there was little colonization in field-grown plants, despite extensive colonization in greenhouse-grown plants, and vice versa, indicating a need for a greater understanding of the ecology of VAM fungi.

## Narrowing the Gap Between Potential and Actual Benefits

There are two options to increase the rate and extent of colonization of plant roots by mycorrhizal fungi. First, agronomic practices can be modified to increase colonization by resident fungi; second, seed or soil can be inoculated with mycorrhizal fungi.

Agronomic practices that maintain or increase mycorrhizal colonization include (1) the growing of plant species that are heavily colonized by mycorrhizal fungi in either rotational or mixed cropping systems, (2) avoidance of fallowing where both soil disturbance and the absence of a host plant can reduce propagule number, (3) avoidance of rotations that include nonmycorrhizal plants (e.g., *Brassica* spp) or plants grown under conditions not conducive to mycorrhizal colonization (e.g., paddy rice), and (4) prevention of topsoil loss either by wind erosion or by leveling.

In several areas, we have insufficient knowledge to predict effects of agronomic practices on the colonization of roots by mycorrhizal fungi. One of these relates to the effect of soil organic matter on the abundance of VAM fungi. There has been speculation that organic matter added to soil encourages the development of mycorrhizae (Hayman 1987), but there are few data to support this speculation (however, see Lee and Wani 1991). In one study, mulching surface soils increased spore numbers in comparison with soils that had been weeded (Nappi et al. 1980). There is a need to further examine the effect of the addition of organic matter on the subsequent colonization of roots by VAM fungi. In these studies, it is important that indirect effects on soil physical structure be separated from more direct benefits of organic matter to the VAM fungi. Another area in which we have insufficient knowledge relates to an abrupt change in agricultural practices. For example, liming an acid soil may reduce mycorrhizal infection, because the resident mycorrhizal fungi are adapted to an acid rather than a neutral or alkaline medium.

The second option to increase the rate and extent of VAM colonization of roots is inoculation. For field crops such as grain legumes, existing techniques for inoculation are inadequate to increase plant growth on a field scale. One, but not the only, difficulty is our inability to grow VAM fungi by standard microbiological techniques. In any case, the inoculation option is probably only appropriate when there is little colonization of roots by resident VA mycorrhizal fungi and where mycorrhizal infection is not limited by the soil physical and chemical environment.

## Alleviating Chemical and Physical Limitations to Root Growth

Root growth and function of pigeonpea may be limited by inadequate aeration associated with intense rainfall (Okada et al. 1991). The vegetative growth and grain yield of pigeonpea was greater in a ridge-and-furrow system than in flatbeds on both Alfisols and Vertisols in several seasons. This beneficial effect was associated with greater emergence and better root growth, presumably due to higher oxygen concentrations with ridges and furrows than with flatbeds. Effects of the improved root growth on nutrient uptake do not appear to have been investigated. What is the distribution of nutrients, including P, with depth? In some situations, effects of waterlogging on plant growth can be overcome by foliar application of nutrients.

While ridges and furrows may enable better growth by alleviating waterlogging, there are some difficulties in their widespread adoption. First, there is some evidence, at least for Alfisols, that this system of soil preparation is more susceptible to water erosion than flatbeds (El-Swaify et al. 1987). Second, this form of land preparation requires the use of specialized equipment that is not readily available to small farmers.

## Placement of Phosphorus Fertilizer

The appropriate method of application of a fertilizer depends upon several soil and climatic factors. First, in soils where nutrients react strongly with soil constituents, higher rates of application will be required when fertilizer is mixed than when it is banded. Second, fertilizers placed in surface layers that are likely to dry to moisture contents insufficient to support root function will provide less nutrient than fertilizer placed deeper. Third, effects of localized supply of fertilizers on root growth can affect greatly the ability of roots to provide sufficient water for unlimited shoot growth.

In both Alfisols and Vertisols, deep (15 cm) banding was more effective than shallow (5 cm) banding of phosphate in increasing vegetative growth and grain yield of chickpea, pigeonpea, and sorghum (Arihara et al. 1991). This result probably reflects the greater moisture supply at 15 cm than at 5 cm.

Effect of P application in reducing grain yield of pigeonpea may also be related to interactions between moisture and nutrient supply. Pigeonpea fertilized with P in Alfisols appears to be more susceptible to moisture stress in short dry spells than nonfertilized pigeonpea. This is presumably associated with effects of P application in reducing the depth of rooting. It is not clear why this effect was not also observed in Vertisols, particularly when root growth was decreased at depth. In some instances, adding P increased vegetative growth but did not increase grain yields, presumably because of moisture depletion or other effects associated with vigorous vegetative growth.

## Conclusion

There are several major research needs: the first is to develop quantitative approaches to estimate the benefits of the VAM symbiosis in particular situations. Important tasks here are to (1) develop a quantitative relationship between potential benefit and root properties for different genotypes, (2) develop procedures to estimate the potential benefit in relation to form of P in soil and adsorption capacity of soil, (3) develop a quantitative relationship between benefit and the rate and extent of mycorrhiza formation in field-grown plants, and (4) develop procedures for predicting mycorrhizal development and the interaction between the supply of moisture and nutrients on grain yield.

The second need is to improve our understanding of the effect of agronomic practices and soil management on the rate and extent of colonization of roots by VAM fungi. In particular, there is a requirement to examine the effect of organic matter addition on mycorrhiza formation.

The third need is for process-oriented research to build a plant-growth model incorporating water balance, shoot growth, root growth, nutrient uptake and distribution, phasic development, and yield formation. Such a model may provide valuable insights into effects of such factors as depth of fertilizer placement.

The final need is to develop land-management procedures that both minimize the effect of waterlogging on plant growth and maintain the soil in a non-erodible form.

## Acknowledgment

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# Part 4

# A Cropping Systems Perspective for Phosphorus Fertilization of Tropical Grain Legumes

# Significance of Legume Crops in Improving the Productivity and Stability of Cropping Systems

**K. Hoshikawa**[1]

*Abstract*

*Leguminous crops are essential components in cropping systems throughout the world. Legumes, which are also an important source of protein in the human diet, can biologically fix considerable amounts of atmospheric nitrogen (N), depending on both species and environment, and therefore have also been an important means of increasing N fertility of soils. Fodder or green-manure legume crops can provide appreciable amounts of N to following crops; while grain legumes usually do not provide as much N, these contributions would become relatively important in soils of low fertility. Even in modern agricultural systems where N fertilizer is widely used, the importance of legumes in crop rotations is still well recognized, suggesting that factors other than $N_2$-fixation are also important.*

*Recently, legumes have been found to use sparingly soluble soil phosphorus (P) in several ways, which could partly explain their importance in the tropics, where most soils are deficient in P. Legumes improve soil physical properties by degradation of soil clods or by the penetration of their taproot system into the soil profile, improving soil tilth and water infiltration and thus benefiting the growth of succeeding crops. Microbiological processes are involved in the degradation of soil clods, even though the mechanisms and effects of degradation are not well understood. The overall importance of legumes in the tropics is discussed.*

## Introduction

Legumes are important components of various cropping systems throughout the world. Many kinds of legumes have been cultivated, primarily because of their importance in the human diet as a protein source, especially in Asia and Africa. A combination of cereals and legumes provides a well-balanced diet for humans.

Another important reason for the cultivation of legumes is their role in improving soil fertility: in China, for instance, the practice was recommended more than 2000 years ago, and in Europe, it was also well known that crop productivity increased with the inclusion of legumes in the crop rotation, an example being the use of red clover (*Trifolium pratense* L.) in a three-course rotation system.

The advantages of legumes in the human diet and in cropping systems are mainly derived from their symbiotic $N_2$-fixing capability. Before the introduction of the Haber-Bosch method to industrially fix atmospheric $N_2$ in 1913 in Germany, cultivation of leguminous crops was indeed the most important way to increase soil N fertility. In modern agricultural systems, since the introduction of N fertilizer, the perceived importance of legumes in improving soil fertility has generally declined; nevertheless, it is still recognized in particular cropping systems. For example, maize (*Zea mays* L.) production in the corn belt of the USA was known to be stabilized after the introduction of soybean (*Glycine max* Merr.) to replace oats (*Avena sativa* L.) in the cropping cycle. This indicates the involvement of factors other than $N_2$-fixation by soybean in increasing maize productivity,

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as the maize was normally given optimum doses of fertilizer N.

In recent years, because of shortages of energy, with consequent increases in N fertilizer prices, and the possibility of pollution caused by N fertilizer, cropping systems that do not require heavy N fertilization have been sought. In tropical agriculture, where both economic reasons and low N fertilizer efficiency make optimum N fertilization difficult, leguminous crops remain an important source of N in cropping systems.

In this brief review, the effects of leguminous crops on increasing productivity of cropping systems are discussed from the soil fertility point of view. Aspects related to weed, pest, and disease control, however, are not covered.

## Nitrogen Fixation by Legume Crops

The amount of $N_2$ fixed by leguminous crops can be quite high, as Table 1 shows. The legumes of main concern at this workshop, chickpea (*Cicer arietinum* L.) and pigeonpea [*Cajanus cajan* (L.) Millsp.], can fix considerable amounts of N under favorable growth conditions. However, despite potential high $N_2$-fixation capacity, legumes cannot always supply enough N to meet internal plant needs by symbiotic $N_2$-fixation. This is especially true for grain legumes, because nodule activity generally decreases during the grain-filling period (Ae 1984; Rupela and Saxena 1987), when there is increasing competition of reproductive structures with nodules for a diminishing photosynthate supply. Indeed, soybean has often been reported to deplete soil N, generally in proportion to realized grain yield. For example, Blumenthal et al. (1982) reported that soybean depleted 9-29 kg $ha^{-1}$ of soil N, depending on population density of the crop. Tanaka et al. (1983) showed that soybean with grain yields of 3.9-4.5 t $ha^{-1}$ depleted the soil to the extent of 12-13 kg N $ha^{-1}$, and Yoshida (1982) reported similar values. Continuous soybean cultivation was reported to have removed around 60 kg N $ha^{-1}$ over a 3-year period (Ozaki 1969).

**Table 1. Estimates of nitrogen ($N_2$) fixation by various legumes under field conditions.**

| Legume | Estimated $N_2$ fixed (kg $ha^{-1}$) | Reference |
|---|---|---|
| Soybean | 20-260 | Yamada (1974) |
| Cowpea | 73- 80 | Yamada (1974) |
| Mung bean | 61 | Yamada (1974) |
| Groundnut | 72-240 | Yamada (1974) |
| Pigeonpea | 69 | Kumar Rao et al. (1983) |
| Chickpea | 1-141 | Rupela and Saxena (1987) |
| Alfalfa | 40-350 | Yamada (1974) |
| Clovers | 50-350 | Yamada (1974) |
| Tropical legumes | 100-280 | Humphreys (1987) |

## Residual Effects of Legumes on Succeeding Crops

Legume crops are known to have a beneficial effect on succeeding crops. In the famous Morrow plots at the University of Illinois, over a 7-year period, maize yielded 17% more in a maize-soybean rotation than with continuous maize (Odell et al. 1982). Maize grain yields following soybean, on average, were superior to continuous maize on a fine sandy loam soil in Alabama over 4 years (Table 2) and on a silty loam and a silty clay loam in Indiana over 12 years (Table 3). The beneficial effect of legumes on succeeding crops is normally exclusively attributed to the increased soil N fertility as a result of $N_2$-fixation.

This speculation may be true when legumes are used as a green manure or as a pasture component. Maize following vetch (*Vicia villosa* Roth), which was used as a winter green-manure crop, did not respond to N application at all (Fig. 1). This suggests

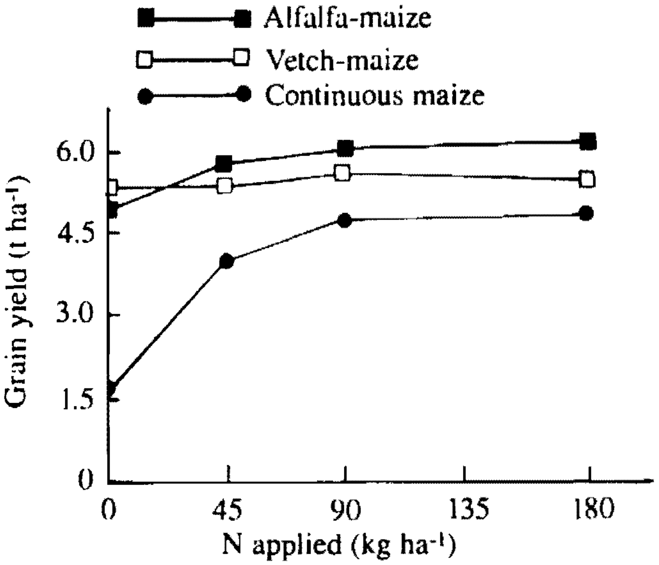

**Figure 1. Effect of previous cropping and nitrogen (N) fertilization on maize yields, 7-year average, Cecil sandy loam. (From Adams 1970.)**

**Table 2. Effects of tillage and crop rotation on maize grain yield in Alabama, USA, 1981-84. (From Edwards et al. 1988.)**

| Tillage system | Grain yield (t ha$^{-1}$) | | | | |
|---|---|---|---|---|---|
| | 1981 | 1982 | 1983 | 1984 | Mean |
| | | | Continuous maize | | |
| Conventional | 6.62 | 9.33 | 7.06 | 10.97 | 8.50 |
| Strip tillage | 6.76 | 7.79 | 7.29 | 10.27 | 8.03 |
| Zero tillage | 5.41 | 9.09 | 6.80 | 11.09 | 8.10 |
| Rotation mean | 6.26 | 8.74 | 7.05 | 10.78 | 8.21 |
| | | | Soybean-maize | | |
| Conventional | 6.70 | 7.91 | 7.32 | 10.83 | 8.19 |
| Strip tillage | 7.26 | 9.39 | 8.51 | 10.72 | 8.97 |
| Zero tillage | 6.34 | 8.86 | 8.23 | 10.86 | 8.57 |
| Rotation mean | 6.77 | 8.72 | 8.02 | 10.80 | 8.58 |

that vetch can provide enough N to sustain the growth of maize. Alfalfa (*Medicago sativa* L.) is reported to provide 85-157 kg N ha$^{-1}$, depending on the number of cuttings (Hesterman et al. 1986). A similar benefit from alfalfa in supplying N to following wheat was reported in Oklahoma, USA (Tucker et al., 1971). In paddy fields in Japan, Chinese milk vetch (*Astragalus sinicus* L.) has been used as a winter green-manure crop and is reported to provide enough N to eliminate the need for basal application of fertilizer N to rice (*Oryza sativa* L.) (Yasue and Iwase 1989).

Where much of the legume biomass is returned to the soil, as in green-manure crops or pastures, a positive soil N balance is to be expected; however, this may not be true for grain legumes or fodder crops, where the bulk of above-ground legume material is removed from the system. The depletion of soil N by high-yielding soybean has already been referred to. Nevertheless, many positive effects of grain legumes, on succeeding crops are still recorded. For example, Kumar Rao et al. (1983) showed that maize following either fallow, sorghum, or a sorghum/pigeonpea intercrop with and without N fertilizer required fertilizer equivalent to 40-50 kg N ha$^{-1}$ in order to attain a grain yield similar to that of nonfertilized maize following sole pigeonpea. Interestingly, the beneficial effect of pigeonpea on the following maize could not be completely compensated for by N application, as Figure 2 shows. Similar cases have been reported for chickpea (Fig. 3), soybean (Hesterman et al. 1986), and Egyptian clover (*Trifolium alexandrinum* L.) and alfalfa (De et al. 1985). Rowland et al. (1988) compared the yield of continuous wheat (*Triticum* spp) and wheat in rotation with lupin at many sites in Western Australia. In 20 cases out of 26, the yield gap between continuous wheat and wheat following lupin could not be compensated for by the application of N. It is interesting to note that similar results were obtained even in the case of green-manure legumes (Fig. 1).

**Table 3. Maize yield response (t ha$^{-1}$) to tillage and rotation in a Chalmers silty clay loam, Indiana, USA. (From Griffith et al. 1988.)**

| Tillage system | Continuous maize | | Maize following soybean | |
|---|---|---|---|---|
| | 1975-86 mean | 1980-86 mean | 1975-86 mean | 1980-86 mean |
| Plow | 10.61 | 10.92 | 11.13 | 11.82 |
| Chisel | 10.19 | 10.47 | 11.04 | 11.63 |
| Ridge | — | 10.47 | — | 11.91 |
| Zero tillage | 9.63 | 9.47 | 10.84 | 11.36 |

These results suggest the involvement of factors other than N contributing to the beneficial effects of legumes on succeeding crops. This speculation seems to be confirmed by the fact that leaving of crop residues usually has little effect on the yield of following crops (Crookston and Kurle 1989) and some-

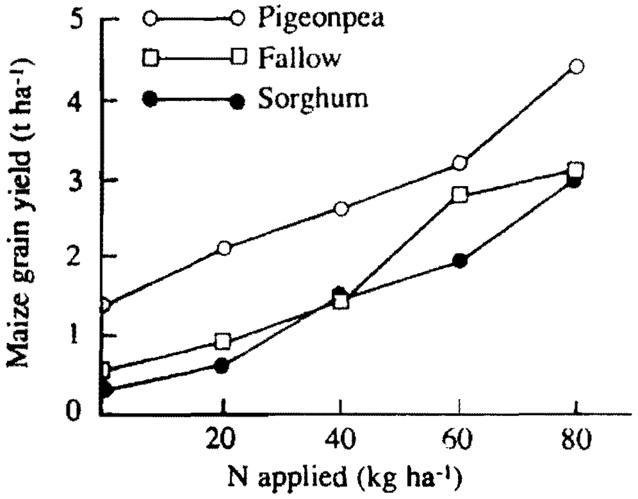

**Figure 2. Effect of previous cropping and nitrogen (N) fertilizer application on maize grain yield on a Vertisol at ICRISAT Center, India. (From Kumar Rao et al. 1983.)**

times can have an adverse effect, even with alfalfa (Fig. 4).

It is possible that ability of grain legumes to improve soil N fertility may be inversely related to yield and that effects are largest in low-N soils. In Rajasthan, India, where most of the soils are low in N and organic matter, the prior cultivation of three grain legumes, mung bean [*Vigna radiata* (L.) Wilczek], moth bean [*Vigna aconitifolia* (Jacq.) Marech.], and cluster bean [*Cyamopsis tetragonoloba* (L.) Taub.], increased the grain yield of succeeding pearl millet [*Pennisetum glaucum* (L.) R. Br.](Kathju et al. 1987). The beneficial effects of soil N were increased in the order mung bean, moth bean, and cluster bean, which was the inverse of the order of grain yield. Similar beneficial effects to wheat were reported in Australia with chickpea, lupin, and faba bean (*Vicia faba* L.) (Marcellos 1984).

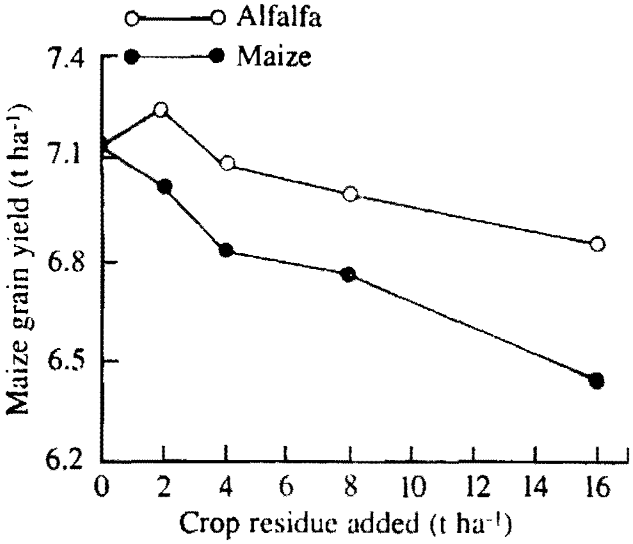

**Figure 4. Effect of maize and alfalfa residue additions on maize grain yields, average for 1963-66. (From Morachan et al. 1972.)**

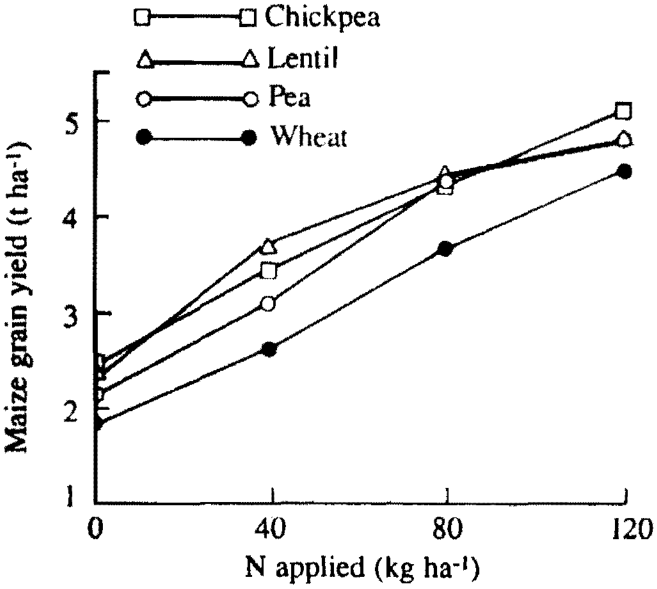

**Figure 3. Effect of the previous crop and nitrogen (N) fertilizer application on maize grain yield. (From Saxena 1981.)**

## Effect of Legumes on Soil Phosphorus Fertility

Some legumes can efficiently utilize occluded soil phosphorus (P). Lupin is tolerant of low soil P levels (Gardner et al. 1981) and can solubilize occluded P by exuding citric acid which, as a chelating substance, solubilizes iron-bound P (Gardner et al. 1983). Chickpea roots also exude a considerable amount of citric acid, which can solubilize calcium-bound P (Ae et al. 1991a). With this characteristic, chickpea can grow well on Vertisols of low available P status, but where much of the soil P is calcium-bound. Pigeonpea can utilize sparingly soluble iron-bound P, as reported by Ae et al. (1991b). For some other leguminous crops, such as soybean, no special mechanisms to utilize highly insoluble soil P have so far been reported. However, it is difficult to explain all of the beneficial effects of legumes on following crops by means of P-solubilizing mechanisms.

## Effect of Legumes on Soil Physical Conditions

In general, the beneficial effects of legumes in a crop rotation seem to be larger on heavy clay soils than on light soils. The effect of soybean cultivation on maize yield is generally larger on poorly drained heavy soil than on well-drained light soil (Van Doren et al. 1976; Hesterman et al. 1986; Griffith et al. 1988). In silt loam soils, Strickling (1950) found no correlation between soil physical conditions as affected by soybean cultivation and maize yield. The beneficial effects of rotation with soybean are also larger on soils under low-tillage systems than under conventional tillage (Dick and Van Doren 1985; Edwards et al. 1988). The beneficial effect of legumes in rotational systems can therefore be related to changes in soil physical properties.

Armbrust et al. (1982) found that the percentage and mechanical stability of dry aggregates of soil larger than 0.84 mm were lower after soybean than after sorghum and wheat (Table 4). Gantzer et al. (1987) observed that incorporation of soybean residue into soil caused small but significantly greater soil splash than incorporation of maize residue. Thus soybean at least appears to loosen soil and thus improve soil tilth. Siemens and Oschwald (1978) observed less resistance to a penetrometer after soybean than after maize (Table 5).

The decrease in size and stability of soil aggregates generally results in harmful rather than beneficial effects on soil physical condition. Soil after a soybean crop is prone to crust under rain impact (Kidder et al. 1943). Soil crusts affect crop growth adversely by increasing resistance to seedling emergence, decreasing air permeability of the soil, and reducing infiltration rate of rainwater. Cultivation of soybean also increases soil and water loss (Laflen and Moldenhauer 1979), with consequent adverse effects on crop growth.

The differences in aggregate size and stability observed just after the cultivation of soybean usually disappear by the following crop season, when the effects of soil physical conditions on crop growth would manifest themselves (Alberts and Wendt 1985; Bathke and Blake 1984). Barber (1959) showed that the aggregation increased in a linear fashion with each additional year of bromegrass or alfalfa up to 4 years, suggesting legumes do not always decrease the size and the stability of aggregates. Thus, differences in the soil aggregation size are not likely to be a major reason for the beneficial effects of leguminous crops on succeeding crops. In fact, maize grain yields are little affected by the aggregation size in a silty clay loam soil (Fig. 5).

**Table 5. Cone index readings[1] from maize and soybean plots in the spring after various types of fall tillage. (From Siemens and Oschwald 1978.)**

| | Tillage | | |
|---|---|---|---|
| Prior crop | Zero | Chisel | Plow |
| Soybean (1975) | 510 | 421 | 296 |
| Maize (1974) | 676 | 627 | 386 |

[1] Average 0-15 cm readings taken with ASAE standard penetrometer.

**Table 4. Effect of crop type on percentage of aggregates 0.84 mm in diameter and on the mechanical stability of the aggregates. (From Armbrust et al. 1982.)**

| | Aggregate percentage | | Aggregate stability (%)[1] | |
|---|---|---|---|---|
| Crop | Fall | Spring | Fall | Spring |
| Wheat | 78.1 a[2] | 77.6 a | 93.2 a | 89.7 a |
| Sorghum | 76.7 a | 70.8 b | 92.3 b | 87.7 b |
| Soybean | 68.7 b | 58.0 c | 90.2 c | 84.3 c |

[1] Aggregate stability was determined by sieving aggregates > 0.84 mm four times.

[2] Mean values over 3 years are given. Means in a column with the same letter are not significantly different at $P = 0.05$ according to Duncan's New Multiple Range Test.

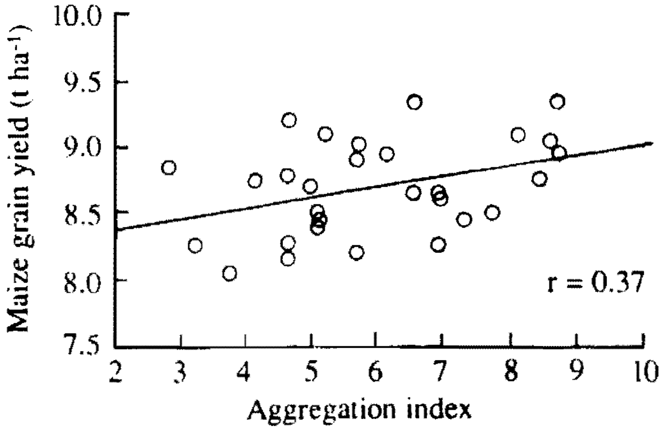

**Figure 5. The relation between soil aggregation index and maize yield on plots that had different prior crops. (From Barber 1959.)**

Soil temperature of a maize field with ridge and zero-tillage systems was higher under maize-soybean rotation than under continuous maize (Griffith et al. 1988). The difference in soil temperature was significantly correlated with the difference in maize yield (Fig. 6), suggesting that the rise in soil temperature benefits growth of following maize by overcoming low-temperature problems associated with a clay soil and soils under conservation-tillage systems. Loosened and less aggregated soil after soybean cultivation might help increase soil temperatures. This type of response applies in environments where temperatures are suboptimal for crop growth. However, in the semi-arid tropics (SAT), where supraoptimal temperatures can limit crop growth, such effects of soybean on soil temperature may adversely affect growth of the companion or subsequent crop.

Water-infiltration rate of soil is clearly improved by the cultivation of legumes (Mannering and Johnson 1969; Carreker et al. 1968; Papendick et al. 1988). Better soil tilth usually is not related to improved water infiltration rate, because infiltration rate generally shows a significant positive correlation with aggregation size (Fig. 7). The development of taproot systems by legumes would be a major reason for the increased water-infiltration rate generally observed after legume cultivation. Alfalfa, known for its vigorous taproot system, is reported to improve water-intake rate into the soil (Carreker et al. 1968). An increase in infiltration rate with the advance of soybean growth suggests that the development of the taproot system is responsible for the increase (Mannering and Johnson 1969), which, in turn, would improve soil aeration and increase soil temperature by quickly draining water on the soil surface.

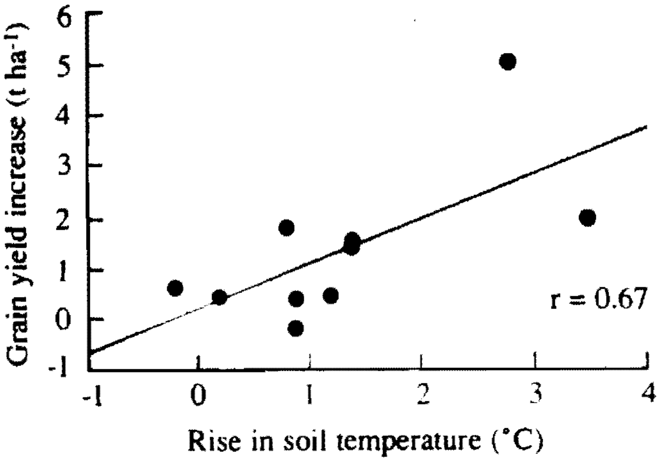

**Figure 6. Relationship of difference in soil temperature and grain yield between rotational and continuous maize. (From Griffith et al. 1988.)**

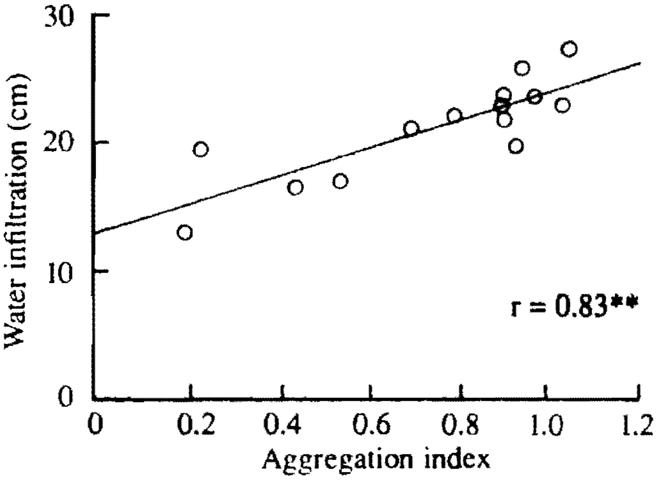

**Figure 7. Relationship between water infiltration into soil and soil aggregation. (From Mannering et al. 1968.)**

Thus the improved soil physical conditions, especially increased water-infiltration rate, seem to be largely responsible for the beneficial effect of a rotation including legumes in clayey soils or soils under low-tillage systems. With the general increase in conservation-tillage practices, such rotations are likely to assume greater importance worldwide.

## Effect of Legumes on Soil Biological Conditions

It is now clear that microorganisms play an important role in the formation and degradation of soil aggregates (Lynch and Bragg 1985). Addition of peptone to soil aggregates was reported to decrease aggregation, presumably because of the extra available N promoting greater microbial utilization of carbon-rich binding agents already present in the soil (Skinner 1979). A decrease in aggregate size after soybean cultivation may be caused by higher activity of soil microorganisms due to the lower carbon:nitrogen ratio of residues of leguminous crops. Thus it is an established fact that there are changes in soil microbial activity with the introduction of leguminous crops after cereal crops; however, because of difficulties in experimental methodology, it is not clear whether these changes are responsible for the differences in crop yields between cropping systems. Vesicular-arbuscular mycorrhizae (VAM) are also reported to be influenced by cropping system, as discussed in detail by Thompson (1991). Further studies in this area are awaited.

## Implications for Crop Production in the Semi-Arid Tropics

Effects of crop rotation on crop productivity can also be readily observed under tropical conditions (Table 6). Soil chemical and physical conditions in the tropics are generally much poorer than in the temperate regions. Improving these properties by fertilizers or tillage is difficult for the farmers in the tropics, especially for peasant farmers in the SAT. The only choice available to them is to improve soil properties through use of appropriate cropping systems.

Soils in the SAT are generally poor in chemical fertility (El-Swaify et al. 1985). Nitrogen fixation by legumes is well documented and has long been used by farmers to improve N fertility of soil. Phosphorus is usually the nutrient most deficient (after N) in soils of the SAT, including Alfisols and Vertisols. The recent discovery of efficient utilization of soil P by chickpea (Vertisols) and pigeonpea (Alfisols) encourages the intensive use of those two legumes to improve P fertility of SAT soils. As potassium (K) is usually not limiting in SAT soils, it is quite feasible to improve soil chemical fertility through the proper utilization of legumes.

Poor physical properties of soils are another major constraint to crop production in the SAT. Generally, soil physical properties are not as easy to improve as soil nutrient deficiencies. Hulugalle and Lal (1986) showed that pigeonpea can improve physical properties of a gravelly Alfisol with a compacted subsoil horizon. Improvement of maize grain yield is also observed after the cultivation of pigeonpea. Studies in this area should be intensified.

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**Table 6. Effect of crop rotation on crop yields (kg ha$^{-1}$) in northern Nigeria. (From Webster and Wilson 1966).**

| Location | First cycle, 1950-52 | | | Second cycle, 1953-55 | | |
|---|---|---|---|---|---|---|
| Bida | | | | | | |
| | Sorghum | Groundnut | Cassava | Sorghum | Groundnut | Cassava |
| Sole cropping | 353 | 305 | 5094 | 397 | 143 | 3128 |
| Rotation | 709** | 388 | 6059** | 749** | 183 | 5296* |
| Samaru | | | | | | |
| | Sorghum | Groundnut | Cotton | Sorghum | Groundnut | Cotton |
| Sole cropping | 1053 | 804 | 471 | 1062 | 781 | 402 |
| Rotation | 1341** | 1160** | 498 | 1248** | 1027* | 489 |

*, ** Significant increases at $P = 0.05$ and $P = 0.01$, respectively.

