



International Workshop



Summary and Recommendations

27-30 Sep 1999, ICRISAT, Patancheru, India

Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities



Japan International Research Center for Agricultural Sciences (JIRCAS)
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)

Adu-Gyamfi, J.J. (ed.). 1999 Food security in nutrient-stressed environments, exploiting plants' genetic capabilities: summary and recommendations of an International Workshop, 27-30 Sep 1999, ICRISAT, Patancheru, India (in En). 1-2 Ohwashi, Tsukuba, Ibaraki 305-8686, Japan and Patancheru 502 324, Andhra Pradesh, India : Japan International Research Center for Agricultural Sciences (JIRCAS) and International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) 148 pp, ISBN 92-9066-411-8, Order code CPE 124.

Attended by 50 international participants, this workshop marked the culmination of Phase III of a 15-year Special Project at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) funded by the Government of Japan Entitled "Sustainable cultivation of upland crops in the semi-arid tropics", the Project was executed in collaboration between ICRISAT and Japan International Research Center for Agricultural Sciences (JIRCAS). The workshop objectives were to: Explore the scope for genetic manipulation of the ability of crop plants to access and use nutrients, prioritize candidate mechanisms of enhancing nutrient uptake and use in terms of their suitability for genetic manipulation, examine appropriate methodologies for genetic enhancement of crop plants' ability to absorb nutrients and use them efficiently, and suggest how genetic options can best be combined with management options to improve nutrient uptake and use. Over 30 papers were presented in sessions on: sustainability of breeding for low-nutrient environments, candidate mechanisms, methodologies, and combining genetic improvement with natural resource management. Extended abstracts of all papers are included, together with an introductory review that includes colored photographs of Project Highlights. Session interpretive summaries, and recommendations for future research needs, priorities and strategies are provided.

Adu-Gyamfi, J.J. (編集) 1999 養分ストレス環境における食糧生産の安定供給 : 植物の遺伝的能力の開発、1999年9月27-30日にインド、パタンチェルにある ICRISAT で開催された国際ワークショップの要旨と推薦 (英語版)、〒305-8686 茨城県つくば市大わし 1-2 とインド、アンドラプラデシュ州パタンチェル 502 324 : 国際農林水産業研究センター (JIRCAS) と国際半乾燥熱帯作物研究所 (ICRISAT) 148pp, ISBN 92-9066-411-8, Order code CPE 124.

本ワークショップは世界各国から 50 人の参加者が出席し、日本政府の拠出金による国際半乾燥熱帯作物研究所 (ICRISAT) での 15 年間にわたる特別プロジェクト“半乾燥熱帯地域における畑作物の持続型栽培”の第三期の成果を公表した。本プロジェクトは、ICRISAT と国際農林水産業研究センター (JIRCAS) との共同研究によって実施された。本ワークショップの目的は以下の通りであった：作物の養分吸収・利用に関連した能力の遺伝子操作に向けた可能性の探査、遺伝子操作を行う上で養分吸収を増大し環境適合性を上げるために利用することの出来る機構の優先度調査、効率的な養分吸収とその体内利用に関する作物の遺伝的能力向上のための方法の探索、養分吸収とその体内利用を増進させるための作物育種と作物管理の最適な組み合わせ方法の提示。30 題以上の論文が以下の 4 つのセッションで発表された：低栄養環境に適した育種の持続、養分吸収と利用に関する機構、養分の有効利用性に関する遺伝子操作の方法論、遺伝的改良と自然資源管理との統合。カラー写真に収めたプロジェクトハイライトの紹介とともに全ての論文要旨を掲載した。各セッション毎の要約、今後必要な調査事項の推薦、優先事項、戦略を提示した。

The opinions in this publications are those of the authors and not necessarily those of JIRCAS or ICRISAT. The designations employed and the presentation of the material in this publication do not imply the expression of any opinion whatsoever on the part of JIRCAS or ICRISAT concerning the legal status of any country territory, city, or area, or of its authorities, or concerning the delimitation of its frontiers or boundaries. Where trade names are used this does not constitute endorsement of or discrimination against any product by either institution.

Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Summary and Recommendations of an International Workshop

27-30 Sep 1999, ICRISAT, Patancheru, India

Edited by

J J Adu-Gyamfi

Sponsored by



**Japan International Research Center for Agricultural Sciences (JIRCAS)
1-2 Ohwashi, Tsukuba, Ibaraki 305-8686, Japan**



**International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)
Patancheru 502 324, Andhra Pradesh, India**

1999

Contents

Opening Session

Welcome Address

L. D. Swindale 3

Government of Japan Project activities at ICRISAT 1984-99

J. J. Adu-Gyamfi, O. Ito , J. Arihara, H. Nakano , and C. Johansen 7

Session 1 Breeding for low-nutrient environments: Is it sustainable?

Physiological traits for crop improvement in low-nutrient environments: The crop physiologists' view

T. R. Sinclair and V. Vadez 19

Prospects for using conventional techniques and molecular biological tools to enhance efficiency of crop plants in low-nutrient environments: The plant breeders' view

C.T. Hash, R. E. Schaffert, and J. M. Peacock 22

Ex-ante impact assessment and economic analysis of breeding for nutrient efficiency and alternate strategies, a conceptual model and research issues: The socio-economists' view

B.I Shapiro, D. Osborne, and M. Ahmed 24

Session I Interpretive Summary

J M Peacock 27

Session 2 Candidate mechanisms

Breeding for low-nutrient environments

Y-G Zhu, C. Huang, N. K. Howes, and S. E. Smith 37

Genetic adaptation of crop plants to low-nutrient environments: Morphological and ecophysiological characteristics of adaptation

H. Nakano, J. J. Adu-Gyamfi, and T. Nakamura 40

Genotypic variability and physiological characteristics of crop plants adapted to low-nutrient environments

J. J. Adu-Gyamfi, S. Ishikawa, T. Nakamura, and H. Nakano 42

Physiological adaptations for nitrogen use efficiency in sorghum J. W. Maranville and S. Madhavan	44
Photosynthesized carbon translocation and distribution of crops adapted to low-nutrient environments K. Fujita, M. I. Chaudhary, A. Fujita, Y. Kai, M. Takayanagi, H.El Sherry, and J.J. Adu-Gyamfi	46
Variability in rooting behavior and nutrient uptake of crop plants in low-nutrient environments T. Nakamura, J. J. Adu-Gyamfi, A. Yamamoto, S. Ishikawa, H. Nakano, and O Ito	48
Genotypic variability in phosphorus solubilizing activity of root exudates by crops grown in low-nutrient environments S. Ishikawa, J. J. Adu-Gyamfi, T. Nakamura, T. Yoshihara, and T. Wagatsuma	50
A proposed new phosphorus (P) uptake mechanism by groundnut and pigeonpea - P solubilizing reaction on the root surface N. Ae and R-F Shen	53
Role of soil microorganisms in improving P nutrition of plants Gyaneshwar P, G. Naresh Kumar, L. J. Parekh, and P.S. Poole	55
Phosphorus use efficiency as related to sources of P fertilizers, rainfall, soil, crop management, and genotypes in the West African semi-arid tropics A. Bationo, J. Henao, and K. Anand Kumar	57
Exploitation of plant genetic differences in solubilizing P from sparingly soluble sources G. R. Findenegg	60
Modelling root-induced solubilization of nutrients G.J.D. Kirk	62
Scope for genetic manipulation of mineral nutrition in chickpea M. Y. Ali, L. Krishnamurthy, N.P. Saxena, O.P. Rupela, Jagdish Kumar, and C. Johansen	64

Aluminium tolerance in nodulated N₂-fixing legume species native to two contrasting savanna sites	
M-L Izaguirre-Mayoral, S. Flores, and T. Oropeza	67
Effect of rock phosphate and superphosphate fertilizer on the productivity of maize var. Bisma	
D. R. Lukiwati	69
Session 2 Interpretive Summary	
J. J. Adu-Gyamfi	71
Session 3 Methodology for genetic manipulation of nutrient availability	
Assessing germplasm collections for traits useful in plant nutrition	
P.J. Bramel-Cox	79
Root exudates as mediators of mineral acquisition in low-nutrient environments	
F. D. Dakora and D. A. Phillips	81
Genetic control of root exudation	
Z. Rengel	83
Transporter genes to enhance nutrient uptake: Opportunities and challenges	
J. Dunlop and T. Phung	85
The phosphate uptake mechanism	
F. W. Smith	88
Breeding for better symbioses	
Z. Rengel	90
Session 3 Interpretive Summary	
F. D. Dakora, and T. R. Sinclair	93

Session 4 Combining genetic improvement with natural resource management

Breeding crops for enhanced nutrient content

R.M. Welch and R.D. Graham 103

Appropriate farm management practices for low-nutrient soils

P.C. Smithson and K.E. Giller 105

Farmer preferences for crop varieties in low-nutrient environments

S. S. Snapp and S.N. Silim 108

Nutrient balances - a guide to improving the management of sorghum- and groundnut-based dryland cropping systems in semi-arid tropical India

T.J. Rego, B. Seeling, V. Nageswara Rao, G. Pardhasaradhi, J.V.D.K Kumar Rao, R.J.K Myers, and C. Johansen 111

Preplant moisture and fertility conditions as indicators of high and stable yields in rainfed cropping systems

C.F Yamoah, G E. Varvel, and J. J. Adu-Gyamfi 114

Role of modelling in improving nutrient efficiency in cropping systems

P.S. Carberry, M. E. Probert, J.P. Dimes, B. A. Keating, and R. L. McCown 116

Session 4 Interpretive Summary

R.M. Welch and C. Johansen 119

Closing Session

Closing Remarks

T Hamazaki 129

Future research needs, priorities, and strategies

133

Participants

137

Opening Session

Welcome Address

L.D. Swindale

Director General International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India

This International Workshop on 'Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities' is the culmination of 15 years' work in partnership between the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) the Government of Japan (GoJ) and various other associates.

In addition to its core contributions to ICRISAT — which have been considerable — the GoJ, through the Japan International Research Center for Agricultural Sciences (JIRCAS) initiated a Special Project with ICRISAT, in November 1984 entitled 'Development of Sustainable Cultivation of Upland Crops in the Semi-Arid Tropics (SAT)'.

The Project was conducted in 3 Phases (I 1984-89, II 1989-94, and III 1995-99). During that time a number of Japanese scientists came to work at ICRISAT. After they returned to Japan, I can assure you, they remained in very close touch with our Institute, both through their work, and through the Friends of ICRISAT Group. During its 15-year period the Project attempted to address the issues of food security and poverty alleviation by exploiting how genetic options can best be combined with management options to improve nutrient availability in SAT cropping systems, with the basic understanding that nutrients are limited in the soils of the region and fertilizer additions are not easy to acquire for various reasons.

In July 1984, I signed the MoU between the Tropical Agriculture Research Center, (TARC), now Japan International Research Center for Agricultural Sciences, Ministry of Agriculture, Forestry and Fisheries, Japan and ICRISAT. Today, I am very privileged to be here to witness the successful completion of the Project and hear about the results. Later in 1984, a team of Japanese scientists, Drs Ae, and Arihara (whom I am delighted to see here today), and Dr Okada joined ICRISAT to begin Phase I of the Project to study the method of soil management and pulses cultivation in the semi-arid tropics with emphasis on the adaptation of pulses to moisture and nutrient, especially phosphorus(P), stress.

We had known for a long time that pigeonpea was unresponsive to P and could use it in ways that other crops could not. We had tried to understand the mechanisms prior to this Project, and had made some progress. But the Project clarified that root exudates had a role to play and specifically for pigeonpea.

That was the central thrust of Phase I - it was much debated - and led to experiments designed to test and prove the hypothesis wrong. So seldom do we follow Karl Popper's axiom that experiments should be designed to prove the hypothesis wrong - we are only too happy to prove ourselves right - but attempting to prove that we are wrong helps the discipline to advance.

Phase I proved there was a mechanism involving root exudates contributing to the availability of P in pigeonpea - this led to consideration of whether additional means to increase utilization of exudates could take place. Results are summarized in the ICRISAT publication, 'Phosphorus Nutrition of Grain Legumes in the Semi-Arid Tropics.'

Phase I led to an FAO-ICRISAT Expert Consultancy Workshop on 'Genetic Manipulation of Crop Plants to Enhance Integrated Nutrient Management in cropping systems-1. Phosphorus,' 15-18 March 1994. The workshop attempted to establish a global consortium of researchers focusing their efforts on improving the ability of crop plants to acquire P, particularly through sources from which it is only sparingly available.

I attended a conference in Japan in early 1998 that brought together people from all over the world who were working on similar tropics. This conference on 'New concepts of plant nutrient acquisition' was held in Tsukuba, Japan, from 22-27 March 1998 to summarize the newly developing concepts on mechanisms of plants to acquire soil nutrients, and to apply them to practical agriculture. I also had the opportunity to make a contribution to a pre-conference symposium on identifying appropriate agricultural technology for Africa and possible research areas for collaboration with the Government of Japan. I would like to quote from my conclusions. "There is evidence of a small but growing number of successes in West Africa with conventional crop improvement research. Input responsive and relatively stable cultivars of the major cereals, sorghum, maize, and millet, the main grain legumes, cowpea and groundnut, and the major root crop, cassava been produced by research institutes, released by governments, and are slowly reaching the hands of the farmers. But one can not avoid the conclusion that some inputs must be obtained and made available to farmers." More that 20 years ago FAO assembled the results of hundreds of fertilizer trials carried out in West Africa by the Freedom from Hunger Fertilizer Program that I led for several years. The results showed consistent improvements in yield from use of fertilizer -with the farmers varieties of crops and landraces. Today with improved cultivars the responses are clearly greater. The obvious input is P and numerous studies have concluded that P is needed by West African soils and that it can be used profitably by a range of crops in a range of situations. P is the nutrient most available in the region, most countries have deposits of rock phosphates - Togo gets its main foreign exchange by exporting rock phosphate to Europe. Deposits exist in Niger and Senegal where phosphoric acid is now

produced to support agronomic productivity in Senegal and India. If N is the most important nutrient and it can not be obtained readily from fertilizers then agriculture based on legumes must be the appropriate response in the region. Legumes in rotation and intercropped can provide food, fodder, fuel, protection from the winds, and cash. They also provide N to subsequent crops.