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# Root Development of Pigeonpea and Chickpea and its Significance in Different Cropping Systems

**J. Arihara,[1] N. Ae,[2] and K. Okada[3]**

## *Abstract*

*Root studies have confirmed that pigeonpea develops a deeper root system than other crops, such as soybean and maize, on Alfisols. This involves penetration by pigeonpea roots of hardpans normally present in Alfisols. The deep-rooting ability of chickpea in Vertisols was also confirmed. The deep-rooting ability of these crops not only explains their greater potential for soil water acquisition but also indicates the possibility of recycling of nutrients from deep soil layers that are not accessed by other crops.*

*Experiments showed that pigeonpea and chickpea left residual benefits for subsequent crops. These effects could not be explained solely in terms of nitrogen (N) additions through $N_2$-fixation, and studies have indicated that these legumes can improve soil water-infiltration rate and available P status for subsequent crops. The improved root development and soil-aeration status of sorghum grown in intercrops with pigeonpea were also demonstrated. The particular advantages of pigeonpea and chickpea in improving soil physical and chemical conditions for companion and subsequent crops in the semi-arid tropics are highlighted and suggestions made for further research.*

## Introduction

The Vertisols, an important soil type of the semi-arid tropics (SAT), have uniform soil profiles that often extend to a depth of several meters. Vertisols are categorized as fertile and relatively young soils formed from basic rocks rich in minerals such as basalt, basic igneous rocks, ash, calcareous sedimentary rocks, and alluvium under seasonal drying environments (El-Swaify et al. 1985). The dominant clay mineral of Vertisols is usually montmorillonite, and the soils have high water-holding capacity. Because of the deep profiles and high water-holding capacity, and sometimes high initial fertility, Vertisols are recognized as one of the most productive soils for dryland agriculture in the tropics and subtropics.

The Alfisols are another important soil type of the SAT. These soils have low water-holding capacity, with kaolinite as the dominant clay mineral, and are characterized by lack of structural aggregation in the soil surface (El-Swaify et al. 1985). Murrum (hardpan) layers in the subsoil restrict root penetration. Thus Alfisols are generally less productive than Vertisols under dryland conditions. However, phosphorus (P) levels can increase with soil depth in Alfisols (Mohr et al. 1972). In Alfisols, clay content increases with depth, and there is an argillic horizon which is moderate in cation-exchange capacity and high in water-holding capacity. Alfisols could be categorized as deep and productive soils if plants growing in them could develop deep root systems to exploit these apparently improved soil conditions at depth. Better uti-

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lization of whole soil profiles with a deep root system would be a key to increasing and stabilizing crop productivity in both Alfisols and Vertisols.

Factors preventing root penetration deep into the profile are poor soil aeration and low P fertility of surface soil in both Alfisols and Vertisols and crust formation on the surface and existence of murrum layers in Alfisols. Because of high bulk density of both Alfisols and Vertisols when wet, about 1.6 g $cm^{-3}$, the porosity in these soils is limited, quite often resulting in poor soil aeration after heavy rain (Okada et al. 1991). The high degree of swelling of clay in Vertisols allows adequate soil aeration at the beginning of the rainy season; however, once the soil is

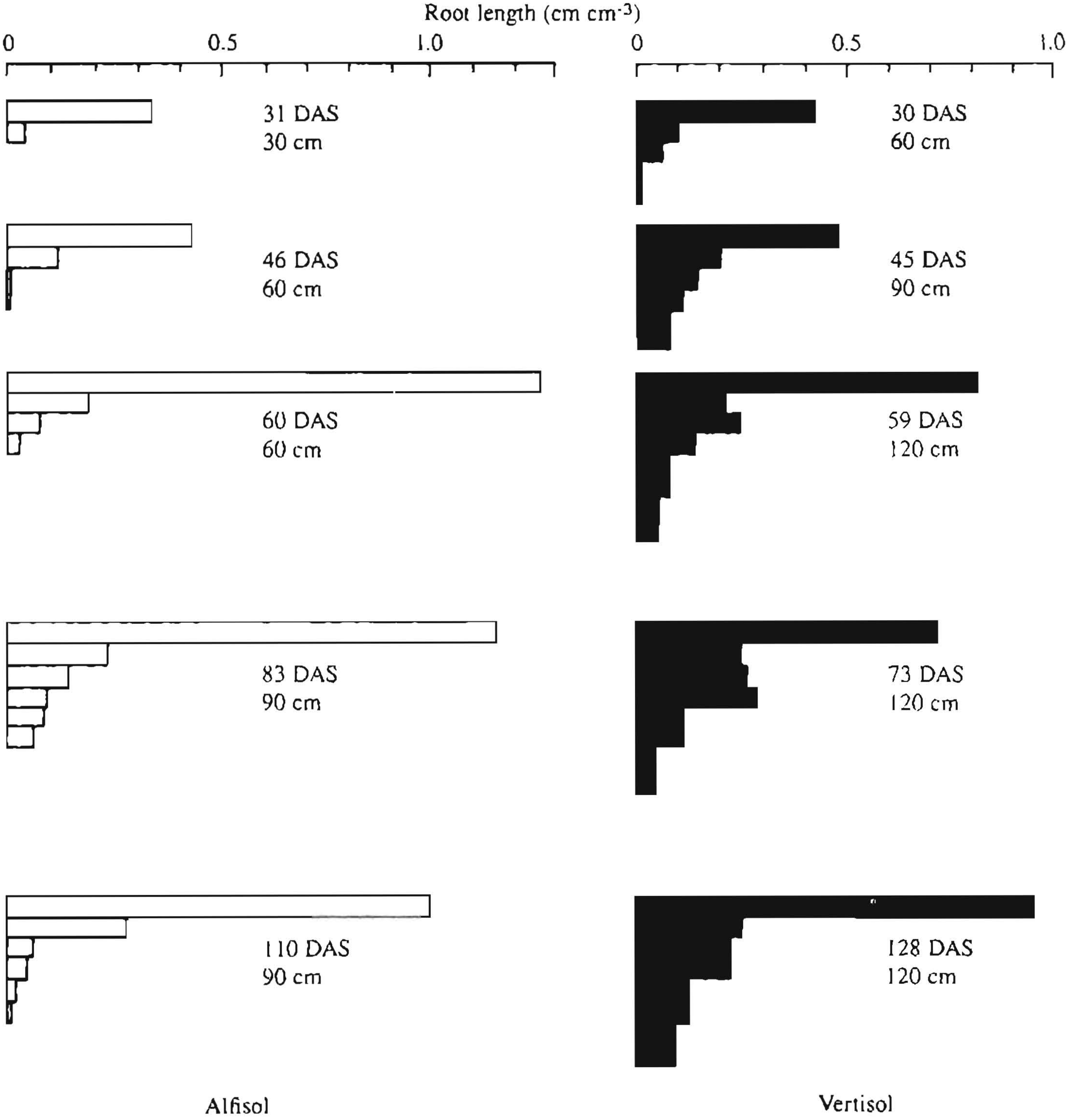

**Figure 1. Root development of soybean grown on an Alfisol and a Vertisol, ICRISAT Center, rainy season 1985. The width of each bar represents 15 cm of soil depth. Sampling time in days after sowing (DAS) and depth of rooting are indicated.**

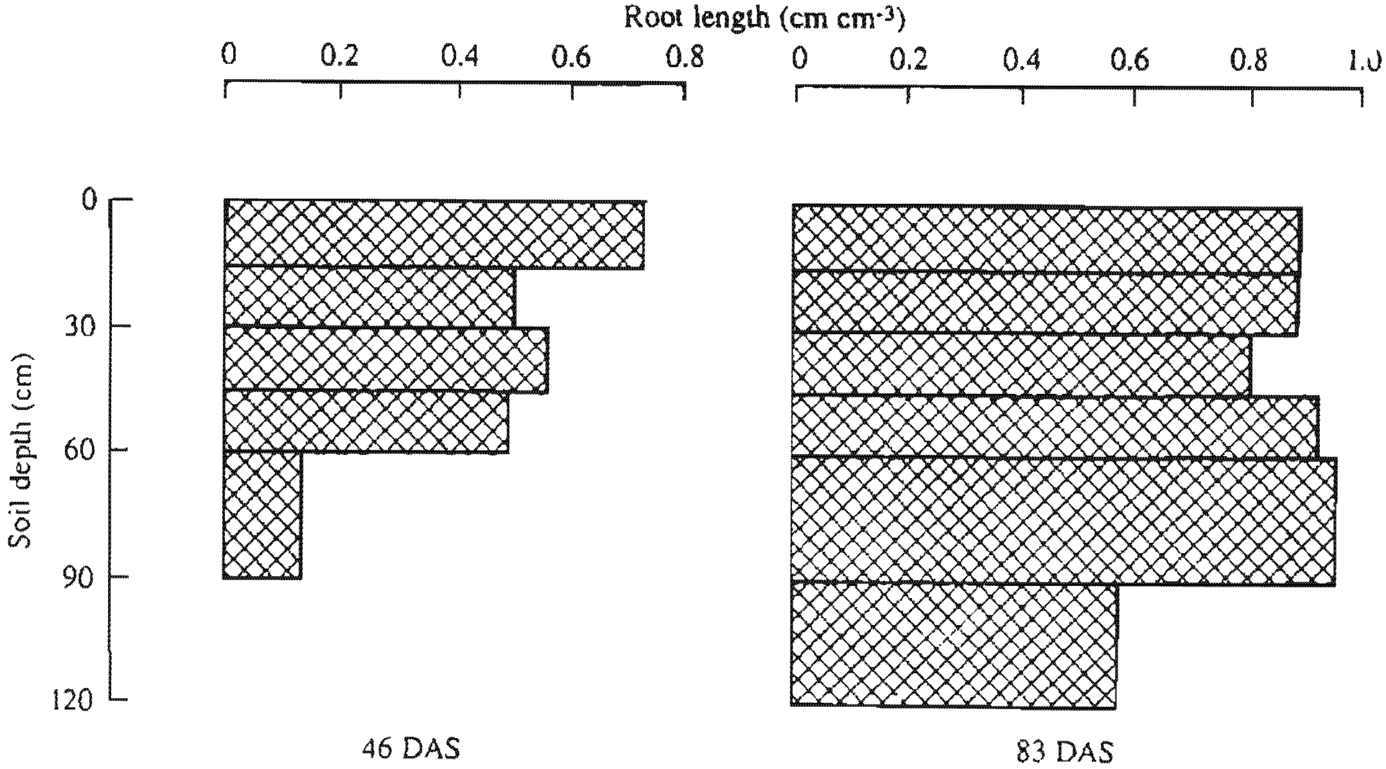

**Figure 2. Root distribution of rainfed chickpea (cv K 850) at two growth stages in a Vertisol, ICRISAT Center, postrainy season 1984/85. DAS = days after sowing.**

saturated with water, air permeability markedly decreases and the soil becomes waterlogged.

In Alfisols, even though saturated water-infiltration rate is not as low as in Vertisols, an unstable aggregation of surface soil enhances crust formation, which can severely restrict air and water permeability. A hard murrum layer in the subsoil presents an obstacle to root development of most crops grown in Alfisols. Low P fertility of surface soils of Alfisols and Vertisols also restricts root development by limiting plant growth, especially in cereals.

In this paper, we characterize the rooting behavior of pigeonpea and chickpea in Vertisols and Alfisols and discuss the beneficial effects of cultivation of these legumes on other crops.

## Root Development of Pigeonpea and Chickpea

The extent of a crop root system in a soil profile depends on crop species and soil type. Generally, crops develop deeper root systems on Vertisols than on Alfisols, an example of soybean being shown in Figure 1. Chickpea is especially able to develop deep root systems in Vertisols, as illustrated by Sheldrake and Saxena (1979) and in Figure 2. Perhaps this ability of deep rooting on calcareous soils is related to its acid exudation ability (Ae et al. 1991a).

In Alfisols, root development of soybean (Fig. 1) and maize (Fig. 3) is generally confined to within 30-45 cm of the soil surface, as roots seem unable to penetrate the murrum layer of iron nodules generally found at 40-60 cm depth. However, pigeonpea seems to be able to penetrate this layer easily and develop a deep root system in Alfisols (Fig. 4). Cracks developed through the murrum layers were observed under pigeonpea rows in several Alfisol fields at ICRISAT Center. This suggests that crops following pigeonpea may be able to develop deeper root systems via the openings left by pigeonpea roots.

When we measured the change in available P level with soil depth in an Alfisol field, we found some very high values below 120-cm depth (Fig. 5). This suggests that the ability of pigeonpea to develop a deep root system on Alfisols represents a considerable advantage to the crop in terms of P nutrition. Further, it can be proposed that this may benefit subsequent crops, pigeonpea—or chickpea in Vertisols—being able to recycle P and other nutrients from deep soil layers; however, this effect is yet to be quantified.

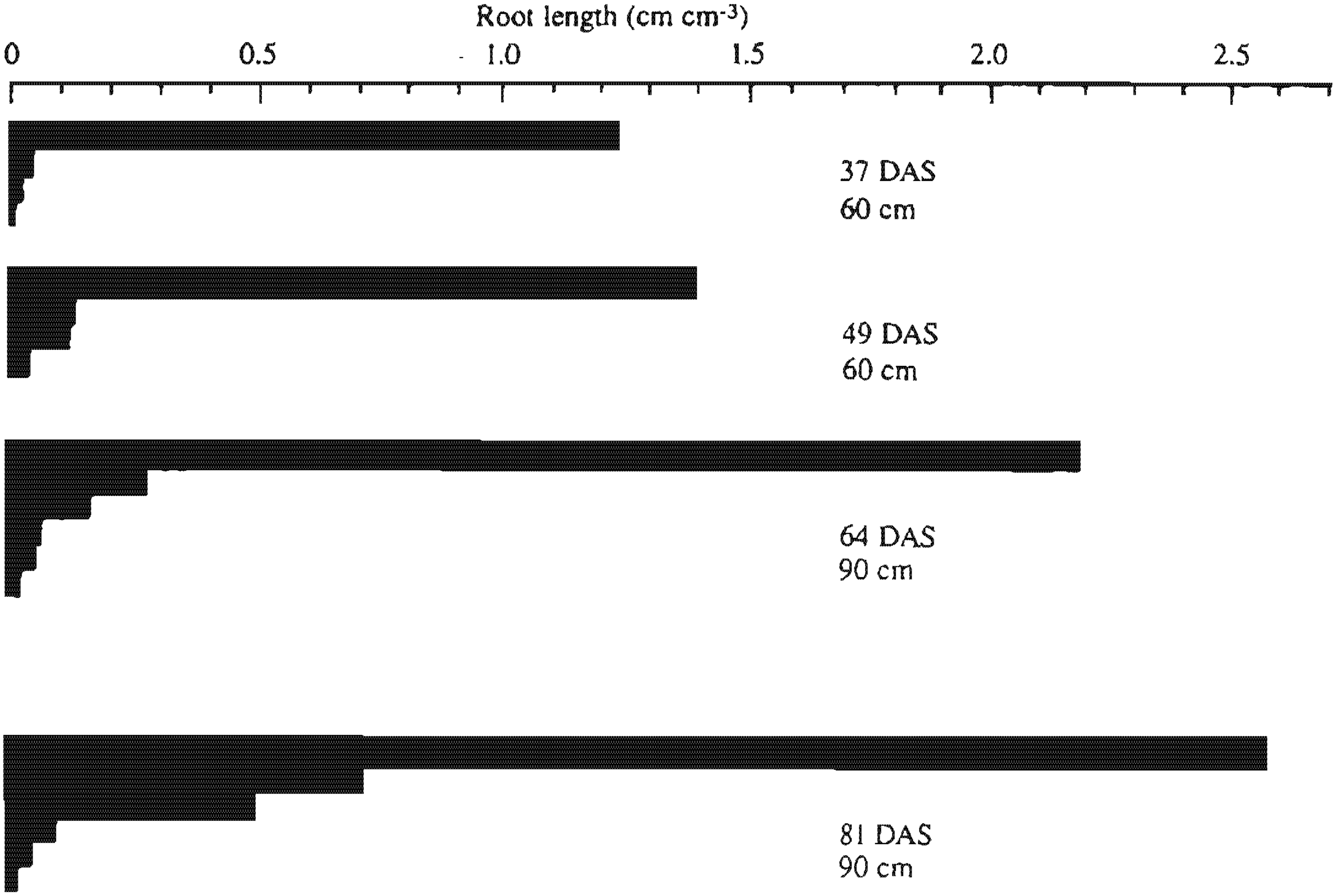

**Figure 3. Root development in maize in an Alfisol, ICRISAT Center, rainy season 1985. Representation as in Figure 1.**

## Residual Effects of Pigeonpea and Chickpea

There are several studies showing beneficial effects of pigeonpea and chickpea on yields of subsequent crops. This is primarily attributed to improvements in soil nitrogen (N) status resulting from $N_2$-fixation by these legumes. Kumar Rao et al. (1983), Kushwaha and Ali (1988), and Johansen et al. (1990) provide examples for pigeonpea; Ahlawat et al. (1981), Jessop and Mahoney (1985), and Keatinge et al. (1988), examples for chickpea. However, not all of the benefit to the subsequent crop is attributable to N addition by the legumes. This is indicated by lack of convergence of N-response curves, at high N application rates, of the subsequent crop following either pigeonpea or the control (fallow or cereal); that is, prior pigeonpea results in superior yield even at high N application levels to the subsequent crop (e.g., Kumar Rao et al. 1983; Johansen et al. 1990). Thus beneficial effects in addition those from residual N are suggested.

In order to investigate these additional beneficial effects, the residual effects of pigeonpea and chickpea cultivation on following sorghum, which was fertilized with 120 kg N ha$^{-1}$, were studied in a Vertisol and an Alfisol. In the rainy season of 1988, short-duration pigeonpea (ICPL 87) was grown without fertilizer under rainfed and irrigated conditions on both soil types. On the Vertisol, sorghum (CSH 5) grain yield following rainfed pigeonpea was similar to that following fallow (Fig. 6). However, following irrigated pigeonpea, the sorghum yield was considerably lower than that following fallow. On the Alfisol, sorghum yield after fallow was less than 1 t ha$^{-1}$ but was more than 2 t ha$^{-1}$ after pigeonpea (Fig. 6).

Similar results were obtained on response of sorghum (CSH 5), fertilized with 120 kg N ha$^{-1}$, to P application in experiments in which sorghum was rotated with pigeonpea (ICPL 87). On an Alfisol field, grain yield of sorghum after pigeonpea increased at all P levels (Fig. 7). Without P, sorghum yield was negligible in the first year but increased to 2 t ha$^{-1}$

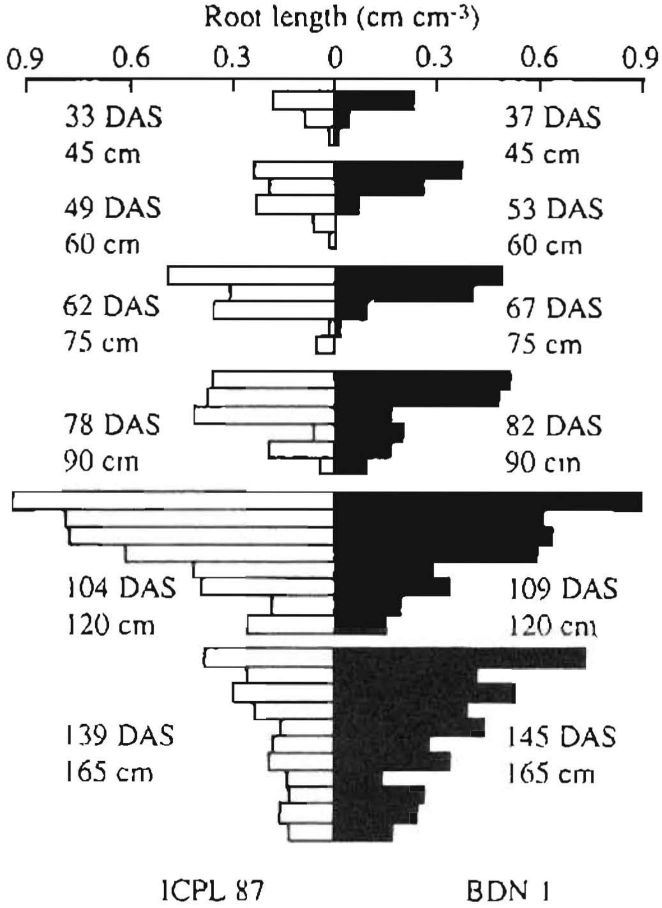

**Figure 4.** Root development of short-duration (ICPL 87) and medium-duration (BDN 1) pigeonpea in Alfisol, ICRISAT Center, rainy season 1985. Representation as in Figure 1.

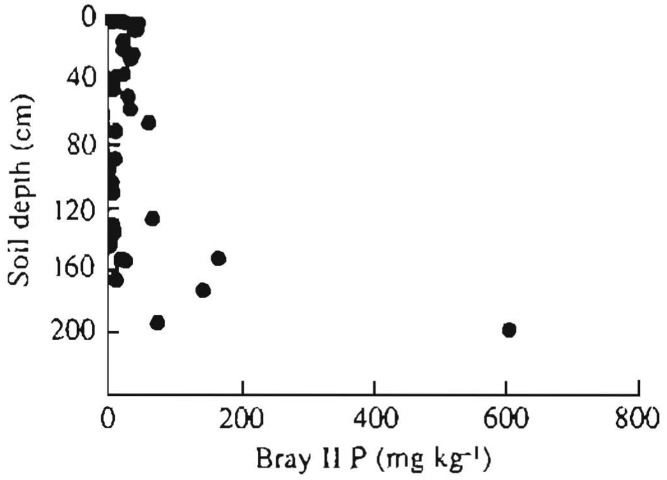

**Figure 5.** Changes in available phosphorus (Bray 2 P) with soil depth of an Alfisol at ICRISAT Center.

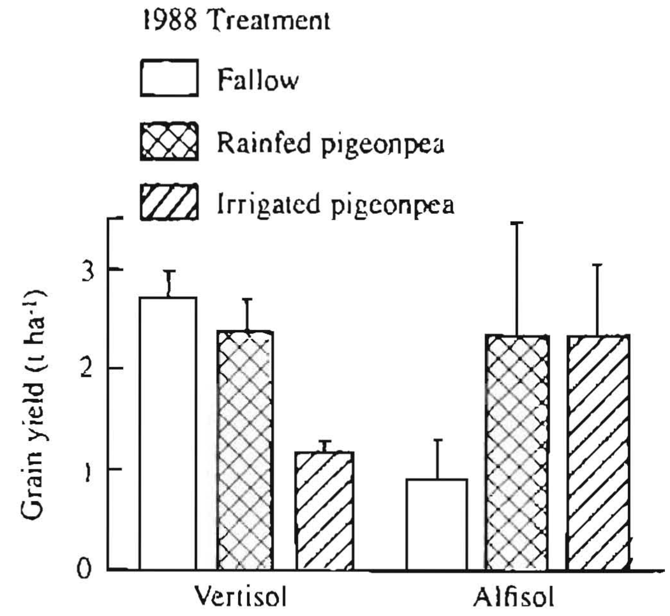

**Figure 6.** Effect of pigeonpea cultivation on grain yield of following sorghum fertilized with 120 kg N ha-1, ICRISAT Center, rainy season 1989. Standard errors indicated.

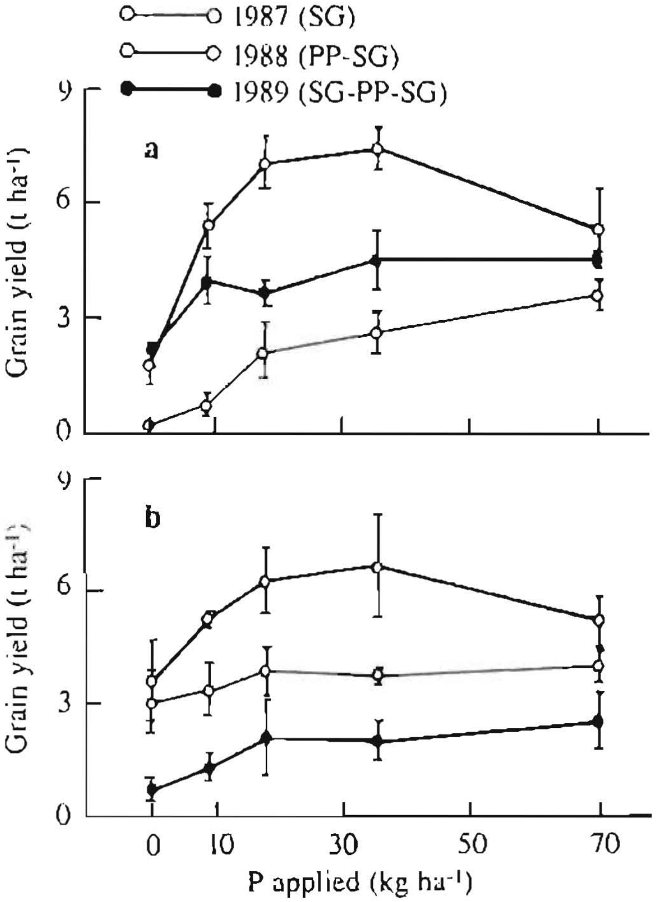

**Figure 7.** Effect of previous pigeonpea (PP) on phosphorus response of sorghum (SG) fertilized with 120 kg N ha-1 on (a) an Alfisol and (b) a Vertisol field of low P fertility, ICRISAT Center, rainy seasons 1987-89. Standard errors indicated.

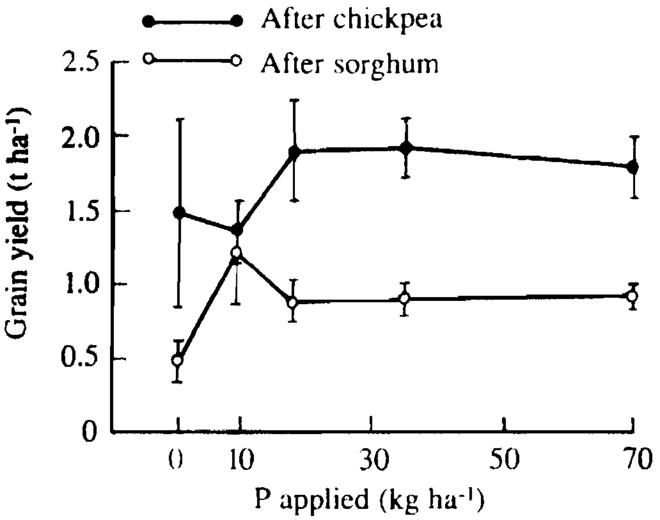

**Figure 8. Effect of previous crop on phosphorus response of short-duration pigeonpea (cv ICPL 87) on a Vertisol field, ICRISAT Center, rainy season 1989. Standard errors indicated.**

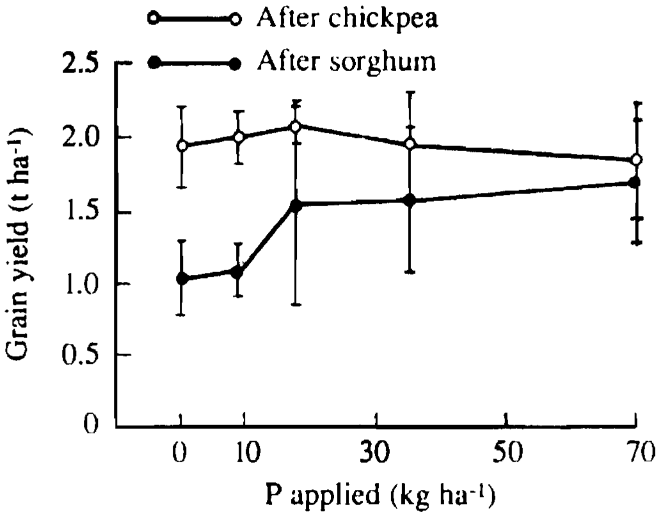

**Figure 9. Effect of previous crop on phosphorus response of short-duration pigeonpea (cv ICPL 87) on an Alfisol field, ICRISAT Center, rainy season 1989. Standard errors indicated.**

after cultivation of pigeonpea. In the third season, after sorghum, yields were intermediate where P was applied. Although these results could have been confounded by effects of different seasons on sorghum growth, a large beneficial effect of growing pigeonpea is indicated. On a Vertisol field, sorghum grain yield in 1988 increased after pigeonpea at all rates of P application but in 1989 it decreased (Fig. 7). Thus pigeonpea improved grain yield of following sorghum on the Alfisol, but depressive effects were apparent on the Vertisol.

Chickpea (K 850) improved the grain production of following pigeonpea (ICPL 87) more than sorghum (CSH 5), at all levels of P application on Vertisols (Fig. 8). On Alfisols, the beneficial effects of chickpea were only apparent at lower P-application rates (Fig. 9).

The improved yield of sorghum following pigeonpea on Alfisols to which N fertilizer was applied, indicates that the beneficial effects of pigeonpea were other than those of residual N. The effects of chickpea in improving pigeonpea yields on Vertisols and Alfisols also could not be attributed to residual N, as we could not measure responses of pigeonpea to N fertilizer on these soils over several years (symbiotic $N_2$-fixation was apparently adequate to meet the N requirements of pigeonpea). One reason for the beneficial effects of these two legumes could be their ability to access P normally not available to other crops, as discussed by Ae et al. (1991a, 1991b) and referred to elsewhere in this paper. An additional reason could be the improvement that these legumes bring about in soil physical characteristics. This is supported by the inability of increased P application to compensate for the beneficial effects of chickpea and pigeonpea (Figs. 7 and 8).

## Effects of Pigeonpea and Chickpea in Improving Water-infiltration Rates

A lack of structural development or stable aggregation in Alfisols in the SAT causes rapid surface sealing following rainfall events and crusting in subsequent drying cycles (El-Swaify et al. 1985). This leads to reduced water-infiltration rate and enhanced runoff early in the rainy season. Thus water-infiltration rate is a good indicator of soil physical conditions of Alfisols. As shown in Figure 10, water infiltration in plots with sorghum following pigeonpea was greater than in plots with continuous sorghum. On the other hand, in pigeonpea plots, water infiltration was the greatest in plots where chickpea had previously been grown (Fig. 11).

These results demonstrate that crop rotations improve water-infiltration rate, as compared with continuous cropping of the same crop. This could be attributed to either total organic matter contribution of roots of previous crops or specific root exudates from particular crops. Further, as previously referred to in the case of pigeonpea growing on Alfisols, water channels may be created in the remains of previous

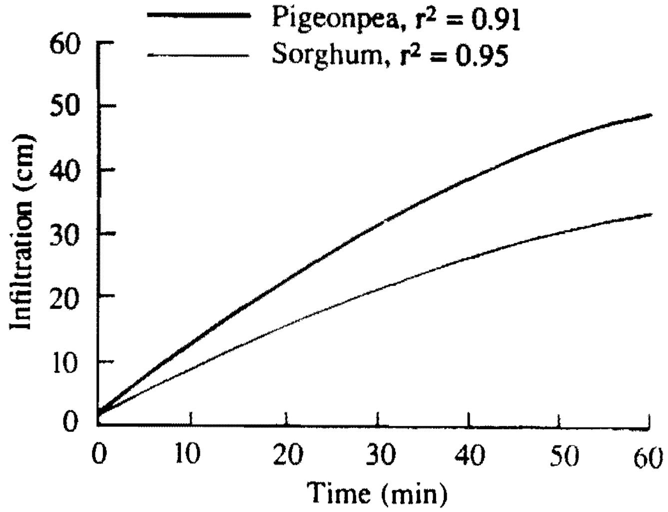

**Figure 10. Effect of previous crop on water-infiltration rate in sorghum plots on Alfisol, ICRISAT Center, rainy season 1989.**

roots. However, these possible effects await quantification.

Root development of sorghum grown on Alfisols is enhanced by the previous cultivation of pigeonpea, as illustrated in Figure 12. In these studies, root development of sorghum was measured in soil pits dug on plots that had previously had either 3 years of pigeonpea or 3 years of fallow. This improved root development with depth could have contributed to the increased grain yield of sorghum following pigeonpea, as depicted in Figure 7.

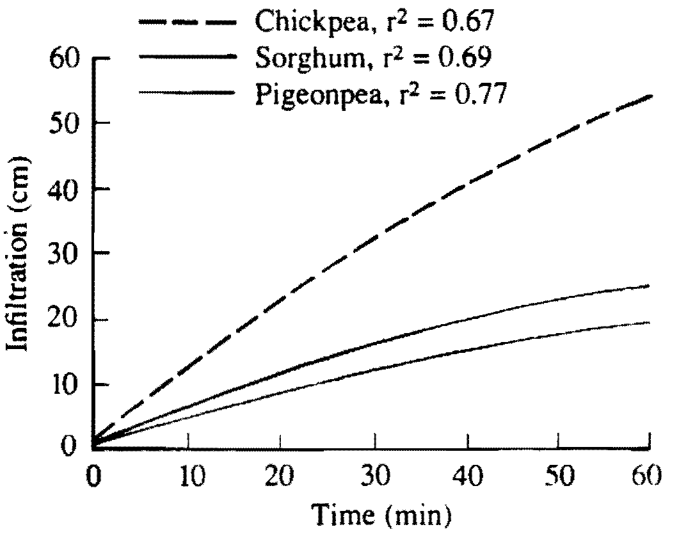

**Figure 11. Effect of previous crop on water-infiltration rate in pigeonpea plots on Alfisol, ICRISAT Center, rainy season 1989.**

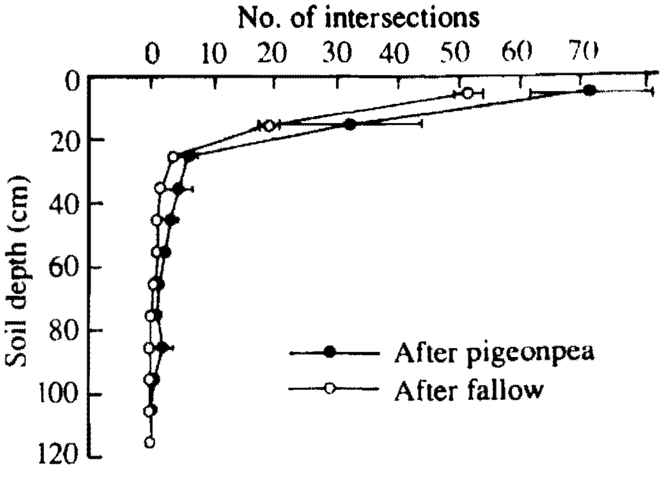

**Figure 12. Effect of pigeonpea cultivation on sorghum root development, as measured by number of intersections in a 5 × 5 cm grid in soil pits, in an Alfisol field, ICRISAT Center, rainy season 1988. Standard errors indicated where they exceed symbol size.**

## Effects of Intercropping Pigeonpea and Sorghum

Intercropping of sorghum and pigeonpea is a widely practiced farming system in the semi-arid regions of India. The beneficial effects of intercropping in terms of increased total grain yield and stability of yield over seasons have been elaborated by Willey (1985) and Ofori and Stern (1987). We examined the basis for improved partial land-equivalent ratios (partial LER = grain yield in intercrop/grain yield in sole crop; Ofori and Stern 1987) of sorghum intercropped with pigeonpea. Sorghum (CSH 5) dry-matter production and grain yield in a sole crop were compared with those in intercrops with medium-duration pigeonpea (C 11) at either one row of pigeonpea to one row of sorghum (1PP:1SG) or one row of pigeonpea to three rows of sorghum (1PP:3SG). Interrow spacing was 60 cm and intrarow spacing 15 cm for both crops (i.e., a replacement intercropping design). Rows were 6 m long and sown on ridges spaced at 60 cm; there were 7 ridges for sole sorghum, 9 for 1PP:1SG and 13 for 1PP:3SG. Experiments were conducted in the 1988/89 season on a Vertisol and on Alfisols of high (a) and low (b) fertility. Fertilizers at rates of 18 kg N ha$^{-1}$ and 20 kg P ha$^{-1}$ were shallow-banded at sowing. Nitrogen fertilizer was topdressed at 40 and 75 days after sowing (DAS) at a rate of 50 kg N ha$^{-1}$ for each application.