Phase II scientists worked on roots themselves rather than exudates. The objectives were :

- To establish methods for quantifying soil-root interactions in various cropping systems
- To study root activities, functions and N uptake by component crops
- To study rooting behavior of pigeonpea in relation to waterlogging and N availability
- To examine soil solutions to estimate the soil's capacity for N supply
- To prepare the N balance sheet in pigeonpea-based cropping systems
- To develop a working model of the rooting profile for pigeonpea in cropping systems
- To compare the different management options of N fertilizer application for the enhancement of N utilization

Considerable work was done. Project staff produced the JIRCAS publication 'Roots and Nitrogen in Cropping Systems of the Semi-Arid Tropics.' Hopefully this will contribute to our knowledge and opportunities for genetic improvement.

In Phase III the Project scope widened to include genetic manipulation. Scientists are aware that no improved cultivar has a reasonable chance of success unless the constraint of soil fertility is addressed through improvement of soil fertility or adaptation of crops. You can not get something for nothing - and no genetic manipulation will help you do it.

Work has continued and achievements are to be reported here. The scientists have been conscientious and well-focused. This reflects on individuals, the organization of the program, and the obvious attention to detail by Japanese scientists who try to make good progress. We learned a lot, but it is a difficult task. However, progress has been made and field-management practices to increase productivity of sorghum and pigeonpea through generation of crop/water/nutrient response curves for optimum nutrient and water management developed. These response curves could be used to model the yield of cultivars in target nutrient and drought-stressed environments of probable productivity and responses and also to learn more about gaps in research.

A lot of basic research still needs to be done on P in plants. We know about the role of P and its relationship to energy transfer. But I don't think we know nearly enough about P partitioning in plants, particularly how that partitioning changes over the growing season as the crop develops.

We have learned from soil scientists about forms of P in soil, their relative solubilities and diffusion of P in soil solutions but there is still a lot to be learned, and the interactions at the root surface between P and plants need to be elucidated. None, or very little of this is going to be done at ICRISAT. That is not our role, but these are things that should be pursued in agricultural research centers and universities, and I hope in 10-15 years we can have another conference like this where that information can be contributed to strategic and applied research of the sort we do here.

The CGIAR over the last 10 years has been working to establish system-wide programs. The Group agrees that centers can not be scientifically autonomous. There is much to be gained from research across centers and a system-wide approach. Several centers work in the same agro-ecological zones, ICRISAT is not the only center in the SAT. System-wide initiatives involve intercenter cooperation and cooperation with governments of the region. But it is very difficult to make such initiatives work properly, it involves institutional cooperation and some institutions have their own infrastructures, and transaction costs can be very high. Only a few system-wide programs are reasonably successful. But the scientists have forged partnerships in other ways. Scientists cooperate because they are interested in each others' work and see opportunities to learn. These partnerships are set up by scientists themselves each contributing to the effort, and interchange is by results. Such partnerships are easy to set up, have low transaction costs, and can be highly effective, like the ones that exist on virtually every study of major viruses in plants and animals. We invite scientists with basic knowledge of the role of phosphorus in plants to share with those working on genetic manipulation and agronomic practices. We want to encourage scientist-to-scientist partnerships.

I shall conclude by expressing my thanks to the Organizing Committee of this conference. I hope you have good meetings and discussions - I will be interested in the results.

Government of Japan Project activities at ICRISAT 1984-99

J. J. Adu-Gyamfi¹, O. Ito², J. Arihara³, H. Nakano⁴, and C. Johansen¹

1. *Natural Resource Management Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Patancheru 502 324, Andhra Pradesh, India*
2. *Japan International Research Center for Agricultural Sciences (JIRCAS), 1-2 Ohwashi, Tsukuba, Ibaraki 305-0851, Japan*
3. *National Agriculture Research Center (NARC), 3-1-1 Kannondai, Tsukuba, Ibaraki 305-8666, Japan*
4. *Hokkaido National Agricultural Experimental Station (HNAES), Shinsei, Meinuro, Kasaigun, Hokkaido 052-0071, Japan*

Introduction

" The little we already know has been very important BUT what we don't yet understand may prove to be our greatest resource for the future PROVIDED that research to deepen our understanding is sustained" - LT Evans.

The Alfisols and Vertisols of the semi-arid tropics (SAT) have the potential to support regional food needs, but are limited by low availability of nutrients, especially phosphorus (P) and nitrogen (N). The situation is further exacerbated by low and unreliable rainfall, and limited groundwater resources. Despite these problems that make food production an unpredictable enterprise, some 850 million (one sixth of humanity) inhabitants of these regions are directly involved in agriculture for their living.

Some say they should not even be there, but if they were to leave their homes, where should they go? Achieving food security - ensuring that sufficient food is available, that supplies are relatively stable, and that those in need can obtain it - has long been the goal of global development investors (donors). Realizing that declining soil fertility in the SAT is the fundamental agronomic cause of declining food production, earlier projects, that aimed to improve soil conditions by increasing fertilizer use to achieve sustainable yields were very successful in the better-endowed regions of the Asian SAT. However, in the less-endowed SAT in Africa and Asia, such approaches have not been successful because the required inputs are either not available to farmers in the right place at the right time, or are unaffordable, and in many case a risky investment. This in turn has led to low rates of adoption of improved crop cultivars because yield gains from them have generally proven transient.

Given the above constraints, one of the possible solutions to enhancing productivity in harsh SAT environments is to improve the adaptation of crop plants to the existing soil conditions by selecting and breeding crops that require only moderate external inputs to approach their genetic potential. This involves improving the nutrient acquisition abilities of existing crops, and/or optimizing nutrient cycling via the use of locally available plant nutrient sources.

The Government of Japan (GoJ), realizing the importance of food security in the SAT, has made substantial contributions to the Consultative Group on International Agricultural Research (CGIAR) to help improve the living conditions and enhance the household income of smallholder resource-poor farmers in the SAT. In addition to its core contributions to the CGIAR, the GoJ, through the Japan International Research Center for Agricultural Sciences (JIRCAS) initiated a special project with ICRISAT, in November 1984 entitled 'Development of Sustainable Cultivation of Upland Crops in the Semi-Arid Tropics.' The Project was conducted in 3 phases (I 1984-89, II 1989-94 and III 1994-99). The Japanese scientists assigned to the Project collaborated with ICRISAT scientists to conduct basic and strategic research to improve and sustain productivity in nutrient- and drought-stressed environments. During its 15-year period, the Project attempted to address the issue of food security and poverty alleviation by exploiting how genetic options can best be combined with management options to improve nutrient availability in SAT cropping systems to thereby enhance the productivity of degraded soils.

Achievements

Realizing that P is a major limiting factor limiting crop productivity in the SAT, during Phase I scientists concentrated on the management options to enhance P availability in cropping systems. The finding that pigeonpea can increase the pool of P available to cropping systems by accessing iron-bound P (Fe-P) via its unique root exudates, provided the first clue to explaining why pigeonpea is better able than other crop species to absorb P from Fe-bound P, the most prevalent form of unavailable P in Alfisols. Phase 1 scientists further identified the mechanisms by which this occurred, particularly the role of organic and phenolic acids of P-solubilizing root exudates. The research identified a phenolic compound "piscidic acid" (p-hydroxybenzyl tartaric acid) that could chelate Fe³⁺ thereby releasing P from Fe-bound P in the soil. These findings, apart from having particular relevance to low-P Alfisols in which Fe-P is the dominant form of soil P, suggested scope for possible enhancement of P efficiency through genetic manipulation of the release of root exudates. Other related research pertaining to the inhibition of root respiration of pigeonpea by waterlogging, developing appropriate diagnostic tests for P, and fertilizer-P management strategy helped accelerate the adoption of pigeonpea in cropping systems as a soil fertility

replenishment crop. The results are summarized in an ICRISAT publication 'Phosphorus Nutrition of Grain Legumes in the Semi-Arid Tropics' (Figure 5a). The findings were also published in refereed journals (Ae et al., 1990, 1993; Otani and Ae 1996; Otani et al., 1996). Phase I led to an FAO-ICRISAT Expert Consultancy Workshop on 'Genetic Manipulation of Crop Plants to Enhance Integrated Nutrient Management in Cropping Systems-1 Phosphorus' held at ICRISAT 15-18 March 1994. This workshop attempted to establish a global consortium of researchers focusing their efforts on improving the ability of crop plants to acquire P, particularly through sources from which it is only sparingly available. During this workshop, research areas with prospects for impact on agriculture in the medium term were identified and appropriate outputs and activities proposed. A further workshop on 'New Concepts of Plant Nutrient Acquisition' was held in Tsukuba, Japan, to summarize the newly developing concepts on the mechanisms by which plants acquire soil nutrients, and to apply these concepts to practical agriculture.

Despite the important role of roots in nutrient and water acquisition, they have been given scant attention in field experiments due to their hidden below-ground nature and to logistical difficulties in data collection (Figure 1). During Phase II in 1989-94, the Project scientists devoted efforts to establishing an overall picture of the profile distribution of water, nitrogen (N), root systems, and root activities and function of ICRISAT mandate crops. They established a relationship between rooting behavior and N flow in pigeonpea-based cropping systems with the establishment of a simple root model using field data on water and nutrient flow, distribution of root systems, N uptake, N₂ fixation, biomass, and yield. The findings of Phase II are unique in that they increased understanding of roots and nutrient dynamics in cropping systems, (Figures 2 and 3) focusing on intercropping, a common practice in the SAT. These studies are summarized in a JIRCAS publication 'Roots and Nitrogen in Cropping Systems of the Semi-Arid Tropics' (Figure 6). Several journal articles (Adu-Gyamfi et al., 1997a, Adu-Gyamfi et al., 1997b; Tobita et al., 1994; Fujita et al., 1995, Matsunaga et al., 1994, Katayama et al., 1995, 1998, 1999; Ito et al., 1996; Rao et al., 1993, 1997; Gayatri Devi et al., 1996) were published as a result of the research conducted during Phase II. In addition to the journal articles, more than 15 conference papers were published (Figure 5c).

With the promising information of possible low-P and low-N mechanisms in pigeonpea, sorghum, and pearl millet evidenced by the root exudates, and deep-rooting ability of these crops, scientists in the current Phase III (1995-99) concentrated on providing a linkage between nutrient physiology and genetic manipulation of crop nutrient use efficiency. The scientists realized that in low-fertility, adverse-rainfall regions of the SAT, no improved cultivar has a reasonable chance of achieving substantial and sustainable yields in farmers'

fields unless the critical constraint of soil fertility is addressed through the adaptation of crops to existing soil conditions. Attention was therefore concentrated on identifying and exploiting physio-genetic systems that increase extraction and utilization of nutrients by crops. Work focused mainly on:

- Understanding the candidate mechanisms of plant adaptation by quantifying the nature and extent of genetic variation in the target production system
- Identifying physiological traits suitable for genetic manipulation of crops that are more stable, and production in nutrient-stressed environments.

These efforts have resulted in a better understanding of the physiological characteristics required for future ideotypes of pigeonpea and sorghum developed for nutrient-stressed environments. Furthermore, the research has helped to strengthen the knowledge base for initiating breeding programs using nutrient-efficient germplasm accessions as parents in crosses. This sets the stage for eventual gene transfer to enhance food security in nutrient-stressed environments. During the past 5 years, scientists established genetic variability in the P-solubilizing activity of pigeonpea root exudates and have quantified the amount of organic and phenolic compounds in these root exudates that could be used as indicators for selection of P-efficient genotypes (Figure 4). This Phase has helped to bridge ICRISAT research on natural resource management and genetic enhancement particularly by establishing links between nutrient physiology and genetic improvement of crops.

Field management practices to increase productivity of sorghum and pigeonpea through generation of crop/water/nutrient response curves for optimum nutrient and water management have been developed. These response curves could be used to model the yield of cultivars in target nutrient and drought-stressed environments.

Capacity building

The Project has supplemented ICRISAT programs in important areas of basic research, not otherwise possible to address, particularly in view of declining core resources. In addition, collaborative ties between ICRISAT and Japanese Universities particularly those of Hiroshima, Hokkaido, and Tokyo were strengthened. The Project also contributed to training Research Fellows - K Okada, S Tobita, J J Adu-Gyamfi, and T Nakamura (currently working in JIRCAS) M Yoshida, and S Ishikawa; Visiting Scientists and Scholars, T Matsumoto, T Goto, H Kokubun, M Moriyama, N Tanaka, K Maeda, Y Ohwaki. A Kubota, M Kondo, J Kashiwagi, and A Yamamoto, to mention but a few, and improved the creativity and job competence of support staff. A total budget of approximately US\$ 4.5m was provided by the Japanese Government during the 15- year period. Besides paying staff salaries, the Project also invested in capital equipment including ¹⁵N spectrophotometer, spectrophotometer, neutron probe,

Project Highlights



Figure 1. During Phase I it was necessary to follow roots underground by going there to find them



Figure 2. By Phase II the minirhizotron (a) could send a tiny video camera (b) into the soil to view roots in situ



Figure 3. Development of the 'porous cup' method (a) enabled non-destructive detailed point sampling (b) of soil solutions



a



b



c



d

Figure 4. Phase III involved detailed investigations of genotypic differences; (a) in the greenhouse in nutrient solution, (b) in the kinetics of N and P uptake, (c) in collaborative greenhouse studies in Japan, and (d) in field trials to verify earlier results.

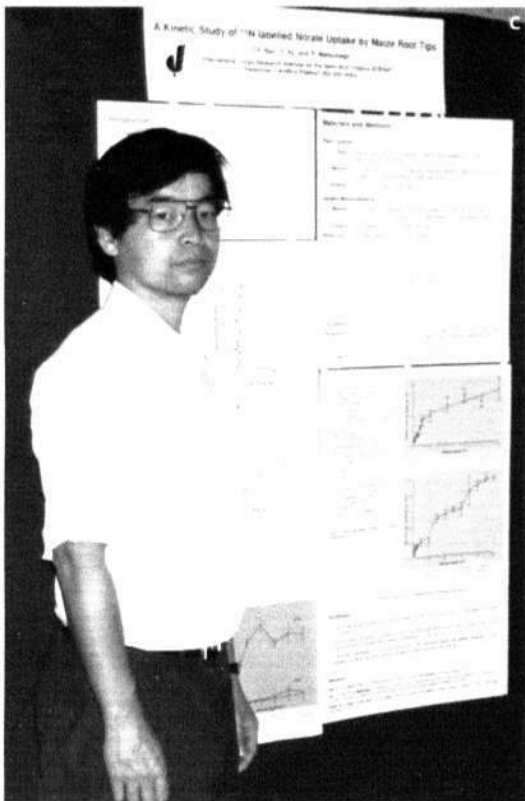
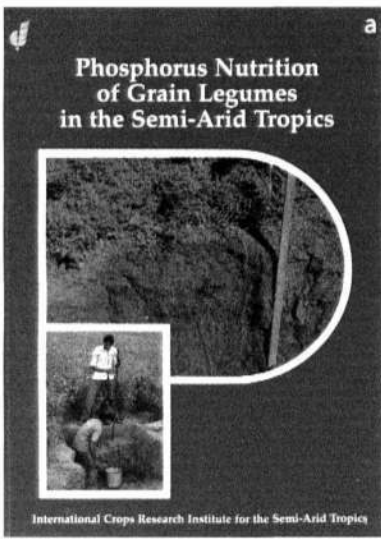


Figure 5. The achievements of the Project have been widely disseminated through; (a) ICRISAT and (b) JIRCAS publications, (c) at numerous conferences where posters on individual topics have been presented, (d) in a commemorative publication '15 Years of Progress, Government of Japan Project at ICRISAT 1984-99' released during the final workshop in September 1999, in both English and Japanese versions, and (e) in many discussions with collaborators such as those in Nigeria



Figure 6. Participants in the International Workshop held at ICRISAT in September 1999 went out into the field to see evidence of research progress.



isotopic analyzer, Kjeldhal digestion and distillation units, ultra-centrifuges, photocopiers, computers, printers, camera, refrigerators, and ovens.

There is now a wealth of accessible knowledge that remains to be blended with the realities of smallholder farming communities in the SAT. ICRISAT must build on these achievements and exploit the comparative advantages in the continuing link between nutrient physiology and genetic manipulation for nutrient efficiency in crops.

This publication (Summary and Recommendations) aims to highlight the extended abstracts of the workshop, the interpretive summaries of each session; and the future research needs, strategies and priorities. The potential contribution of physiological research to genetic improvement of crop plants has long been expanded, but the traditional separation of physiological and breeding research tend to persist. It is hoped this publication will stimulate interest in this fascinating dimension of improving the adaptation of crop plants to nutrient-stressed environments through an integral approach involving workshop plant breeders, crop physiologists, statisticians, and crop modelers.

Acknowledgements

We thank all who have worked on the Project and our collaborators in ICRISAT and other advanced research institutions for their dedication and hard work, all who have contributed to the organization and running of this meeting, and all the participants for their attendance and diligence in preparing and participating in discussions. We acknowledge the help of Sue Hainsworth in the preparation of material prior to the meeting, the production of the commemorative publication in English and Japanese, and for editorial work on this publication and on the full proceedings that will be published by Kluwer Academic Publishers, Dordrecht, The Netherlands.

References

- Adu-Gyamfi J J, Ito O, Yoneyama T, Gayatri Devi and Katayama K 1997a** Timing of N fertilization on N, fixation, N recovery and soil profile nitrate dynamics on sorghum/pigeonpea intercrops on Alfisols of the semi-arid tropics. *Nutr. Cycl. Agro.* 48, 197-208
- Adu-Gyamfi J J, Ito O, Yoneyama, T, Gayatri Devi and Katayama K 1997b** Nitrogen management and biological nitrogen fixation in sorghum/pigeonpea intercropping on Alfisols of the semi-arid tropics. *Soil Sci. Plant Nutr.* 43, 1061-1066.
- Ae N, Arihara J, Okada K, Yoshihara T and Johansen C 1990** Phosphorus uptake by pigeonpea and its role in cropping systems of the Indian subcontinent. *Sci.* 284, 477-480.
- Ae N, Arihara J, Okada K, Yoshihara T, Otani T and Johansen C 1993** The role of piscidic and secreted by pigeonpea roots grown in an Alfisol with low P fertility. *In Genetics Aspects of Plant Mineral Nutrition*. Eds P J Randall, E Delhaize, R A Richards and R Munns. pp 279-288. Kluwer Academic Publishers, Dordrecht, The Netherlands.

- Fujita K, Chaudhary M I, Adu-Gyamfi J J and Yoshizawa D 1995** Dinitrogen fixation and growth responses to phosphorus and aluminium application in pigeonpea (*Cajanus cajan* L). Soil Sci. Plant Nutr. 41,729-735
- Gayatri Devi, Ito O, Matsunaga R, Tobita S, Rao T P, Vidyalakshmi N and Lee K K 1996** Simulating root system development of short-duration pigeonpea. Exp. Agric. 32, 67-78
- Ito O, Johansen C, Adu-Gyamfi J J, Katayama K, Kumar Rao J V D K and Rego T J (eds). 1996** Roots and nitrogen in cropping systems of the semi-arid tropics. JIRCAS (Japan International Research Centre for Agricultural Sciences) International Agriculture Series No.3. 691 pp.
- Ito O, Matsunaga R, Katayama K, Tobita S, Adu-Gyamfi JJ, Kashiwagi J, Rao T P and Gayatri Devi 1996.** Dynamics of roots and nitrogen in cropping systems of the semi-arid tropics. JIRCAS J. 3,33-47.
- Johansen C Lee K K and Sahrawat K L (eds) 1991** Phosphorus Nutrition of Grain Legumes in the Semi-Arid Tropics ICRISAT (International Crops Research Institute for the Semi-Arid Tropics) Patancheru, Andhra Pradesh, India. 264 pp.
- Ito O, Matsunaga R, and Rao T P 1996** Diurnal changes in non-structural carbohydrates in pigeonpea leaves. Soil Sci. Plant Nutri. 42, 419-424.
- Katayama K, Ito O, Matsunaga R, Adu-Gyamfi J J, Rao T P and Anders M M 1995** Nitrogen balance and root behavior in four pigeonpea-based intercropping systems. Fert. Res. 42, 315-319.
- Katayama K, Ito O, Adu-Gyamfi J J, Rao T P, Dacanay E V and Yoneyama T 1999** Effects of NPK fertilizer combinations on yield and nitrogen balance in sorghum or pigeonpea on a Vertisol in the semi-arid tropics. Soil Sci. Plant Nutr. 45, 143-150.
- Katayama K, Ito O, and Rao TP 1998** Seeding characteristics and retention of current photosynthates in leaves in relation to initial growth in pigeonpea (*Cajanus cajan* L. Millsp.) and cowpea (*Vigna sinensis* Endl.) Soil Sci. Plant Nutr. 44 (3), 477-480.
- Matsunaga R, Ito O, Tobita S, Rao T P and Johansen C 1994** Response of short-duration pigeonpea to nitrogen application after short-term waterlogging on a Vertisol. Field Crops Res. 38, 167-174.
- Otani T, Ae N and Tanaka H 1996** Phosphorus (P) uptake mechanisms of crops grown in soils of low P status: II Significance of organic acids in root exudates of pigeonpea . Soil Sci. Plant Nutr. 42, 553-560.
- Otani T and Ae N 1996** Phosphorus (P) uptake mechanisms of crops grown in soils of low P status I. Screening of crops for efficient P uptake, Soil Sci. Plant Nutr. 42, 155-163.
- Rao T P, Ito O, Matsunaga R and Yoneyama T 1997** Kinetics of ¹⁵N-labelled nitrate uptake by maize (*Zea mays* L) root segments. Soil Sci. Plant Nutr. 43, 491-498.
- Rao, T P, Ito O and Matsunaga R 1993** Differences in uptake kinetics of ammonium and nitrate in cereals and legumes. Plant Soil 154, 67-72.
- Tobita S, Ito O, Matsunaga R, Rao T P, Rego T J, Johansen C and Yoneyama T 1994** Field evaluation of nitrogen fixation and use of nitrogen fertilizer by sorghum/pigeonpea intercropping on an Alfisol in the Indian semi-arid tropics. Biol. Fertil. Soils. 17,241-248.

Session 1

**Breeding for low-nutrient
environments: Is it sustainable ?**

Physiological traits for crop improvement in low-nutrient environments: The crop physiologists' view

T. R. Sinclair and V. Vadez

*United States Department of Agriculture-Agricultural Research Service (USDA-ARS),
and Agronomy, Physiology, and Genetics Laboratory, University of Florida, PO Box
11095 Gainesville, FL 32611-0965, USA*

Nitrogen (N) and phosphorous (P) are essential nutrients intimately involved in the biochemistry and physiology of plant life. The roles of each of these elements is well documented and quantitative relationships exist between levels of nutrient in plants and physiological activity. Therefore, to maximize yield under low-nutrient conditions the challenge is to maximize nutrient uptake and to optimize the use of the elements among competing processes. The intent of this review is to examine the current physiological understanding of N and P uptake and use, and to evaluate various options for optimizing plant performance under limited-nutrient conditions.

Biochemical background

Nitrogen is an essential component of amino and nucleic acids. Consequently, without N it is not possible to synthesize the necessary proteins, enzymes, DNA, and RNA required in virtually all plant processes. Deficiency or reduced N in plants necessarily means that there is less biochemical machinery to catalyze plant metabolism and to generate new cells. Not surprisingly, one of the most obvious symptoms of N deficiency is a decrease in the size of plant tissue. During vegetative development N deficiency results in decreased leaf sizes, which have the lasting consequence of decreased light interception and capacity for growth. To sustain high photosynthetic activity, large quantities of the enzyme RuBisCO must be synthesized in leaves. In fact, more than half of the protein, and consequently N, in C₃ plants is in RuBisCO. Much of the variation in photosynthetic activity per unit leaf area that exists among leaves is directly linked to their N content. In addition, developing seeds have N requirements that are constrained to rather narrow ranges of concentrations. Without a continuing N supply to developing seeds, seed growth is necessarily restricted. The obligate need in many plant processes for N at fairly high content levels imposes a severe restriction that prohibits increasing crop yields.

Phosphorous is essential for plant structures, including nucleic acids and phospholipids in cell membranes. The bonding properties of phosphorous make it crucial for metabolic processes that are nucleotide-based, e.g., ADP, NAD,

and NADP, because of its unique energy-transfer properties. Inorganic P, that exists in concentrations as high as 10 mM in the cytoplasm, is also directly involved in the generation of high-energy phosphate compounds such as ATP from ADP. Consequently, P is critical in establishing the enzymatic machinery in energy storage and transfer, which in many cases involves membrane processes. Therefore, an inadequate P supply results in dramatic decreases in plant development and growth.

Use efficiency

Nitrogen use in plants is usually quite efficient. It is readily incorporated into organic materials and commonly partitioned in the plant to optimize crop growth. For example, N is commonly distributed among leaves so that those receiving the greatest amount of light also have the most N in order to maximize canopy photosynthetic activity. Further, N can be readily mobilized to new tissue and developing seeds from older tissue when current uptake into the plant is inadequate to meet these needs. It is not uncommon for more than 75% of the total accumulated N to be in the seeds at maturity. Plants appear to have few physiological options to greatly increase the efficiency with which N is used once it has been accumulated by the plant.

Less is known about the efficiency of P use than N use in plants. Certainly, P is readily mobilized in the plant and there appears to be a priority for the use of P. Particularly intriguing is the issue of P partitioning in plants to optimize overall growth. For example, is it more desirable to partition P to roots for more root growth to obtain more soil nutrients, or to shoots to increase leaf area development and photosynthetic activity for greater overall mass accumulation? Also, there is the possibility for metabolic adaptations for sustained activity when the level of P in cells is low. Physiological investigations on the partitioning and use of P in crop plants, and the possibility of genetic variations are topics that need further investigation.

Uptake

The critical needs for both N and P are, not surprisingly, associated with uptake processes in roots with high affinities for each element. If the elements are available at the root surfaces and there is a physiological deficiency in the plant, roots have the capacity for uptake that is many fold greater than that observed under normal field conditions. There appear to be few physiological options in the uptake processes themselves that would increase element uptake by crops. The key limitation is the availability of each of the elements at the root surface.

Nitrogenous compounds tend to be very mobile in the soil. As a result, N is readily transferred to root surfaces by both diffusion and mass flow in the soil. A rather modest root length density of 1.0 to 1.5 cm cm⁻³ appears to be sufficient

to extract N from the soil at the rate required by the plant. Little opportunity appears to exist for increasing N uptake by physiological modification.

On the other hand, the chemistry of P in the soil is complex and soil-P compounds have very low mobility in the soil. These limitations on P availability in the soil lend themselves to several approaches for amelioration by physiological modifications of crops. Exudates from crop roots are an option for altering soil chemistry, particularly by soil acidification, to increase the availability of insoluble forms of P. The low mobility of P in soils means that crops need a high density of absorbing surfaces in the soil in order to ensure that contact is made with P stores. High root length densities are obviously an important feature since they allow full exploration of the soil for P. Also, associations between roots and mycorrhizae offer a good possibility to increase the effective P-acquiring surface area in the soil. Extended crop growth cycles could lengthen the time in which P can be recovered from the soil. Consequently, in soils where P exists but is poorly acquired by crops, there are several major physiological modifications that likely would result in increased P acquisition.

Yield improvement

An obligate need for both N and P in the biochemical and physiological processes for assimilating crop mass, and the fact that they are quantitatively essential compounds in seeds, means that crop yield increases are rigidly limited by the amount of N and P acquired by a crop. Therefore crops in a low-nutrient environment are doomed to produce low yields unless new sources of these elements can be made available. Options to open new sources of P by plant exudates to alter soil chemistry, increasing the absorbing surface area, or lengthening the time for P uptake have been discussed. These options do not improve N accumulation. In reality, N accumulation under most conditions can only be increased by providing more N to crops.