Leaf-area indices (LAI) in the different cropping systems at 83-90 DAS, the midripening stage of sorghum, are presented in Table 1. The LAI of sole pigeonpea was about double that of sole sorghum on all fields, indicating vigorous shoot growth of pigeonpea. In the 1PP:1SG intercrop system, LAI of pigeonpea was greater than that of sorghum in Vertisol and Alfisol (b), but the reverse was true in Alfisol (a). Light-

**Table 1. Leaf-area index (LAI) of sorghum and pigeonpea and light extinction coefficient (k), with standard errors in parentheses, in different cropping systems at the midripening stage of sorghum, ICRISAT Center, rainy season 1988.**

| Cropping system | Parameter | Vertisol | Alfisol(a) | Alfisol(b) |
|---|---|---|---|---|
| Sole pigeonpea | | | | |
| | LAI | 4.41 (±0.40) | 3.85 (±0.40) | 4.16 (±0.22) |
| | k | 0.82 (±0.13) | 0.81 (±0.07) | 0.81 (±0.04) |
| Intercrop (1PP:1SG) | | | | |
| Pigeonpea | LAI | 1.85 (±0.20) | 1.66 (±0.14) | 1.75 (±0.16) |
| Sorghum | LAI | 1.53 (±0.10) | 1.84 (±0.11) | 1.25 (±0.08) |
| Total | LAI | 3.37 (±0.14) | 3.50 (±0.22) | 3.01 (±0.16) |
| | k | 0.58 (±0.05) | 0.63 (±0.04) | 0.75 (±0.05) |
| Intercrop (1PP:3SG) | | | | |
| Pigeonpea | LAI | 0.79 (±0.05) | 0.66 (±0.04) | 0.87 (±0.06) |
| Sorghum | LAI | 1.84 (±0.11) | 2.28 (±0.18) | 1.63 (±0.20) |
| Total | LAI | 2.63 (±0.13) | 2.94 (±0.18) | 2.50 (±0.21) |
| | k | 0.58 (±0.04) | 0.71 (±0.07) | 0.66 (±0.08) |
| Sole sorghum | | | | |
| | LAI | 2.05 (±0.13) | 2.38 (±0.17) | 1.95 (±0.12) |
| | k | 0.59 (±0.05) | 0.60 (±0.06) | 0.57 (±0.06) |

**Table 2. Total dry matter at flowering time of sorghum and grain yield per 6-m row and partial land-equivalent ratios (LER) of sorghum in different cropping systems, ICRISAT Center, rainy season 1988.**

| | | At flowering | | At harvest | |
|---|---|---|---|---|---|
| Field | Cropping system | Total dry matter (g row$^{-1}$) | Partial LER | Grain yield (g row$^{-1}$) | Partial LER |
| Vertisol | | | | | |
| | Sole sorghum | 839 (±70)[2] | | 349 (±4) | |
| | Intercrop[1] | | | | |
| | (1PP:1SG) | 860 (±103) | 0.51 | 389 (±7) | 0.56 |
| | (1PP:3SG) | 688 (±36) | 0.61 | 374 (±3) | 0.80 |
| **Alfisol (a)** | | | | | |
| | Sole sorghum | 1397 (±182) | | 1001 (±13) | |
| | Intercrop | | | | |
| | (1PP:1SG) | 1915 (±304) | 0.69 | 1778 (±17) | 0.89 |
| | (1PP:3SG) | 1425 (±220) | 0.77 | 1339 (±11) | 1.00 |
| **Alfisol (b)** | | | | | |
| | Sole sorghum | 918 (±97) | | 831 (±11) | |
| | Intercrop | | | | |
| | (1PP:1SG) | 1159 (±240) | 0.63 | 1040 (±12) | 0.63 |
| | (1PP:3SG) | 1109 (±380) | 0.90 | 936 (±16) | 0.85 |

1. 1PP:1SG = one row pigeonpea: one row sorghum. 1PP:3SG = one row pigeonpea : three rows sorghum.

2. Standard errors in parentheses.

extinction coefficients (k) of each intercrop system were equal to or larger than those for sole sorghum on all fields, indicating that light interception of the whole canopy of intercropped sorghum was not superior to that of sole sorghum. These results suggest that, at least during the ripening period, sorghum intercropped with pigeonpea in these experiments did not benefit from better light interception as compared with sole sorghum. This finding constrasts with the report by Willey (1985) that the major benefit to sorghum in an intercrop is increased light interception.

Dry-matter yield at flowering and grain yield per row increased in intercropping treatments on the Alfisols but there was little such increase on the Vertisols (Table 2). Partial LERs of sorghum exceeded expected values (equal row yields irrespective of spacing) of 0.50 for 1PP:1SG and 0.75 for 1PP:3SG for dry matter at flowering on the Alfisols and for grain yield on all soils. As these increases in partial LER do not seem to be a result of less competition for light in intercropped sorghum, it can be assumed that the relatively better growth of intercropped sorghum must be due to below-ground, rather than above-ground, effects. Among possible below-ground factors, differences in growth would be difficult to attribute to differences in water use, as rainfall was adequate to maintain the soil moist throughout the sorghum growth period in this season. Further, possible stimulatory effects of $N_2$ fixed by pigeonpea are unlikely, as 118 kg N ha$^{-1}$ was applied as fertilizer to all treatments.

Root mass of sorghum, as measured by the soil pit method, was greater in the intercrops than in the sole crop (Table 3). By contrast, root mass of pigeonpea in the intercrop was the same as or less than that in the sole crop. The top:root ratio of intercropped sorghum tended to be less than that of sole-cropped sorghum, but the reverse was true for pigeonpea. These results demonstrate the enhanced rooting capacity of sorghum plants in an intercropping system, which would

**Table 3. Root dry mass for a 6-m row (g row$^{-1}$) and top:root (T:R) ratio of pigeonpea and sorghum in different cropping systems at the midripening stage of sorghum, ICRISAT Center, rainy season 1988.**

| | Cropping system[1] | | |
|---|---|---|---|
| | Sole | 1PP:1SG | 1PP:3SG |
| Vertisol | | | |
| Pigeonpea | | | |
| Root mass | 160 (±17) | 160 (±16) | 114 (±11) |
| T:R ratio | 9.4 | 10.3 | 9.3 |
| Sorghum | | | |
| Root mass | 236 (±24) | 372 (±18) | 249 (±22) |
| T:R ratio | 11.5 | 10.3 | 11.0 |
| Alfisol (a) | | | |
| Pigeonpea | | | |
| Root mass | 98 (±15) | 67 (±5) | 71 (±7) |
| T:R ratio | 13.6 | 13.9 | 14.8 |
| Sorghum | | | |
| Root mass | 181 (±5) | 323 (±25) | 211 (±33) |
| T:R ratio | 16.5 | 15.1 | 16.6 |
| Alfisol (b) | | | |
| Pigeonpea | | | |
| Root mass | 156 (±16) | 150 (±17) | 146 (±16) |
| T:R ratio | 9.7 | 9.9 | 10.4 |
| Sorghum | | | |
| Root mass | 271 (±29) | 313 (±39) | 294 (±20) |
| T:R ratio | 10.8 | 10.6 | 9.8 |

1. 1PP:1SG = one row pigeonpea:one row sorghum intercrop; 1PP:3SG = one row pigeonpea:three rows sorghum intercrop. Standard errors in parentheses.

undoubtedly assist in nutrient and moisture acquisition.

Poor soil aeration can be a factor reducing plant growth not only in Vertisols but also in Alfisols (Okada et al. 1991). We have observed that sorghum appears to suffer less waterlogging damage when grown in an intercrop with pigeonpea than as a sole crop. Soil-aeration measurements (as per Okada et al. 1991) taken over an 18-day period, following flowering of sorghum in the above-mentioned intercropping studies, confirmed the differences in soil oxygen status between intercrop and sole-crop treatments. In one Alfisol (b) (Fig. 13) and a Vertisol (Fig. 14), soil oxygen concentrations in sole sorghum plots were considerably reduced following rainfall events, with improvements in soil oxygen concentration directly proportional to the proportion of pigeonpea in the system. Thus intercropped sorghum has better soil-aeration conditions, which may result in better root growth, and, ultimately, higher yield per plant than in sole-cropped sorghum. However, in Alfisol (a), which showed the highest partial LERs for sorghum grain yield, soil aeration in intercropped plots was not consistently higher than in sole sorghum plots (Fig. 15). Thus the beneficial effects of intercropping cannot be completely explained in terms of improved soil aeration. Further careful studies are required for a full understanding of the beneficial effect of intercropping with pigeonpea on grain production of sorghum.

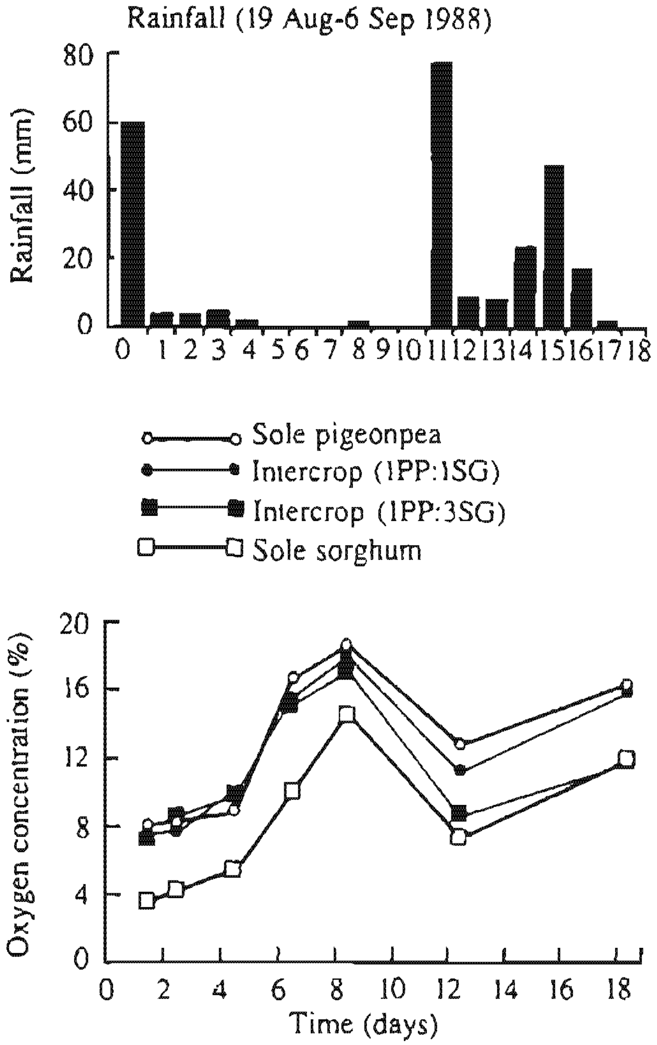

**Figure 13. Soil oxygen concentration at 15-cm depth following flowering of sorghum in Alfisol (b) field with different cropping systems, ICRISAT Center, rainy season 1988. Rainfall during the period is also depicted. PP = pigeonpea; SG = sorghum.**

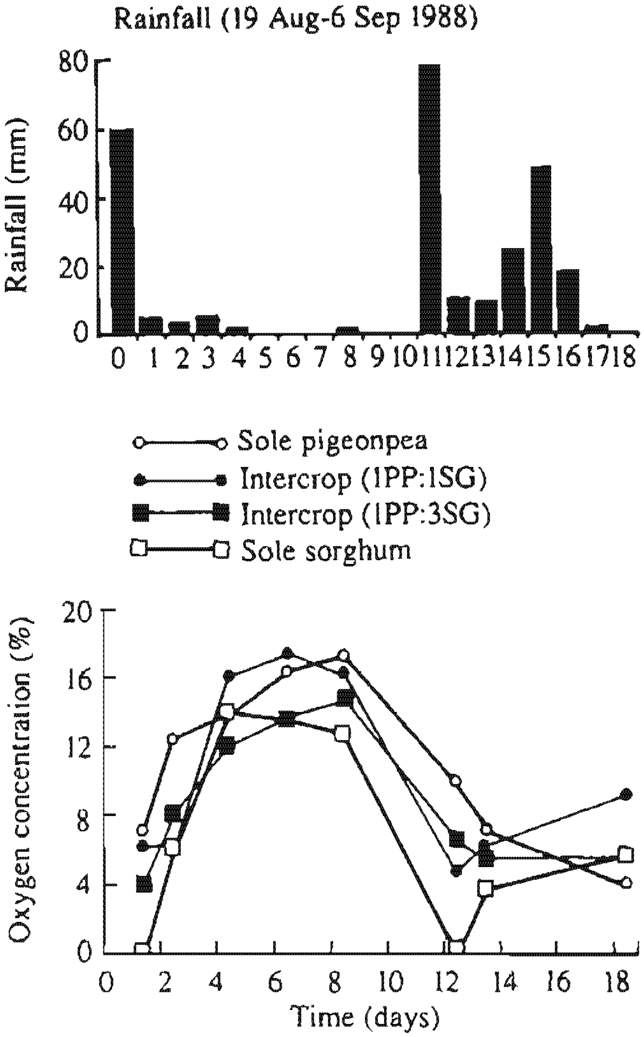

**Figure 14. Soil oxygen concentration at 15-cm depth following flowering of sorghum in a Vertisol field with different cropping systems, ICRISAT Center, rainy season 1988. Rainfall during the period is also depicted. PP = pigeonpea; SG = sorghum.**

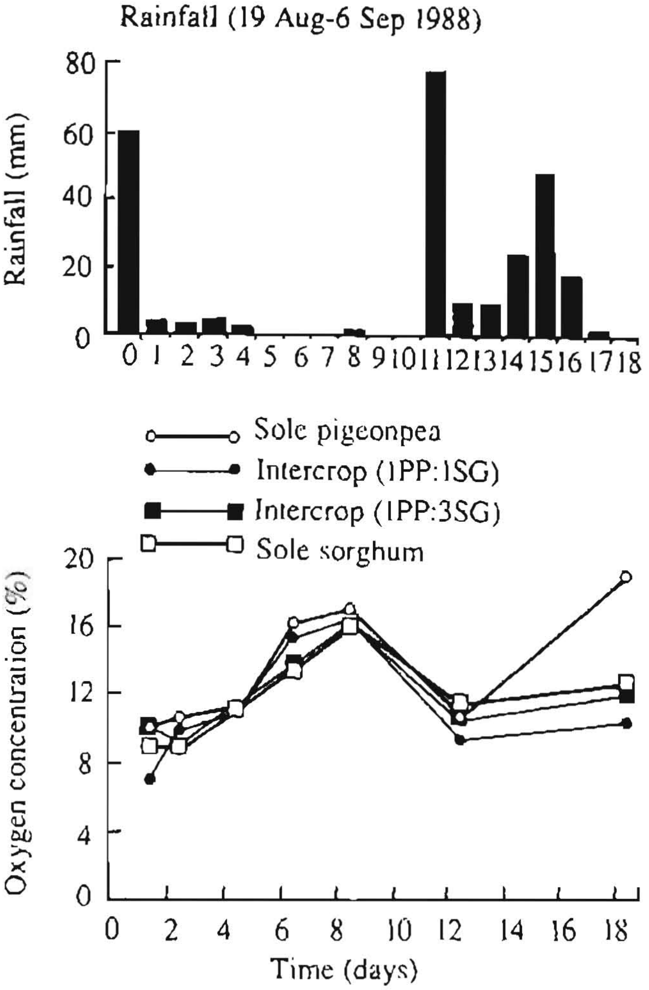

Figure 15. Soil oxygen concentration at 15-cm depth following flowering of sorghum in Alfisol (a) field with different cropping systems, ICRISAT Center, rainy season 1988. Rainfall during the period is also depicted. PP = pigeonpea; SG = sorghum.

## Effects of Pigeonpea and Chickpea on Phosphorus Status

The particular advantages of chickpea root exudates in being able to access calcium-bound P and of pigeonpea root exudates (piscidic acid) to access iron-bound P have been explained by Ae et al. (1991a, 1991b). This raises the question as to whether these legumes can increase the available P pool of the soil not only to their own advantage but also to that of subsequent crops growing in that soil.

This hypothesis was tested in a pot experiment where several crops were grown four times in succession in Alfisol and Vertisol of low P status. Maize was subsequently grown twice to estimate available P remaining in the soil. Pigeonpea and a pigeonpea/sorghum mixture extracted more P from the Alfisol over four growth cycles than did sole sorghum or chickpea (Table 4). The growth of succeeding maize was better after pigeonpea than after sole sorghum. This demonstrates that pigeonpea on the Alfisol not only extracts more P for its own use but also makes more P available for use by subsequent crops. A chickpea/sorghum mixture on Alfisol also extracted a large amount of P and had a large beneficial effect on P status. On the Vertisol, the effect of pigeonpea and chickpea on P status was not clear even though the pigeonpea/sorghum extracted the most P. However, the beneficial effect of chickpea on P uptake of subsequent maize on Vertisols was demonstrated in another pot experiment of similar design (data not shown here). The effect of pigeonpea and chickpea on the P status of Alfisols and Vertisols needs further exam-

Table 4. Phosphorus uptake of sorghum, pigeonpea, chickpea, and sorghum-pigeonpea and sorghum-chickpea mixtures grown in pots filled with Alfisol or Vertisol of low P fertility and the effects on growth of succeeding maize.

| Soil | Sorghum (a) | Pigeonpea (b) | Chickpea (c) | Mixture a+b | Mixture a+c |
|---|---|---|---|---|---|
| | | | P uptake of each crop (mg pot$^{-1}$) | | |
| Alfisol | 143 (±15)[1] | 165 (±17) | 91 (±4) | 199 (±14) | 209 (±26) |
| Vertisol | 378 (±73) | 284 (±27) | 276 (±16) | 408 (±14) | 321 (±34) |
| | | | Dry mass of maize (g pot$^{-1}$) | | |
| Alfisol | 54 (±7) | 70 (±6) | 68 (±3) | 54 (±3) | 65 (±5) |
| Vertisol | 96 (±3) | 106 (±5) | 104 (±8) | 88 (±5) | 59 (±7) |

[1] Standard errors in parentheses.

ination under pot and field conditions to determine the significance to cropping systems of the SAT.

## Conclusions

These studies confirm the deeper rooting ability of pigeonpea in Alfisols and chickpea in Vertisols, as compared with other crops, and suggest the possible advantages of this ability. Improved water extraction from deeper in the soil profile is an obvious advantage, but there is also the possibility of recycling of nutrients from deeper soil layers; this latter possibility needs to be quantified. Residual benefits of pigeonpea and chickpea to subsequent crops that are additional to N effects have been demonstrated. Evidence is presented that these additional effects could be a result of these legumes improving water infiltration rate and soil P availability. However, further quantification of these effects under field conditions is required. Studies on intercropping have shown that sorghum intercropped with pigeonpea is benefited by belowground factors, as compared with sole-cropped sorghum. Further careful studies are required for a complete understanding of the beneficial effects of intercropping in increasing LER. It is suggested that further quantification of these apparent beneficial effects of pigeonpea and chickpea is required to demonstrate the importance of these particular legumes to the sustainability of cropping systems in the SAT.

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# Nutrient Dynamics in Tropical Cropping Systems Involving Legumes

**H. Imai**[1]

### *Abstract*

*The nutrient dynamics in multiple cropping systems involving legumes was studied in a humid tropical environment over 4 years. Relevant soil nutrients, as well as pH and electrical conductivity (EC), vary considerably according to cropping sequence, cropping season, and the amounts of fertilizer and compost applied. Soil pH varied by only one unit through eight successive cultivations of different crops, and available nutrients in soils, except phosphorus (P), varied in inverse proportion to the amount of rainfall.*

*Neither soil nutrient concentrations before sowing nor those after harvest were closely related to the overall crop yields. Therefore, it is more important to provide a timely fertilizer application than to progressively increase soil fertility for high crop yields in the humid tropics.*

*Nutrient uptake by the same crop remained similar across different crop rotations. Soybean absorbed nearly three times as much nitrogen (N) and twice as much P as other crops. To produce 4 t of dry seed, 300 kg N $ha^{-1}$ and 18 kg P $ha^{-1}$ must be taken up by the shoots of soybean plants. Of total uptake, soybean accumulated nearly 80% N, 75% P, and 60% potassium (K) in its seeds. Calcium (Ca) and magnesium (Mg) were mainly deposited in leaf and stem tissue.*

*Variation in the total dry-matter production of rotation crops can be explained by three variables, i.e., P, N, and Mg uptake. Uptake of P alone could explain 77% of the variation, while N and Mg uptake increased $R^2$ by only 5 and 6%, respectively. A component effects plot also showed that only P provided useful information in predicting dry-matter production. Thus P is a nutrient of primary importance for high yields of tropical legumes; hence, development of cultural practices to enhance its uptake and translocation to seeds is highly recommended.*

## Introduction

Legume-based crop rotation is generally beneficial to the soil: it preserves organic matter, increases soil nitrogen (N), balances soil nutrients, improves soil physical properties, and breaks soilborne disease cycles (Ruthenberg 1971; Haynes 1980; Chandrapanya et al. 1982; Ofori and Stern 1987; Francis 1989; Imai 1990a; Imai et al. 1989, 1990). In the tropics, crops can potentially be cultivated throughout the year if water is available. Multiple, intensive cropping is widely practiced in East Asia to maximize land productivity per unit area and time. To illustrate the nutrient dynamics in multiple-cropping systems involving legumes, this chapter reports the results of a study on vegetable-legume rotations in a humid tropical environment, which permits continuous and intensive cropping. This system would exaggerate the changes occurring in a semi-arid environment, where water availability limits biomass production, but provides an example of the principles involved. This study began in 1983 and was aimed at developing appropriate vegetable-legume rotation systems for tropical conditions and evaluating effects of previous

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[1] Tropical Agriculture Research Center, Tsukuba, Ibaraki 305, Japan.

ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1991. Phosphorus nutrition of grain legumes in the semi-arid tropics (Johansen, C., Lee, K.K., and Sahrawat, K.L., eds.). Patancheru, A.P. 502 324, India: ICRISAT.

crops and application of fertilizers, mulch, and compost on crop yields and nutrient dynamics.

## Experimental Details

Experiments were conducted at the Asian Vegetable Research and Development Center (AVRDC) experimental farm at Tainan, Taiwan. Average maximum temperatures there are in the range 29-32°C during May-October and 21-24°C during December-February. Respective minimum temperatures for these periods are 21-24°C and 12-14°C. Total average annual rainfall during 1983-86 was 1600 mm, with 86% falling during May-September. Evaporation exceeded rainfall in all months except May, June, and August.

Six rotation systems were begun in the autumn of 1983 and then extended to ten sequences from the summer of 1984 (Table 1). From the autumn of 1985, spring and summer mung bean was replaced by soybean, and corn and buckwheat, which had been cultivated for green manure, were replaced by sweet corn for the fresh market. Individual crops were planted on 50-m$^2$ plots in a completely randomized design with two replications. With the exception of Chinese cabbage, all plant parts remaining after harvest were plowed back into the soil. Fertilizers and compost applied to each crop in sequence are given in Table 2. With the change of crop types from 1986, N application was increased to 200 kg ha$^{-1}$ year$^{-1}$ in all rotations, which may have contributed to a discontinuity in the 1986 results.

After crops were harvested to determine yield and total biomass production, soil samples were collected from the top 10-cm soil profile of each plot. These samples, except those destined for inorganic N analysis, were air-dried, passed through a 2-mm sieve, and analyzed.

The pH and electrical conductivity (EC) of air-dried soils were determined at soil:water ratios of 1:2.5 and 1:5, respectively, after 1 h of shaking. Total N was measured by Kjeldahl distillation. Inorganic N in the soil was determined after extraction in 1 N KCl, followed by ammonium-N and then nitrate-N analysis of the filtrate. Available P was determined according to Olsen's extraction method, namely, soil extraction with 0.5 M $NaHCO_3$ at pH 8.5. Morgan's extraction solution, 0.735 M NaOAc-HOAc, was used to determine available potassium (K), calcium (Ca), and magnesium (Mg) in the soil.

For plant analysis of N, P, K, Ca, and Mg, oven-dried plant samples were block-digested in concentrated $H_2SO_4$, with $H_2O_2$ subsequently added to clarify the digest.

## Yield Data

The yield of mung bean cultivated in the spring and autumn was always very low (Table 3); it was neglig-

**Table 1. Cropping systems tested for vegetables and legumes at the Asain Vegetable Research and Development Center, Tainan, Taiwan.**

| Rotation No. | Spring (Feb-May) | Summer (Jun-Sep) | Autumn (Oct-Jan) |
|---|---|---|---|
| 1 | Rice (Local 90)[1] | Mung bean (V 1973A) | Tomato (CL 1561-6-0) |
| 2 | Mung bean (V 1973A) | Rice (Local 90) | Sweet potato (CN 1108-13) |
| 3 | Soybean (AGS 129) | Chinese cabbage (ASVEG#1) | Buckwheat |
| 4 | Tomato (CL 1131-43-8) | Corn (Tainan 6) | Soybean (AGS 129) |
| 5 | Soybean (AGS 129) | Tomato (CL 1131-38-4) | Chinese cabbage (Fong-Luh) |
| 6 | Chinese cabbage (Pin-Luh) | Tomato (CL 1131-38-4) | Mung bean (V 1973A) |
| 7 | Chinese cabbage CM[2] (Pin-Luh) | Tomato (CL 1131-38-4) | Mung bean (V 1973A) |
| 8 | Chinese cabbage M[3] (Pin-Luh) | Tomato M (CL 1131-38-4) | Mung bean (V 1973A) |
| 9 | Rice (Local 90) | Tomato CM (CL 1131-38-4) | Soybean CM (AGS 129) |
| 10 | Rice (Local 90) | Tomato M (CL 1131-38-4) | Soybean (AGS 129) |

1. Cultivars used at the beginning of this trial are given in parentheses. Tomato cultivar was changed to Tainan 2 in spring and autumn sowings and to CL 5915-153 in the summer sowing from 1985. Sweet potato was changed to CN 1232-9 from autumn 1985. From autumn 1985, spring and autumn mung bean was replaced by soybean (AGS 129), and corn and buckwheat were replaced by sweet corn (Tainan 6).
2. CM: In addition to the fertilizer application shown in Table 2, 30 t ha$^{-1}$ compost plus 10 t ha$^{-1}$ rice straw mulch were provided.
3. M: 10 t ha$^{-1}$ rice straw mulch was applied.

**Table 2. Application of fertilizer in each rotation system tested at Tainan, Taiwan.**

| Rotation No. | Sowing time | Crop | Fertilizer used[1] | Dressing | Fertilizer applied (kg ha$^{-1}$) N | P | K | Compost (t ha$^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| 1 | Autumn | Tomato | CF#4 | Basal | 70.0 | 15.3 | 116.2 | 0 |
| | | | CF#1 | Top | 30.0 | 3.2 | 12.5 | 0 |
| | Spring | Rice | CF#39 | Basal | 25.0 | 16.5 | 20.8 | 0 |
| | Summer | Mung bean | CF#4 | Basal | 25.0 | 5.5 | 41.5 | 0 |
| 2 | Autumn | Sweet potato | CF#4 | Basal | 40.0 | 8.7 | 66.4 | 0 |
| | | | CF#39 | Top | 20.0 | 13.1 | 16.6 | 0 |
| | Spring | Mung bean | CF#39+KCl | Basal | 30.0 | 19.7 | 41.5 | 0 |
| | Summer | Rice | CF#1 | Basal | 60.0 | 6.6 | 24.9 | 0 |
| 3[2] | Spring | Soybean | CF#4 | Basal | 50.0 | 30.6 | 83.0 | 0 |
| | Summer | Chinese cabbage | CF#5 | Basal | 100.0 | 21.8 | 62.3 | 0 |
| 4[2] | Autumn | Soybean | CF#39 | Basal | 40.0 | 26.2 | 33.2 | 0 |
| | Spring | Tomato | CF#5 | Basal | 70.0 | 15.3 | 43.2 | 0 |
| | | | CF#4 | Top | 40.0 | 8.7 | 66.4 | 0 |
| 5 | Autumn | Chinese cabbage | CF#5 | Basal | 70.0 | 15.3 | 43.8 | 0 |
| | Spring | Soybean | CF#39 | Basal | 40.0 | 26.2 | 33.2 | 0 |
| | Summer | Sweet potato | CF#4 | Basal | 40.0 | 8.7 | 66.4 | 0 |
| 6 | Autumn | Mung bean | CF#39+KCl | Basal | 15.0 | 9.8 | 20.8 | 0 |
| | Spring | Chinese cabbage | CF#39 | Basal | 50.0 | 32.8 | 41.5 | 0 |
| | Summer | Tomato | CF#1+KCl | Basal | 85.0 | 9.2 | 93.4 | 0 |
| 7 | Autumn | Mung bean | CF#43+superphosphate | Basal | 20.0 | 14.0 | 16.6 | 0 |
| | Spring | Chinese cabbage | CF#39 | Basal | 50.0 | 32.8 | 41.5 | 30 |
| | Summer | Tomato | CF#1+KCl | Basal | 80.0 | 8.7 | 83.0 | 30 |
| 8 | Autumn | Mung bean | CF#43+superphosphate | Basal | 20.0 | 14.0 | 16.6 | 0 |
| | Spring | Chinese cabbage | CF#39 | Basal | 50.0 | 32.8 | 41.5 | 0 |
| | Summer | Tomato | CF#1+KCl | Basal | 80.0 | 8.7 | 83.0 | 0 |
| 9 | Autumn | Soybean | CF#2 | Basal | 40.0 | 14.0 | 53.9 | 30 |
| | Spring | Rice | CF#43 | Basal | 25.0 | 10.9 | 20.8 | 0 |
| | Summer | Tomato | CF#43 | Basal | 50.0 | 21.8 | 41.5 | 30 |
| | | | CF#39 | Top | 35.0 | 23.1 | 29.0 | 0 |
| 10 | Autumn | Soybean | CF#2 | Basal | 40.0 | 14.0 | 53.9 | 0 |
| | Spring | Rice | CF#43 | Basal | 25.0 | 10.9 | 20.8 | 0 |
| | Summer | Tomato | CF#43 | Basal | 50.0 | 21.8 | 41.5 | 0 |

1. Compound fertilizers (CF) N-P-K; #1=20-2.2-8.3; #2=10-3.5-13.7; #4=11-2.4-18.3; #5=16-3.5-10;#39=12-7-10; #43=15-6.6-12.8.
2. Corn and buckwheat, which had been cultivated for green manure until 1985, did not receive any chemical fertilizer. After 1986, 50 kg N ha$^{-1}$ was supplied through CF#1 to the replaced sweet corn.

ible in the second cultivation on the same plot because of serious root damage caused by *Fusarium oxysporum*. However, mung bean yielded well in the summer sowing and did not show any symptoms of root disease even in the second sowing. Thus use of mung bean in such rotations in the subtropics is only recommended for summer sowing. Soybean, on the other hand, showed no growth or yield retardation in autumn and spring. Spring soybean yielded nearly 4 t ha$^{-1}$ even in the second cultivation (Table 4). Thus, soybean is far more tolerant to continuous cropping than mung bean.

**Table 3. Mung bean yields in different cropping sequences.**

| Rotation No.[1] | Sowing time | Previous crop | Marketable yield (t ha$^{-1}$) |
|---|---|---|---|
| 6 | Autumn 1983 | Rice[2] | 0.78 |
| 2 | Spring 1984 | Sweet potato | 1.06 |
| 1 | Summer 1984 | Rice | 2.09 |
| 6 | Autumn 1984 | Tomato | 0 |
| 7 | Autumn 1984 | Tomato | 0.85 |
| 8 | Autumn 1984 | Tomato | 0.49 |
| 2 | Spring 1985 | Sweet potato | 0.36 |
| 1 | Summer 1985 | Rice | 1.89 |
| 1 | Summer 1986 | Rice | 1.83 |
| SE | | | ±0.25 |

1. Rotation numbers: see Table 1 for details.
2. Before the experimental cropping sequences were begun in autumn 1983, rice was planted in the experimental field to even out possible variations due to previous cropping.

## Changes in Soil Chemical Parameters

### Soil pH and EC

Change in soil pH was traced over the ten successive cultivations for different cropping sequences (Fig. 1). The soil pH increased slightly over time but there was little seasonal fluctuation. Soil pH increased significantly after Chinese cabbage but decreased with rice cultivation. Compost application slightly lowered the pH. However, soil pH varied within one unit through ten successive cultivations of different crops and it remained within the desired range for crop growth (6.5-7.5).

Soil EC remained constant over years after an initial reduction in the first year (Fig. 1). Autumn (dry-season) sowing resulted in higher soil EC than the other sowings, because more than 90% of annual rainfall was received during the spring and summer sowings, thereby leaching salts from the topsoil. Moreover, about 72 g of Ca and 9 g of Mg were introduced into each experimental plot through every 1000 L of irrigation water in the dry season. The EC was always higher after spring rice than after rice sown in summer, when more than 60% of annual rainfall was received. Cropping sequence had little effect on soil EC, and changes mainly corresponded to the amount of fertilizer and compost applied.