An excellent possibility for increasing N supply to is to take full advantage of the symbiotic N₂ fixation capability of some plants. Especially in low-N environments where fertilizer N is not available, the development of superior legume germplasm with high N₂-fixation activity could lead directly to high yields by the legume and increased yields of non-legumes grown in cropping schemes involving legumes. Increased emphasis on legumes, however, is likely to require substantial investigation of their uptake and use of P. Nevertheless, legume crops are likely to be critical to increasing crop yields in low-nutrient environments.

Prospects for using conventional techniques and molecular biological tools to enhance efficiency of crop plants in low-nutrient environments: The plant breeders' view

C.T. Hash¹, R. E. Schaffert², and J. M. Peacock³

1. *Genetic Resources and Enhancement Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India.*
2. *Embrapa Milho e Sorgo (Embrapa/CNPMS), Sete Lagoas, Minas Gerais, Brazil.*
3. *International Center for Agricultural Research in the Dry Areas (ICARDA), Arabian Peninsula Regional Program (APRP), PO Box 13979, Dubai, United Arab Emirates*

Sustainable increases in global production of food and feed-grain crops - both legumes and cereals - will increasingly require integration of improved cultivars and cultural practices to economically achieve improvements in crop productivity and stability of this productivity. This can be brought about in favorable environments in part by increasing the amounts of soil nutrients available to crops by application of mineral and organic fertilizers, and selection for short-statured crop genotypes that are more responsive to fertilizers and less prone to lodging. However, high rates of fertilizer application in such environments can result in pollution of surface and sub-surface water supplies since much of the applied fertilizer nutrients are not taken up by the crop and instead leach into the subsoil, or are carried away with soil particles in runoff water. In environments less favorable for production, moisture and soil toxicity constraints can interact very strongly with soil nutrient availability, sometimes making it difficult to obtain economic responses to individual fertilizers or other soil amendments. Enhancing crop growth under such conditions requires improvement of nutrient uptake ability, as there appears to be little opportunity to enhance the efficiency of biomass production from a fixed amount of nutrients. Thus, in both favorable and less favorable crop production environments, genetic improvements in the ability of crops to take up soil nutrients - both indigenous and applied - will be critical to sustainably increasing agricultural productivity. Genetic enhancement of root traits, including root-related changes in the chemistry of the rhizosphere that can enhance nutrient availability, will be critical to improving crop uptake of soil nutrients.

Molecular biology, combined with Mendelian and quantitative genetics in quantitative trait locus (QTL) mapping and marker-assisted selection (MAS), provides powerful new tools to facilitate efficient genetic manipulation by plant

breeders of such complex traits as drought tolerance and phosphorus (P) uptake ability. Current opportunities for genetically manipulating the ability of crop plants to more efficiently take up essential soil nutrients, using as examples P and several of the crops in ICRISATs crop improvement mandate are examined. It is concluded that for at least some of these important, but often academically and economically orphaned tropical food crops, the genetic variation and molecular tools that will be needed already exist, or can be expected to become available in the very near future. With appropriate, targeted research, these tools can permit the empirical exploration of the potential for marker-facilitated mapping and manipulation of major genes that can contribute to enhanced P uptake ability of these crops. With these tools, delivery of new versions of currently popular, high-yielding, high-quality, disease-resistant crop cultivars, with genetically improved ability to take up P currently in soils but unavailable for crop growth, could take as little as 5 to 7 years. Sustainable use of such improved cultivars would require that they be used as components of integrated soil fertility management systems.

Ex-ante impact assessment and economic analysis of breeding for nutrient efficiency and alternate strategies, a conceptual model and research issues: The socio-economists' view

B.I Shapiro¹, D. Osborne¹, and M. Ahmed²

1. *Natural Resource Management Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), B P 320 Bamako, Mali*
2. *International Livestock Research Institute (ILRI), P O Box 5689, Addis Ababa, Ethiopia.*

The stated impact goal of the technology strategies under consideration during this workshop is food security in nutrient-stressed environments. To do a meaningful ex-ante impact assessment of any proposed technology requires first placing that technology in the context of the broader issues of what is needed in developmental terms to achieve such a goal, and the relevant development possibilities of the target population(s). Considering the development needs and possibilities establishes the relevance of the new technologies for making the required impact. Once this is established the specific question of whether the low-input strategies due to be discussed, in this workshop, or high-input strategies, or a combination of the two are most relevant for the arid and semi-arid tropics (ASAT) can be addressed.

Firstly the agricultural development needs of the target population(s) if food security is to be improved need to be defined. Food security is dependent upon food availability and accessibility - thus a combination of food production and cash income is required. To produce a surplus that would enable commercialization and provide cash income to help ensure security, an annual increase in per capita food production of around 1% on average would have to be achieved. This would require an increase in output of about 4.0% per year, given the current population growth rate of 2.9-3.1%. Historically, such a rate of output growth has been unattainable without intensification involving external cash inputs.

What then are the development possibilities for the ASAT? Substantial empirical evidence shows that basically two main development pathways are relevant - an extensive path that involves increasing cultivated area or improving extensive livestock production, and an intensive path that results in increasing yields through more intensive use of land and more cash inputs. The evidence shows that the pathway ultimately occurring depends upon rainfall amount and distribution, buttressed by the forces of population pressure and market access.

What are the implications for the ASAT? Extensive, low-input systems will generally work where rainfall is below 500 mm, population pressure is low, and market access is remote. Here attempts at crop intensification are not appropriate since the use of cash inputs is not profitable. Meanwhile, livestock activities, even when improved, will not increase incomes much when population pressure is high and land holdings are small. In this scenario improved livestock production, which can substantially increase farmer incomes, will ultimately require replacement of crops with livestock activities and eventual consolidation of landholdings to enable improved, but extensive animal production. The key development challenge in livestock production in the dryer parts of the ASAT region is the shift to improved forages. Technological change through introduction of forage production and feeding cereals to livestock is eventually expected to take place throughout the African ASAT as it is already doing in southern Africa and in parts of Asia. Where this extensification process is not yet occurring in dryer areas, land degradation and desertification are taking place.

Intensive systems require external inputs and will work where rainfall is high enough (above 500 mm) to make inorganic fertilizer use profitable. This profitability is supported by high population pressure and good access to markets. The first response to increasing population pressure is an expansion of cultivated area to maintain crop output. Continuing population growth eventually reduces farm sizes as land becomes more constrained. Land values go up and the cost of labor declines. With continuing population growth and low use of inputs, yields and incomes decline. Where rainfall is sufficient to ensure profitability, as yields decline and the land supply becomes more limited, the potential returns to more intensive production practices increase. In most areas of the ASAT where rainfall is sufficient to make inorganic fertilizer use profitable, there is very little room for expansion of cropland, so the needed output increase will have to come from agricultural intensification on existing land. In the Asian ASAT, the land constraint is even more pronounced, especially on land that can be irrigated, so the need to intensify rainfed agriculture is the same.

Are more nutrient-efficient crops relevant where crop intensification is possible? Low cash-input systems that include legumes are possible as a short-term solution. However, they would limit, but not entirely eliminate the need for purchased inputs. Increasing the availability of one nutrient increases the demand for others. The income gains from such low-input systems would also be small because farm sizes are usually small. Where the conditions are appropriate for intensification, continuation of low-input methods will ultimately lead to progressive land degradation. Ultimately in such circumstances, there will be a return to extensive livestock production if intensification with external inputs does not take place. To rely solely on low-input methods in such circumstances will not help to create sustainable systems.

Breeding for nutrient efficiency is one of a set of low-input strategies that include improved use of manure, crop residues, composting, biological nitrogen fixation or the application of rock phosphate, etc. At the present time, the available empirical evidence shows that imported inorganic fertilizers are the only technically efficient and economically profitable way to overcome the soil fertility constraints faced by most farmers in ASAT regions where rainfall is high enough for intensification to take place. Such low-input strategies are complements, but not substitutes for fertilizer use in raising the production of smallholder agriculture in this situation.

The main constraint to yield increases where rainfall is high enough for inorganic fertilizer use to be effective is not germplasm, but policies that affect the availability of external cash inputs, especially inorganic fertilizer. African governments need to further improve the already more conducive policy environments that have come about in recent years. Policies are needed to encourage importation of inorganic fertilizers and their sale in the private market, along with public investments in infrastructure that would lead to better functioning markets. Dissemination of technical information is also required to make farmers more aware of potential benefits and how best to use inorganic fertilizers and their complements.

Session 1 Interpretive Summary

Breeding for low-nutrient environments: Is it sustainable?

J.M. Peacock

Introduction

This conference set out to address the important issue of how physiological mechanisms of nutrient uptake can best be combined with genetic options to improve the adaptation of crops to low-nutrient availability, thereby enhancing productivity of nutrient-poor soils in the semi-arid tropics. The first session, attempted to address the question from the viewpoint of three interrelated disciplines; physiology, breeding, and socio-economics.

The crop physiologists⁹ view

The physiologist's task was to give some perspectives about opportunities for physiological improvement that might result in increased yields in low-nutrient environments. Interestingly, physiologists went about their task by posing six related and important questions.

- 1. What are the essential physiological roles of nitrogen (N) and phosphorus (P) in crop growth?**
- 2. Can the need for N and P in plant growth be decreased?**
- 3. Can the allocation of N and P to grain be improved to achieve increased grain yield?**
- 4. What is the quantitative yield limitation based on N and P accumulation?**
- 5. Can N and P uptake from the soil be increased in low-nutrient environments?**
- 6. What is the opportunity for legumes in low-nutrient environments?**

The authors did an admirable job in addressing these and came to some pertinent conclusions (Sinclair and Vadez, 2000).

In summary, after listing all the important physiological roles of N and P they conclude that both N and P are essential and the need for both elements cannot be decreased. Low levels of either invariably mean lower yields. It seems clear that little opportunity exists to increase N recovery in low-nutrient environments, apart from adding more N, and we learn later that this is sometimes neither economical nor environmentally acceptable. Alternatively, having longer-duration varieties and improving the plant architecture could provide a larger leaf area and duration and thus more storage (Sinclair and Sheehy, 1999). But, low-nutrient

conditions are often associated with low water and high temperature conditions and as such, long-duration varieties and larger leaf areas are often not well adapted.

One approach suggested is to increase N uptake by the use of more legumes in the farming systems. However, Wood et al. (1997) showed that growing chickpea and lentil in a wheat/legume rotation did not provide a net input of N. These data also indicated that the inclusion of these grain legumes in rotation with wheat may reduce the rate of depletion of soil N compared with a continuous wheat crop, but it is unlikely to yield a positive N balance. It must be concluded therefore that these particular grain/legume rotation systems do not offer the immediate prospect of a sustainable cropping system. The case is likely to be the same for many other cereal/legume rotations and may account for the reason why in the Mediterranean region, grain legumes are grown on only 3.5% of the crop land (Buddenhagen, 1990).

On the other hand, several short-term options can be investigated for increasing P accumulation and the authors look closely at roots; long root hairs are highlighted and although selection for these could be time-consuming, this seems a possible route to take. The interaction of root hairs with mycorrhiza or "managing mycorrhiza" must be regarded as an essential area for further research.

In summary, the physiologists point to concentrating on trying to increase the P uptake by plants with the help of the plant breeders and molecular biologists.

It is therefore an appropriate point in the summary to turn to the views of applied geneticists, but before doing so I would like to quote from a section taken from Ghazanfer and Fisher (1998). "Endomycorrhiza (in desert plants) increase absorption of nutrients, particularly phosphorous and bacterial nitrogen fixation may be an important nutrient aid in the vascular plants of dune areas. Bowers (1982) lists several genera, including *Aristida* and *Artemesia* that have associated nitrogen-fixing bacteria. There is growing evidence that the rhizosheaths, characteristic of the root systems of desert perennial grasses, such as *Stipagrostis plumosa*, *Cenchrus ciliaris*, and *Coelachyrum piercie* may be important aids both to nitrogen nutrition and water absorption. Nitrogen-fixing bacteria have been associated with the cylindrical root sheaths formed of matted root hairs and sand grains held by the secreted mucilage (Danin, 1991; 1996a, b)".

Under P scarcity in soil, P influx into roots is immensely affected by root hairs; nearly 90% of root P uptake could be accounted for by root hairs (Fohse et al., 1988). Prolific root hair formation can increase P exploitation efficiency of tomato plants. "Cottony root" (crt) hair trait that increases P absorption is such an example (Hochmuth et al., 1985). It is well known that plant tolerance to low-P in soil can be significantly influenced by the mycorrhiza! component in the roots because vascular-arbuscular mycorrhiza (VAM) can extract P more efficiently at lower concentrations through better soil exploitation and absorption (Krishna, 1997).

Earlier at ICRISAT, this group (Ae et al., 1990) demonstrated the importance

of secretions (piscidic acid) from pigeonpea in acidifying the soil to increase P uptake. Indeed, many acids have been identified viz. acetic, glycolic, malonic, oxalic, and formic in the root exudates of a number of plants (Vancura and Hovadik, 1965; Dakora and Philips, 2000; Fox and Comerford, 1990).

These root exudates, as shown by many (Dakora and Phillips, 2000) play a crucial role in enabling desert grasses to survive under very low-nutrient conditions, usually with little water. Now the ICRISAT breeders and crop improvement scientists have a problem, or better stated a challenge; how to make their mandate crops more productive under low-nutrient conditions. If one considers the case of pearl millet (*Pennisetum glaucum*) and the farmers in the Sahel and northern India. *Pennisetum glaucum* is well-adapted in Rajasthan, as is the related forage grass, *Cenchrus ciliaris*; the two species are growing alongside each other. Krishna and his colleagues again at ICRISAT (1985) showed that pearl millet in the presence of VAM was able to take up more P. Genes that code for transporter proteins for all inorganic nutrients and some of the minor nutrients have been cloned from plants (Chrispeels et al., 1999). The question is, is the desert grass system more effective in taking up P and if so, can we identify the genes responsible and get them into *Pennisetum glaucum*?

The plant breeders' view

In recognizing that the nitrogen route may be a dead end, the breeders quite rightly focus their attention on how to genetically enhance the crops' ability to access the small amounts of available P and/or increase the amounts of available P in the soil solution. Genotypic differences in P use efficiency (PUE) due to mycorrhiza occur in many crops (Smith et al., 1992) but the genetics of this phenomenon are still not clearly understood. Many reports support the possibility of increasing the VAM component in roots, and its effect on P efficiency of the host genotype via selection and breeding (Manske, 1990; Smith et al., 1992).

The breeders go straight to the core of the problem, and address the issue of how the genetic enhancement of root traits (Lynch, 1995), including root-induced changes in the chemistry of the rhizosphere, can enhance nutrient availability (Hinsinger, 1998). They argue, like others (Dunlop and Phung 2000; Dakora and Philips, 2000) that this will be critical to improving uptake of soil nutrients, particularly P. They also argue that molecular biology, combined with Mendelian and quantitative genetics in quantitative trait locus (QTL) mapping and marker-assisted selection (MAS), provide powerful new tools to facilitate efficient genetic manipulation by plant breeders of complex traits. They examine current opportunities for genetically manipulating the ability of crop plants to more efficiently take up essential soil nutrients, using as examples P and ICRISAT's mandate crops-chickpea, groundnut, pearl millet, pigeonpea, and sorghum. They conclude as do others (Dunlop and Phung, 2000) that for at least some of these

important food crops, the genetic variation and molecular tools already exist, or can be expected to become available in the very near future. With appropriate, targeted research, these tools can permit us to empirically explore the potential for marker-facilitated mapping and manipulation of major genes that can contribute to the enhanced P uptake ability of these crops.

The authors show that there is overwhelming evidence that associations of plant roots with VAM and the exudation of organic acids and enzymes from plant roots can contribute to significant increases in the supply of P to plant roots. They therefore have two sets of target traits for assessment and possible utilization by plant breeders and physiologists.

If we turn to the conclusions drawn by the physiologists on identifying genes associated with roots exudates, then this is very encouraging, and is clearly a route to be followed. However, each set of traits is complex, and difficult to measure, but despite this the authors argue that cultivars with a genetically improved ability to take up P could take as little as 5 to 7 years to develop. This time frame will also be dependent to some extent on the availability of reliable screening procedures for roots, but experience shows that this has never been easy or really mastered.

It is over 15 years since some of these ideas on root exudates were being discussed and worked out (Krishna et al., 1985). With so many new breeding and molecular tools now available the way forward is clearer, and it is a matter of the physiologists, breeders, agronomists, molecular biologists, and soil scientists finishing the job. The subsequent papers in this workshop set out to show us the way.

The socio-economists' view

The socio-economist posed three important research and development questions pertinent to the problem of low-nutrient soils.

- 1. What are the development needs in the arid and semi-arid tropics (ASAT)?**
- 2. How are agricultural systems likely to evolve and what are the implications for technology research strategies?**
- 3. What are the critical research questions related to alternative technology strategies?**

In order to address these important questions an example from Sub-Saharan Africa (SSA) was used.

It is clear that agricultural systems in SSA are in crisis, in response to increasing population and growing markets, and that with the current population increases (approx. 3 % per year) the region will require a per capita food production increase of about 4.0% per year. It is also recognized that the two major constraints to primary production in SSA are water availability and soil fertility, and that these should be addressed together and not in isolation from each other.

A simple model is presented that indicates which pathway could be followed as a function of population pressure and access to markets. The result of the model is also strongly affected by rainfall. The model allows crop improvement scientists to focus on the priority issues as they relate to improving crop production in low-nutrient soils.

It can be seen that in the driest areas, low-input strategies with traditional crops are not viable because of population pressure and that therefore, extensive livestock activities may have to replace existing systems. Here, the focus would be on improving forages and pastures rather than food or feed crops. In contrast, in the wettest areas the best scenarios are to use inorganic fertilizers, that are clearly profitable. It is the transition zone that requires the most research input and is probably the climatic zone that this workshop must address.

Good local cultivars such as Sadore Local already exist in the Sahelian zone of SSA. What is now required is to find ways to breed similar varieties that can better utilize and obtain P, and at the same time do not enhance land degradation through the mining of soil nutrients and the total depletion of soil organic matter. Land degradation must be avoided at all costs.

In conclusion, economists admit that there are no silver bullets, and that a combination of technologies will be required. Breeding solutions will need to be combined with crop and water management strategies. Higher productivity, more sustainable systems in the ASAT will require location-specific strategies, that will be dependent on population, markets, and rainfall. Two of the listed technologies, the use of more legumes in the ecosystems, and the use of physiological and molecular biological tools to improve P uptake through plant breeding are addressed.

References

- Ae N, Arihara J, Okada K, Yoshihara T and Johansen C 1990** Phosphorus uptake by pigeonpea and its role in cropping systems of the Indian subcontinent. *Science* 248, 477-480.
- Bowers J E 1982** The plant ecology of inland sand dunes in western North America. *J. Arid Environ.* 5, 199-220.
- Buddenhagen I W 1990** Legumes in farming systems in Mediterranean climates. *In* The Role of Legumes in Farming Systems of the Mediterranean Areas. Eds A E Osman, M H Ibrahim and MA Jones, pp 39. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Chrispeels M J, Crawford N M and Schroeder J I 1999** Proteins for transport of water and mineral nutrients across the membranes of plant cells. *Plant Cell* 11, 61-675.
- Dakora F D and Phillips D A 2000** Root exudates as mediators of mineral acquisition in low-nutrient environments. *In* Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. *Developments in Plant and Soil Sciences* volume 00. Ed JJ Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).

- Danin A 1991** Plant adaptation in Desert Dunes. *J. Arid Environ.* 21,193-212.
- Danin A 1996 a** Adaptations of *Stipagrostis* spp. to Desert Dunes. *J. Arid Environ.* 34, 279-311.
- Danin A 1996 b** Plants of Desert Dunes. Springer-Verlag, Berlin, Germany.
- Dunlop J and Phung T 2000** Transporter genes to enhance nutrient uptake: Opportunities and challenges. *In* Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00. Ed JJ Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Fohse D, Claasen N, and Jungk A 1988** Phosphorus efficiency in plants 1. External and internal P requirements and P uptake efficiency of different plant species. *Plant Soil* 110, 101-109.
- Fox T R and Comerford N B 1990** Low-molecular weight organic acids in selected forest soils of the southeastern USA. *Soil Sci. Soc. Am. J.* 54, 1139-1144.
- Ghazanfar S A and Fisher M 1998** Vegetation of the Arabian Peninsula, Kluwer Academic Publishers, Dordrecht, The Netherlands. 352 pp.
- Hinsinger P 1998** How do plant roots acquire mineral nutrients? Chemical processes involved in the rhizosphere. *Adv. Agron.* 64, 225-265.
- Hochmuth G J, Gabelman WH and Gerloff GC 1985.** A gene affecting tomato root morphology. *Hort. Sci.* 20,1099-1101.
- Krishna KR, Sheety KG, Dart P J and Andrews D J 1985** Genotype dependent variation in mycorrhizal colonization and response to inoculation of pearl millet. *Plant Soil* 86, 113-125.
- Krishna K R 1997** Phosphorus efficiency of tropical and semi-dryland crops. *In* Accomplishments and Future Challenges in Dryland Soil Fertility Research in the Mediterranean Area. Ed J Ryan, pp 343-363. International Center for Research in the Dry Areas (ICARDA), Aleppo, Syria.
- Lynch J P 1995** Root architecture and plant productivity. *Plant Physiol.* 109, 7-13.
- Manske G G B 1990** Genetical analysis of the efficiency of VA mycorrhiza with spring wheat. 1. Genotype differences and a reciprocal cross between efficient and non-efficient variety. *In* Genetic Aspects of Plant Mineral Nutrition. Eds N El-Bassam, M Dambroth and B C Loughman. pp 397-405. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Shapiro B I, Osbourne D and Ahmed M 2000** Ex-ante impact assessment and economic analysis of breeding for nutrient efficiency: The socio-economists' view *In* Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00. Ed JJ Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Sinclair T R and Sheehy J E 1999** Erect leaves and photosynthesis in rice. *Science* 283, 1456-1457.
- Sinclair T R and Vadez V 2000** Physiological traits for crop yield improvement in low N and P environments. *In* Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00. Ed JJ Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).

- Smith SE, Robson AD and Abbot LK 1992** The involvement of mycorrhizas in assessment of genetically dependent efficiency of nutrient uptake and use. *Plant Soil* 146, 169-179.
- Vancura V and Hovadik A 1965** Root exudates of plants. II. Composition of root exudates of some vegetables. *Plant Soil* 22, 21-32.
- Wood M, Philbeam C, McNeil A, and Harris H 1997** Nitrogen cycling in a dryland cereal-legume rotation system. *In Accomplishments and Future Challenges in Dryland soil Fertility Research in the Mediterranean Area*. Ed J Ryan, pp 71-78. International Center for Research in the Dry Areas (ICARDA), Aleppo, Syria.

Session 2

Candidate mechanisms

Breeding for low-nutrient environments

Y-G. Zhu^{1,2,3}, C. Huang⁴, N. K. Howes⁵, and S. E. Smith^{1,2,3}

1. Department of Soil and Water 2. CRC for Molecular Plant Breeding 3. Centre for Plant Root Symbioses, Waite Campus, The University of Adelaide, Glen Osmond, SA 5064, Australia
4. Department of Plant Science, Waite Campus, The University of Adelaide, Glen Osmond, SA 5064, Australia
5. Field Crops Pathology Unit, South Australia Research and Development Institute (SARDI), Glen Osmond, SA 5064, Australia

With the mounting pressure from the ever-increasing population throughout the world, sustainable production of quantity and quality food has now been prioritized by many international organizations and national governmental agencies. Management of soil fertility is a key component of any food production system. Low-fertility soils are widely distributed in many parts of the world. On nutrient-deficient soils, the traditional approach is to change the soil to fit the plant, i.e., fertilizers and other soil amendments are applied to increase soil fertility and/or to make soil nutrients available for plant uptake. However, application of chemical fertilizers means extra costs for farmers and could also lead to greater risks of off-site non-point water pollution by nitrogen (N) and phosphorus (P) from agricultural land. The exploitation of plant genetic variation to increase the efficiency with which plants absorb and use nutrients has been increasingly emerging as an alternative approach towards low-nutrient environments. Varietal differences in plant tolerance to low-nutrient soils have been observed for many elements and in many crop species. An overview of the achievements made in this research field is provided, in order to identify new research directions and initiatives for future development of genetic resources.

Definitions of nutrient efficiency

Nutrient efficiency is broadly considered as the ability of a genotype to grow well in a soil deficient in that nutrient (very low bioavailability) and produce higher biomass, especially in the harvestable component, than other genotypes. From an agronomic aspect, the definition of nutrient efficiency is likely to be specific to particular agricultural systems, soils, and plant products (e.g., grain or total above-ground biomass). However, physiologically plant nutrient efficiency contains two components, i.e., uptake efficiency and utilization efficiency. The practicality of these definitions varies with the crop involved and the product of concern.

Plant adaptation to low-nutrient environments

Wild plants of native vegetation have evolved various strategies to ensure their survival under different environmental conditions, in response to low soil fertility, including both slow growers (Type I) and ruderal species (Type II). Slow-growing plants often have high root/shoot ratios, and low maximum potential growth rate, even at high nutrient supply; these types of plants can store nutrients (i.e., luxury consumption and higher internal concentration) for later utilization when supply is limited. Another characteristic of some Type I plants is a large seed reserve of nutrients used in seedling establishment that also contributes to grain quality. Ruderal species are more responsive to external nutrient supply and can easily display visual deficiency symptoms; Type II plants have relatively low nutrient storage. Apart from growth strategies, plants have also evolved other mechanisms to acquire nutrients from low-nutrient environments, these are discussed.

Plant characteristics related to nutrient efficiency

For the purpose of breeding programs, identification of plant traits important for nutrient uptake and utilization efficiency is essential. This will allow the development of marker-assisted selection (MAS) for particular quantitative traits. Identification of these traits is also useful in understanding the mechanisms of nutrient efficiency which leads to possible manipulation to produce nutrient-efficient crop cultivars. These characteristics include differences in the architecture of the plant root system, the ability of a plant to modify the rhizosphere chemically and thus increase nutrient bioavailability, root symbioses such as arbuscular mycorrhizae, and absorption mechanisms. These characteristics have been identified on various plant species as of particular significance for the uptake of different nutrients.

Strategies for breeding nutrient-efficient cultivars

Reliable screening for crop cultivars using appropriate parameters is a prerequisite to breeding for cultivars with enhanced tolerance to low-nutrient environments. Bioassay systems should reflect the soil type in which the plants will be grown, the particular definition of nutrient efficiency for which the tests are required, and dominant mechanisms of importance in the plant species in question. The advent of molecular-marker technology has led to the development of genetic maps that reveal quantitative trait loci (QTLs) related to nutrient efficiency. MAS is a relatively new technology and there has been only limited application in breeding programs aimed to design nutrient-efficient crop cultivars. It is expected that this approach will be particularly useful for nutrient efficiency, that is almost certainly controlled by multiple genes. The use of doubled haploid (DH) populations provides an option for improved selection if molecular marker technology is not available.

There have also been major developments in recent years on the molecular basis of plant acquisition of nutrients, with the identification and characterization of some ion transporters/channels. Attempts are being made to improve plant nutrient acquisition by genetically manipulating these transporters/channels. However, in most soil-plant systems, the process of nutrient uptake is often limited by the mobility of ions in the soil and their diffusion to the root surface, rather than the kinetics of uptake across the plasma membrane. In consequence, justification of the importance of transporters/channels in the context of nutrient efficiency will require more information.