**Table 4. Soybean yields in different cropping sequences.[1]**

| Rotation No.[2] | Sowing time | Previous crop | Yield (t ha$^{-1}$) |
|---|---|---|---|
| 4 | 1983 Autumn | Rice | 2.59 |
| 3 | 1984 Spring | Buckwheat | 3.74 |
| 5 | 1984 Spring | Chinese cabbage | 3.87 |
| 4 | 1984 Autumn | Corn | 2.62 |
| 9 | 1984 Autumn | Tomato | 3.08 |
| 10 | 1984 Autumn | Tomato | 2.31 |
| 3 | 1985 Spring | Buckwheat | 3.85 |
| 5 | 1985 Spring | Chinese cabbage | 3.72 |
| 4 | 1985 Autumn | Corn | 2.38 |
| 6 | 1985 Autumn | Tomato | 2.63 |
| 7 | 1985 Autumn | Tomato | 2.45 |
| 8 | 1985 Autumn | Tomato | 2.59 |
| 9 | 1985 Autumn | Tomato | 2.75 |
| 10 | 1985 Autumn | Tomato | 2.73 |
| 2 | 1986 Spring | Sweet potato | 4.42 |
| 3 | 1986 Spring | Buckwheat | 3.93 |
| 5 | 1986 Spring | Chinese cabbage | 3.82 |
| 4 | 1986 Autumn | Corn | 3.14 |
| 6 | 1986 Autumn | Tomato | 2.92 |
| 7 | 1986 Autumn | Tomato | 2.95 |
| 8 | 1986 Autumn | Tomato | 3.08 |
| 9 | 1986 Autumn | Tomato | 3.47 |
| 10 | 1986 Autumn | Tomato | 2.77 |
| 2 | 1987 Spring | Sweet potato | 4.13 |
| 3 | 1987 Spring | Corn | 4.32 |
| 5 | 1987 Spring | Chinese cabbage | 4.19 |
| SE | | | ±0.13 |

1. Spring and autumn mung bean were replaced by soybean from the autumn of 1985.
2. Rotation numbers: see Table 1 for details.

### Soil Nutrients

The annual variation in available soil nutrients is shown in Figure 2. Inorganic N gradually decreased with time, while soil P increased in the first 3 years and then appeared to reach a plateau. Available K increased to a constant level of around 80 mg kg$^{-1}$ after 1984, and soil Mg increased up to 1986.

The seasonal variation of soil nutrients during the 1983-87 period is summarized in Figure 3. Concentration of such divalent cations as Ca and Mg decreased sharply during the summer sowing. Soil N and K concentrations were higher after the autumn sowing because of limited rainfall and irrigation. Sowing time did not significantly affect soil P. Fertil-

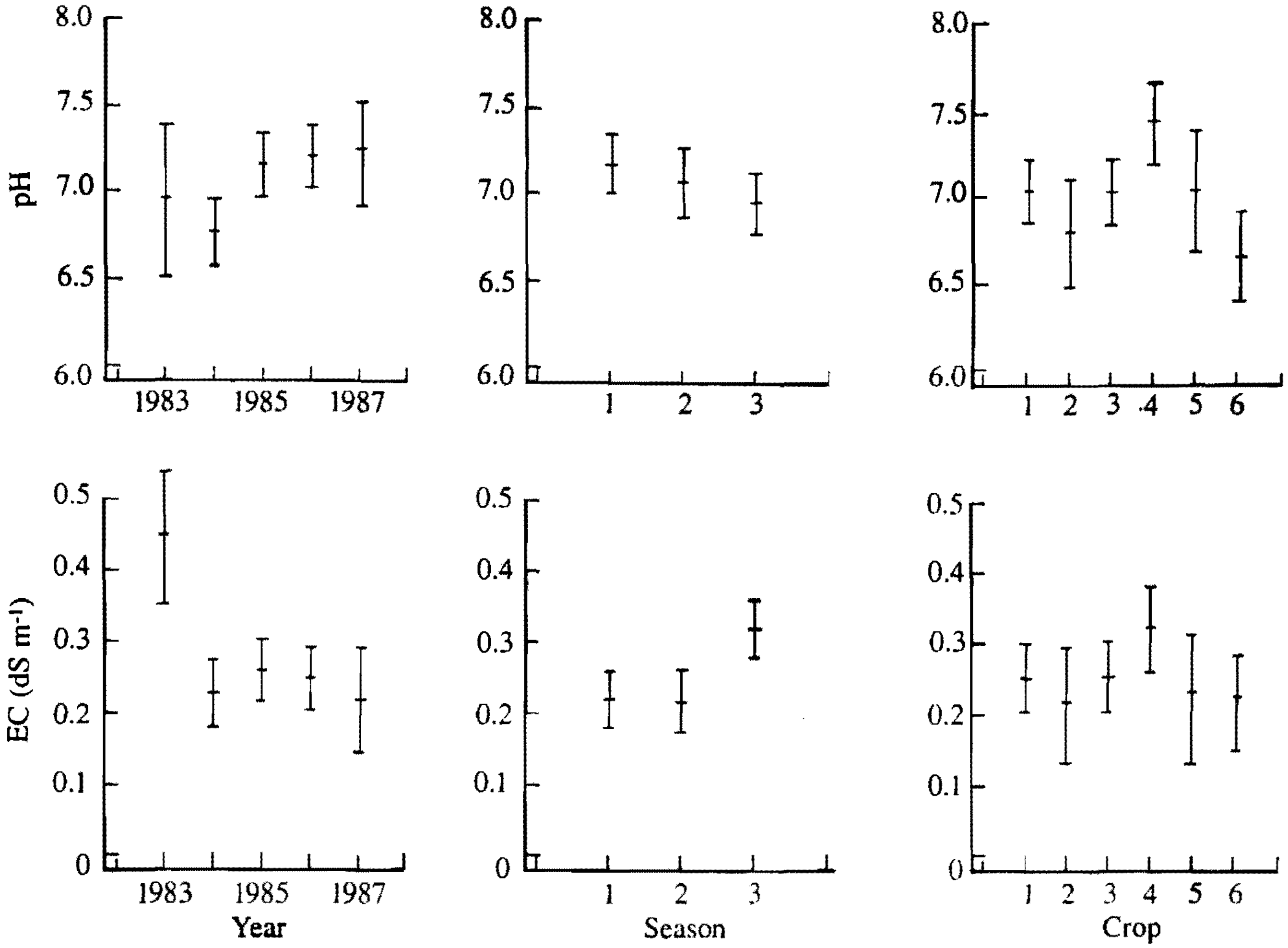

**Figure 1. Plots of means and 95% confidence intervals for changes in soil pH and EC with year and season of sowing and crops cultivated. Season: 1 = spring, 2 = summer, 3 = autumn. Crop: 1 = soybean, 2 = mung bean, 3 = tomato, 4 = Chinese cabbage, 5 = sweet potato, 6 = rice.**

izer P is bound by soil components and this prevents leaching by rain (Imai et al. 1981).

Figure 4 shows soil nutrient variations according to the crops cultivated. Inorganic N was not markedly increased by introduction of legumes into the crop rotation, and decreased significantly following rice cultivation. Available P was higher after soybean and tomato cultivation but decreased following sweet potato and rice. Soil K was higher following soybean cultivation. Tomato cultivation decreased available Ca level. Available Mg increased with cultivation of soybean, Chinese cabbage, or rice, while it decreased with the introduction of mung bean and tomato.

Two main factors contribute to the increase in soil available nutrients following cultivation of soybean and Chinese cabbage: sowing time and compost and/or mulch application. Soybean was cultivated in both autumn and spring, but not in summer, and Chinese cabbage was mainly sown in spring. On the other hand, tomato was mostly introduced into various cropping sequences as a summer crop, when more than 60% of the annual precipitation was received. In addition, only three crops—soybean, Chinese cabbage, and tomato—received compost and mulch, which contained substantial amounts of available nutrients (pH, 7.5; EC, 2.95 dS $m^{-1}$; total C, 16.5%; total N, 1.85%; $NH_4$-N, 22 mg $kg^{-1}$; $NO_3$-N, 203 mg $kg^{-1}$; available P, 1212 mg $kg^{-1}$; available K, 2065 mg $kg^{-1}$).

Cropping sequence did not affect available nutrient status in soil greatly (Fig. 5), but compost application did increase total N (Rotation Nos. 7 and 9). Compost and rice-straw mulch were very effective in increasing soil P and K. Use of rice-straw mulch, therefore, is a technique of primary importance not only for overcoming damage caused by heavy rain and a decrease in soil temperature, but also for increasing available soil P and K. Although compost increases soil P and K, its application in association

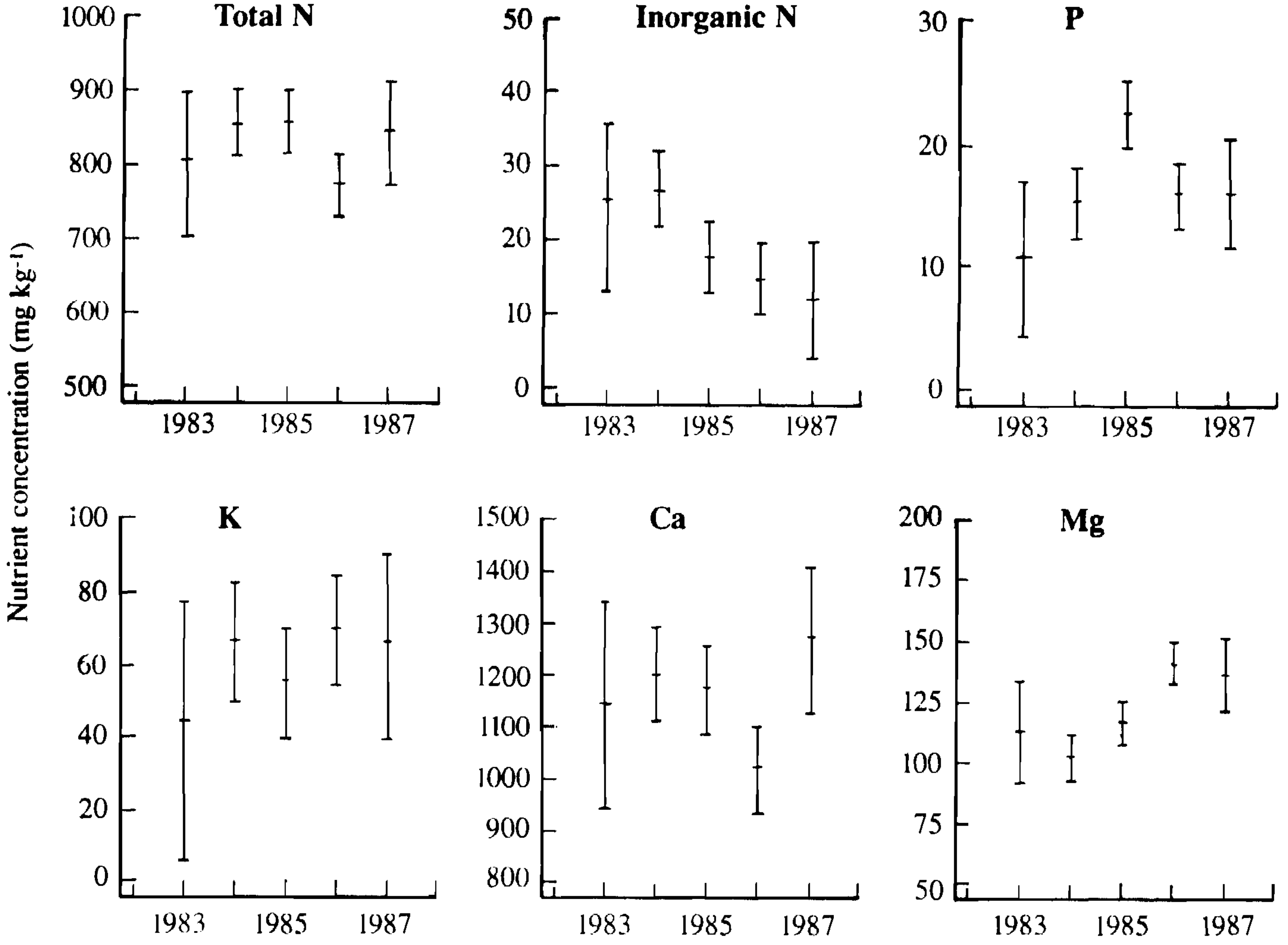

**Figure 2. Plots of means and 95% confidence intervals for annual variations in total N and available soil nutrients, 1983-87.**

with deep plowing should be avoided in the rainy season, because a deeply plowed field acts as a water reservoir during heavy rain, collecting runoff from the surrounding area, which results in serious root damage to the rotation crops. Application of unmatured compost associated with the deep plowing aggravates root damage, due to a sharp decrease in soil Eh. Only fully matured compost should therefore be used in this season.

## Relation of Soil Nutrient Concentrations to Crop Yields

Multiple-regression analysis was applied to this data set to clarify factors affecting yield. "F-enter," a value for the F-ratio above which variables would be entered into the model, was set to 4.0. The best-fit model contains three independent variables: pH, inorganic N (IN), and available P (P). Although pH and IN are both significant at 0.01 probability level and P also shows a significant t-value at 0.05 probability level, the coefficient of determination ($R^2$) is 0.206, with an adjusted $R^2$ of 0.18, indicating that only 18% of the variation in the yield is explained by the three factors included in the model (Table 5).

From this data set, multiple-regression analysis was then applied to soybean data only to elucidate the effect of soil nutrient status on a specified crop. Nearly one-third of the yield variation of soybean is explained by only soil EC, and the other nutrients are not significant even at $P = 0.05$ (Table 5).

Next, multiple-regression analysis was conducted for yield of succeeding crops as a dependent variable and nutrients left in the soil after harvest of the preceding crop. P, K, and Mg are included in the best-fit

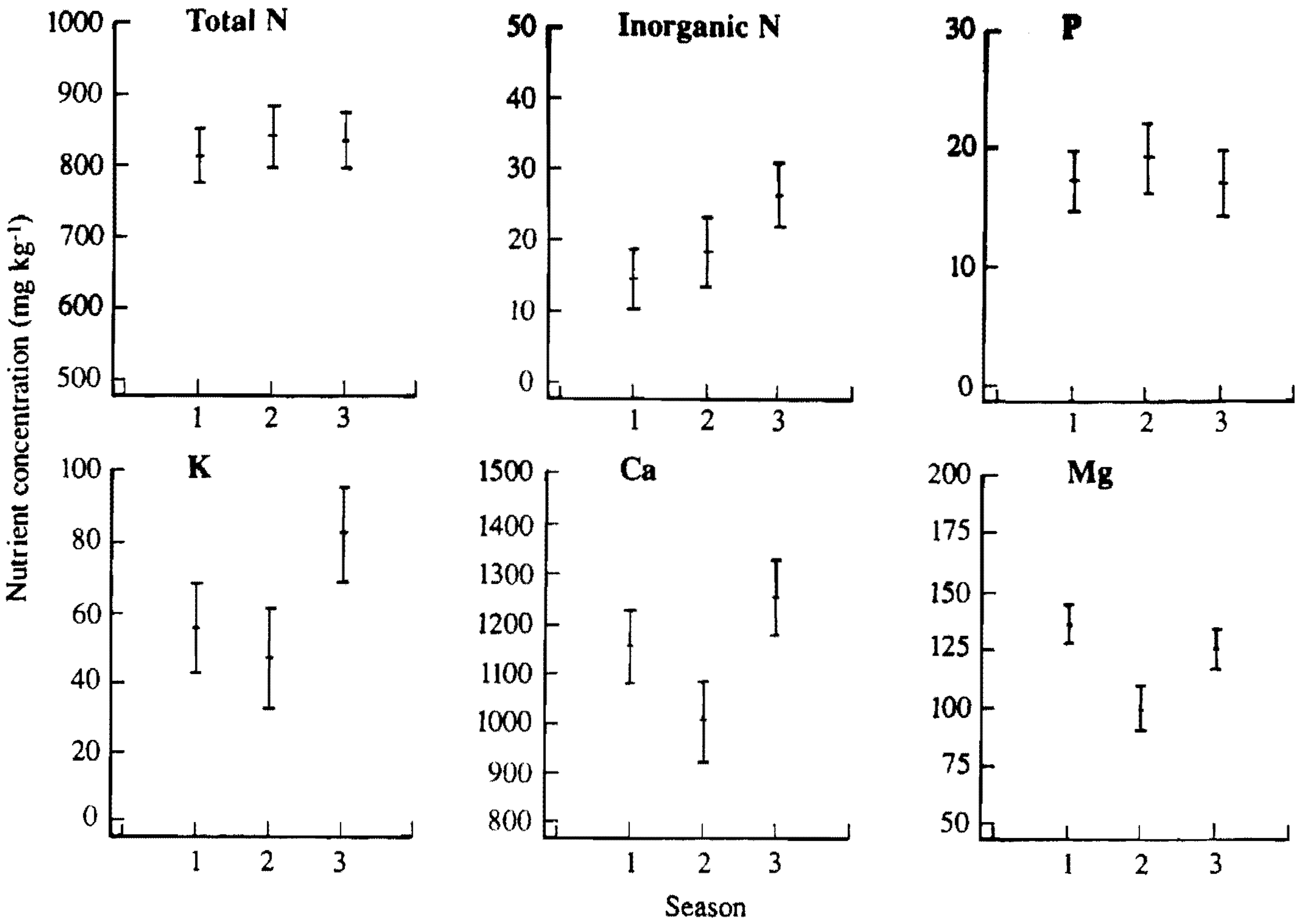

**Figure 3. Plots of means and 95% confidence intervals for seasonal variations in total N and available soil nutrients. Season: 1 = spring, 2 = summer, 3 = autumn.**

**Table 5. Fitted relationships of relevant soil chemical properties to crop yields.**

| Independent variable | Coefficient | Standard error | t-value | Significance level ($P <$) |
|---|---|---|---|---|
| All rotation crops | | | | |
| Constant | -59.30 | ±22.14 | -2.68 | 0.009 |
| Soil pH | 8.67 | ± 3.10 | 2.80 | 0.006 |
| Soil EC | 0.35 | ± 0.11 | 3.28 | 0.002 |
| Available P | 0.20 | ± 0.10 | 2.04 | 0.044 |
| Adjusted $R^2 = 0.180$ | | | | |
| Soybean alone | | | | |
| Constant | 3.93 | ± 0.24 | 16.47 | 0.000 |
| Soil EC | -2.72 | ± 0.84 | -3.24 | 0.004 |
| Adjusted $R^2 = 0.275$ | | | | |

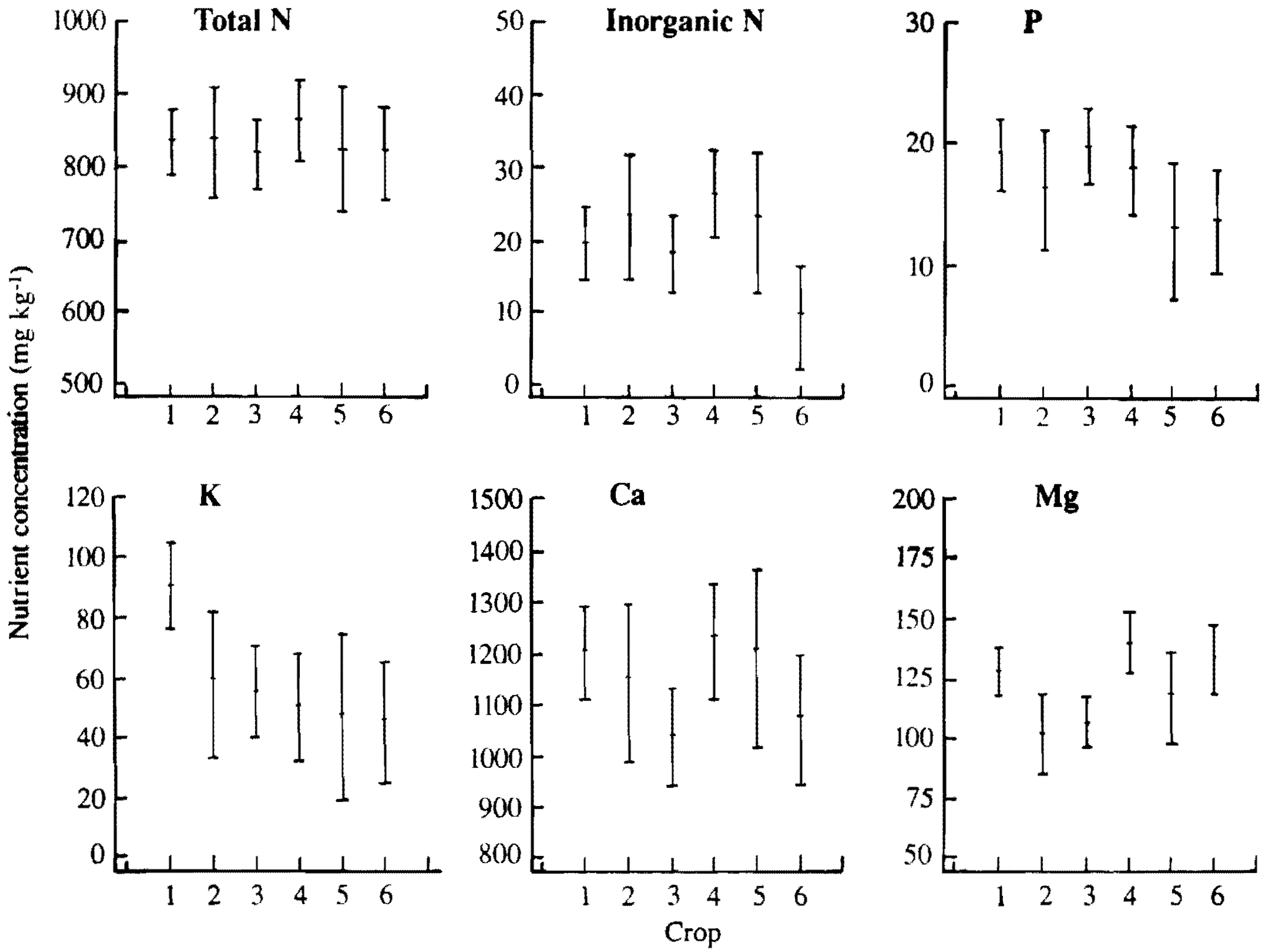

**Figure 4. Plots of means and 95% confidence intervals for changes in total N and available soil nutrients with crop cultivated. Crop: 1 = soybean, 2 = mung bean, 3 = tomato, 4 = Chinese cabbage, 5 = sweet potato, 6 = rice.**

model, with an adjusted $R^2$ of 0.22. Thus the model does not fit well to the experimental data, and only P has a positive coefficient, indicating that a cumulative effect of soil nutrients in the humid tropics may only be expected for P.

Thus, soil nutrient concentrations, measured either before sowing or after harvest, are not closely related to crop yield. Therefore, it is more important to provide timely application of fertilizer than to try to increase soil fertility over time, to maintain high yields of legumes and vegetables in the humid tropics.

## Nutrient Uptake by Crops in Various Rotations

Nutrient uptake by various crops grown under different cropping sequences is presented in Figure 6. The pattern of nutrient uptake by the same crop was similar among different crop rotations. Soybean absorbed nearly three times as much N as other crops. It also absorbed 11 kg P $ha^{-1}$, while mung bean absorbed only half this amount. Tomato had the highest K uptake, followed by rice and soybean. Calcium uptake was highest in tomato and soybean and lowest in rice. Magnesium uptake was highest in soybean, followed by tomato.

Soybean accumulated nearly 80% of the total N uptake, 75% of the P uptake, and 60% of the K uptake in its seed (Fig. 7); however, Ca and Mg were mainly deposited in leaf and stem. This indicates that plowing back of soybean residues into the soil does not appreciably increase the soil N, P, and K, but does increase soil Ca and Mg. In mung bean also, N and P were mainly deposited in the seed. Mung bean accumulated less nutrients than soybean; therefore, a max-

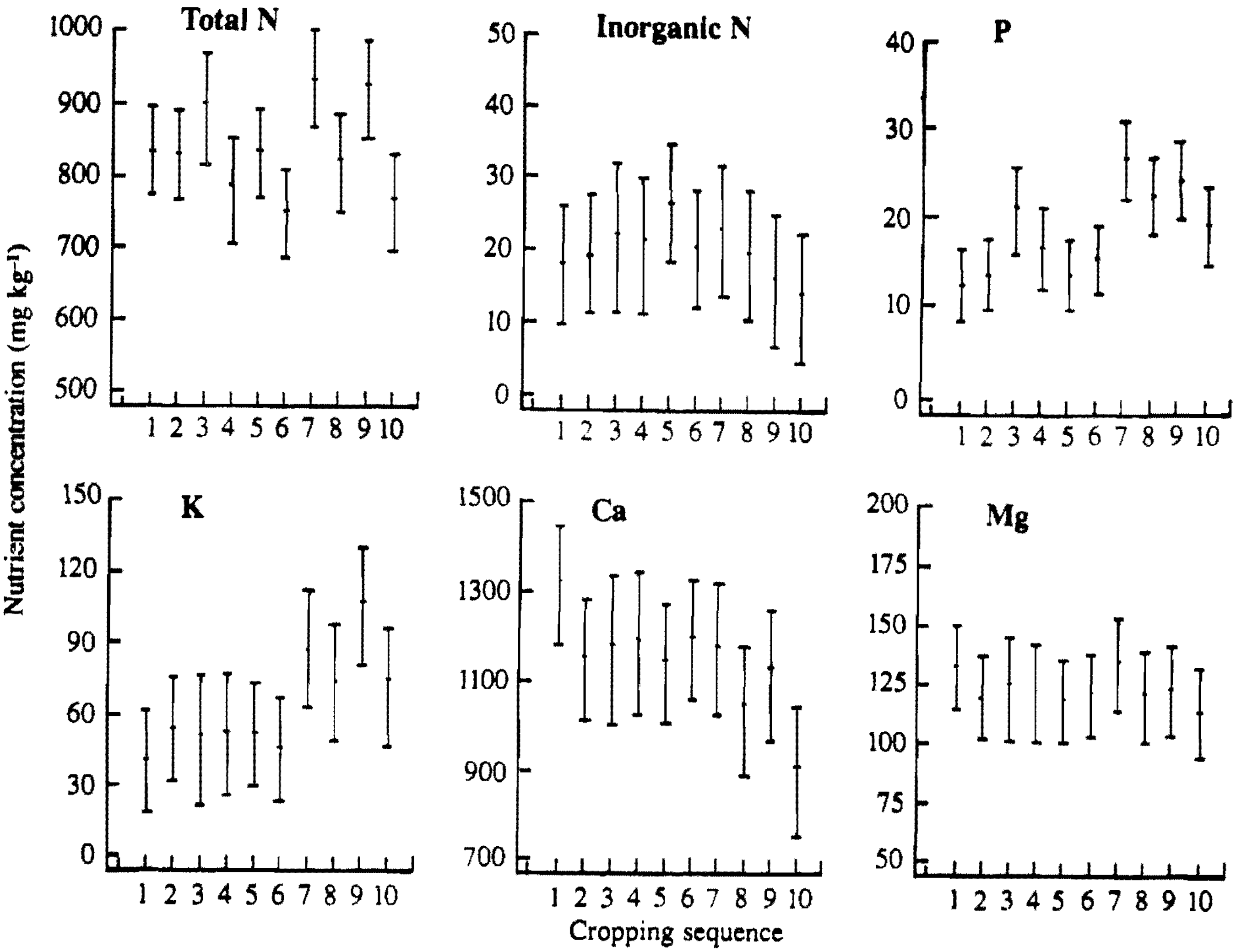

**Figure 5. Plots of means with 95% confidence intervals for changes in total N and available soil nutrients with cropping sequence (as defined in Table 1).**

imum of 30 kg N, 2 kg P, and 25 kg K ha$^{-1}$ could be returned to the soil through decomposition of mung bean residues. Rice accumulated nearly 60% of its total N uptake and 70% of its P uptake in the seed, but translocated only 10% of total K uptake to the seed (Fig. 7). Most of the Ca taken up was stored in stem and leaf tissue, while nearly one-half of the Mg was found in the seed.

More than 50% of total uptake of N and K, and nearly 60% of P, were found in the fruits of tomato (Fig. 7); most of the Ca and Mg accumulated in stem and leaf tissue.

## Relation between Nutrient Uptake and Crop Yields

The dry mass of each plant part for eight different crops over seven seasons increased linearly with increasing N uptake, with three distinctive straight lines for different crop groups (Fig. 8). Rice and sweet potato had the highest rate of dry-matter production per unit N uptake, with a value of 102.6 kg ha$^{-1}$ per kg N absorbed ($R^2 = 0.91$), followed by tomato (slope = 48.5, $R^2 = 0.97$); soybean (slope = 21.0, $R^2 = 0.83$) and Chinese cabbage, the least. In other words, soybean and Chinese cabbage required the highest N absorption to produce a unit amount of dry matter. Thus, N absorption by each rotation crop accurately reflects its dry-matter production.

A plot of dry mass of fruit or seed against N uptake could also be categorized into three different groups: the first for soybean, the second for mung bean and tomato, and the third for rice (Fig. 9). To produce 4 t of dry seed, for example, 300 kg N ha$^{-1}$ needs to be absorbed by whole soybean plants and

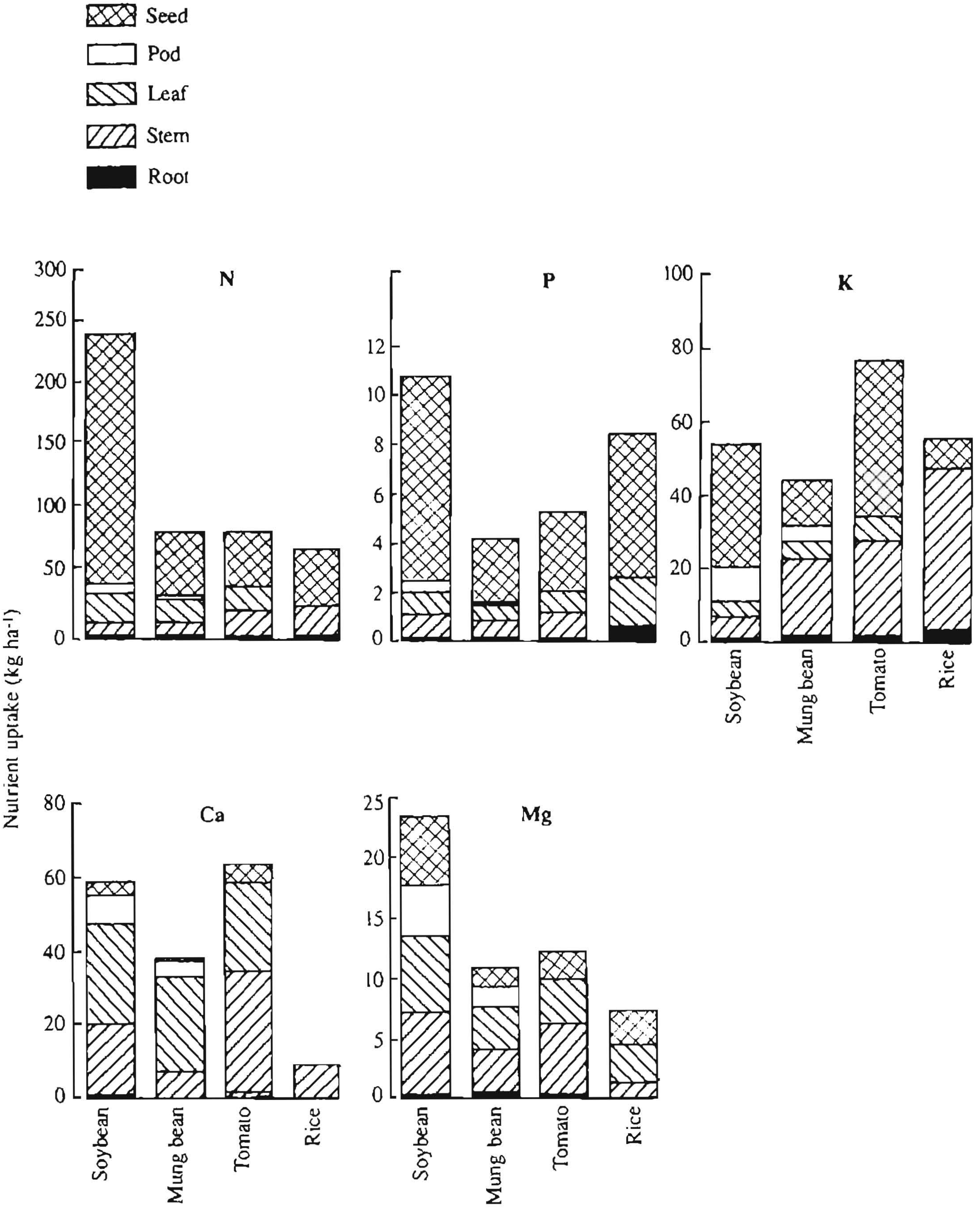

Figure 6. Uptake of N, P, K, Ca, and Mg by the major rotation crops. Data were collected continuously from the spring of 1985 to the spring of 1987, over seven seasons, and statistically analyzed.