Conclusion

The existence of genetic variation in plant nutrient acquisition and adaptation to low- nutrient environments provides the rationale for breeding crop cultivars for such situations, to secure a sustainable food supply. Screening strategies should be devised on the basis of ecophysiological understanding of plant nutrient efficiency. QTLs can be established using reliable bioassay and appropriate parameters, that will overcome current limitations in breeding for low-nutrient environments. Recent developments in molecular biology and gene technologies to genetically modify plants provide further opportunities for enhancement of nutrient efficiency, but this requires more information before the approach can be justified.

Genetic adaptation of crop plants to low-nutrient environments: Morphological and ecophysiological characteristics of adaptation

H. Nakano¹, J. J. Adu-Gyamfi², and T. Nakamura³

1. *Hokkaido National Agricultural Experimental Station (HNAES), Shinsei, Memuro, Kasaigun, Hokkaido 052-0071, Japan*
2. *Natural Resource Management Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India*
3. *Japan International Research Center for Agricultural Sciences (JIRCAS), 1-2 Ohwashi, Tsukuba, Ibaraki 305-8686, Japan*

Considerable effort, money, and time have been invested in core collections of huge numbers of crop germplasm accessions by international agricultural institutions (including ICRISAT). These accessions are only useful if a knowledge base for classification and identification of traits is established. New and diversified traits are discovered through the application of improved screening methods on broader genetic collections and in special environments that enable the detection of useful differences among lines. While considerable efforts have been concentrated on screening large numbers of accessions of germplasm collections for such specific traits as pest, disease, and drought resistance, very little has been achieved in screening for traits controlling nutrient [particularly nitrogen (N) and phosphorus (P)] use efficiency. For breeding programs, identification of and classification of plant traits associated with nutrient uptake and utilization efficiency is useful in the development of marker-assisted selection (MAS) for desirable quantitative traits. The morphological and ecophysiological classification of these traits is an aid to understanding the mechanisms of nutrient use efficiency in crop cultivars. The development of reliable screening methods using appropriate parameters is a prerequisite to breeding for cultivars with enhanced tolerance of low-nutrient environments.

Field and greenhouse screening of 100 genotypes each of sorghum and pigeonpea accessions held in the gene bank at ICRISAT, Patancheru were conducted on Alfisols and Vertisols during both rainy and postrainy seasons. Morphological and plant growth characteristics that are contrasting in adaptability to low N and P conditions were identified and classified. The sorghum genotypes used included hybrids, breeding lines, lines that are dwarf and exotic, drought-tolerant, capable of quick early growth, local, low-yielding, high-tillering improved, forage, and some originating from China. The 100 pigeonpea accessions included hybrids, lines from acid and arid regions, high altitudes,

pod borer tolerant, pod fly tolerant, local, dwarf, drought-tolerant, and breeding lines. The N treatments were; no N application (NO), or N applied at 100 kg N ha⁻¹ in two splits (N100). Similarly, two P treatments were; no P applied (P0), and 40 kg P ha⁻¹ (P40). Plant growth characteristics, leaf area, plant height, node numbers, tiller numbers, days to 50% flowering / booting, grain weight, shoot weight, harvest index, and N and P concentrations in leaf and grain were recorded. Correlations between dry matter, harvest index, and N and P concentrations in grain were calculated. The ability of plants to produce high grain yields in soils with low N and P concentrations and hence remove as little N and P as possible from the cropping systems were evaluated.

Results showed that for sorghum, the hybrids, and the forage and improved lines produced higher grain and shoot yields in low-N and -P environments than the other lines. Pigeonpea accessions collected from arid, high-altitude areas and hybrids were the most adapted to low-P environments. Dry matter yield was positively correlated to leaf size, leafweight, and leaf/ stem ratio but not to specific leaf weight (SLW mg DW cm⁻²). The criterion for selection of nutrient efficiency for sorghum depends on the whether breeding is for stover quality or for grain yield. Lines with low phosphorus harvest indices (PHIs) and low nitrogen harvest indices (NHIs) would yield straw that is valuable to livestock and more easily decomposed to produce high quality manure. High PHIs and NHIs are desirable for grain sorghum used as food.

Hybrids and newly improved cultivars produced more biomass and high grain yields in low-nutrient availability conditions than local varieties in this 2-year experiment. The reasons for the low adoption of hybrids and improved varieties by smallholder farmers need further investigation. Questions have been raised about the sustainability of hybrids and the improved varieties that effectively exploit nutrients in low-nutrient environments. Are these hybrids and improved varieties mining the soils and contributing to land degradation?

Genotypic variability and physiological characteristics of crop plants adapted to low-nutrient environments

J. J. Adu-Gyamfi¹, S. Ishikawa¹, T. Nakamura², and H. Nakano³

1. *Natural Resource Management Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India*
2. *Japan International Research Center for Agricultural Sciences (JIRCAS), 1-2 Ohwashi, Tsukuha, Ibaraki 305-8686, Japan*
3. *Hokkaido National Agricultural Experimental Station (HNAES), Shinsei, Memuro, Kasaigun, Hokkaido 052-0071, Japan*

Despite the considerable progress made in breeding for high-yielding, pest and disease resistant cultivars of crop plants, yields realized on smallholder farms in the semi-arid tropics (SAT) remain in the range of 20-30% of those achieved on experimental or research stations. Low nutrient availability particularly of nitrogen (N) and phosphorus (P) rather than the total N and P contents in soils, is one of the major causes of this yield gap. The USAID Title XII International Sorghum/Millet Collaborative Research Program (INTSORMIL) has made significant progress in improving the N-use efficiency of sorghum and millet. There is however, little progress in enhancing P-use efficiency. The availability of differing pools of P in soil and the varietal differences in the adaptation of crops to low-P conditions, provide considerable scope for breeding cultivars for enhanced P-use efficiency.

A series of field and greenhouse (solution culture) experiments were conducted on sorghum and pigeonpea lines during 1996 to 1998, to assess the extent of genotypic variation among cultivars, identify physiological and agronomic traits, and investigate and prioritize candidate mechanisms responsible for the adaptation of the crops to low-N and -P environments. Fifteen genotypes each of sorghum and pigeonpea (hybrids and improved, local, drought-tolerant, and breeding lines selected from an initial screening of 100 genotypes) were evaluated in low-N or low-P Alfisols. The N levels were 0, 25, and 100 kg ha⁻¹ applied as two split doses to sorghum. The P levels were 0 and 40 kg ha⁻¹ applied to sorghum and pigeonpea. In the greenhouse, combinations of two N levels (0.2 and 1.0 mM N) and three P levels (4, 20, and 100 µM P) were supplied in solution culture. To compare the uptake, translocation, and distribution of N, P, and carbon (C), isotopes ³²P, ¹⁵N, and ¹³C were used. Plant growth characteristics, and N and P concentrations at the early vegetative stage, booting, and final harvest were recorded. Lipid, inorganic, ester, and residue P fractions in plant parts were determined. Nutrient efficiencies, uptake, incorporation, and utilization were calculated.

Biomass, grain yield, and N and P accumulation were highest in the hybrids, improved cultivars, and Chinese lines compared to the local cultivars, breeding lines, and drought-tolerant cultivars. The few exceptions were a medium-duration breeding line of pigeonpea and a drought-tolerant forage sorghum that recorded high biomass but low grain yields. N uptake was significantly increased by P supply. Low-P supply depressed leaf area and shoot weight more than root weight and root length. Whereas there were small differences in uptake efficiency, large and significant differences in incorporation and utilization efficiencies were observed among the cultivars and crop species. At low-P the hybrids, and improved and Chinese lines translocated more N, P, and photosynthates from lower leaves to the growing plant parts (flag leaf and terminal buds) and grains than did local and breeding lines. The sequential translocation of N, P, and photosynthates from roots to leaves (particularly to the flag leaves) by the hybrids and the improved genotypes compared to local ones could be used as a selection criterion for N- and P-efficient cultivars. Differences in the utilization of P fractions among cultivars were observed.

Leaf area expansion, the rapid and efficient translocation of nutrients from old leaves to the growing parts, and the ability to take up nutrients (particular P) at low-P availability are important characteristics for adaptation to nutrient-stressed environments. However, selection and manipulation need to be made in consideration of the end product, be it forage or grain yield. For forage sorghum, uptake efficiency seems to be more important than utilization efficiency. Other experiments on soil/water/nutrient/genotype interactive effects on sorghum and pigeonpea are discussed.

Physiological adaptations for nitrogen use efficiency in sorghum

J. W. Maranville¹ and S. Madhavan²

1. Department of Agronomy, and

2. Department of Biochemistry P O Box 880 664, University of Nebraska, Lincoln, NE 68583-0817, USA

Among other definitions, nitrogen use efficiency (NUE) has been defined as the amount of grain or biomass produced per unit of nitrogen (N). Biomass per unit N is simply the inverse of plant N concentration and can conceptionally imply some physiological efficiency for N use contrasted to other definitions that account for uptake from soil. The exact biochemical/physiological mechanism(s) by which plants may derive greater NUE are not known. To increase NUE, a plant must maintain photosynthesis while leaf N is being reduced. This would imply that some entity related to both photosynthesis and N metabolism might be involved, such as carboxylating enzymes that not only catalyze CO₂ fixation, but also store organic N. This hypothesis was tested in sorghum by conducting a series of greenhouse experiments using two genotypes from China known to have high NUE (95-105 g DM g⁻¹ N) compared to U.S. genotypes known to be low for NUE (65-75 g DM g⁻¹ N) when grown under deficient soil N conditions. Carboxylase activity was estimated by plotting carbon assimilation rate (A) against internal leaf CO₂ concentration (C_i) over time, and chlorophyll concentration, PEP carboxylase, RuBisCo, and NADP-malic enzyme activities and amounts, carbon isotope discrimination, and NUE were also determined. Experiments contained two soil-N levels (sufficient and deficient) and had five to seven replicates per run.

Results of these studies confirmed the high NUE values of the China lines (g biomass g⁻¹ N). Chlorophyll concentration in leaves of the high NUE lines was lower at both soil N treatments. A plant profile of leaf chlorophyll showed that China lines senesced lower leaves quicker than U.S. lines which may indicate more N translocation to upper leaves with N stress. Carbon isotope discrimination values were able to distinguish N stress, but were not different between the two sorghum groups. Carboxylation efficiency indices (A_{ci}) were significantly greater for the China lines than the U.S. lines at each soil-N level by about two-fold, indicating greater carboxylation enzyme activity. Photosynthesis rates measured at flowering did not differ between the high and low NUE groups at adequate soil-N. However, when severe N-stress was imposed, the China lines had photosynthesis rates 37% lower than those at high soil-N compared to a

drop of 44% for the less-efficient U.S. lines. While the amounts of PEP carboxylase and RuBisCo enzymes were dramatically reduced, the amount of NADP-malic enzyme appears to not be affected by severe N-stress. Activity of PEP carboxylase was maintained at a comparatively higher rate than the other enzymes with N-stress in the China lines, especially China 17 compared to the U.S. lines.

From these results, it appears that sorghums with greater NUE and more tolerance to low N-stress have the ability to maintain photosynthesis by a preferential maintenance of an active PEP carboxylase enzyme. This, in part, helps maintain growth and productivity under conditions where soil-N is severely limiting.

Photosynthesized carbon translocation and distribution of crops adapted to low-nutrient environments

K. Fujita¹, M. I. Chaudhary¹, A. Fujita¹, Y. Kai¹, M. Takayanagi¹,
H.El Sherry¹, and J.J. Adu-Gyamfi²

1. Faculty of Applied Biological Science, Hiroshima University, 1-4-4 Kagamiyama, Higashi-Hiroshima 739-8528, Japan
2. Natural Resource Management Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India

Reduction in plant leaf area and growth as a consequence of phosphorus (P) limitation have been attributed to the direct effects of P shortage on the expansion of individual leaves, and to a reduced production of assimilate required for growth. A series of field and pot experiments were conducted to assess the effect of low-P supply on photosynthesis, photoassimilate partitioning, leaf area expansion, and on the ethanol-soluble (cytosol) and cell wall fractions (pectin hemicellulose and cellulose). The crops used were pigeonpea, mashbean, mungbean and soybean. Phosphorus levels were 5 and 200 kg P ha⁻¹ for the field experiments and 5 and 250 kg P ha⁻¹ for the pot experiments. Leaves were exposed to ¹³CO₂/¹²CO₂ (99.5 atom % ¹³C) for 2 hours in natural light conditions using a steady state ¹³CO₂/¹²CO₂ feeding system. The carbon (C) content and the ¹³C abundance in ethanol and water-soluble cellulose and hemicellulose fractions were determined using a mass spectrometer (MAT 252[®], Finnigan, San Jose, California, USA)

Biomass and leaf area expansion were severely decreased by low P, however, there was genotypic variation among the pigeonpea cultivars used. Low-P treatment resulted in a decrease in P concentration in whole leaves and cell walls but an increase in the cytosol fraction. P limitation resulted in the partitioning of more ¹³C assimilates to roots and less to leaves and stems. For pigeonpea, a hybrid (ICPH 8) which is more adapted to low-P conditions than the non-hybrids (ICPL 87 and UPAS 120) recorded a relatively higher amount of ¹³C in leaves and stems than the non-hybrids. The sorghum genotype (IS 37005), that is more adapted to low-P, distributed more ¹³C to its growing leaves and culms but less to the roots than the hybrid CSH 9. The ¹³C fractions in cytosol and cell walls decreased with low-P in the sorghum hybrids but increased in the non-hybrids.

These results suggest that at low-P availability there is increased partitioning of photoassimilates to roots and less to the growing leaves. The synthesis into hemicellulose and cellulose in leaves is suppressed, causing an inhibition of leaf area expansion. Leaf area expansion is an important trait related to increased

crop productivity. The variability among crop plants in the translocation of photoassimilates to leaves and the other growing parts at low-P availability provides a scope for genetic manipulation of this trait to improve the adaptation of crops to P-stressed environments.