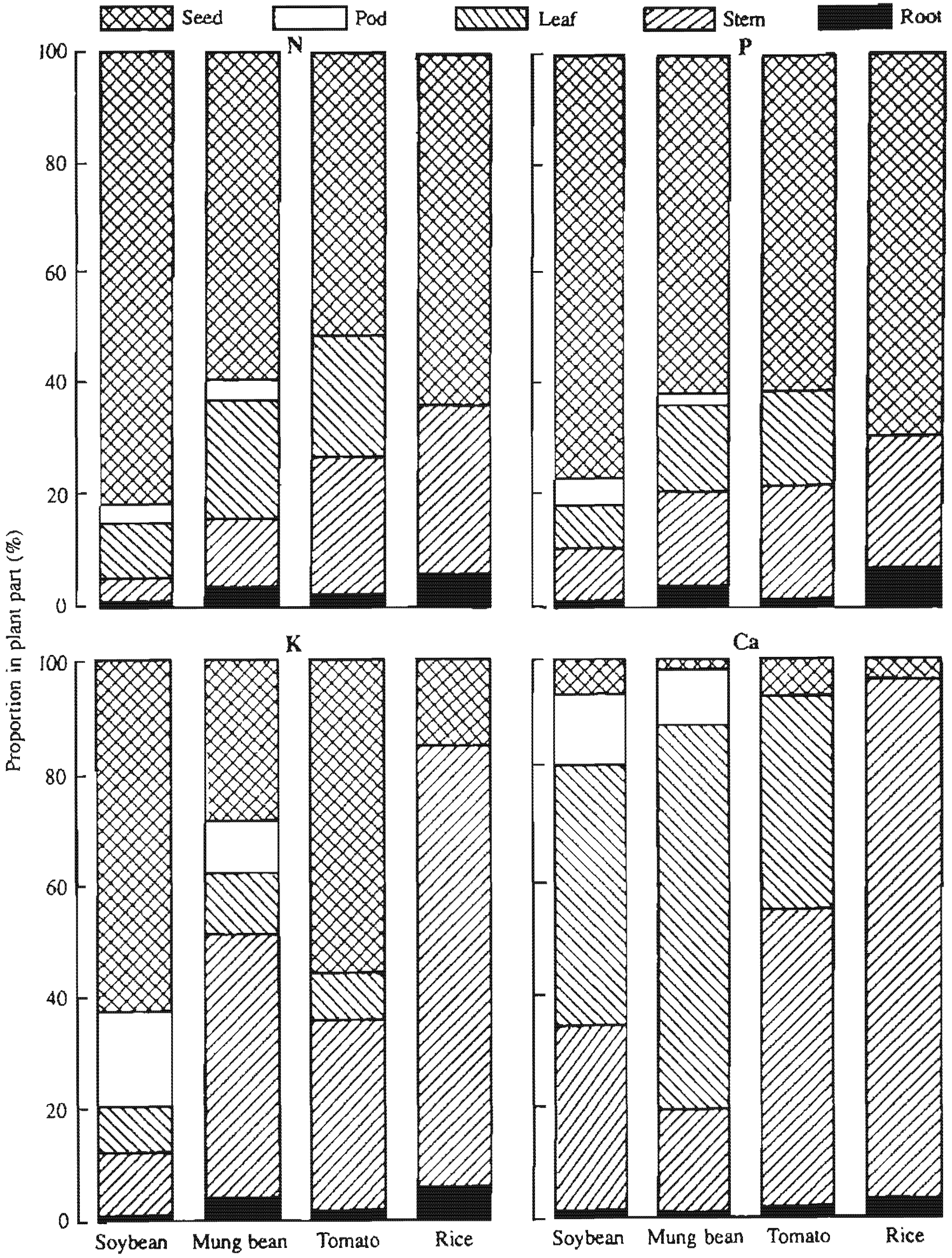

Figure 7. Distribution of N, P, K, and Ca between plant parts of major rotation crops.

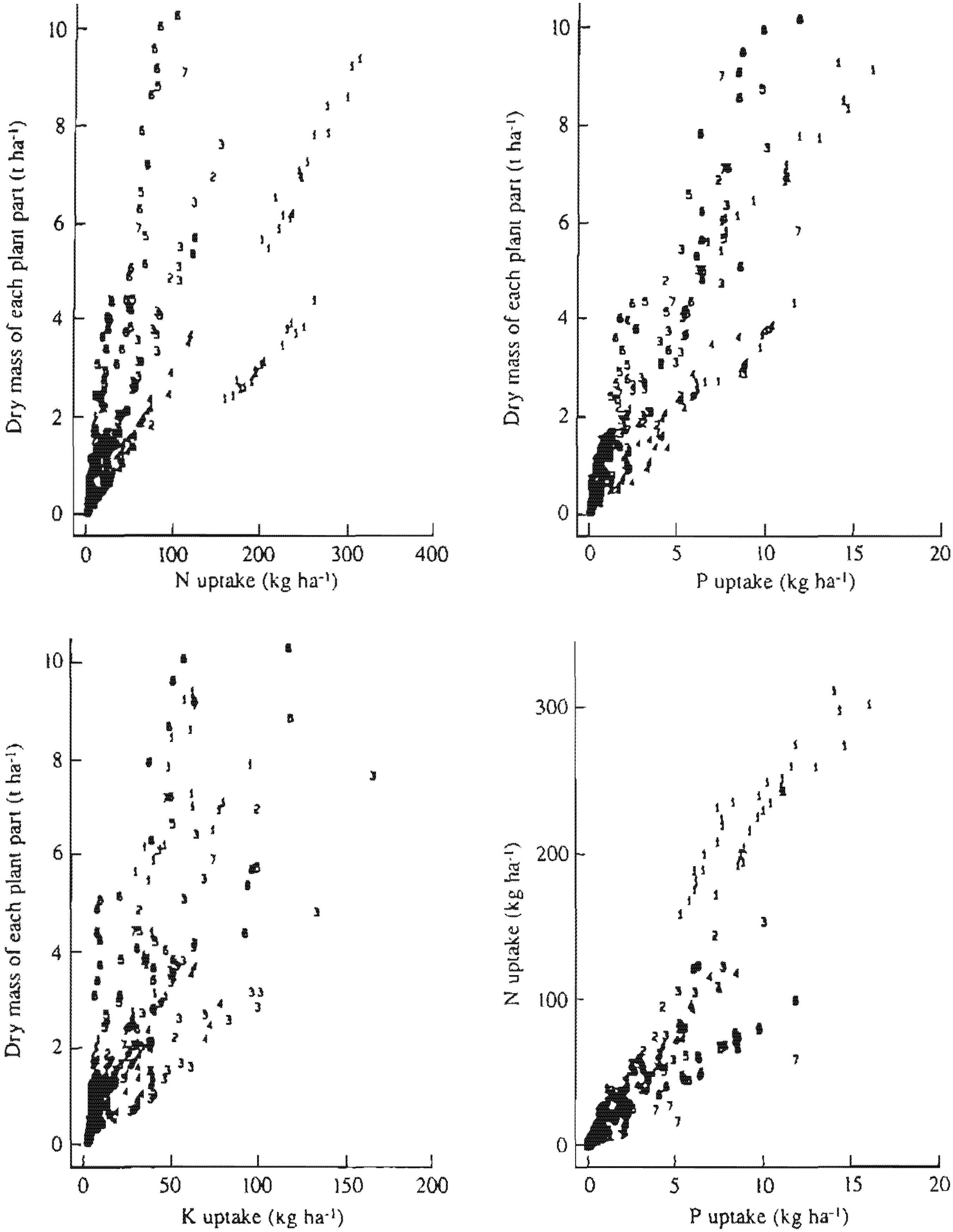

**Figure 8. Relationship between dry mass of different plant parts and uptake of N, P, and K and between N uptake and P uptake. Crop: 1 = soybean, 2 = mung bean, 3 = tomato, 4 = Chinese cabbage, 5 = sweet potato, 6 = rice, 7 = corn, 8 = buckwheat.**

250 kg N $ha^{-1}$ accumulated in the seed. The corresponding values for rice are only 70 kg and 50 kg N $ha^{-1}$. Recent promising varieties of soybean contain nearly 40% or more of protein, while rice contains less than 10%; therefore, soybean accumulates four to five times as much N in its seed as rice during the period from pod-filling stage (R4) to physiological maturity (R7) (Fehr and Caviness 1977). This implies that soybean should continuously fix N symbiotically during the reproductive stage, and efficiently transfer it to the seed, unless successive split applications of N are provided as late as the R6 stage (Kuwahara et al. 1986).

The dry mass of the rotation crops also increased linearly with increasing P uptake, with no clear differences in relationships between crops (Fig. 8). However, $R^2$ was substantially increased, from 0.77 to 0.86, when soybean data were excluded.

Similar relationships were also obtained in the plots of dry mass of fruit or seed against the total P uptake (Fig. 9). Experimental points fell roughly on two lines: tomato and rice on one and soybean and Chinese cabbage on the other. Soybean absorbs 15 kg P $ha^{-1}$ ($R^2 = -0.93$), while tomato ($R^2 = 0.92$) and rice ($R^2 = 0.95$) each absorb 8 kg P $ha^{-1}$, to produce 4 t of the dry seed or fruit. Soybean also absorbs more P per unit of dry matter produced than other crops. However, its uptake of P—unlike the uptake of N—is less than double that of the other crops. As previously described, soybean accumulates more than 80% of its total N and P in the seed, thereby requiring considerable amounts of both these nutrients to support high grain yields. In plots of N uptake by different crops against their P uptake, N uptake was found to increase linearly with P uptake (Fig. 8; $R^2 = 0.81$). However, soybean showed a relationship different from the other crops in that it had a greater slope above 150 kg N $ha^{-1}$. Therefore, soybean absorbs more N than P when its N uptake exceeds 150 kg $ha^{-1}$. Cultural practices that accelerate N uptake and its efficient transfer to the seed during the reproductive growth stage are of primary importance in achieving more than 2.5 t $ha^{-1}$ of soybean grain yield. Topdressing of N both at R1 and R4 is therefore strongly recommended for high yield of soybean (Kuwahara et al. 1986).

When dry mass is plotted against K uptake, tomato, Chinese cabbage, and buckwheat tend to fall on one line; legumes, rice, and sweet potato on another (Fig. 8). Tomato and Chinese cabbage, for example, have slopes of fitted regression lines of 35.1 ($R^2$ = 83.5) and 33.5 ($R^2$ = 67.3), respectively, while the slope for soybean is steeper, with a value of 84.8 ($R^2$ = 82.3). Tomato is one of the fruit vegetables that show high response to K (Imai 1990b). The magnitude of the slope for rice is intermediate, but the fit of experimental points to a regression line is not as good for rice as for the other crops. Thus, the total K uptake is not correlated to total dry-matter production as closely as total N and P uptake.

In the plot of dry mass of fruit or seed against total K uptake, the correlation deteriorated (Fig. 9). No correlation could be found for soybean, tomato, and rice. Only Chinese cabbage head mass was highly correlated with the K uptake ($R^2 = 0.91$).

As previously described, K accumulated less in the fruit or seed than N and P, and only 10% of total K uptake was translocated to the seed in rice. This indicates that, unlike N and P, K is not necessarily associated with the major plant constituents. Although K has several physiological and biochemical roles, e.g., in protein synthesis and in the mechanism of opening and closing of stomata, it is not known to be a constituent of any essential organic compound in plants (Mengel and Kirkby 1980).

Finally, for quantitative determination of the contribution of each nutrient taken up to increased dry-matter production, multiple-regression analysis was applied to the total dry mass of rotation crops as a dependent variable, and nutrients absorbed as independent variables. P, N, and Mg uptake are included in the fitted model for total dry-matter production of eight different rotation crops, with an adjusted $R^2$ of 0.87. Of these three factors, P uptake alone explained about 77% of the variation in dry-matter production. As is well known, P plays an important role in the numerous enzyme reactions that depend on phosphorylation; hence, it has a key role in the conversion and transfer of energy for a wide range of biochemical processes (Moorby and Besford 1983; Wild and Jones 1988). Phosphorus is also a constituent of nucleic acid and of phospholipids, including those of cytoplasmic membranes. Thus, P is a nutrient of primary importance in tropical legume and vegetable production.

Introduction of Mg and N into the fitted model increased adjusted $R^2$ by only 5% and 6%, respectively. Magnesium plays a major role in numerous reactions as a cofactor of most of the enzymes that act on phosphorylated substrates. Because of its role, the distribution of Mg in plants is often similar to that of P.

Nitrogen directly or indirectly interacts with P to enhance crop growth. Ammoniacal-N fertilizer increases P availability. Application of nutrient N—

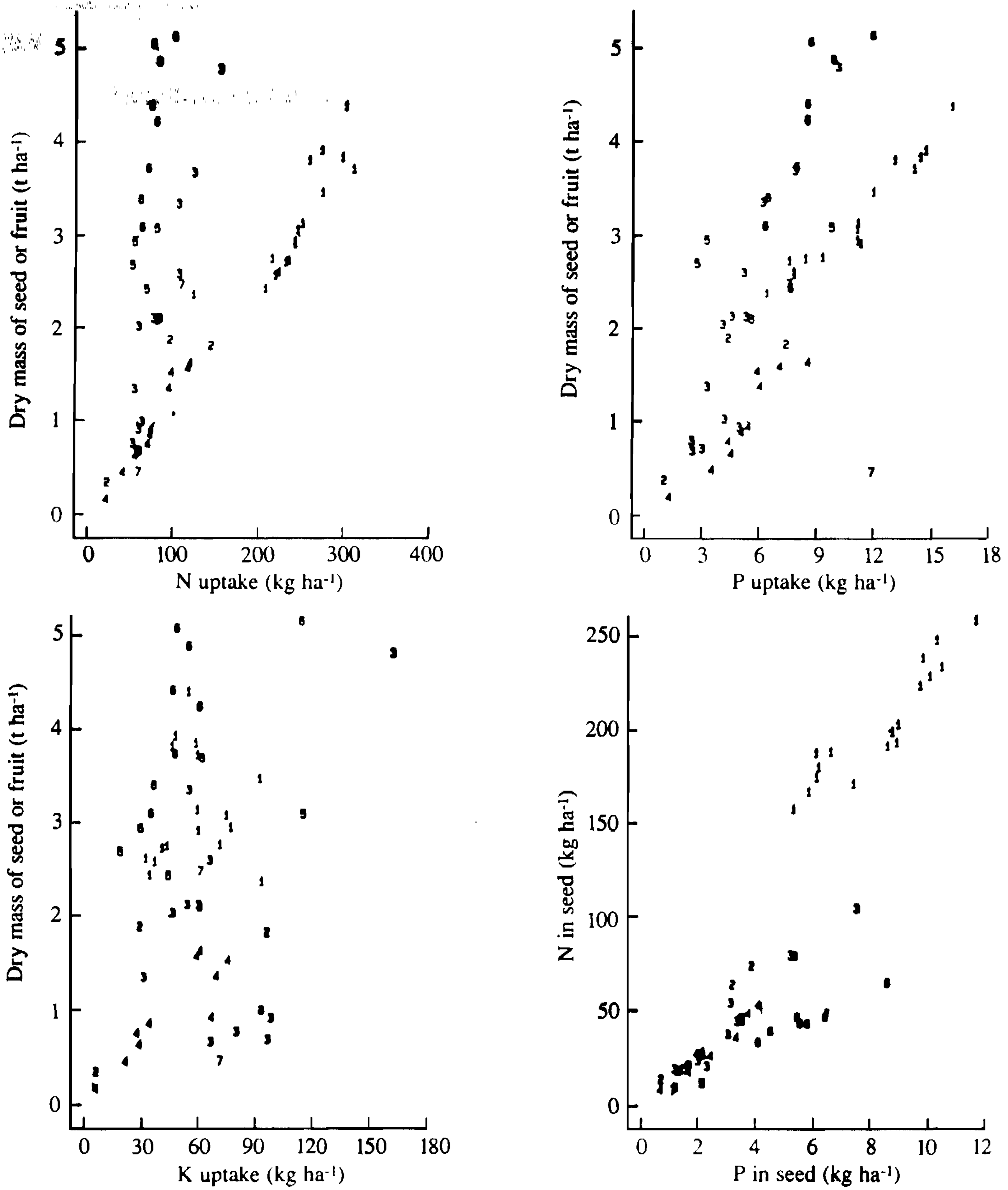

**Figure 9. Relationship between seed or fruit production of the different rotation crops and total uptake of major nutrients, and between N and P in seed. Crop: 1 = soybean, 2 = mung bean, 3 = tomato, 4 = Chinese cabbage, 5 = sweet potato, 6 = rice, 7 = corn.**

which plays an essential role in the growth of most plants as a constituent of proteins, nucleic acids, chlorophyll, and growth hormones—encourages initiation and extension of primary and secondary lateral roots and also increases top growth and its duration, thus resulting in an increase in P uptake by crops (Silberbush and Barber 1983; Wild and Jones 1988).

Phosphorus also increases N uptake by accelerating top and root growth, and P-deficient plants have a stunted root system and an even more stunted leaf and stem (Bouma 1983). Phosphorus enhances the symbiotic $N_2$-fixation process in legumes. Nodules develop faster and become active sooner in response to P fertilization, and P application increases the concentration and content of N in the harvested portion of the host legume. Thus, the three nutrients, N, P, and Mg, seem to interact closely with one another in plant tissues.

To examine the validity of the fitted model in terms of the magnitude of components and residual effects, a component-effects plot was applied to the three variables of N, P, and Mg. By definition, the plot produces a component-plus-residuals plot of the residuals around a line defined by the term $B_j(X_{ij}-\overline{X}_j)$, which multiplies the centered value of the independent variable $X_j$ by the associated value of its regression coefficient $B_j$. The term $(X_{ij}-\overline{X}_j)$ indicates deviations from sample means for the independent variable X (e.g., P). Therefore, the component-effects plot is considered as a type of residual plot of the regression line, which is estimated by the product of the partial regression coefficient for each independent variable (Table 6) and the deviations from sample means. The residuals are relatively small compared with the change in dry-matter production predicted by P uptake (Fig. 10). This indicates that P uptake provides useful information in predicting the dry-matter production of the rotation crops. For N uptake, however, the residuals are comparatively large in relation to its component effect, and they become even greater for Mg uptake. These results also indicate that P uptake provides valuable information in predicting dry-matter accumulation, but neither N uptake nor Mg uptake alone can predict its variation as well.

Concentration of N varied greatly not only between the plant organs but also between the rotation crops. Average N concentration in each plant organ ranged from 1% in stems to 3.5% in seed or fruit and the N concentration in the seed or fruit—major accumulators of this nutrient—varied greatly, in the range of 1% for rice to 7% for soybean (Fig. 11). Concentration of P in plant tissues is as low as one-tenth of N concentration and does not differ greatly among the crops: it ranges from 0.3% in rice to 0.5% in soybean and from 0.15% in stems to 0.45% in the seed. Thus P is well distributed throughout plant tissue and proportionally reflects plant growth. Hence it is a better index than other nutrients of dry-matter production of the eight crops considered here.

A similar relationship was obtained between the harvested portion of the crops and total nutrient uptake. Uptake of P, N, and Mg are included in the fitted model, which has an adjusted $R^2$ of 0.80; P uptake alone can explain about 56% of the variation in the seed or fruit production. Introduction of N and Mg into the fitted model increases the values of $R^2$ by

**Table 6. Fitted relationship between nutrient uptake and dry-matter production of rotation crops.**

| Independent variable | Coefficient | Standard error | t-value | Significance level ($P <$) |
|---|---|---|---|---|
| Whole plant | | | | |
| Constant | 235.59 | ± 69.74 | 3.38 | 0.0008 |
| N uptake | -19.10 | ± 1.68 | -11.37 | 0.0000 |
| P uptake | 761.19 | ± 33.29 | 22.87 | 0.0000 |
| Mg uptake | 138.24 | ± 11.20 | 12.35 | 0.0000 |
| Adjusted $R^2 = 0.869$ | | | | |
| Reproductive organ | | | | |
| Constant | 382.45 | ±167.15 | 2.29 | 0.0261 |
| N uptake | -19.43 | ± 2.48 | -7.83 | 0.0000 |
| P uptake | 552.91 | ± 69.96 | 7.90 | 0.0000 |
| Mg uptake | 368.35 | ± 86.96 | 4.24 | 0.0001 |
| Adjusted $R^2 = 0.784$ | | | | |

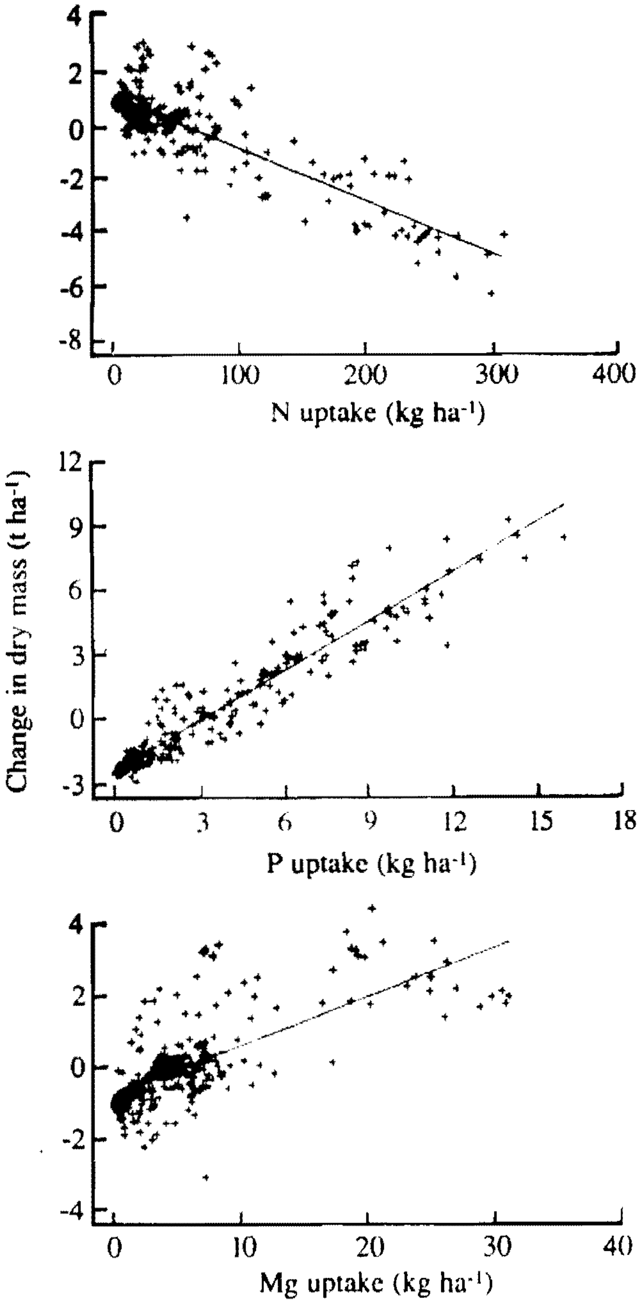

**Figure 10. Component-effects plot for the three variables included in the fitted model of Table 6.**

17% and 7%, respectively. Thus the contribution of P uptake to seed production was lower than to total dry-matter production, but N contribution increased greatly. This reflects the fact that N is predominantly accumulated in the seed or fruit of these crops.

The relationship between the total nutrient uptake and the seed or fruit mass of a specified rotation crop was also examined by multiple-regression analysis. Ninety-three percent of the variation in soybean seed production can be explained by P uptake alone; P uptake also explains about 92% of the yield variation of legumes (soybean and mung bean). In the fruit production of tomato, however, N uptake is the factor of primary importance ($R^2 = 0.90$), and addition of both the P-uptake and the K-uptake parameters increase $R^2$ by only 4%. The variation of Chinese cabbage head mass can be adequately explained by two factors, N and Mg uptake ($R^2 = 0.98$). Therefore, high seed production of legumes is primarily dependent on the amount of P absorbed, while high yields of leafy and fruit vegetables are more dependent on N uptake.

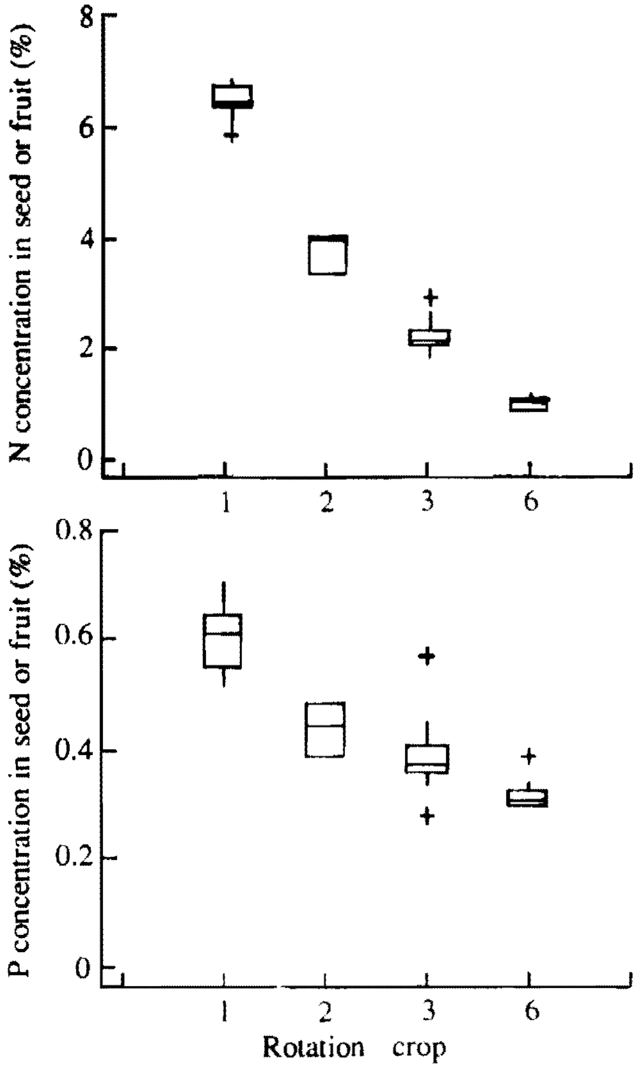

**Figure 11. "Box-and-whisker" plot of N and P concentrations in the reproductive organs of the major rotation crops (1 = soybean, 2 = mung bean, 3 = tomato, 6 = rice). The central box covers the 50% of data points between the upper and lower quartiles. The whiskers extend to the extreme minimum and maximum values. The line within the box is the median. Apparent outliers are represented by +.**

Legumes have a high P requirement due to the production of protein-containing compounds of which N and P are important constituents. The P concentration in legumes is generally much higher than that found in grasses. The vital role that high-energy P storage compounds play in reactions involving energy transfer, especially those of the elemental $N_2$-fixing enzyme, nitrogenase, is perhaps the reason that legumes, dependent on symbiotic N, have a higher P requirement than grasses, which depend on absorption of mineral N. Hence, development of cultural practices to accelerate absorption of P and its efficient transfer to reproductive organs during later growth stages is highly recommended.

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# Fertilizer Management Strategies for Legume-based Cropping Systems in the West African Semi-Arid Tropics

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### *Abstract*

*A major constraint the smallholder farmer faces in the West African semi-arid tropics (WASAT) is the low productivity of soils, which is often combined with land and labor shortage, caused in part by low productivity of labor, lack of cash resources, and limited access to credit. Groundnut and cowpea are two of the predominant grain legumes in the WASAT; they are important components of the mainly cereal-based cropping system, the most important cereals being pearl millet and sorghum. Production of these legumes is low and unstable because of the lack of adaptable cultivars with some resistance to the major biotic and abiotic stress factors, inherent low fertility of soils, uncertain rainfall distribution, and the short duration of the growing season. A current review of literature reveals that nitrogen (N), phosphorus (P), calcium (Ca), magnesium (Mg), and molybdenum (Mo) are the most important nutrients limiting legume production in the WASAT. Improvement of legume-based production systems will depend on amelioration of the low soil fertility, use of appropriate fertilizers, improved cultural practices, and use of appropriate cultivars. This chapter discusses these aspects and highlights research findings at the ICRISAT Sahelian Center. Experiments on rotation of cereals with groundnut and cowpea are demonstrating that it is possible to intensify and sustain the cereal-legume-based cropping systems in this drought-prone region.*

## Introduction

Groundnut (*Arachis hypogaea* L.) and cowpea [*Vigna unguiculata* (L.) Walp.] are two of the predominant grain legumes in the West African Semi-Arid Tropics (WASAT). Groundnut occupies 2.7 million ha of arable land and cowpea 6 million ha. The two legumes are important components of the mixed cropping patterns of resource-poor farmers. The most important cereals are pearl millet and sorghum, and legumes are often intercropped with these (Steiner 1984). Legumes serve as food as well as cash crops.

The countries of sub-Saharan West Africa have been traditional exporters of groundnut, but production has declined recently (Morris 1989). Cowpea production, on the contrary, has increased over the years and in some countries, such as Niger, it has more than doubled (Anonymous 1987), largely because of an increase in the area cultivated. Yields of cowpea grain are generally low, varying between 50 and 300 kg ha$^{-1}$, in marked contrast to yields of over 1000 kg ha$^{-1}$ obtainable on research stations and by large-scale commercial enterprises in northern Nigeria. The potential for increased yields in the region is therefore high.

The most common cropping system in the WASAT

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involves growing several crops in association as mixtures or intercrops. This practice provides the farmer with several options for returns from land and labor, often increases efficiency with which scarce resources are used, and reduces dependence upon a single crop that is susceptible to environmental and economic fluctuations. Types of crop associations differ from place to place, with ecological zone, farm size, human population, and soil fertility, as well as with cultural and socioeconomic factors.

In the Northern Guinean and the Sudan Savanna Zones, sorghum-based cropping systems are common. Millet, maize, groundnut, and cowpea form important components of this system (Steiner 1984), whereas in the Sahelian Zone, the cropping system is millet-based, with millet/cowpea and millet/groundnut being the most important cropping patterns. While considerable information is available on fertilizer requirements for sole-cropping of various crops, little is known on fertilizer requirements for intercropping.

The importance of fertilizers as key inputs in accelerating food production in the WASAT is well recognized by researchers and policy-makers. Sub-Saharan Africa accounts for about 9% of the world's population; the population growth rate of about 3% annually in this region is among the world's highest. But sub-Saharan Africa uses less than 1% of the world's fertilizer; in 1983, the use of chemical fertilizers averaged a low 7 kg ha$^{-1}$, compared with 82 kg ha$^{-1}$ in Asia and 32 kg ha$^{-1}$ in Latin America, and some of the West African countries experienced a negative growth (Table 1).

**Table 1. Characteristics of fertilizer use in West African countries (derived from Muhamadar 1986).**

| Country | Nutrient 1978-82 (kg capita$^{-1}$) | Nutrient 1978-82 (kg ha$^{-1}$) | Growth[1] (%) |
|---|---|---|---|
| Bénin | 0.53 | 1.10 | -8.9 |
| Burkina Faso | 1.23 | 3.27 | 25.5 |
| Côte d'Ivoire | 5.33 | 11.00 | 6.5 |
| Gambia | 4.30 | 16.43 | 2.0 |
| Ghana | 1.40 | 7.03 | 23.5 |
| Guinea | 0.27 | 0.87 | -4.8 |
| Guinea-Bissau | NA | 2.1 | NA |
| Liberia | NA | 11.1 | 7.3 |
| Mali | 1.67 | 5.63 | 7.0 |
| Mauritania | 0.67 | 5.83 | 28.2 |
| Niger | 0.40 | 0.70 | 23.1 |
| Nigeria | 1.87 | 4.87 | 33.5 |
| Sénégal | 4.33 | 4.70 | 8.7 |
| Sierra Leone | 0.30 | 0.77 | 1.4 |
| Togo | 0.90 | 1.70 | 23.6 |

[1] Annual compound growth rate from 1969/70-1971/72 average to 1980/81-1982/83 average.

In this chapter we discuss the characteristics of the crop-production environment, review the previous work in the region, and present experience of the ICRISAT Sahelian Center (ISC) at Sadoré, near Niamey in Niger.

## Characteristics of the Crop-production Environment

### Climate

The WASAT is an extensive area, covering Sénégal, The Gambia, Mali, Mauritania, Burkina Faso, Niger, and northern Nigeria. These are the major growing areas of both groundnut and cowpea. In this region, particularly the Sahel, evapotranspiration exceeds rainfall during at least 5 months of the year. Only one rainfed crop per year is possible without irrigation. The legumes are usually sown in June or July and harvested in September-October. The growing period is 2-$4^{1}/_{2}$ months. Temperatures are warm (annual mean 25°C). The rainfall is generally low (annual range 300-1000 mm), variable, and undependable. End-of-season drought is common. Sivakumar (1989) reported that the reduction in the mean annual rainfall in Niger from 1969 was a geographical mean pattern, not an isolated occurrence. The intensity of rainfall is normally very high, and the aggressiveness of rainstorms has important implications for soil and crop management.

### Soil

Throughout the WASAT, shifting cultivation has been a widely used land-management system. Basically, it involves the cultivation of a piece of land for a few years, followed by a rest period in which the land is allowed to return to native vegetation, improving nutrient status and soil structure. In this system, the bush is cleared and burned before cultivation, causing loss of most of the nitrogen (N), sulfur (S), and carbon (C). Soils are also prone to nutrient loss by erosion and leaching. The destruction of humus leads to deterioration of soil physical properties.

The WASAT is now experiencing rapid population growth, and the increased demand for cropland has led to a decrease in fallow periods for stable traditional agriculture. With continuous cultivation, the productivity of the soil is reduced because of (1) lowering of organic matter below critical levels, (2) physical removal of the soil by wind or water erosion, (3) leaching of nutrients, especially in light-textured soils, and (4) exhausting of soil nutrients by crop removal.

## Physical Properties

The physical and chemical properties of some typical WASAT surface (0-15 cm) soils are given in Table 2. The WASAT soils are predominantly sand to sandy loam. Clay content ranges from 1 to 5% and the soils have a weakly coherent massive to subangular blocky structure. Due to their sandy nature, the surface soils have a friable consistence and they can crust when dry. The sandy soils of the Sahelian Zone have bulk densities ranging from 1.4 to 1.7 Mg m$^{-3}$, corresponding to a porosity of 36-43% (Sivakumar et al. 1990). The dune soils of the Sahelian Zone have a very high hydraulic conductivity (150-200 cm day$^{-1}$) and therefore a rapid internal drainage. But in the Sudanian Zone, with increased clay content and the formation of crusts, the internal drainage is reduced. The available soil moisture can be as low as 0.07 g cm$^{-3}$ at the soil surface. The sandy dune soils are prone to wind erosion and, with the strong storms that characterize the beginning of each rainy season, crop establishment can be severely affected by sandblasting and burial of seedlings.

## Chemical Properties

One striking feature of the WASAT is low soil fertility, which is expressed through the low level of organic C, total N, and effective cation-exchange capacity (CEC) (Table 2). Among 31 topsoils of the WASAT, total N value ranged from 31 to 1800 mg kg$^{-1}$, with a mean of 266 mg kg$^{-1}$ (Bationo et al. 1989). The main source of N is organic matter, and the natural low levels of this in these soils are reflected in low total N values.

The value of exchangeable acidity is very low, indicating that these soils are likely to have little problem related to aluminum (Al) toxicity.

Phosphorus (P) has been shown to be one of the most limiting nutrients. The low levels of available P are due to low levels in soil parent material and organic matter.

**Table 2. Physical and chemical properties of some selected soils (0-15 cm) of the West African Semi-Arid Tropics (Bationo et al. 1989).**

| Soil property | Sadoré (Niger) | Gobéry (Niger) | Gaya (Niger) | Dapaong (Togo) | Sotuba (Mali) | Samaru (Nigeria) |
|---|---|---|---|---|---|---|
| Clay (%) | 1.0 | 1.5 | 3.9 | 1.7 | 3.0 | 5.3 |
| pH (KCl) | 4.1 | 4.2 | 4.3 | 5.8 | 4.9 | 4.9 |
| Exchangeable acidity (cmol kg$^{-1}$) | 0.23 | 0.21 | 0.20 | 0.20 | 0.06 | 0.10 |
| Organic matter (%) | 0.22 | 0.32 | 0.52 | 0.51 | 0.48 | 0.96 |
| Total N (mg kg$^{-1}$) | 74 | 103 | 226 | 219 | 142 | 299 |
| Effective cation-exchange capacity (cmol kg$^{-1}$) | 0.54 | 0.64 | 1.87 | 1.68 | 1.89 | 3.14 |
| Base saturation (%) | 57.0 | 61.8 | 89.2 | 87.9 | 36.9 | 97.0 |
| Total P (mg kg$^{-1}$) | 68 | 73 | 96 | 82 | 87 | 132 |
| Available P (Bray 1) (mg kg$^{-1}$) | 6.9 | 2.0 | 3.2 | 4.1 | 1.7 | 9.6 |
| Maximum P sorbed (b) (mg kg$^{-1}$) | 51.7 | 61.4 | 101.0 | 52.1 | 93.1 | 130.5 |

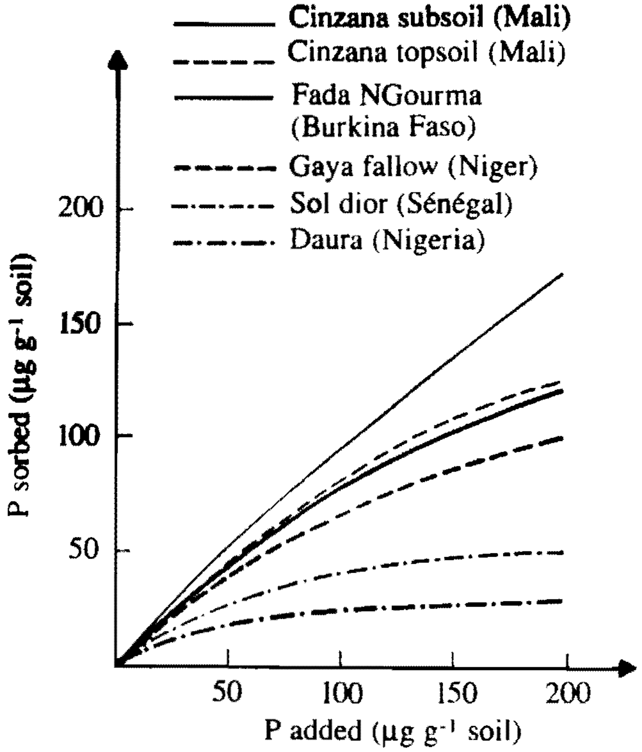


**Figure 1. Phosphorus-sorption isotherms of selected soils from millet-growing areas of West Africa.**

## Phosphorus-sorption Isotherms

The study of the P-sorption characteristics is important for an understanding of the availability of P to the plant. The method of Fox and Kamprath (1970) was used to carry out studies on P fixation of some soils in West Africa, and selected adsorption isotherms are presented in Figure 1. Sorption data were fitted to the Langmuir equation and P-adsorption maxima calculated. The soils of the WASAT have low adsorption capacities due to their low buffering capacities, and as a result, only small quantities of P fertilizers are needed to give significant crop response to P (Table 1).

## Review of Nutritional Research in the WASAT

### Nitrogen

Legume response to N fertilization tends to be site-specific. Drevon (1980) observed chlorosis in groundnut in acid soils and attributed this to Al and manganese (Mn) toxicity. Zengbe (1980) and Ahmad et al. (1981) found that 400 genetically diverse lines of cowpea responded positively to N fertilization, indicating inadequate infectivity or efficacy of indigenous rhizobia and a potential for improvement by rhizobial inoculation. It is commonly found that applications of small amounts of N are needed to ensure good nodulation of soybean and cowpea in soils of low N status. On the contrary, Ofori (1975) and Olofintoye (1986) found that application of N neither enhanced nodulation nor increased yield significantly. Agboola (1978) reported that there was no response to N in cowpea on soils with more than 2% organic matter. Nodulation and $N_2$-fixation in groundnut, as measured by the acetylene reduction assay, is drastically reduced by soil nematodes and drought stress (Drevon and Diabaye 1981; Meyer et al. 1982).

### Phosphorus

Several investigators have shown that P deficiency constitutes the major constraint to food production in West Africa (Milne 1968; Pichot and Roche 1972; Bationo 1982; Bationo et al. 1986). The low organic matter content in the sandy soils of the WASAT contributes to the P problem (Agboola and Oko 1976). It has been reported that the use of Kpeme rock phosphate in Togo (Dossou and Cretenet 1975), Tahoua rock phosphate in Niger (Nabos et al. 1974), and Tilemsi rock phosphate in Mali (Jenny 1973; Charoy 1980; Thibout et al. 1980) can significantly increase yields. Bikienga (1985) found that partially acidulated Kodjari rock phosphate increased groundnut yields in Burkina Faso.

In different experiments in Nigeria, it was shown that the application of P fertilizer increased nodulation of cowpea as well as uptake of other nutrients (Olofintoye 1986). The importance of inoculation with vesicular-arbuscular mycorrhizae (VAM) to increase P utilization by cowpea and groundnut was reported by Sanni (1976) and Islam et al. (1980).

### Potassium, Sulfur, Calcium, Magnesium, and Micronutrients

Response of groundnut to potassium (K) has been reported by researchers in West Africa (Lombin et al. 1985; Lombin and Singh 1986). Nangju (1976) and Fox et al. (1977) reviewed the importance of S for cowpea production in the tropics and recommended addition of elemental S to rock phosphate for groundnut production in northern Nigeria. With continuous cultivation and the use of high analysis fertilizers in northern Nigeria, deficiencies of calcium (Ca), magnesium (Mg), S, and some trace elements have been observed in groundnut production (Balasubramanian et al. 1981), and S supply seems to be the main factor responsible for better performance of groundnut fertilized with single superphosphate. In fertilizer trials in Nigeria, application of gypsum did not significantly increase groundnut yield (Yayock and Owonubi 1983).

Pieri (1976) reported that a 2% increase in Al saturation decreased groundnut pod yield by 75 kg $ha^{-1}$ and that ammonium sulfate had a greater effect on soil acidity than urea. The application of lime has been widely shown to increase groundnut nodulation (Dennis 1977; Wey and Obaton 1978; Singh et al. 1985; Wey et al. 1987).

The assessment of the seriousness of micronutrient deficiencies in the WASAT on the basis of presently available data seems impossible, but some responses of legumes to micronutrients have been reported. Balasubramanian et al. (1981) and Lombin et al. (1985) found responses of groundnut to boron (B) and molybdenum (Mo) in a long-term experiment in northern Nigeria.

### Soil Fertility Aspects under Intercropping and Rotations

Steiner (1984) pointed out that intercropping systems in general allow more efficient use of limited natural resources. From the results of recent research in the Sudano-Sahelian Zone, it has been concluded that millet/cowpea intercropping generally improves and stabilizes yield, with yield advantages of up to 60% (Fussel and Serafini 1987; Ntare et al. 1989). All fertilizer experiments in the WASAT have been carried out on sole crops, and our knowledge of fertilizing intercropping systems or crop rotations with inorganic fertilizers is still rudimentary. The practical quantity and timing of fertilizer application in these systems need to be studied.

For fertilizer management in intercropping, it is important to understand the growth characteristics of the crops in specific cropping patterns and recognize that the component crops have different nutritional needs. For example, the application of N to a cereal/legume intercrop can decrease the use efficiency of N, as it suppresses symbiotic $N_2$-fixation in legumes. The response of intercrops to fertilizers, as compared with sole crops, can be measured by calculating land-equivalent ratios (LER). The LER is the sum of ratios of yield of a component in an intercrop over its sole-crop yield. Should the LER increase with increasing fertilizer rates, then this indicates that the fertilizer efficiency is higher in the intercrop than in the sole crop (Steiner 1984).

Intercropping systems can increase the plant population, leading to increased total nutrient uptake and thus a greater depletion of the soil (Reddy and Willey 1981).

In millet/cowpea intercrop studies, it was observed that, with the application of P fertilizer, millet can suppress the cowpea crop, particularly when cowpea is sown 3 weeks after millet (A. Bationo, unpublished results). Well-fertilized millet dominates the legume (ICRISAT 1986).

Steiner (1984) reported that, in legume/nonlegume associations, there is no direct evidence for a quantitatively significant transfer of N from legumes to nonlegumes. It is mainly the following crops in the rotation that profit from the residual N effect (Singh et al. 1984).

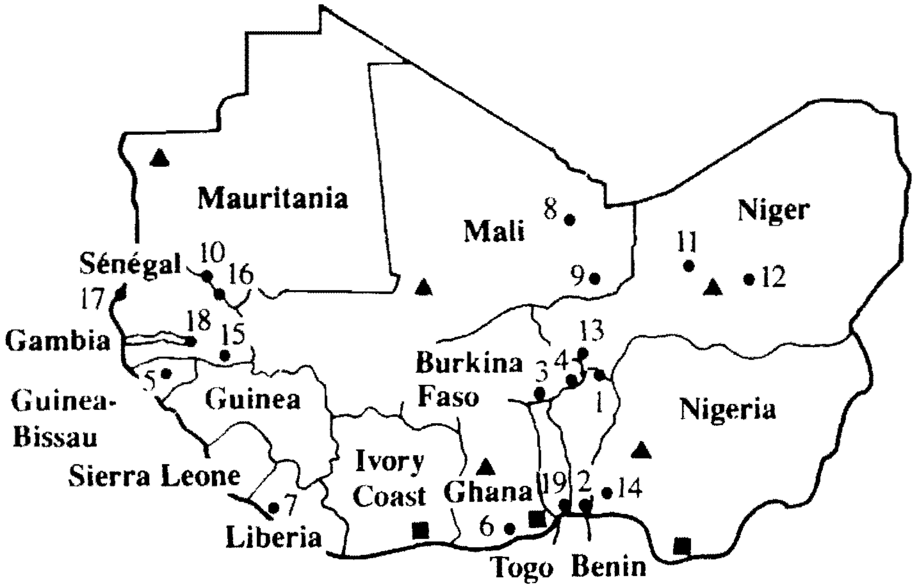
Nitrogen fixation by legumes in pure crops is more than in intercropping systems and can reach considerable amounts (Tiessen 1988). During 9 years of trials in Côte d'Ivoire, Sement (1983) found that seed yields of cotton grown after groundnut, cowpea, or soybean, were up to 0.29 t $ha^{-1}$ more than those following maize. In Burkina Faso, Stoop and Staveren (1981) reported that when sorghum without fertilizer application followed cowpea, yields were higher than when sorghum followed millet. Further, when millet followed cowpea, yield was affected by both the cowpea cultivar and its density. Cowpea can fix between 64 and 134 kg N $ha^{-1}$ (Balasubramanian et al. 1980; Dakora et al. 1987) and these amounts may supply a major part of the N taken up by the following cereal crop in a rotation. Eaglesham et al. (1982), however, reported that the contribution of N fixed by some legume crops can be negligible in soils rich in total N and can even cause greater N depletion because of the large fraction of N in the grain.

## The Experience at ICRISAT Sahelian Center

Work at ISC on soil fertility and fertilizer management has concentrated on millet and sorghum as sole crops, and we have just begun to gather knowledge on legumes as sole crops or intercropped with cereals. In the WASAT, it is believed that the use of fertilizer is too risky, and policy-makers tend to believe that water availability is the major constraint to increased agricultural production. In the past 50 years, however, grain yields on cultivated land have steadily declined, even in years of very good rainfall (A.U. Mokwunye and L.L.Hammond, 1989, The myths and science of fertilizer use in the tropics. Unpublished ms). Evidence from recent work at ISC clearly indicates that in the WASAT low soil fertility is a more serious problem for the farmer than rainfall (Bationo et al. 1989). The water-use efficiency (WUE) is much higher with than without the application of fertilizers (Table 3).

**Table 3. Water use (WU), grain yield (Y), and water-use efficiency (WUE) of pearl millet with and without fertilizer at two sites in Niger (ICRISAT 1986). Fertilizers were applied at 30 kg N ha$^{-1}$ as urea, 17 kg P ha$^{-1}$ as single superphosphate, and 25 kg K ha$^{-1}$ as potash (KCl).**

| | Sadoré | | | Dosso | | |
|---|---|---|---|---|---|---|
| Treatment | WU (mm) | Y (kg ha$^{-1}$) | WUE (kg ha$^{-1}$ mm$^{-1}$) | WU (mm) | Y (kg ha$^{-1}$) | WUE (kg ha$^{-1}$ mm$^{-1}$) |
| Fertilizer | 382 | 1570 | 4.14 | 400 | 1700 | 4.52 |
| No fertilizer | 373 | 460 | 1.24 | 381 | 780 | 2.04 |
| SE | ± 3.7 | ±162 | ±0.44 | ± 3.0 | ±103 | ±0.26 |



● **Phosphate rock deposit**

Bénin
1 Mekrou
2 Pobe

Burkina Faso
3 Arly
4 Diapeqa-Kodjari

Guinea-Bissau
5 Farim Saliquinhe

Ghana
6 Sekondi

Liberia
7 Bambuta-Bomi Hill

Mali
8 Assakerei
9 Tilemsi

Mauritania
10 Bofal-Loubboira

Niger
11 Aschia Tinamou
12 Tahoua
13 Tapoa

Nigeria
14 Abeokula

Sénégal
15 Gambia Namel
16 Matam
17 Taiba Thies
18 Ziguinchor (Casamance)

Togo
19 Akoumape-Hahotoe

▲ **Anhydrite gypsum deposit**

■ **Natural gas deposit**

**Figure 2. Phosphate rock, anhydrite, gypsum, and natural gas deposits in West Africa (after McClellan and Notholt 1986).**

## Indigenous Raw Materials

As previously indicated, fertilizer consumption in the WASAT is very low, the high cost of imported commercial fertilizers being one of the reasons. Several countries in West Africa are known to have agromineral deposits (Figure 2). The use of indigenous phosphate deposits can be an economic alternative to imported, more expensive, commercial fertilizers and would allow savings of much-needed foreign exchange. According to the classification for direct application of rock phosphate proposed by Diamond (1979), only the rock phosphates of Tahoua in Niger, Tilemsi in Mali, and Matam in Sénégal are medium in their reactivity. By acidulating rock phosphate with only a portion of the sulfuric acid or phosphoric acid required to fully convert the insoluble phosphate to water-soluble phosphate monohydrate, the solubility of rock phosphate can be increased. Rock phosphate thus treated is termed partially acidulated rock phosphate (PARP), with PARP50 indicating that 50% of the acid required to produce fully acidulated superphosphate has been used to make the product. PARP may be attractive, because it is one means of utilizing unreactive rock by increasing the content of plant-available P and also a means of achieving significant savings in foreign exchange. For example, the factory-gate cost of available P obtained from sulfuric-acid-based PARP50 is estimated to be about 80% of that obtained with single superphosphate.

Table 4 shows response of grain and total dry-matter yield of millet and cowpea to fertilizers and changes in soil pH and available P. In both millet and cowpea, the application of fertilizers can increase total dry matter more than 250% over the control and the application of 10 t ha$^{-1}$ of farmyard manure (FYM) can produce yields comparable to those obtained with the addition of commercial fertilizers. For both crops, the application of Parc-W rock phosphate (PWRP) from Niger, acidulated at 50%, gave a relative agronomic effectiveness of 87% as compared with single superphosphate for total dry-matter production, while the relative agronomic effectiveness ranged between 27% and 54% for Tahoua or Tilemsi rock phosphates. The application of N fertilizer alone did not significantly increase millet yield. As P deficiency is the major constraint in WASAT soils, responses to other limiting nutrients are found only in

**Table 4. Grain and total dry-matter response of pearl millet and cowpea to fertilizer sources and change in soil P and available P, Sadoré, Niger, rainy season 1989.**

| | Millet[1] | | | | Cowpea[1] | | | |
|---|---|---|---|---|---|---|---|---|
| Treatment | Grain yield (t ha$^{-1}$) | Total dry-matter (t ha$^{-1}$) | pH (1:2.5) | Bray-I P (mg kg$^{-1}$) | Grain yield (t ha$^{-1}$) | Total dry-matter (t ha$^{-1}$) | pH (1:2.5) | Bray-I P (mg kg$^{-1}$) |
| No fertilizer | 0.27 | 1.77 | 4.1 | 12.1 | 0.39 | 1.19 | 4.0 | 4.0 |
| N | 0.35 | 1.93 | 4.1 | 2.7 | 0.52 | 1.65 | 4.1 | 3.4 |
| P, as SSP | 0.65 | 3.10 | 4.2 | 11.7 | 0.72 | 2.30 | 4.3 | 7.0 |
| NP, P as SSP | 0.68 | 3.88 | 4.2 | 9.4 | 0.72 | 2.72 | 4.1 | 5.7 |
| NPK, P as SSP | 0.73 | 4.48 | 4.0 | 3.2 | 0.98 | 3.05 | 4.1 | 6.8 |
| NPK, P as TSP | 0.71 | 4.26 | 4.1 | 11.7 | 0.97 | 3.03 | 4.1 | 5.5 |
| NPK, P as Tahoua rock phosphate | 0.65 | 3.00 | 4.1 | 9.1 | 0.76 | 2.19 | 4.2 | 4.6 |
| NPK, P as Tilemsi rock phosphate | 0.59 | 3.00 | 4.1 | 10.6 | 0.69 | 1.71 | 4.0 | 5.9 |
| NPK, P as PARP | 0.71 | 4.13 | 4.1 | 6.3 | 0.85 | 2.80 | 4.2 | 6.2 |
| FYM | 0.68 | 3.85 | 4.3 | 4.5 | 0.90 | 3.12 | 4.4 | 13.9 |
| SE | ± 0.058 | ± 0.341 | ± 0.028 | ± 0.009 | ± 0.048 | ± 0.269 | ± 0.005 | ± 0.097 |
| CV (%) | 19 | 20 | 1.4 | 23 | 13 | 23 | 2 | 31 |

1. Millet was cropped twice and received two doses of fertilizer, while cowpea was cropped and fertilized once.

2. Fertilizers were applied at 30 kg N ha$^{-1}$, 13 kg P ha$^{-1}$, and 25 kg K ha$^{-1}$ and FYM (farmyard manure, derived from cowdung) at 10 t ha$^{-1}$. K was applied as KCl and N as urea. SSP = single superphosphate; TSP = triple superphosphate; PARP = Parc-W rock phosphate, partially acidulated, at 50%.

the presence of adequate P (Traore 1974). The application of N did not affect the cowpea yield significantly, indicating adequacy of symbiotic $N_2$-fixation. The application of FYM significantly increased the soil pH. The first year of application of rock phosphate or PARP significantly increased available P, indicating that a strong residual effect can be expected from all P fertilizer sources.

At the end of the 1989 cropping season, total N was significantly higher in the cowpea plots than in the millet plots. Averaged across treatments, 234 and 272 mg $kg^{-1}$ total N (SE ±5.02) were measured in the millet and cowpea plots, respectively.

At Tara in the Sudanian Zone, we compared PWRP, Tahoua rock phosphate (TRP), and PARP50 with single superphosphate (SSP) and triple superphosphate (TSP) on groundnut cultivar 55-437. The haulm and pod yields increased significantly with the application of SSP, TSP, and PARP50 (Fig. 3). PARP50 was as good as imported fertilizers (SSP and

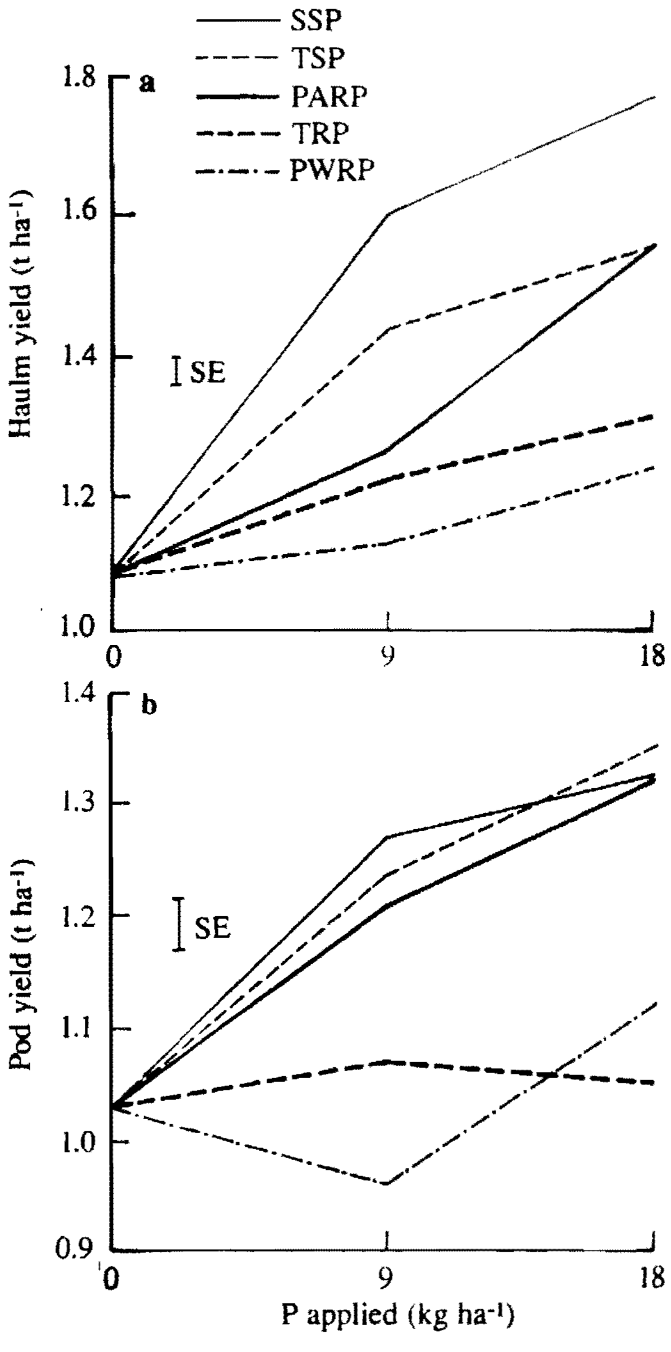


**Figure 3. Relationship between different sources and rates of P fertilizer on groundnut (a) haulm and (b) pod yields, Tara, Niger, rainy season 1988. SSP = single superphosphate; TSP = triple superphosphate; PARP = partially acidulated rock phosphate; TRP = Tahoua rock phosphate; PWRP = Parc-W rock phosphate.**

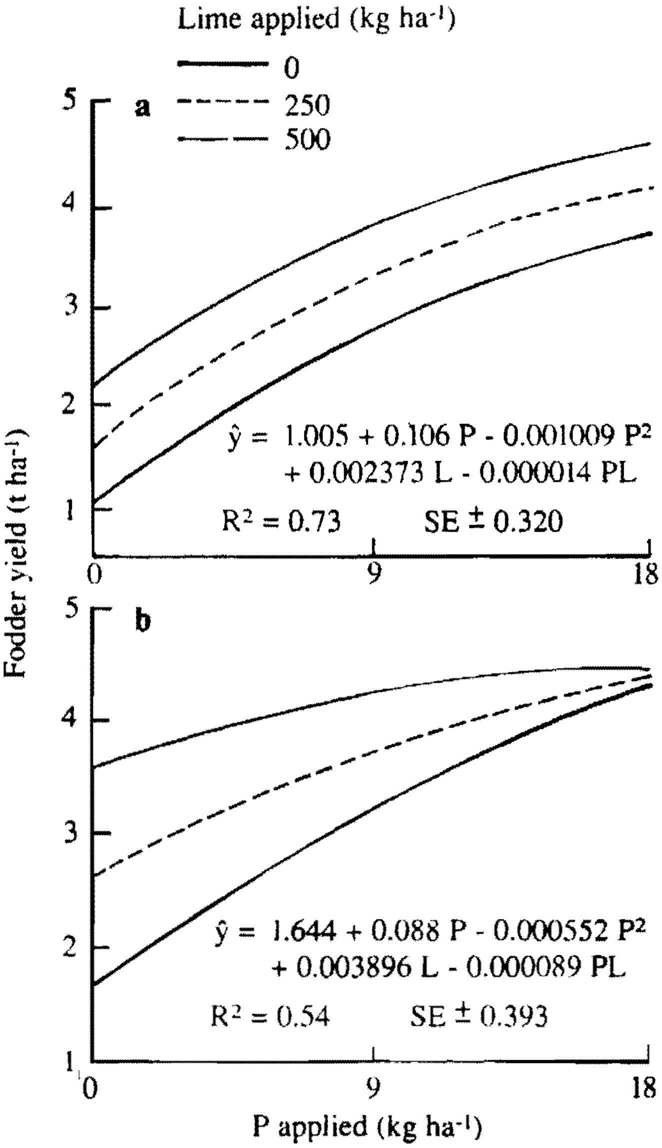


**Figure 4. Relationship between phosphorus and lime application on fodder yield of cowpea (a) cv TN 66-88 and (b) cv Local Sadoré at Sadoré, Niger, rainy season 1988.**

TSP) in increasing pod yield. A response to S may have been responsible for the difference between SSP and TSP, which was significant.

## Interaction between Phosphorus and Lime

Application of dolomite (36% Ca and 20% Mg) significantly increased fodder yields of cowpea cultivars TN 88-63 and Local Sadoré, and there was a significant interaction between lime and P (Fig. 4). Further research is needed on the importance of Mg and Ca as nutrients for cowpea and on the effect of liming on exchangeable acidity.

## Intercropping and the Use of Fertilizers

Traditional intercropping systems cover over 75% of the cultivated area in the WASAT (Steiner 1984). The principal reasons for farmers to intercrop are flexibility, profit, resource maximization, risk minimization, soil conservation and maintenance, weed control, and nutritional advantages (Norman 1974). At ISC, yield advantages of 20-70% have been obtained with millet/cowpea intercropping practices (Table 5) and 28-53% for millet/groundnut systems (Table 6).

From examination of different cowpea cultivars at different fertility levels in intercropping with pearl

**Table 5. Land-equivalent ratios (LER) for pearl millet/cowpea intercrops and sole-crop yields at ICRISAT Sahelian Center, Sadoré, Niger, rainy season 1985. (From Ntare 1989).**

| Millet cultivar | Cowpea cultivar[1] | Millet grain | Cowpea grain | Cowpea hay | Total |
|---|---|---|---|---|---|
| | | | **LER[2]** | | |
| Local cv | Local cv | 0.98 | 0.31 | | 1.29 |
| CIVT | Local cv | 0.74 | 0.64 | | 1.38 |
| 3/4 KH-B78 | Local cv | 0.87 | 0.47 | | 1.34 |
| ICMS 7703 | Local cv | 0.67 | 0.87 | | 1.54 |
| Local cv | TN 88-63 | 1.10 | 0.29 | | 1.39 |
| CIVT | TN 88-63 | 0.77 | 0.45 | | 1.22 |
| 3/4 KH-B78 | TN 88-63 | 1.13 | 0.46 | | 1.59 |
| ICMS 7703 | TN 88-63 | 1.03 | 0.54 | | 1.57 |
| Local cv | IT 82E 60 | 1.05 | 0.43 | | 1.48 |
| CIVT | IT 82E 60 | 0.74 | 0.96 | | 1.70 |
| 3/4 KH-B78 | IT 82E 60 | 1.10 | 0.58 | | 1.68 |
| ICMS 7703 | IT 82E 60 | 0.89 | 0.74 | | 1.63 |
| **SE** | | ± 0.113 | ± 0.126 | | ± 0.179 |
| | | | **Sole-crop yields (kg ha$^{-1}$)** | | |
| Local cv | | 1300 | | | |
| CIVT | | 1100 | | | |
| 3/4 KH-B78 | | 770 | | | |
| ICMS 7703 | | 780 | | | |
| | Local cv | | 421 | 1780 | |
| | TN 88-63 | | 951 | 1320 | |
| | IT 82E 60 | | 193 | 366 | |
| **SE** | | | ±72.5 | ± 164.0 | |

1. Local cv: photoperiod sensitive, long-duration (120-150 days).
TN 88-63: photoperiod insensitive, medium-duration (75-80 days).
IT 82E 60: photoperiod insensitive, short-duration (55-60 days).
2. LER = sum of ratios of yield of each crop in mixture over yield of sole crop.

Table 6. Yields of pearl millet and groundnut in sole crops and intercrops, and resultant land-equivalent ratio (LER) at Tara, Niger, rainy season 1989.

| Treatment[1] | Groundnut pods (t ha$^{-1}$) | Millet grain (t ha$^{-1}$) | LER[2] | Groundnut haulms (t ha$^{-1}$) | Millet straw (t ha$^{-1}$) | LER |
|---|---|---|---|---|---|---|
| Sole crop | | | | | | |
| Groundnut (28-206) | 1.29 | | | 2.62 | | |
| Groundnut (47-16) | 0.99 | | | 3.13 | | |
| Groundnut [ICGS(E)11] | 1.40 | | | 2.59 | | |
| Millet (CIVT) | | 1.29 | | | 3.70 | |
| Intercrop | | | | | | |
| CIVT and 28-206 | 0.71 | 1.20 | 1.48 | 1.28 | 2.95 | 1.29 |
| CIVT and 47-16 | 0.66 | 1.04 | 1.46 | 1.44 | 3.05 | 1.28 |
| CIVT and ICGS(E)11 | 0.71 | 1.31 | 1.53 | 1.22 | 3.32 | 1.37 |
| SE | ± 0.08 | ± 0.05 | | ± 0.17 | ± 0.17 | |
| CV (%) | 16.6 | 16.2 | | 16.8 | 19.0 | |

1. Randomized complete block design with 4 replications. Millet planted at 1 × 1 m and groundnut at 50 × 10 cm.

2. LER = Sum of ratios of yield of each crop in mixture over yield of sole crop.

millet, it can be concluded that there is a differential response among genotypes (Table 7) and that cereal yield responds better to fertilizer when cowpea densities are low (ICRISAT 1986). Thus cowpea cultivars best suited to intercropping with millet should not strongly compete with the cereal crop but should themselves maintain high yields of both grain and fodder in an intercrop situation.

## Role of Rotations in Soil Fertility Maintenance

By using $^{15}$N-labeled fertilizers to assess the fate and efficiency of fertilizer N in millet production in Niger, Christianson et al. (1990) found that total plant N uptake from fertilizer was low (20-37%) and losses could be up to 53%. The majority of N remaining in the soil was found in the 0- to 15-cm layer, and the

Table 7. Effect of fertilizer level[1] on cowpea cultivars intercropped with pearl millet at Gobéry, Niger, 1988.

| Cowpea cultivar | Cowpea grain (t ha$^{-1}$) | | | Cowpea hay (t ha$^{-1}$) | | |
|---|---|---|---|---|---|---|
| | Low | Medium | High | Low | Medium | High |
| TV × 4659-03E | 0.10 | 0.11 | 0.21 | 0.51 | 0.36 | 0.61 |
| TN 5-78 | 0.17 | 0.18 | 0.41 | 0.19 | 0.28 | 0.54 |
| Dan Illa | 0.12 | 0.14 | 0.22 | 0.15 | 0.15 | 0.32 |
| Suvita 2 | 0.12 | 0.17 | 0.18 | 0.13 | 0.23 | 0.20 |
| TN 88-63 | 0.22 | 0.21 | 0.26 | 0.27 | 0.24 | 0.27 |
| Tera Local | 0.11 | 0.26 | 0.30 | 0.23 | 0.44 | 0.58 |
| Local Sadoré | 0.27 | 0.36 | 0.41 | 0.55 | 0.79 | 0.91 |
| SE | | ±0.04 | | | ±0.005 | |
| Mean | 0.16 | 0.20 | 0.25 | 0.25 | 0.36 | 0.48 |
| SE | | ±0.02 | | | ±0.004 | |

1. Low = no fertilizer; medium = 18 kg P ha$^{-1}$ and 22.5 kg N ha$^{-1}$; high = 36 kg P ha$^{-1}$ and 45 kg N ha$^{-1}$. N applied to millet only.

mechanism of N loss is believed to have been ammonia volatilization.

In an attempt to find alternative ways of supplying N to cereals, we initiated trials in 1988 at Sadoré in the Sahelian Zone and Tara in the Sudanian Zone to study the effect of rotations involving pearl millet, cowpea, and groundnut. Figure 5 shows that legumes such as cowpea or groundnut have a large effect on succeeding millet yields. With no application of N fertilizers, millet yield after cowpea increased by 58% at Tara and 100% at Sadoré. The contribution of the residual N is yet to be quantified.