Variability in rooting behavior and nutrient uptake of crop plants in low-nutrient environments

T. Nakamura¹, J. J. Adu-Gyamfi², A. Yamamoto³, S. Ishikawa²,
H. Nakano⁴, and O Ito¹

1. Japan International Research Center for Agricultural Sciences (JIRCAS), 1-2 Ohwashi, Tsukuba, Ibaraki 305-8686, Japan.
2. Natural Resource Management Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India
3. Experimental Farm of Tohoku University, Tohoku University, Miyagi 989-67, Japan
4. Hokkaido National Agricultural Experimental Station (HNAES), Shinsei, Memuro, Kasaigun, Hokkaido 052-0071, Japan

Despite the important role played by roots in nutrient and water acquisition from soils, roots have been given little attention in field experiments because of their hidden nature, and the technical difficulties of below-ground data collection. The ability of roots to acquire and use soil and fertilizer nitrogen (N) is an important adaptation of crops to the infertile soils of the semi-arid tropics. While developing and releasing hybrids and improved varieties to farmers in nutrient-stressed semi-arid environments, there has been insufficient focus on such resource management aspects as N uptake and N-use efficiency. Unless the basic and critical constraints of nutrient efficiency are addressed, no hybrid or improved cultivar can achieve sustainable yields in less-endowed environments.

Sorghum hybrids are known to outyield local varieties when given high inputs of fertilizer N. However, under N-limiting conditions farmers prefer local varieties to hybrids because they may be adapted to limited-N conditions. Field and greenhouse experiments were conducted to compare the physiological basis of growth and dry matter production in a hybrid and a local variety of sorghum by examining the relationship between root growth and N absorption rate. Sorghum hybrid (CSH 9) and a local variety (FSRP) were grown on an Alfisol. Two N levels; no fertilizer (ON) and 100 kg N ha⁻¹ (100 N) were applied as urea at sowing. For the kinetic experiments, NO₃-N uptake rates at different nitrate solution concentrations ranging from 0.05 to 2.0 mM were calculated. The kinetic parameters Michaelis constant (K_m) and maximum uptake rate (V_{max}) were determined.

The N absorption rate of the plant was calculated from the amount of N accumulated by the plant per day, and the relative N absorption rate (RAR) as the N absorption rate divided by the dry weight of the plant. Specific N absorption rate per root mass (SRA), the distribution of dry mass to the root (FWR), specific

N absorption rate per root length (SRAL), and specific root length (SRL) were calculated using the following equations:

$$\text{RAR} = \text{SRA} \times \text{FWR}$$

$$\text{SRA} = \text{SRAL} \times \text{SRL}$$

Results showed that the grain yield and harvest index (HI) of the hybrid (CSH 9) were higher than those of the local variety (FSRP) irrespective of the rate of applied N (0 and 100 kg N ha⁻¹). The grain yield of the hybrid was reduced less than that of the local variety when no N was applied. The SRA was highly correlated to RAR, but not to FWR, it was also highly correlated to SRAL, but not to SRL. The SRA and SRAL at physiological maturity were higher in the hybrid than in the local variety and were better maintained in the hybrid when no N was applied. Similar results were obtained from the pot experiments.

For the kinetic analysis of nitrate uptake by roots, V_{\max} in the hybrid roots was higher than that in the local variety. K_m in the hybrid was slightly higher than that of the local variety. The V_{\max}/K_m ratio of the hybrid was higher than that of the local variety. This indicated that the roots of the hybrid were more able to absorb N than those of the local variety. The finding that N absorption ability of hybrid roots is higher than that of local variety suggests that the hybrid is better adapted to limited-N conditions than the local variety because the hybrid had greater root proliferation than the local variety.

Genotypic variability in phosphorus solubilizing activity of root exudates by crops grown in low-nutrient environments

S. Ishikawa¹, J. J. Adu-Gyamfi¹, T. Nakamura², T. Yoshihara³, and T. Wagatsuma⁴

1. *Natural Resource Management Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India*
2. *Japan International Research Center for Agricultural Sciences (JIRCAS), 1-2 Ohwashi, Tsukuba, Ibaraki 305-8686, Japan*
3. *Department of Bioscience and Chemistry, Hokkaido University, Kita - 9, Nishi-9, Kita-ku, Sapporo 060- 8589, Japan*
4. *Laboratory? of Plant Nutrition and Soil Science, Yamagata University, Tsuruoka, Yamagata 997-8555, Japan*

The release of organic acids from roots in response to phosphorus (P) deficiency is an effective way plants can acquire and utilize such relatively immobile ions as sparingly soluble P in soils. Pigeonpea is known to solubilize iron (Fe)-bound P by exuding piscidic acid from its roots. The exploitation of plant genetic variation in the acquisition of unavailable insoluble P accumulated in soils has been increasingly emerging as an alternate approach to improve productivity in low-nutrient environments. This study aimed to investigate the genotypic differences in P solubilizing activity of pigeonpea exudates and the role of organic acids and phenolic compounds (piscidic acid) in P acquisition from soils low in available P.

A pot experiment was conducted to compare the growth and P uptake of plants at flowering stage among four pigeonpea genotypes [ICPH 8 (hybrid), ICPL 87 (improved), Manak (local), and ICPL 88039 (drought-tolerant)]. The soil used was an Alfisol containing 4.1 mg available P (Bray 11) kg⁻¹ and 35 mg Fe-bound P kg⁻¹. Four different forms of fertilizers, namely aluminium phosphate (AlPO₄; Al-P), iron phosphate (FePO₄H₂O; Fe-P), apatite [Ca₅OH(PO₄)₃; Ca-P], and single superphosphate (SSP) at 40 mg P kg⁻¹ were applied at sowing. There was also a control (no P applied; P₀). The dry weight and P uptake in all the genotypes tested except for Manak were in the order of P₀ < Al-P, Fe-P < Ca-P < SSP, and those of Manak were in the order of P₀, Al-P < Ca-P < Fe-P < SSP. The dry weights and P uptakes by Manak in the P₀ and Fe-P treatments were higher than in the other genotypes. The results suggest that there is a genotypic variation in the ability of pigeonpea to acquire and utilize Fe-P in Alfisols. The local variety (Manak) has a higher ability to utilize Fe-P in Alfisols than the other

genotypes. A qualitative Fe-P solubilizing activity by root exudates was observed by spotting root exudates on a filter paper permeated with FePO_4 and stained with molybdenum blue. A visible white spot indicate that the sample was able to dissolve Fe-P. A white spot was observed when seedlings were grown in low-P conditions, indicating that root exudates contained Fe-P solubilizing substances. A nondestructive technique based on this assay method showed that Fe-P solubilizing substance was released mainly from root tips. The Fe-P solubilizing activity of carboxylic acid compounds was also tested and found to be in the order of citric acid > piscidic acid, malic acid >> succinic acid. Therefore, such carboxylic acids as citric and piscidic acids in root exudates of pigeonpea were thought to be implicated in the solubilization of Fe-P.

The amount and composition of carboxylic acids in root exudates were determined and compared among pigeonpea genotypes grown in nutrient solutions containing 2 or 80 μM P for 15 or 30 days. The amounts of citric and piscidic acids released from their roots by all the genotypes increased at low-P treatment. There was a significant difference in the release of piscidic acid between treatments after 30 days. To examine the effect of change in P concentration in shoots and roots on carboxylic acid secretion from the roots, seedlings pre-exposed to 2 μM P for 15 days were transferred to the nutrient solution containing 2 or 80 μM P and incubated for 7 more days. A continuous low-P treatment induced a greater release of piscidic acid without a change of internal P concentration in all the genotypes tested. The internal P concentration of plants significantly increased with increasing external P concentration. Consequently, a decrease in citric acid release from the roots was observed, but piscidic acid was continuously released, regardless of the significant increase of P concentration in shoots. Two temperature treatments (25° and 35 °C) had no significant effect on the release of carboxylic acid by the genotype. These results suggest that citric acid may be released from the roots in response to internal P concentration. On the other hand, the release of piscidic acid from roots may depend on the duration of the low-P treatment and plant age in addition to the internal P concentration.

Citric acid was more able to dissolve insoluble P in Alfisols than piscidic, malic, or succinic acids. At least 100 μM of organic acids were required to dissolve approximately 5 μM P from insoluble P in Alfisols. Phosphate release from Alfisols by root exudates collected at the low-P treatment was undetectable.

No correlation was found between genotypic variability in the release of piscidic acid from the roots under low-P treatment (Manak, ICPL 88039 > ICPH 8 > ICPL 87) and in the growth and P uptake of plants on Alfisols (Manak > ICPL 87, ICPH 8 > ICPL 88039).

Although pigeonpea has a specific Fe-P solubilizing ability because it can exude carboxylic acid from its roots in P-deficient conditions, the difference in

the growth and P uptake among pigeonpea genotypes grown in an Alfisol could not be explained by the amounts of citric and piscidic acids secreted from the roots. It will be necessary to investigate the concentration in the rhizosphere, the characteristics of adsorption to soils, and the effect of microorganisms on organic acids released from roots in soils low in available P.

A proposed new phosphorus(P) uptake mechanism by groundnut and pigeonpea - P solubilizing reaction on the root surface

N. Ae and R-F Shen

*Division of Soil Sciences, National Institute of Agro-Environmental Sciences (NIAES),
3-1-1 Kannondai, Tsukuba, Ibaraki 305-8604, Japan*

Groundnuts take up more phosphorus (P) from soils of low P fertility than sorghum and soybean. This ability could not be attributed to differences in root development, in P uptake parameters such as K_m and C_{min} or to the excretion of root exudates capable of solubilizing iron (Fe) and aluminium (Al) bound P, the sparingly soluble P forms in soils. Root exudates were not detected in significant quantities throughout the groundnut-growing season. Because neither root length nor root exudates could explain the superior ability of groundnuts to survive in P-deficient soils, their superior P uptake must be due to a yet unidentified mechanism. Plant roots acquire P by diffusion rather than mass flow because P concentrations in the soil solution are very low due to the strong adsorption of P to the surface of clay minerals. These low-P concentrations subsequently reduce P-diffusion coefficients particularly in soils of low-P fertility.

Groundnuts, sorghum, and soybean were grown in an extremely P-deficient soil. Groundnuts grew and set pods but soybeans and sorghum could not survive. The fact that other crops did not survive in this P-deficient soil indicates that P concentrations in the soil solution must have been negligible, and that diffusion of P to the root surface of plants must have been equally negligible. If transport of P to roots is insufficient, P solubilization in groundnuts has to occur in the contact zone between root and soil. Attention was therefore focused on the interaction between root surfaces and soil particles, that is the "contact reaction" between epidermal root cell walls and P-fixing minerals.

Fresh roots of groundnut, soybean, and sorghum were collected from plants grown in sand culture. Roots were harvested 2 months after sowing. Crude cell walls were obtained by grinding and subsequently washing root samples with 0.5 M HCl to remove minerals from the root surface. A pure cell wall was obtained after component washing with sodium deoxycholate to remove plasma membranes and organelles.

The P-solubilizing reaction between the root cell wall preparation and Fe - or Al-phosphates was observed. Root cell walls of groundnut solubilized more Fe/Al-P than cell walls of sorghum and soybean. These results were repeated with naturally occurring P-containing minerals such as hematite and allophane.

The cell wall activity of groundnut roots thus partly explains the superior growth of this crop under P-deficient conditions. To characterize the active site for P solubilization, the effect of pH, heat, enzyme digestion, and addition of other cations on P solubilization were investigated. Furthermore, it was investigated whether the cation exchange capacity (CEC) of root cell walls, derived from polygalacturonic acid in the cell wall pectin, is the primary cause for the solubilization of P. Results indicate that; 1. the solubilizing ability is not related to root CEC because soybean, with a higher root CEC than groundnut, was inferior in solubilizing P, 2. the reaction site of groundnut root cell walls is stable against heating and digestion with cellulose and pectinase, and 3. pre-treating cell walls with either Al^{3+} , Fe^{3+} , or Ga^{3+} decreased solubilization, but cations with lower valency such as Na^+ , K^+ , Ca^{2+} , or Mg^{2+} had no effect. The active site for solubilization therefore appears to be specific to tri-valent cations.

In previous work, it was shown that pigeonpea also has the ability to take up P from sparingly soluble Fe- and Al-bound P forms. This ability was associated with the excretion of root exudates that form chelates with Fe or Al in the soil, thus releasing P. Piscidic acid was the first carboxylic acid with chelating ability detected in exudates from pigeonpea roots and further experiments revealed the presence of malonic and oxalic acids that also have a chelating ability with Al^{3+} and Fe^{3+} . To determine the quantity of organic acids in root exudates, pigeonpea was cultivated at three P levels and exudates were collected in weekly intervals. Exudation of organic acids with chelating ability sharply increased during the flowering stage (9-11 weeks after sowing). Exudation of malonic, citric, malic, and piscidic acids and the P-solubilizing capacity of the exudates were enhanced by excess P rather than by P-deficiency. These results suggest that the exudation of chelating organic acids from pigeonpea seem to be controlled by the plant growth stage, not by P-deficiency. This phenomenon led to the question of how young pigeonpea can take up P from a low-P soil before the onset of root exudation.

Pigeonpea roots were grown in sand and collected at an early growing stage to test the hypothesis that the "contact reaction" similar to that in groundnut root cell walls is able to solubilize P. The solubilizing ability of pigeonpea cell walls was compared to those of soybean, maize, and groundnut. Pigeonpea root cell walls solubilized as much P as groundnut root cell walls and significantly more than soybean and maize. This finding suggests that the "contact reaction" theory may not be unique to groundnut.

Recently a new concept termed "contact reaction" was proposed. This postulates that P-solubilization occurs at the interface of root surface with P-containing soil particles. The better adaptation of crop species like groundnut and pigeonpea to P-deficient soils may be explained by the higher P solubilizing ability of their root cell walls than that of other crops. The identification of chemical structure(s) of these active sites in groundnut and pigeonpea root cell walls is, however, needed to fully establish the theory.