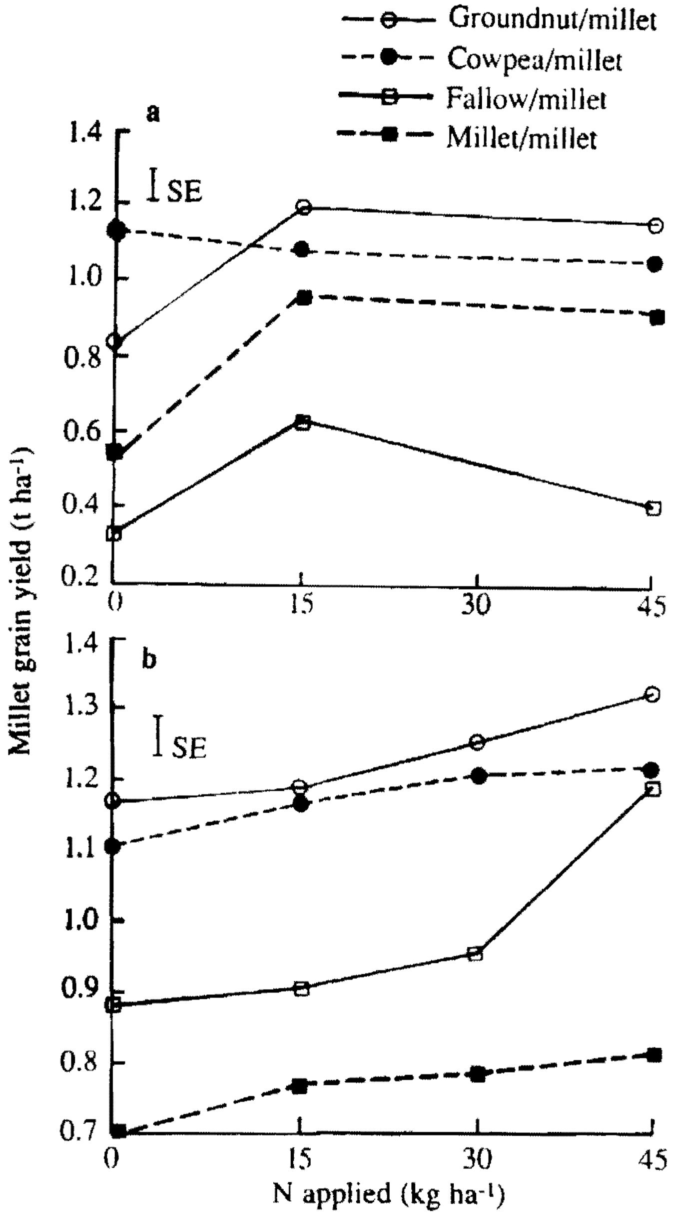


**Figure 5. Effect of crop rotation and N fertilizer on grain yield of pearl millet after one cycle of rotation at (a) Sadoré and (b) Tara, Niger, 1989.**

## Conclusion

The research findings discussed here underline the importance of legumes in the predominantly cereal-based cropping systems of the WASAT. There is, however, a scarcity of research information regarding the effects of crop mixtures and rotations on soil productivity and the N benefit from legumes to succeeding crops. Understanding of these factors will aid in developing cropping system strategies for sustaining agriculture in the WASAT.

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# Strategies for Maximizing the Efficiency of Phosphorus Utilization in Cropping Systems Involving Chickpea and Pigeonpea

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### Abstract

*This chapter summarizes current knowledge on phosphorus (P) fertilizer requirements of chickpea and pigeonpea in different cropping systems and suggests means of maximizing efficiency of P fertilizer use in both traditional and evolving cropping systems. In many of the P fertilizer trials conducted for both of these crops in India, mostly under dryland conditions, significant responses occur up to application rates of 15-30 kg P* $ha^{-1}$*. With the evolution of new cropping systems with higher potential yields and biomass production, and hence demand for P, fertilizer P requirements based on studies of traditional systems need to be reexamined. More rational and combined use of soil maps, soil analysis, plant analysis, pot trials, and field trials is suggested for diagnosis of P deficiency and determination of P fertilizer response functions.*

*As chickpea and pigeonpea are usually grown in complex cropping systems, an integrated approach to determining P requirements of the entire system, rather than those of the individual crops alone, through modeling of the P cycle is recommended. A major impediment to this approach is inadequate knowledge of the residual value of P fertilizer in the soils and cropping systems of concern. In increasing efficiency of P fertilizer use, care should be taken to evolve optimum application procedures for particular cropping systems. Deep placement seems mandatory where the topsoil is prone to drying and in situations where phosphate fixation is a problem, but may be unnecessary in well-watered systems. There is scope for further evaluation of partially soluble fertilizer P sources for these crops, especially in view of the activity of their root exudates in solubilizing P and their mycorrhizal associations. The various mechanisms proposed by which chickpea and pigeonpea can enhance the available P status of the total cropping system need to be quantified, so that their significance and scope for exploitation can be determined. The extent of genotypic difference in P-use efficiency needs to be adequately studied in these crops so that the genetic improvement option can be appropriately assessed.*

## Introduction

Chickpea (*Cicer arietinum* L.) and pigeonpea [*Cajanus cajan* (L.) Millsp.] are usually grown as rainfed grain legume crops in semi-arid regions. The biotic and abiotic constraints that they usually face, with few inputs given by farmers to overcome the constraints, result in the low yield levels obtained in the major growing regions of the world: in 1987, the world average productivity of chickpea was 691 kg $ha^{-1}$ and that of pigeonpea 707 kg $ha^{-1}$ (FAO 1988). However, phosphorus (P) deficiency does not rank as a major

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ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1991. Phosphorus nutrition of grain legumes in the semi-arid tropics (Johansen, C., Lee, K.K., and Sahrawat, K.L., eds.). Patancheru, A.P. 502 324, India: ICRISAT.

constraint in traditional growing areas, as evidenced by the marginal responses to P fertilizer measured for these crops, as discussed later. This apparent lack of responsiveness has perhaps resulted in less than adequate study of the P requirements of these crops in the different cropping systems in which they are found.

The major cropping systems of chickpea and pigeonpea referred to in this chapter in relation to P requirements are summarized in Table 1. It is understandable that at least one of the reasons for the low P responsiveness of these crops in traditional systems would be less P demand due to limited biomass and yield realization, caused by other constraints. With the recent development of chickpea and pigeonpea cropping systems with high biomass and yield potential, as in short-duration pigeonpea sole crops, it is expected that P demand, and hence P fertilizer requirements, will increase. These newly evolving cropping systems have received little research attention to date as to their mineral nutrient limitations and fertilizer requirements.

The objective of this chapter is to summarize current knowledge on P fertilizer requirements of chickpea and pigeonpea in different cropping systems and suggest means of maximizing efficiency of use of P fertilizer in both traditional and evolving cropping systems.

## Phosphorus Responses Recorded

Most knowledge concerning response of chickpea and pigeonpea to P fertilizer has been generated in India, where these crops are predominantly grown and most research on them done. Tandon (1987) has summarized the results of 2181 P fertilizer trials with chickpea and calculated a mean increase in yield of 310 kg $ha^{-1}$ over a nonfertilized control mean yield of

**Table 1. Major chickpea and pigeonpea cropping systems considered in this chapter.**

| | Cropping system | Major region | Major constraints |
|---|---|---|---|
| **A. Chickpea** | | | |
| 1. | Long- and medium-duration rainfed in South Asia | Subtropical South Asia | Foliar diseases, pod borer, terminal heat and drought stress, cold stress (pod-filling stage) |
| 2. | Short-duration rainfed in South Asia | Peninsular India | Drought stress, soilborne diseases, pod borer |
| 3. | Irrigated short- and medium-duration in South Asia[1] | Central and peninsular India | Initial and terminal heat stress, pod borer |
| 4. | Spring-sown in West Asia | Mediterranean and West Asia | Terminal drought and heat stress, leaf miner |
| 5. | Winter-sown in West Asia[1] | Mediterranean and West Asia | Ascochyta blight, cold stress (vegetative stage) |
| 6. | Rice fallow crop | Subtropics | Establishment, soilborne diseases, drought stress |
| **B. Pigeonpea** | | | |
| 1. | Perennial (agroforestry)[1] | Potential for semi-arid regions | Drought, pod borer, soilborne diseases |
| 2. | Medium- and long-duration types, as intercrops | South Asia and eastern Africa | Terminal drought, pod borer, pod fly, sterility mosaic disease, fusarium wilt |
| 3. | Short-duration sole crops in rotation (e.g. wheat)[1] | Northern India | Pod borer, phytophthora blight, waterlogging, drought |
| 4. | Short-duration multiple harvest[1] | Peninsular India | Pod borer, drought |
| 5. | Extra-short-duration for contingency cropping[1] | Low and variable rainfall environments | Drought, pod borer |
| 6. | Rice fallow crop[1] | Tropics | Establishment, low-temperature stress, drought stress, pod borer |

1. Relatively recent system.

770 kg ha$^{-1}$, up to an application level of 17 kg P ha$^{-1}$. The same mean P response was calculated for 503 trials with pigeonpea, but from a nonfertilized control yield of 460 kg ha$^{-1}$ (Tandon 1987). Tomar et al. (1987) also report many P fertilizer trials with chickpea in India giving P responses up to about 20 kg P ha$^{-1}$ but not beyond. For trials done exclusively on farmer's fields, similar levels of response to P fertilizer are also found (e.g., Table 2; Joshi et al. 1988). Thus, biological optimum P application rates appear to be in the range 15-30 kg P ha$^{-1}$ for both crops and the normally recommended P fertilizer rates for these crops in India are in the vicinity of 20 kg P ha$^{-1}$. However, there are also many reports of nonresponsiveness to P application in both chickpea (e.g., Saxena 1980; Saxena 1984) and pigeonpea (e.g., Sheldrake 1984). Further, we have noted that results of many P fertilizer trials where no P response is found are simply not reported.

Outside India, the P response of chickpea and pigeonpea has been less thoroughly documented. In West Asia, responses of chickpea to P fertilizer are varied (Murinda and Saxena 1985; Matar et al. 1988). Large P responses of pigeonpea have been recorded in Africa (Ogunwale and Olaniyi 1981; Rhodes 1987) and the Caribbean (Dalal and Quilt 1977; Hernandez and Focht 1985), mainly on acid soils.

In comparing P responsiveness between crop types, Matar et al. (1988) reported that in West Asia chickpea responds to P in a manner similar to lentil, faba bean, pea, and vetch. In Pakistan, chickpea is less responsive to P than other crops normally grown in the same season, such as lentil, wheat, and mustard (Rashid et al. 1988). Pigeonpea response to P application is comparatively less than that of other nonlegume crops normally grown in the same season (Johansen 1990), but is similar to that of other tropical grain legumes (Nandal et al. 1987).

**Table 2. Pooled mean phosphorus response of chickpea grain yield in trials on farmers' fields in Chittorgarh and Alwar Districts of Rajasthan, India. (From Rawal and Bansal 1986, and Rawal and Yadava 1986.)**

| P level (kg ha$^{-1}$)[1] | Grain yield (kg ha$^{-1}$) | |
|---|---|---|
| | Alwar | Chittorgarh |
| 0 | 1808 | 1142 |
| 8.5 | 1864 | 1356 |
| 17.0 | 1976 | 1525 |
| 25.5 | 2186 | - |
| SE | ±36 | ±26 |
| No. of trials | 48 | 58 |
| Period of trials | 1975-77 | 1978-82 |
| Chickpea variety | RS 10 | C 235 |

[1] In the presence of 20 kg N ha$^{-1}$.

## Major Factors Determining Phosphorus Response

The magnitude of P responses of chickpea and pigeonpea in the field can be primarily attributed to the following major factors:

- Capacity of the particular soil type to supply P. Alkaline, calcareous soils, where these crops are mostly grown, generally show less response to P fertilizer application than acid soils with high P-fixation capacities.
- Plant or crop demand for P. The potential biomass production of these crops is usually limited by the various constraints mentioned in Table 1, and it would be expected that P demand and P responsiveness would increase as biomass potential increases. This is illustrated in data showing an increased responsiveness of pigeonpea to P application at higher plant densities (Ahlawat and Saraf 1981). Although average yields of chickpea and pigeonpea in India are low, and similar to world averages (FAO 1988), there are large yield variations between districts (Sharma and Jodha 1982). For example, in the state of Uttar Pradesh in 1978/79, district average yields for chickpea varied from 200 to 1153 kg ha$^{-1}$ and those for pigeonpea from 489 to 2924 kg ha$^{-1}$ (Sharma and Jodha 1982). Such variation needs to be taken into account in comparing P responses and developing P fertilizer recommendations on a regional basis.
- Soil moisture availability during crop growth. As these crops are traditionally grown under rainfed conditions, the topsoil (e.g., 0-15 cm) is subject to drying. Thus P response can be reduced under low soil moisture conditions due to both decreased availability of applied P and reduced plant demand for P because of limitation of biomass production by drought. This is illustrated by increasing responsiveness to P with

increasing soil moisture supply (irrigation) measured in chickpea (Singh and Sharma 1980; Borgohain and Agarwal 1986; Kulhare et al. 1988). However, Sharma and Yadav (1976) found a negative interaction between P application and irrigation in chickpea. Further, in a survey of many P fertilizer experiments in India, Rajendran et al. (1982) found that irrigated chickpea responded less to P than rainfed chickpea. This may have been a consequence of irrigated sites having a higher initial P status, perhaps from residual P from fertilizer applied to previous crops, than would rainfed areas, which generally receive little P fertilizer. Irrigation and P treatments need to be included in the same experiment to enable conclusions to be drawn about the interaction of these factors.

- Other possible factors affecting P response, such as mycorrhizal infection, root distribution, and root exudates, have been discussed in earlier chapters and will also be referred to later in this chapter.

## Methods of Determining Phosphorus Requirements

Multilocation fertilizer experiments conducted over many seasons in major chickpea- and pigeonpea-growing areas, primarily in India, have given some idea as to the extent of P limitation in specific regions and provided a basis for fertilizer recommendations. Nevertheless, for any given site, even on research stations, considerable uncertainty remains as to the P status of these crops and continued quantification is warranted, particularly where cropping systems are changing. The P status of these crops can be diagnosed by several possible methods, which offer differing degrees of precision. A stepwise use and combined interpretation of these methods is recommended. These are described as follows in approximate increasing order of precision of the information they can offer.

### Soil and Geological Maps

Soil and geological maps are usually available for even the most remote of regions, to varying degrees of precision. Examination of these gives a first approximation as to possible problems of P deficiency as well as other nutrient imbalances for a given region; for example, they would indicate the likelihood or otherwise of P-fixation problems in acid soils.

### Symptoms

In chickpea, P deficiency usually results in stunted plants of darker green color and anthocyanin pigmentation, with older leaflets then gradually losing their green color to become bronze (Smith and Pieters 1983). There are no distinct symptoms of P deficiency in pigeonpea, but in cases of severe deficiency plants remain stunted, with their foliage dark green, and the older leaves are eventually shed (Johansen 1990). However, symptoms are of little value in assessing P status, because of their similarity to and interactions with symptoms caused by other nutrient imbalances and biotic and abiotic stresses. The manifestation of symptoms would also differ between genotypes with different inherent levels of pigmentation; further, symptoms would only be apparent when plant growth has been severely impaired by P deficiency.

### Soil Analysis

Although many soil P tests have been done in the chickpea- and pigeonpea-growing regions of India, there is a dearth of information on critical P levels applicable to these crops under field conditions in the various soil types and cropping systems. For calcareous soils of pH 8.1-8.4 in northern Syria, Cate-Nelson analysis (Cate and Nelson 1971) of P fertilizer trials indicates a critical level of available soil P for winter-sown chickpea of 5-7 mg P kg$^{-1}$, as Olsen's bicarbonate-extractable P (Fig. 1). This critical range also applies to other legumes comparable to chickpea in this region, namely, faba bean, pea, vetch, and lentil (Matar et al. 1988). For field-grown pigeonpea in an acid (pH 4.8) soil in Sierra Leone, Rhodes (1987) determined a critical level to be an equilibrium soil solution concentration of 0.26 $\mu$M P. As a broad generalization based on experience on Alfisols and Vertisols at ICRISAT, for the 0-15 cm soil horizon, Olsen-P values above 5 mg kg$^{-1}$ would indicate a P response of chickpea and pigeonpea to be highly unlikely; 2-5 mg kg$^{-1}$ would be a zone of uncertainty; and below 2 mg kg$^{-1}$, responses to P would be probable. The inadequacies of using standard soil P tests for chickpea and pigeonpea are explained by Ae et al. (1991a, 1991b). Nevertheless, in view of the large data base on P responses of these crops in India at least, it would seem worthwhile to subject these data to a

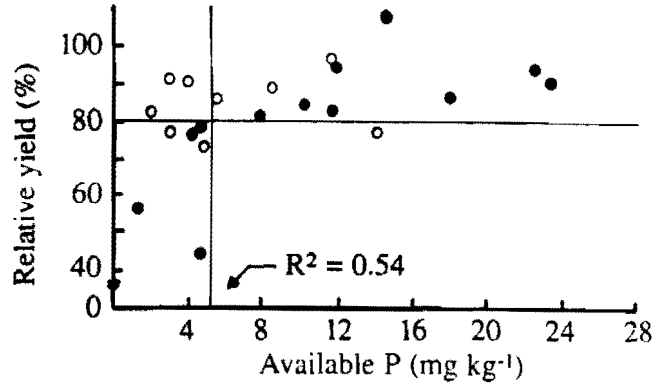

**Figure 1. Cate-Nelson plot of relative grain yield of chickpea (yield without P relative to maximum yield with P) against bicarbonate-extractable P for field sites in Syria in 1985/86 (○) and 1986/87 (●) seasons. (From Matar et al. 1988.)**

Cate-Nelson analysis on a soil type and regional basis in order to determine critical soil levels and the variability associated with them. The minimum data required for each experiment would be soil-test value without P fertilizer added, grain yield without P, and maximum grain yield with P. However, critical values obtained would need to be interpreted in the light of other environmental factors and stresses affecting yield.

### Plant Analysis

Various estimates have been made of critical P concentrations in tissues of chickpea (Reuter 1986) and pigeonpea (Johansen 1990), but considerable care is required in interpreting these values, as they are strongly influenced by plant part sampled, plant growth stage, interactions with other nutrients, growth environment, and genotype (Bates 1971; Smith 1986). Further complications are the indeterminate growth habit of chickpea and pigeonpea and variability of phenology, which would make it difficult to standardize sampling time and plant part sampled. However, plant analysis may be more feasible for monitoring P status of short-duration, determinate sole crops of pigeonpea grown under assured soil moisture regimes, but the necessary calibrations are yet to be done.

### Plant Growth Tests

The above suggests that symptoms or soil and plant analysis cannot be relied upon for diagnosing P status of chickpea and pigeonpea, let alone for suggesting P fertilizer requirements. Plant growth tests are required both for reliable diagnosis and for arriving at fertilizer recommendations. Pot trials, conducted in an environment as nonlimiting as possible, so as to maximize chances of expression of any nutrient imbalance (e.g., in a greenhouse), can provide information as to the potential of a particular soil to supply P, or any other nutrient, for plant growth (Andrew and Fergus 1976). However, for chickpea and pigeonpea, only response of the vegetative growth stage can be adequately measured in such pot tests because of atypical growth during the reproductive phase, resulting in inferior pod formation, in the greenhouse as compared with field conditions. The magnitude of P response found in pots can indicate the extent of P deficiency likely to be observed in the field and thus assist in efficient design of field experiments, with P application rates covering an appropriate range.

It is necessary to establish plant growth and yield response functions under field conditions if biological and economic optimum rates of fertilizer or amendment application are to be precisely known. Fertilizer rate trials need to be conducted over several seasons and at different sites within a region before an accurate picture of fertilizer requirement can be established. This is because of the various growth and yield limitations interacting with P response in the field, particularly interactions between soil moisture and P application when the crops are grown under dryland conditions.

Where some knowledge exists of P status and fertilizer requirements in particular fields, small-plot field trials can be used to monitor P status; for example, to confirm whether fertilizer recommendations are indeed correct. At ICRISAT Center, such trials have been effectively used to demonstrate that chickpea and pigeonpea do not need P fertilizer in fields where P is regularly applied to other crops in a rotation. Indeed, in view of uncertainties in the applicability of currently used soil tests to predict P response of chickpea and pigeonpea, it is suggested that such small-plot trials (e.g., plot size of 8 rows, 4 m long, for chickpea and short-duration pigeonpea sole crops) are necessary for monitoring P status of these crops.

## Modeling of Phosphorus Cycles

Chickpea and pigeonpea are usually grown as minor components of complex cropping systems. Thus an integrated approach is required to determine P fertilizer requirements of the entire system rather than of individual crops in it. It is therefore useful to consider the P cycles operative in given cropping systems, preferably formalized into a mathematical model. To our knowledge, no detailed P modeling exercises have been attempted so far for particular chickpea or pigeonpea cropping systems. However, a simplified P budgeting approach for cropping systems involving these crops has been developed by the All India Coordinated Research Project on Soil Test-Crop Response Correlation, using the concept of fertilizer application for targeted yields (Velayutham et al. 1985). Although calculations by this methodology rely on gross assumptions about nutrient availability from fertilizer and soil, it is reported to be a useful framework for arriving at fertilizer recommendations and in promoting understanding of, and stimulating research in, P cycling in particular cropping systems. In the recent literature, there are several examples of cropping system P models that could be adapted for chickpea and pigeonpea cropping systems, such as those of Bennett and Bowden (1976), Blair et al. (1976), Jones et al. (1984), Probert (1985), and Wolf et al. (1987).

For chickpea and pigeonpea cropping systems, information that is particularly required for modeling purposes, but is lacking, includes estimates of labile P available to these crops and residual value of fertilizer P applied to previous crops. As discussed earlier, there are difficulties in using standard soil analyses to measure labile P; it could perhaps be better estimated from extrapolated intercepts on the "x" axis of P-response curves, determined in pots or in the field (Russell 1978). However, response curves of good fit would be required to do this with any accuracy.

It is the normal practice for cropping systems involving chickpea and pigeonpea, in South Asia at least, to apply P fertilizer, if indeed it is applied, to other apparently more remunerative components of the cropping system (Jha and Sarin 1984). Mathur et al. (1979) found that, for acid (pH 5.0-5.5) soils in Bihar state of India, chickpea responded to P applied in the previous three seasons to a maize-chickpea rotation. Residual effects were greater with rock phosphate (phosphorite) than with single superphosphate. In northern Syria, chickpea responded to P applied to barley in the previous season (Matar et al. 1988).

In pigeonpea, Rao and Bhardwaj (1981) found that P applied to a preceding wheat crop enhanced subsequent pigeonpea yields (System B3 in Table 1). It has also been found that P applied to pigeonpea has residual benefits for following crops. For example, application of P to pigeonpea has been reported to increase growth, yield, and P uptake of a following wheat crop (Pannu and Sawhney 1975; Singh et al. 1983; Ahuja 1984; Dahama and Sinha 1985; Singh and Faroda 1985). This can primarily be attributed to P fertilizer stimulating pigeonpea growth and $N_2$-fixation such that more residual fixed N is made available to the subsequent wheat crop. However, data on P uptake by wheat indicate that P applied to the preceding pigeonpea crop can be taken up by wheat (Singh et al. 1983; Dahama and Sinha 1985; Singh and Faroda 1985). Unlike the stimulatory residual effect mentioned above, P application to a previous pigeonpea crop had little effect in stimulating wheat yields, although the pigeonpea itself responded to P; Rao and Bhardwaj (1981) therefore concluded that, for their particular pigeonpea-wheat rotation, the best strategy was to fertilize each crop with 18 kg P $ha^{-1}$.

Residual effects of P have also been measured in a rotation of a sorghum/pigeonpea intercrop with castor under rainfed conditions on an Alfisol (System B2 of Table 1; Venkateswarlu et al. 1986). Castor could benefit from P applied to the prior sorghum/pigeonpea intercrop to the extent that the P fertilizer recommendation for this system was 22 kg $ha^{-1}$ applied to the intercrop only. There was also an indication (differences not significant) that pigeonpea could benefit from P applied to a prior castor crop.

For chickpea and pigeonpea cropping systems, more detailed studies are needed to allow calculation of rates of decay (e.g., half life) in availability of applied P over time. The methodologies for doing this are well documented (e.g., Russell 1978; Barrow 1980; Widjaja-Adhi et al. 1985; Janssen and Wolf 1988). Generally, decay rates are exponential, and half lives are in the order of 1 year, but parameters vary, primarily due to initial P status, crop removal, and the buffering capacity of the soil for P (Tisdale et al. 1985). It would be dangerous to extrapolate from other studies to chickpea and pigeonpea cropping systems. Calculation of appropriate decay rates would be fundamental to developing appropriate P balance models.

## Phosphorus Requirements of New and Evolving Cropping Systems

The pattern of chickpea and pigeonpea cultivation is changing in traditional production areas, and these crops are being introduced into new areas. The P fertilizer requirements of new systems cannot simply be extrapolated from those of the traditional ones, particularly when there seems to be a high degree of uncertainty concerning P requirements of traditional cropping systems in the first place. For example, the particular P requirements of pigeonpea in a traditional intercrop system (B2) are very difficult to estimate. As can be generalized from trials conducted by the All India Coordinated Agronomic Research Project (Ahlawat et al. 1985), it seems that the P requirement of an intercrop would be the sum of the requirements of the individual components when grown as sole crops at similar spacings as in the intercrop.

Although it is recognized that more research is needed to establish P requirements in traditional cropping systems, especially in relation to interactions of P availability with soil moisture, following are some considerations for establishing P requirements of some newly evolving cropping systems with chickpea and pigeonpea.

## Winter-sown Chickpea in West Asia (A5)

Winter-sown chickpea in Mediterranean regions has greater biomass accumulation and grain yield potential than the normal spring-sown crop and would thus have a higher P requirement, as illustrated in Table 3. Phosphorus responses of winter- and spring-sown chickpea have not been directly compared to determine whether the increased demand results in a greater response to P fertilizer. However, if root volume of the winter-sown crop stays in proportion to its above-ground biomass, then extra native soil P could be accessed, thus minimizing a P response. Another consideration is that P applied to the winter-sown crop at sowing is likely to have a greater relative availability, because it would remain in moist surface soil throughout the winter and be available for uptake during much of the vegetative growth period. By contrast, P applied to spring-sown chickpea in a receding soil moisture situation is likely to become increasingly unavailable as the surface soil dries out.

## Irrigated Chickpea (A3)

With increased understanding of the extent of drought limitation to rainfed chickpea in central and peninsular India (N.P. Saxena 1987) and with relatively high prices for chickpea in recent years, irrigated chickpea is becoming increasingly popular in these regions. Considerations similar to those described for winter-sown chickpea in West Asia apply to irrigated chickpea; i.e., the increased biomass potential would cause increased P demand and hence increased fertilizer needs (Table 3). Again, however, available soil moisture would enhance the relative availability of fertilizer P. Also, the possible increasing importance of residual P in irrigated systems, (previously referred to with respect to the data of Rajendran et al. 1982), needs to be considered.

**Table 3. Total biomass, grain yield, and calculated phosphorus content of above-ground parts (assuming 0.30% P in grain and 0.10% P in rest of shoots, based on P analyses at ICRISAT Center) of chickpea in different cropping systems.**

| Cropping system | Biomass ($t\ ha^{-1}$) | Grain yield ($t\ ha^{-1}$) | Above-ground P content ($kg\ ha^{-1}$) |
|---|---|---|---|
| Spring-sown West Asia[1] | 1.56 | 0.80 | 3.2 |
| Winter-sown West Asia[1] | 3.55 | 2.09 | 7.7 |
| Rainfed, peninsular India[2] | 2.09 | 0.91 | 3.9 |
| Irrigated, peninsular India[3] | 6.20 | 3.18 | 12.6 |

1. From M.C. Saxena (1987).
2. Mean of 16 genotypes in Vertisol at ICRISAT Center in 1985/86 (N.P. Saxena, ICRISAT, unpublished data).
3. Cultivar Annigeri in Vertisol at ICRISAT Center in 1980/81 (Saxena and Johansen 1990).

## Chickpea in Rice Fallows (A6)

Although this has been a traditional and popular cropping system in subtropical South Asia, yields have remained low, as the seed is hand-broadcast at about the time of the rice harvest and no further inputs are generally given. Responses to P fertilizer are generally not found in such systems, because of both low P demand and, possibly, availability of residual P applied to the rice crop (Meelu and Rekhi 1981). With attempts to improve chickpea agronomy, and hence yield potential, in rice fallow systems (Johansen et al., in press), the P requirements of chickpea in rice fallows will need to be reevaluated, in terms of both increased P demand and residual value of P applied to rice. Indeed, it may be necessary to rely on P applied to the previous rice crop, because of the difficulty of fertilizer application and tillage to mix it into the soil surface in rice fallows. It will also be necessary to determine root configuration in relation to available P, due to the usually poor soil structure of rice fallows. The P model of Probert (1985) has been effectively applied to mung bean grown in a rice-based cropping system (Sreekantan and Palaniappan 1988); such a model could be adapted for chickpea in rice fallows.

### Pigeonpea in Agroforestry (B1)

Perennial long-duration pigeonpea, with resistance to sterility mosaic disease and fusarium wilt, is showing promise as a tree component in agroforestry systems in peninsular India (Daniel and Ong 1990). For this use, the P requirements of pigeonpea as a tree crop need to be considered. In the first place, it is difficult to measure P response of such pigeonpea, as optimum methods of fertilizer placement are yet to be established. Along with P placement, other important considerations are: the extent of mycorrhizal activity and whether this can be enhanced, the ability to extract P from deep soil (e.g., below 1 m), and the extent to which P fertilizer is required for regrowth after the first year.

### Short-duration Sole Pigeonpea in Rotation (B3)

There is already considerable knowledge on P response of short-duration pigeonpea, mainly indeterminate types grown in rotation with a cool-season crop such as wheat in northern India (Kulkarni and Panwar 1981). Generally, responses seem larger than reported for long-duration pigeonpea in intercrops, the traditional method of pigeonpea cultivation in the region. There has been a recent trend towards developing pigeonpea genotypes for this system that are determinate and shorter in stature (<1.5 m tall) and duration (<120 days). The P nutrition of this recently bred material has not yet been examined in any detail and, again, extrapolation from types where P response has been examined is unwise. For example, earlier types would have a shorter period in which to absorb P from the soil, and determinate types may have P translocation and retranslocation patterns different from indeterminate ones. Evidence suggests that the more recently developed short-duration determinate types have a lower rooting ability than traditional pigeonpea (Chauhan, in press) and this may limit access to native soil P. Changes in biomass production of the new types need to be considered in terms of possible P demand. It has been observed that P deficiency can delay maturity of short-duration pigeonpea (Chauhan et al., in press; and A. Kubota, ICRISAT, 1989, personal communication), and this needs to be borne in mind when fitting pigeonpea into particular rotations.

### Short-duration Multiple-harvest Pigeonpea (B4)

In tropical environments with warm winters, it is possible to exploit the perennial nature of short-duration pigeonpea to take multiple harvests from the same crop (Chauhan et al. 1987). Thus a total of 5 t $ha^{-1}$ grain and 10 t $ha^{-1}$ remaining above-ground biomass may be produced from the same plot of land over a 9-month period, exerting a large P demand (estimated at 35 kg $ha^{-1}$ P for above-ground production). There is evidence that second-flush yield may respond to an initial P application where the first-flush yield and above-ground dry-matter production did not. For instance, on an Alfisol with 5 mg $kg^{-1}$ Olsen P at ICRISAT Center, first-flush yields with and without applied P were similar; however, second-flush yield was 46% higher with 200 kg $ha^{-1}$ single superphosphate applied at sowing than with no P (Y.S. Chauhan and C. Johansen, ICRISAT, 1987, unpublished data). Further work is urgently needed to understand the P requirements of such multiple-harvest systems with high biomass potential.

### Contingency Cropping with Extra-short-duration Pigeonpea (B5)

With the breeding of extra-short-duration pigeonpea genotypes that can mature in 90 days or less in tropical environments, studies are under way to evaluate these genotypes in contingency or catch-cropping systems where periods of available soil moisture supply are likely to be short. That is, such genotypes should be able to escape drought as can other short-season legumes, such as cowpea, mung bean, and urd bean. Again, the P requirements of this type of pigeonpea are yet to be evaluated. Limited periods of available soil moisture will undoubtedly limit biomass production and hence P demand. However, further improvements to this plant type will require increased capacity for initial growth rate for more rapid development of leaf area. This will also require increased rates of P uptake by seedlings, a process which may then become limiting in marginal P environments.

### Pigeonpea in Rice Fallows (B6)

The development of short- and extra-short-duration pigeonpea has increased possibilities of using pigeonpea as a rice fallow crop in the tropics. The same considerations as discussed for chickpea would be applicable here.

## Appropriate Fertilizer Type and Application Method

In India, in the rare instances that any fertilizer is used on chickpea and pigeonpea, diammonium phosphate (DAP) is the most commonly used form of P fertilizer (Tandon 1987). This is a convenient fertilizer for these legumes, as it supplies an often-required starter dose of N as well; responses to starter doses of N are common in both chickpea (Rajendran et al. 1982) and pigeonpea (Kulkarni and Panwar 1981). Other P sources used are superphosphate and various compound fertilizers. All of these fertilizers have high levels of water-soluble phosphate, immediately available to the crop if the soil is moist. However, in view of the likely increases in costs of manufacturing soluble P sources and the desirability of considering the longer-term P needs of whole cropping systems, sparingly soluble sources of P need to be considered for these crops.

The efficiency of rock phosphate in supplying the P needs of tropical legumes in acid soils is well documented (Kerridge 1978). Although many studies have been done on rock phosphate and other sparingly soluble P sources in Indian cropping systems (Tandon 1987), there are relatively few reports relating to chickpea and pigeonpea. On an acid (pH 5.0-5.5) soil, chickpea responded to rock phosphate and single superphosphate in a similar manner on a total P content basis (Mathur et al. 1979). The better residual value of rock phosphate in this study has already been referred to. In pot studies, rock phosphate stimulated growth of chickpea in alluvial sandy soils of Haryana, India, of pH 8 and low P status (Jalali and Thareja 1985). Further growth stimulation was obtained by mycorrhizal inoculation. In a presumably alkaline Vertisol from Pune, India, rock phosphate could also stimulate chickpea growth in pots, with a further stimulation when cellulolytic and phosphate-solubilizing fungi were added (Rasal et al. 1988). There are earlier reports of phosphate-solubilizing organisms enhancing yield and P uptake of chickpea (e.g., Subramanian and Purushothaman 1974; Ahmad and Jha 1977). Prabhakar and Saraf (1990) confirmed that growth response of chickpea on a sandy-loam soil of pH 7.6 was at least as good with rock phosphate inoculated with phosphate-solubilizing bacteria as with superphosphate. In field studies on granitic soils in Thailand, addition of 400 kg ha$^{-1}$ rock phosphate in the presence of gypsum increased pigeonpea grain yield by 30-80%, at different spacings, in 1976 and 1977 (Andrews and Manajuti 1980). The ability of chickpea and pigeonpea to utilize P from rock phosphate over time, especially in view of their mycorrhizal and other microbial associations and their root exudates, warrants further study.

Although P fertilizer application for chickpea and pigeonpea is most feasible at or before sowing, there are situations where application during crop growth would be desirable, particularly for longer duration crops or in multiple-harvest systems. However, any topdressing of fertilizer, additional to an application at sowing, would require that the topsoil be moist for the applied fertilizer to be solubilized. Another alternative for nutrient addition to established crops is the use of foliar sprays or dusts. Some positive responses to foliar sprays of P have been demonstrated for chickpea (e.g., Sharma et al. 1975), but the results of such experiments often remain ambiguous. For example, where there are positive responses to the application of DAP, it is not possible to distinguish between the relative contributions of N and P (e.g., for chickpea, Pathak et al. 1985; for pigeonpea, Reddy et al. 1987).

For predominantly rainfed crops, lack of responsiveness to fertilizers can at least partly be attributed to drying of the surface soil to which the fertilizer is applied, and thus reduced P availability during dry periods. There are many reports demonstrating positive effects of deep placement of P fertilizer on chickpea yield under rainfed conditions in India (e.g., Sharma and Richharia 1962; Sinha 1972; Kumbhare et al. 1978). However, some studies attempting to further demonstrate this principle have obtained anomalous results, for example the pot study of Ghosh (1985), where no interaction was found between soil moisture regime and P placement; thus, additional interacting factors perhaps need to be considered. For short-duration pigeonpea cv T 21 grown in Punjab, India, placement of P fertilizer at a depth of 10 or 15 cm increased yield by 35% over broadcast application (Pannu and Sawhney 1975). The ICRISAT experience with P placement is presented by Arihara et al. (1991); generally deep placement was beneficial under rainfed conditions. While it can be concluded that the most appropriate mode of P fertilizer placement is largely determined by the likely moisture status of the soil profile during crop growth, other factors—such as P-fixation capacity of the soil, availability of appropriate equipment for deep placement, and the economics of P fertilizer application—would need to be considered in formulating any recommendations about P fertilizer placement method.

## Exploiting the Ability of Chickpea and Pigeonpea to Mine Phosphorus

In summary, as discussed in detail in earlier chapters of this volume, it has been proposed that chickpea and pigeonpea can access more native soil P than other comparable crops through the following mechanisms:

- strong development of mycorrhizal associations;
- deep-rooting ability of both crops and, presumably, ability to retrieve P from deeper soil layers;
- acid exudates from chickpea, which allow it to access more P in alkaline soils; and
- exudates from pigeonpea which allow it to utilize iron-bound P in the soil.

The extent to which additional P is made available by these mechanisms needs to be quantified; only then can their significance in contributing to the P status of the total cropping system be estimated. If indeed chickpea and pigeonpea can access extra P for their own use, then this can also be considered as an addition to the total cropping system, in terms of conversion from otherwise unavailable P to organic P in chickpea and pigeonpea tissue, which could eventually release labile P from organic residues of these crops. If such effects are significant, then this should be considered in the overall economic evaluation of the crop, along with the direct products of food, fuel, and fodder, and established indirect values, such as contribution of $N_2$-fixation to the N economy of the cropping system.

If these mechanisms do prove quantitatively significant, then it would be worthwhile to examine the extent of genotypic variation, to assess whether genetic enhancement of the particular trait is feasible. However, it must be recognized that traits such as deeper rooting ability and increased root exudation would probably involve penalties of reduced potential for above-ground biomass formation. This aspect should tie in with an overall understanding of genotypic differences in P-use efficiency—including P-uptake capacity and P translocation and retranslocation. There have been several studies where P response of a range of chickpea genotypes has been measured but interaction effects—that is, comparative P response between genotypes—were not presented (Raju and Varma 1984; Singh et al. 1984; Ahlawat et al. 1985; Yadav et al. 1985). Manjhi et al. (1973) demonstrated genotypic differences in P response between pigeonpea genotypes: variety Sarada reached a yield plateau at lower P application rates than T 21 or AS 10. There is scope for much wider assessment of the extent of genotypic differences in P response, including further analysis of existing data, and determination of the basis of these differences.

## Future Research Emphases

In view of the many unanswered and newly raised questions in this and earlier chapters, and thus the many possible research directions that can be taken, it seems appropriate to prioritize research areas where greater practical returns could be expected. We suggest that:

- in developing new cropping systems for chickpea and pigeonpea, determination of P and other nutrient requirements be considered an integral part of the research involved, rather than an afterthought;
- P models be developed for the main cropping systems of interest, to provide a basis for P management strategies and highlight gaps in knowledge;
- a coordinated attempt be made to decide on best methods of measuring labile P for these systems;
- residual values of fertilizer P be determined for the major chickpea and pigeonpea cropping systems;

- more realistic assessment be made of the usefulness or otherwise of plant tissue analysis in determining plant P requirements, especially for newer cropping systems where water supply is more assured, phenology more predictable, and plants have a more determinate habit;
- less soluble—i.e., less processed—sources of P be evaluated for chickpea and pigeonpea on a long-term cropping system basis;
- more research be done on the engineering aspects of deep placement of P fertilizer in rainfed, water-limited environments;
- the contributions of various mechanisms of increasing P accessibility proposed for chickpea and pigeonpea be quantified and their significance assessed; and
- genotypic differences in P-use efficiency be further assessed and their basis understood.

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# Interpretive Summary of Part 4: A Cropping Systems Perspective for Phosphorus Fertilization of Tropical Grain Legumes

C.W. Hong[1]

## Introduction

In legume/nonlegume cropping systems, it has been traditionally believed that the merit of legumes is their ability to restore plant-available nitrogen (N) to the soil. With the advance of research, it has been gradually revealed that legumes can improve other factors also. Our understanding of these aspects is still far from perfect; it is as yet intuitive and qualitative rather than analytical and quantitative.

The papers presented in Part 4 attempted to:

- overview the existing information on the various effects of legumes in legume/nonlegume cropping systems, wherever possible quantitatively and analytically (Hoshikawa 1991);
- identify the mechanisms whereby legumes such as chickpea and pigeonpea improve soil conditions for subsequent crops other than by N accretion (Arihara et al. 1991);
- observe the dynamics of plant nutrients under different cropping systems (Imai 1991);
- highlight some actual fertilizer experiment results involving the legume/nonlegume cropping systems in the West African Semi-Arid Tropics (WASAT), to appreciate the implications of the use of legumes in resource-poor environments (Bationo et al. 1991); and
- suggest strategies for maximizing the efficiency of P fertilizers in cropping systems involving chickpea and pigeonpea, based on current knowledge of the response of these crops to P fertilizers (Johansen and Sahrawat 1991).

The papers covered the topics very thoroughly, not only in presenting data and reviewing the existing information, but also in interpreting them in terms of practical applicability, leaving little for this author to add as an interpretive review. Still, an attempt is made here to add a few points, particularly regarding practical applicability.

## Significance of Legumes in Cropping Systems

Hoshikawa (1991) attempted to logically analyze the mechanisms involved in the beneficial effects of legumes in improving the productivity of soils; restoring available N to soil by biological $N_2$-fixation, solubilizing sparingly soluble P, affecting soil aggregate stability, increasing the water-infiltration rate, raising soil temperature, and altering the biological conditions of soils.

Legumes are generally, if not universally, considered to significantly restore available N to the soil. This notion, however, is far too qualitative. Unfortunately, this qualitative notion prevails and misleads the public, making them believe that whichever legumes are used in cropping systems, additional supplemention of fertilizer N would not be needed. Although Hoshikawa did not comprehensively present the quantitative aspect of the contribution of N by different legumes, he came up with points of practical importance, implying that only when legumes are used as green manure without harvesting the grain would the N contribution be practically significant, but not when the grain is harvested. He even further pointed out that a crop like soybean, when cultivated for grain, depletes the soil N instead of restoring it. Reviewing a few research results on the interaction between N application rate and the response of cereal

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ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1991. Phosphorus nutrition of grain legumes in the semi-arid tropics (Johansen, C., Lee, K.K., and Sahrawat, K.L., eds.). Patancheru, A.P. 502 324, India: ICRISAT.

crops, Hoshikawa inferred that the beneficial effects of legumes in legume/nonlegume rotations cannot be explained by N alone.

Citing a few references, he noted that some sparingly soluble P compounds in the soil can be solubilized by the root exudates of some legumes; for instance, lupin and chickpea excrete citric acid, which solubilizes occluded P and Ca-P, and pigeonpea excretes compounds that can dissolve Fe-P. The reviewer, however—perhaps due to inadequate information—did not touch upon the quantitative aspects of this effect. Considering the complications involved, it may not be reasonable to expect that such information would be available in the near future.

The cultivation of legumes generally results in an increase in water-infiltration rate and an improvement in soil aeration. Hoshikawa concluded, on the basis of existing research results, that these particular beneficial effects of legume cultivation are not due to increased soil aggregate stability but due to the rooting habits of the legumes: legumes produce taproots. The cavities created when taproots die and decay would serve as channels for water to infiltrate and for the air to diffuse at a faster rate. Here, the question arises as to how stable the cavity would be in different soil types. For instance, when Vertisols are wetted, the clay swells and seals even large cracks; would the taproot cavity survive saturation of a soil such as a Vertisol?

Increased water-infiltration rate in the soil has advantages and disadvantages. When rainfall is heavy on heavy-textured soils, high infiltration rate would be beneficial for crops, shortening the period of excessive wetting of the soil. On the other hand, too high an infiltration rate could cause harm by increasing leaching of water-soluble nutrients, particularly nitrate. The question is how to balance these two effects. The answer lies in more thorough studies into the quantification of these effects.

Hoshikawa touched upon the effect of raising the soil temperature by cultivating legumes, citing an experimental result obtained in a temperate region. How relevant this information would be in the tropics is an interesting question. Apart from this, the point is a complex one. In the field, after heavy rainfall, soil temperature can vary, depending on how quickly the field is drained; the higher the infiltration rate, the more quickly the field would be drained and the more rapidly the soil temperature would rise. Thus, any positive effect due to higher infiltration is a compounded effect; an effect of high soil temperature and an effect of better aeration (due to better drainage). Accordingly, the experimental results cited need more careful interpretation.

It is obvious that introduction of different crops would affect the activities of soil microbes. However, at the present level of knowledge, it appears rather difficult to know how the changes brought about by legumes on the microbial activities would affect the productivity of the soil. Citing the work of Skinner (1979), Hoshikawa inferred that the cultivation of legumes may result in the destabilization of soil aggregates, because it would add organic material to the soil, which would reduce binding effects in carbon-rich soil. This is a significant point in a practical sense. Destabilization of soil aggregates may be beneficial if not too extreme; as the reviewer points out, it may improve soil tilth. At the same time, it would increase the chance of crusting in some soils, particularly in some Alfisols. It seems that sufficient information is not yet available to judge the validity of this inference.

Hoshikawa implied that, since legumes not only restore plant-available soil N, but also increase the availability of soil P and improve soil physical properties, the increased use of legumes would be beneficial to farmers. In principle, there is no doubt about this thought. In reality, however, farmers cannot accept this idea unconditionally. Where traditional farming practices prevail, the land area planted to legumes is far smaller than that planted to nonlegumes. For instance, in Ghana and Ethiopia, the ratio of land area planted to nonlegumes and legumes is about 7:1 (The World Bank 1987, 1988). It would be logical to investigate the reasons why farmers are planting more nonlegumes than legumes, before trying to recommend that farmers plant more legumes than they have hitherto done. One reason is obvious: they do not have enough labor. Often, there is land available to plant more legumes than they are doing at present. When the productivity of nonlegumes under traditional farming practices is extremely low, the highest priority in allocating labor (and land) is given to these nonlegumes, to secure the required quantity of produce from these crops. Unless the farmers are able to meet their needs for nonlegumes with less labor and land, they cannot plant more legumes. This fact has been overlooked by many scientists and sometimes by extensionists.

## Significance of Root Development of Pigeonpea and Chickpea

Arihara et al. (1991) presented voluminous experimental data on the various beneficial effects of pigeonpea and chickpea on the cereals either accompanying or succeeding them. Basically, the data reconfirmed the legume effects observed elsewhere with other legumes, and actually provided evidence as to possible mechanisms for the beneficial effects of legumes. The uniqueness of this study lies in the fact that the authors intensively studied the characteristics of roots and rhizosphere of the crops to explain the mechanism of the beneficial effects of pigeonpea and chickpea on the cereals associated with or succeeding them. The following points are of special interest or deserve special recognition:

- Analysis of available P at different depths in an Alfisol revealed that beyond the depth of 120 cm, the available P content of soil can be very high (>100 mg $kg^{-1}$). Whether or not this is a localized phenomenon is yet to be determined. Nevertheless, this phenomenon deserves further investigation. If it occurs extensively, the means to tap this resource should be worked out, perhaps not by mechanical means but by biological means.
- The data confirmed that the beneficial effects of chickpea and pigeonpea on the cereals succeeding them are complex, and much more than simply increasing the available N in the soil. Although the paper did not adequately evaluate the different beneficial mechanisms, quantitative evidence was given for improvement in soil physical properties and increased availability of P.
- Sorghum and pigeonpea intercropping is one of the most widely practiced cropping systems in some parts of SAT India. It is known that the system is significantly more productive and stable than a sole-crop system, but so far, the explanations offered for this superiority have not included the factors in and around the rhizosphere. The present study, however, examined the roots and rhizosphere more closely to seek additional explanations for the superiority of intercropping. So far, it has been believed that more effective interception of solar energy, higher water-use efficiency and higher nutrient-use efficiency result in the superiority of intercropping. Arihara et al. found that intercropping improves rhizosphere conditions, increasing the water-infiltration rate and improving soil aeration. This, in turn, increases development of roots, in terms of both the total root mass and the expansion of the rooting zone to deeper soil layers. In other words, in the presence of intercropped pigeonpea, water infiltration was high, free oxygen content in the soil profile was higher when soil was wet after heavy rains, sorghum roots extended to deeper layers, and the root mass per plant was higher than in sole-cropped sorghum. The authors speculated that such improvements in the conditions of the root zone, especially at deeper layers, would be a very important reason for the higher productivity of intercrop systems. This speculation sounds logical and seems to bear practical significance.
- Through experiments-conducted in the field and in pots, Arihara et al. reconfirmed and expanded upon the fact that pigeonpea and chickpea possess unique characteristics in utilizing soil P; pigeonpea better utilizes soil P in Alfisols where Fe-P dominates, and chickpea better utilizes soil P in Vertisols, which contain much more Ca-P than Alfisols.
- The findings of this study have significant practical implications, two outstanding ones being: (1) both pigeonpea and chickpea can be used to pump up soil P from deep soil horizons, because they are deep-rooting crops and there may be substantial amounts of available P at depth in some soils. In attempting to do so, pigeonpea would be more effective in Alfisols and chickpea more effective in Vertisols; (2) where temporary waterlogging of the field would constrain the performance of crops, such as sorghum, intercropping with pigeonpea would be effective in reducing this constraint.

## Nutrient Dynamics in Vegetable and Legume Cropping Systems

Imai (1991) reported the results of research conducted at the Asian Vegetable Research and Development Center in Taiwan. The objective of the research was to examine changes in soil chemical properties and plant nutrient contents under intensive cropping with relatively high inputs. The information from this type of research may not have a direct bearing on discussion of the present topic of cropping systems involving legumes in the semi-arid tropics. There is a large gap between the two systems, particularly in terms of cropping intensity and the level of inputs. Nevertheless, the paper offers much, in terms of concept and principle, for the understanding of the effects of cropping sequences on nutrient dynamics, an understanding essential to the establishment of soil fertility management strategies for sustainable agriculture.

The paper looked at the seasonal and annual changes in soil chemical properties, influence of crop combinations on the chemical properties of soils, relationships between nutrient content of soil and crop yield, nutrient uptake and partitioning within the plant, and the relationship between amount of nutrient uptake and crop yield.

The study indicated how soil chemical properties can change seasonally, and how different crops affect the soil chemical properties. For instance, the soil electrical conductivity (EC) varies with rainfall; in the rainy season, the EC tends to be lowered, and soil EC increases when the field is irrigated in the absence of rainfall. Soil pH changes under different crops; rice tends to lower the soil pH, while Chinese cabbage increases it. In spite of the continued heavy application of fertilizers, the available nutrient content in the soil did not change significantly, except for available P, which increased gradually to reach a plateau in the fourth year. Contrary to expectation, soybean cultivation did not increase the mineral N content in the soil.

Under the experimental conditions wherein the available nutrient concentrations in the soil varied in the range of 5-46 mg $kg^{-1}$ for N (mineral N), 10-58 mg $kg^{-1}$ for P (by Olsen's method), 5-110 mg $kg^{-1}$ for K (exchangeable), and 150-250 mg $kg^{-1}$ for Mg (exchangeable), there was no significant correlation between the nutrient content in the soil and the yield of the crop. This observation is suggestive to those who are trying to use soil testing for fertilizer recommendations.

The data on the partitioning of plant nutrients within crop plants is informative. For instance, the paper indicates that in soybean 80% of the N and 75% of the P taken up is translocated to the seed. This convincingly demonstrates for legumes like soybean that, if the seed is harvested, even when the entire crop residue is returned to the soil, the addition of N to the soil would not be very significant.

In the range of fertilizer application where the crop yield increases more or less linearly in relation to the amount of the nutrient applied, there would be linear correlation between these two parameters. The data presented in the paper are in conformity with this logic. What is interesting is the large difference in the correlation coefficients between different crops. For instance, the values for the total dry-matter yield per kg of nutrient absorbed are: 103 for N, 445 for P, and 123 for K in rice; 21 for N, 114 for P, and 85 for K in soybean. This information can be used to estimate crop fertilizer requirements, pattern of nutrient partitioning, and the fertilizer-uptake efficiency for different crops.

## Fertilizer Management Strategies for Legume-based Cropping Systems

Bationo et al. (1991) discussed the characteristics of the crop production environment in the WASAT and reviewed the work on improving crop productivity in the region, with special reference to the use of a legume component in the cropping systems.

In one word, the crop production environment in the WASAT is "fragile." The soils, being mostly sandy and exposed to high temperatures throughout the year, have very low nutrient-supplying and -holding capacity. For instance, because organic-matter content in the soil is low (due to low supply because of slow growth of vegetation and high decomposition rate because of high temperatures), the natural N-supply capacity is low. Further, because of their low CEC and high infiltration rate, soils cannot hold applied N effectively; ammonium-N is easily lost via ammonia volatilization and nitrate-N is easily lost via leaching. Not only N, but also P and several other essential nutrients are present in WASAT soils at only low concentrations.

Another unfavorable factor in the crop-production environment is the rainfall pattern. Rainfall is insufficient and irregular, the irregularity often being more problematic than the insufficiency. Frequently, a heavy downpour occurs in a short period of time, and a prolonged dry spell follows before the next rainfall event. This unfavorable rainfall pattern and the fragile soil characteristics combine to worsen the situation. In the event of heavy rainfall, with the water-holding capacity of the soils being low, much rainwater would escape from the field by runoff. Further, with the infiltration rate of the soil being high, leaching of mobile plant nutrients, particularly nitrate-N, would occur. If these events occur when the crop is young, plant growth would be retarded, resulting in eventual poor crop performance.

The crop-production environment is fragile not only in terms of physical characteristics but also in terms of socioeconomics. The farmers in the region generally do not have income sources other than farming, which gives them a very low income; because they are generally poor, they cannot improve their farming practices to improve their farming productivity. Therefore, they remain poor. Indeed, this vicious circle of poverty characterizes the crop-production environment not only in the WASAT, but in many other developing regions as well.

Our common sense tells us that where crop productivity is low due to low soil fertility, improvement of soil fertility is essential to improving crop productivity. Our common sense also tells us that using chemical fertilizers is an effective and convenient way to improve the soil fertility. On the other hand, it is also obvious that where rainfall is unreliable and there are no other means to maintain adequate moisture in the field, the use of costly fertilizers is risky. So, technologies need to be sought to improve soil fertility without involving costly purchased inputs. One of these is the use of legumes as components of cropping systems. There are two different patterns in the cropping systems involving the legumes: intercropping and rotation. The beneficial effects of of both have been well established. Their effectiveness is not disputable. However, there are two important questions: (1) Can the rational use of legumes in the cropping system eliminate the need to use chemical fertilizers? (2) If cropping systems involving legumes are so effective, why have farmers not adopted such systems more intensively and extensively?

It would be unrealistic to try to answer these questions without information on what level of improvement of productivity is needed for different crops in a country. One may, however, attempt an answer at the macro level, in comparative terms. For instance, if in a particular country, there is a need to increase crop production by about 20%, disregarding the crop ratio, wide adoption of legume/cereal intercropping may be the solution. At the micro level, however, intercropping may not be an attractive or practical option. Not attractive, because in intercropping the benefit as measured by the land-equivalent ratio (LER) is about 20% or so, while the adequate use of fertilizers on sole crops of nonlegumes and legumes may double, triple, or even quadruple, yields. Not practical, because in intercropping the intention is to maximize the total LER, not to meet the farmers' needs. For instance, in pearl millet/groundnut intercropping, the LER is about maximum when the land allocation for the two crops is in the ratio of 1 millet:3 groundnut. This system may maximize the land-use efficiency, but does not suit farmers' needs, particularly those of subsistence farmers, who may need three times more millet than groundnut. If these two crops are intercropped in the ratio of 3 millet:1 groundnut to suit the farmers' needs, the benefit of intercropping shrinks to an insignificant level. The point made here is not that intercropping is not useful, but that its use is bound to be limited.

In terms of the productivity of nonlegumes, the legume-nonlegume rotation seems to be a better option. The data presented in the paper by Bationo et al. are particularly impressive, showing that the yield of pearl millet following cowpea or groundnut was three to four times higher than that following pearl millet. However, impressive though the results may be on experimental plots, can such legume-nonlegume rotations be widely adopted by farmers in a short period of time? Many resource-poor farmers cannot allocate much land for legumes in the current year and wait until the next year to reap a good harvest of cereals. They need the cereals now, in this year and in every year, and, with the productivity of the cereals being low under their practices, they need to allocate as much of their land as possible to cereals.

If they adopted the improved technologies for nonlegumes, allowing them to allocate less land than usual for the nonlegumes, farmers could be in a position to allocate more land and labor to legumes. In conclusion, it appears to be unrealistic to expect that legumes can eliminate the need for the chemical fertilizers. Rather, when chemical fertilizers are adequately used, legumes have a better chance of being more widely used.

The question of why farmers have not been using legumes more extensively was answered above indirectly and in the section reviewing Hoshikawa's paper. In short, planting more legumes at the sacrifice of nonlegumes under traditional practices—even though in so doing a substantial increase in purchased inputs is not necessary—is very risky and costly to the farmers. Resource-poor farmers would not accept this risk and cost.

Bationo et al. really did not touch upon the issue of fertilizer-management strategy explicitly. Nonlegume/legume intercropping and rotation possess many merits other than just restoring available N to the soil. These include risk aversion, suppression of diseases and pests, and solubilizing some nutrients existing in sparingly soluble forms in the soil. At the same time, experience indicates that legumes alone cannot solve all the problems. Experience also tells us that chemical fertilizers, although costly, are effective and convenient in improving the crop productivities phenomenally. The question now is to look at these two components not separately but complementarily.

Would intercropping and use of chemical fertilizers be synergistic, neutral, or antagonistic? Many experiments have been conducted so far regarding this question. According to the authors, it seems that clear-cut answers are not available yet. A similar question can be raised with regard to rotation and fertilizer use. The answer to this question seems easy. The use of chemical fertilizers would allow farmers to allocate more resources to legumes, and the increased use of legumes would increase the efficiency of use of chemical fertilizers.

## Strategies for Maximizing Efficiency of Phosphorus Utilization in Cropping Systems

Johansen and Sahrawat (1991) summarized current knowledge on P fertilizer requirements of chickpea and pigeonpea and identified what should be done for the scientists to be able to suggest the means to maximize P fertilizer-use efficiency in cropping systems involving these two crops. Indeed, the authors covered all the relevant topics very thoroughly, leaving little to be added. Existing information was critically reviewed and suggestions made as to what should be further learned. All points are acceptable. One point not adequately covered is the practical suggestion of what should be done to make better use of these two crops on the basis of what is known so far. As the authors pointed out, by suggesting that more studies are required, there may be more unknown than known. Still, the farmers are looking to scientists and expecting some guidance. There is no question that the research should be continued, but at the same time, while continuing such research to improve knowledge, the farmers should be serviced with whatever knowledge is already available.

The authors stated in their introduction that the objective of the paper was to summarize the current knowledge on P fertilizer requirements of chickpea and pigeonpea in different cropping systems and *suggest means of maximizing efficiency of use of P fertilizer in both traditional and evolving cropping systems*. As mentioned earlier, they summarized the current knowledge thoroughly, but gave no concrete suggestions for maximizing the efficiency of P fertilizers in the cropping systems involving these crops. What they suggested was the type of further research that should be done. For the research scientists, doing more research may be the means to maximize something. For the farmers, however, to make something happen in the field may be the means to maximize something.

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# Part 5

# Future Research Needs

# Research Requirements for Improving the Phosphorus Nutrition of Chickpea and Pigeonpea in Different Cropping Systems

**K. Kyuma**[1]

I comment as a soil scientist who has worked mainly on aquic soils in humid regions, such as paddy soils and peat soils, and who is not very familiar with soils and crops of the semi-arid tropics (SAT). Nevertheless, I would like to give a broad overview of my impressions of the meeting, realizing that the chairmen of the respective sessions have already given specific comments and recommendations relating to the subject matter of those sessions. I will concentrate on summarizing the work conducted and presented by the Government of Japan (GOJ) Special Project team and will suggest some possible future research directions, particularly for any followup special projects.

I have confessed to my ignorance of SAT soils and crops, but I understand that all members of the Japanese team were similarly ignorant at the start of their assignment. But this was in a sense fortunate, as it allowed them to take a fresh look at the soils (Alfisols and Vertisols) and the crops (chickpea and pigeonpea). They set about this task by growing chickpea and pigeonpea themselves, both in pots and in the field, thus gaining first-hand experience of all of the environmental factors influencing crop growth and yield ability. Prime findings of these studies were that:

- chickpea grown on Vertisols did not respond to phosphorus (P) fertilizer application and its P uptake was greater than on Alfisols, despite the fact that Olsen-P values were higher for Alfisols than Vertisols.
- pigeonpea performed much better than other crops on Alfisols in the absence of P fertilization.

The explanation for the first result appears to reside in the ability of chickpea to exude more citric acid from its roots than other crops. This acid exudate can solubilize calcium-bound P (Ca-P) from two to three times more space around roots as compared with other crops. This finding caused the Japanese scientists to cast doubt on the validity of bicarbonate extraction, such as Olsen's P test, as a soil test applicable to chickpea growing on Vertisols. They argued that a dilute acid extractant would better simulate the ability of crop roots, and chickpea roots in particular, to extract P on Vertisols. Furthermore, by correcting for the buffer capacity of Vertisols, they could establish a good correlation between P uptake and the acid-soluble P test value even for other crops grown on Vertisols and which exude less acid than chickpea.

However, further elaboration is needed here. In terms of running a practical soil-testing program for a region having diverse soils and crops, it is essential to have one soil P test that is applicable to all soil types of the region—even soils as different as Alfisols and Vertisols—and that is able to reasonably predict response of a wide range of crops to P application. The Japanese team proposed a simple titration method to determine a correction factor for the acid dissolution test to predict the response to P of different crops grown on Vertisols. Is it not possible to devise a simple technique to determine a correction factor for different types of soils, say at the series level? Once such a matrix of correction factors for both crops and soils has been established, a single soil P test could be used with more confidence for different crops growing on different soils in a region.

From the second major result, the better performance of pigeonpea on Alfisols of low P status, the

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Japanese team proceeded to identify a substance exuded by pigeonpea roots that could release iron-bound P (Fe-P). This substance, piscidic acid, could chelate Fe, thereby releasing P for uptake by the crop. However, this finding has also raised further questions that require detailed and careful research. From S. Takagi's research on mugineic acid, presented in this volume, it is obvious that many aspects need further investigation. Phytochemical and phytophysiological aspects of piscidic acid need to be elucidated. Importantly in the SAT context, it is necessary to clarify the agronomic implications of piscidic acid in relation to the P nutrition of pigeonpea. Studies are needed on such factors as temporal changes in secretion pattern, effect of crop P status, and effects of various soil conditions on secretion.

The Japanese team also tackled problems of a direct practical nature, such as the best method to apply P fertilizer under situations where a P response was likely. They confirmed that deep banding was necessary under rainfed conditions, where the topsoil dried out during the growing season, but that broadcasting and mixing in the surface soil was adequate under well-watered conditions.

The significance of chickpea and pigeonpea as components of crop rotations and intercropping was also evaluated, particularly from the standpoint of their P-uptake characteristics. Not only were advantages and improvements in P-use efficiency demonstrated, but also beneficial effects of these legumes on soil physical properties shown, probably primarily as a consequence of their deep-rooting habit. However, these studies on cropping systems have not been carried out long enough to elucidate the overall nutrient dynamics of the various cropping systems. Therefore, further research along these lines is recommended, whereby not only the behavior of P but also of N and other possible growth-limiting nutrients should be accounted for. Furthermore, in cropping systems research, it is highly recommended that a careful study be made of traditional cropping systems evolved in the SAT. India has a wealth of such traditional practices in dryland cultivation, from which Japanese scientists could learn of the wisdom of farmers that has been accumulated over centuries. Such an approach may provide valuable clues to further scientific advancement.

Another important piece of research undertaken in this Special Project pertains to the inhibition of root respiration of pigeonpea by waterlogging. After quantifying the detrimental effects of reduced oxygen concentration in the soil atmosphere, the Japanese scientists highlighted the importance of ridging, even in Alfisols, to alleviate problems of excess water accumulation under field conditions.

A common theme was apparent in the research carried out under the first phase of the Special Project: close attention to crop roots and the rooting zone. In the SAT, meeting the crop's demand for water is a key factor in successful crop production. Just as important is the ability to acquire nutrients under low-input situations. Both requirements are met by better matching rooting behavior to potentially available soil moisture and nutrients. It therefore seems appropriate that the Japanese scientists focused their efforts on crop roots and the functioning of the rhizosphere, even though this is a very difficult type of research. Nevertheless, there is still much to be learned about root behavior under the marginal and fluctuating conditions of soil moisture and nutrients in the SAT.

Another feature of the Special Project work was its interdisciplinary approach. Research in the rooting zone and, more specifically, the rhizosphere demands a joint effort of soil and plant scientists. The team, fortunately, was comprised of an appropriate blend of disciplines. It is therefore strongly recommended that the second phase of the Special Project maintain the same interdisciplinary approach. This is often desired, but rarely found in Japanese research institutions, which are usually somewhat isolated from the practicalities of agricultural production.

In conclusion, and particularly on behalf of the delegates from Japan, I thank the organizing committee of the workshop for their efforts to ensure a high standard of paper presentation and discussion. I wish to express sincere thanks to all of the Workshop participants from India and abroad for the kindness with which they shared their knowledge and experience with us. I also wish to extend special thanks to those who assisted the Japanese team in field and laboratory; without their assistance it would have hardly been possible to attain the results presented at this Workshop. I hope that the team for the second phase of the Special Project will enjoy the same support and assistance from ICRISAT staff.

# Requirements for Future ICRISAT Research on the Phosphorus Nutrition of Legumes

**J.R. Burford**[1]

In these concluding comments, it is appropriate to place the recent work on phosphorus in pulses at ICRISAT into perspective, both in terms of ICRISAT's broad research objectives and the ways that these are achieved, and to indicate the research that appears to be needed in the future. The Institute's first two mandates direct us to collect and enhance the germplasm of five crops of the semi-arid tropics—pearl millet, sorghum, pigeonpea, chickpea, and groundnut—and to determine the best ways of using the resources, crops, and environment of the zone. Germplasm collection and enhancement is mainly conducted within our Genetic Resources Program and our two crop improvement programs—Legumes and Cereals. Optimum utilization of resources is the aim of our Resource Management Program. As will be seen shortly, the recent research on the P nutrition of pigeonpea and chickpea has implications for both germplasm and resource management research in the future.

The earlier research at ICRISAT by Sheldrake, Narayanan, and Saxena provided a good physiological characterization of pigeonpea and chickpea. This and subsequent work by several disciplines in the Legumes and Resource Management Programs indicated clearly that pigeonpea and chickpea are phosphorus-efficient crops. What was not clearly understood was the mechanisms or crop traits that resulted in this efficiency. For chickpea, the solubilizing action of acidic root exudates (organic acids) had been identified as one possible mechanism, but no such specific solubilizing compounds were known for pigeonpea. Research in the Government of Japan Special Project has provided an invaluable lead, in the discovery that piscidic acid is exuded by pigeonpea and that this compound enhances pigeonpea's ability to take up phosphorus from iron phosphates in the soil. This research is an excellent example of the advantages of associations between ICRISAT and mentor institutes; in this case, scientists in Japan who provided expert techniques and in-depth knowledge to help investigate a specific problem that had been identified by more generally based research in the Institute.

At this stage, it is appropriate to consider the direction of future research for these two legumes. First, by considering the whole plant, it is apparent that much more basic research is needed on their nutrition. In this respect, there is a need to separate clearly the different aspects of the uptake and utilization of phosphorus in the plant. The questions that need to be addressed are the following.

- Has the internal requirement for P been adequately characterized for each crop species; for example, are the critical limits for tissue P concentration well known?
- Have all possible uptake mechanisms been explored? And how do these uptake mechanisms relate to the supply of phosphorus in the soil, both that in solution or in different solid species (iron phosphate being a specific example)?
- And, relevant to the above point, are critical limits now well established for any soil test?

Clearly, despite the advances made by this project on one mechanism for P uptake by pigeonpea, there is need for much more research into the various other factors that contribute to P uptake. We need to know the role of the morphology of the root systems, especially in relation to appropriate soil moisture status for absorbing P, the role of mycorrhiza (*in the field*), and the critical level of the P in the soil solution in

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contact with the root. These factors all merit serious consideration because it is clear that—in contrast to most temperate legumes—pigeonpea and chickpea have evolved to be efficient at survival in low-P, droughty soils. The traits responsible for this P efficiency should be understood, so that they are not lost in subsequent breeding efforts to improve yield, especially as the breeding process is commonly carried out on soils of research stations with adequate to high P levels. It is clear that such further research will involve a combination of both germplasm and resource management disciplines.

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