Role of soil microorganisms in improving P nutrition of plants

Gyaneshwar P.¹, G Naresh Kumar², L. J. Parekh², and P.S. Poole³

1. Soil and Water Sciences Division, International Rice Research Institute (IRRI), MCPO Box 3127, 1271 Makati City, Philippines
2. Department of Biochemistry, M. S. University of Baroda, Vadodara 390 002 Gujarat, India
3. School of Animal and Microbial Sciences, University of Reading, Whiteknights, P O Box 228, Reading RG 6 6 AJ, UK

Phosphorus (P) is one of the major plant growth-limiting nutrients even though it is abundant in soils in both inorganic and organic forms. However, available P concentration in soils is extremely low due to its high reactivity with calcium (Ca), iron (Fe), and aluminium (Al) leading to its precipitation and resultant unavailability to plants. To alleviate the P deficiency in agricultural soils, chemical fertilizers are added. However, 75-90% of the added P is not available to the plants as it becomes immobilized by the cations present in the soils. The added fertilizers usually far exceed the crop requirement, resulting in an increase in the total P concentration in agricultural soils. It has been estimated that accumulated P is sufficient to sustain maximum crop yields for 100 years. Microorganisms can play an important role in retrieving this accumulated P that could enhance plant growth in an eco-friendly and sustainable manner.

Phosphate-solubilizing microorganisms (PSMs) are ubiquitous in soils and there have been extensive studies with PSMs to determine their effect on the P status of inoculated plants. However, the results have been variable. In spite of the importance of PSMs in agriculture, the detailed biochemical and molecular mechanisms of P solubilization are not known. Doubts have been raised about the efficiency of the PSMs in soils, as the soil conditions are different from those in the laboratory.

Recent work has shown that the present screening procedure employed is not effective in selecting the better PSMs, and that there are significantly fewer PSMs that can probably solubilize soil P than those solubilizing P during screening. Incorporating a buffer in the screening medium and using such sparingly soluble P as rock phosphates can isolate better PSMs. Using such a modified medium a P-solubilizing *Enterobacter asburiae* was isolated, this bacterium could release P from soil. The bacterium secreted gluconic acid and the activity of glucose dehydrogenase (GDH) was induced by phosphate starvation. Mutants in the GDH activity failed to solubilize soil P, indicating that secretion of gluconic acid was the major factor involved in P solubilization

Understanding the genetic basis of P solubilization can help in transforming the more rhizosphere-competent bacteria into PSMs. Genes involved in gluconic acid production have been cloned from P-solubilizing *Pseudomonas cepacia* and *Erwinia herbicola*. Additionally it has been shown that mineral phosphate solubilizing (*mps*) genes could be cloned from non-P solubilizing *Synechocystis* PCC 6803. These results imply that the *mps* genes are not restricted to PSMs and that metabolic engineering of such plant growth promoting bacteria as *Pseudomonas* and *Rhizobium* for solubilizing mineral P will help in generating novel PSMs that will have better chances of being effective in field conditions.

Phosphorus use efficiency as related to sources of P fertilizers, rainfall, soil, crop management, and genotypes in the West African semi-arid tropics

A. Bationo¹, J. Henao², and K. Anand Kumar³

1. *International Fertilizer Development Center / International Crops Research Institute for the Semi-Arid Tropics (IFDC/JCRISAT) BP 12404, Niamey, Niger*
2. *International Fertilizer Development Center (IFDC), PO Box 2040, Muscle Shoals, Alabama, AL 35662, USA*
3. *International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), BP 12404, Niamey, Niger*

In the West African semi-arid tropics, lack of volcanic rejuvenation has caused the region to undergo several cycles of weathering, erosion, and leaching, leaving soils lacking many nutrients. Low and erratic rainfall, high soil temperatures, the poor native fertility of the soil, surface crusting, and the soils' low water-holding capacity are major constraints to crop production.

The aforementioned adverse conditions combined with management practices inadequate to replenish soil nutrients have led to low soil fertility resulting in low productivity. Among soil fertility factors, phosphorus (P) deficiency is a major constraint to crop production. Both total and available P values are very low. Response to nitrogen (N) is substantial only when both moisture and P are not limiting. Although lack of water limits crop production in the drier zones in the Sahel, all available evidence indicates that inherent low fertility (mainly P) is a more serious problem.

Phosphorus dynamics in the soils are complex, because they involve both chemical and biological processes and the long-term effects of sorption (fixation) and desorption (release) processes. In soils that are used for pearl millet production, total P ranged from 25 to 349 mg kg⁻¹ with a mean of 109 mg kg⁻¹. The majority of these soils have available P levels far below the critical P levels needed for most of the crops grown in the region. The maximum P sorbed ranged from 28 to 253 mg kg⁻¹ with a mean of 129 mg kg⁻¹. Soils of this region can be considered as having relatively low P-sorption capacities compared to the clay-rich Ultisols and Oxisols found in the more humid tropical regions. As a result of the low P-sorption capacity, only small quantities of P-fertilizers are needed to satisfy crop requirements.

Research has been undertaken over several years and locations to assess the extent of P deficiency in the soils, to estimate the P requirement of major crops, and to evaluate the agronomic potential of various phosphate fertilizers including

phosphate rock (PR) from local deposits. Here, water-soluble P fertilizers, PR sources from Niger (Parc-WPR and Tahoua PR), Mali (Tilemsi PR), and Burkina Faso (Kodjari PR) and modified partially acidulated phosphate rocks (PAPR) are compared for their effects on P-use efficiency (grain yield kg/P applied kg). Partially acidulated phosphate rock improved the P-use efficiency of PR sources. Among the four PR sources in the region, Tilemsi and Tahoua PR gave the highest P-use efficiency compared to Kodjari or Parc-W sources. Soil acidity and rainfall affected the agronomic efficiency of the different PR sources. PR performance is enhanced in the flooded systems used for rice production.

P-use efficiency differs among the main cereals (sorghum, pearl millet, and rice) and legumes (cowpea and groundnut) grown in the region, but very little research has been undertaken to relate this to the root system. In a comparison among 9 pearl millet genotypes, the P-use efficiency ranged from 20 to 80 kg grain/kg P applied, but there was no significant relationship between P-use efficiency and the yield of these genotypes under control (no P application) conditions.

In the Sudano-Sahelian Zone of West Africa, end-of-season drought is a common phenomenon. The analysis of data from long-term soil fertility management trials indicates a significant relationship between pearl millet biomass production and the total amount of rain received in September, the last of the 4-5 month growing season. P-use efficiency for total dry matter varied from 125 kg/kg P with 50 mm rainfall to 230 kg/kg P with 200 mm rainfall received in September for pearl millet total dry matter with the application of single superphosphate.

Soil and crop management play an important role on P acquisition. The application of crop residues enhances root growth, root colonization with vesicular arbuscular mycorrhizae (VAM), and P uptake. Whereas P-use efficiency was 67 kg grain / kg P with fertilizer application, it increased to 137 kg grain / kg P when an additional 4 t ha⁻¹ of crop residues was applied.

Rotation of cereals with legumes also plays an important role in P nutrition. P-use efficiency in continuous pearl millet cropping system was 46 kg grain / kg P, whereas it increased to 73 kg / kg P when pearl millet was rotated with cowpea. Methods of P-fertilizer application have a significant effect on P-use efficiency. Recent research indicates that hill placement of small quantities of P fertilizers (4 kg P ha⁻¹) will increase P-use efficiency compared to the present recommendation of broadcasting 13 kg P ha⁻¹. Opportunities for increased efficiency of P utilization through cultivar improvement, include selection for treatments that favor strong plant demand such as late maturity, increased rootlet activity, and increased P solubilization capacity.

Future research needs to focus more on understanding the factors affecting P uptake including the ability of plants to; 1. solubilize soil P through pH changes

and the release of chelating agents and phosphate enzymes, 2. explore a large soil volume, and 3. absorb P from low soil solution concentration. Understanding the relationship between uptake efficiency and utilization efficiency needs further investigation. The potential gains in improved nutrient acquisition are not clear and need to be estimated to set breeding priorities. As total P in most of the soils is very low, emphasis should be put on selection of genotypes for improved P utilization from locally available rock phosphate.

Exploitation of plant genetic differences in solubilizing P from sparingly soluble sources

G.R.Findenegg

Wageningen Agricultural University, Broekemalaan 18, 6703 GM Wageningen,
The Netherlands

When making use of the plants' genetic capabilities for improving crop nutrient acquisition in poor environments, three research phases can be distinguished:

1. Identification of physiological mechanisms in nutrient acquisition under nutrient-poor conditions and specification of growth conditions and plant genotypes where these mechanisms are active. This involves laboratory experiments.
2. Estimation of the efficiency of the identified mechanisms under laboratory and field conditions and their quantitative contribution in total uptake of the limiting nutrient. Laboratory and field experiments and computer simulations are required.
3. Identification of the genes involved in the efficient mechanisms and transfer of these genes into suitable crop genotypes. Assessment of performance in the field is required.

Investigations on phosphate acquisition from mineral organic, and adsorbed sources are reported.

Mineral sources

Excretion of organic acids from the roots of rape plants is dramatically increased under phosphate-starved conditions. When grown in the absence of phosphate, citric and malic acids are excreted from a specific part of the roots - behind the root tips - at a rate of ~1 nmol per cm root length during 2 hours. In a well-defined rooting medium (sand with rock phosphate moistured with phosphate-free nutrient solution) the rhizosphere acidification resulting from this excretion is sufficient to make rock phosphates available for uptake. This experimental finding was verified by computer simulation of the rhizosphere processes.

Simulation studies have also revealed that the concentrated excretion of organic acids from a limited part of the root surface is more efficient in phosphorus (P) solubilization than the excretion of the same amount of acids would be, when distributed homogeneously over the whole root surface. The efficiency of the localized excretion is strongly intensified by the fact that when rock phosphate is locally available in the rooting medium, the excretion of organic acids shifts along the root so that the organic acid are excreted in the vicinity of the rock phosphate particles.

In *Sisymbrium* sp., a weed species taxonomically related to rape, phosphate starvation does not result in an enhanced excretion of organic acids from the

roots. Nevertheless, deficiency of P results in a similar degree of citric and malic acid accumulation in the leaves and roots of both species. However, only in rape but not in *Sisymbrium* are the organic acids are excreted from the roots.

Organic sources

The phytase activity of roots is another mechanism of potential importance for the mobilization of phosphates from soils. However, the solubility of such organic phosphates as phytates in the soil is low, and precipitated phytates are not attacked by phytase. When phytase is externally added to a sand moistened with P-free nutrient solution, P availability from added phytate is clearly increased for maize roots. But, if soil is used instead of sand, no significant positive effect is observed from the addition of phytase.

Adsorbed sources

The acidification effects of excreted organic acids on P availability observed with rape plants seem to be of importance for applied rock phosphates and for high pH soils. In order to estimate the effect of organic (especially citric) acid on P availability in tropical soils other experiments have been conducted with P adsorbed to goethite, again mixed with sand, and moistened with P-free nutrient solution. As expected, P-availability for maize roots (known to have only low organic acid excretion rates) depended strongly on the amount of P loaded. For the computer simulation of the rhizosphere sorption processes a physico-chemical charge model of the goethite surface that took into account the adsorption of phosphate, citrate, and other components of the nutrient solution was used. Simulation results agreed well with experimental observations at a high P adsorption density on the goethite, but underestimated it at a low adsorption density. Detailed studies in homogeneous media (suspension culture) of different compositions have shown that this disagreement was due to the fact that competition of the sulphate in the nutrient solution with phosphate and citrate for the goethite adsorption sites was not taken into account in the simulation model.

The adsorption model has been extended to include the combined effects of pH, sulphate, and citrate on phosphate adsorption on goethite in the rhizosphere. Subsequently, the effect of citrate excretion has been estimated by running the simulation model for maize roots with imposed citrate excretion rates comparable to those reported in the literature for other species. At a high P adsorption density of $1.9 \mu\text{mol m}^{-2}$ goethite surface area, a citrate excretion of $0.5 \text{ nmol cm}^{-1} \text{ day}^{-1}$ (corresponding to an investment of approximately 3 to 11 % of the plant dry matter increase) increased P uptake by about 10%. However, at a lower adsorption density ($1.1 \mu\text{mol m}^{-2}$) the same excretion rate increased P uptake more than 10-fold. These calculations emphasize the importance of citric acid excretion for P acquisition of roots in tropical soils.

Modelling root-induced solubilization of nutrients

G.J.D. Kirk

*Soil and Water Sciences Division, International Rice Research Institute (IRRI), MCPO
Box 3127, 1271 Makati City, Philippines*

Roots interact with the soil around them in various complicated ways, and identifying the processes that are important in regulating nutrient dynamics, and, from these, processes that might be manipulated by plant breeding or agronomy, is a complicated matter. Mathematical modelling can help. In fact it may be essential where several interacting rate-processes must be considered and plant physiological and soil processes linked together. Early models of nutrient uptake by roots considered the roots to behave as cylindrical sinks to which nutrients moved by mass flow and diffusion. Root demand for the nutrient could vary, but the roots did not otherwise influence the soil. These models worked reasonably well for the more soluble nutrient ions, such as NO_3^- . But for the less soluble nutrients, such as phosphorus (P), it was evident that the roots played a more active role and were in some cases able to bring about an increase the concentration of the nutrient in the soil solution.

At IRRI a theory developed for such situations has been applied to solubilization of P by rice plants (a) growing in aerobic soil, and (b) growing in flooded, anaerobic soil.

For rice growing in aerobic soil the solubilization involves excretion of organic anions from the roots. Measurements of the P pools depleted by rice growing in an aerobic, highly weathered P-deficient soil showed that the bulk of the P was solubilized from an alkali-soluble inorganic pool. The solubilization could not be explained by root-induced pH changes, nor by increased mineralization of organic P. Subsequent measurements showed a substantial excretion of organic anions, principally citrate, from rice roots into nutrient solution and soil, and it is postulated that this was responsible for the solubilization. A mathematical model was used to demonstrate that the amounts of citrate excreted and their P solubilizing effects were sufficient to account for the observed P solubilization and uptake. The model allows for the diffusion of citrate away from the roots, its decomposition by soil microbes, its reaction with the soil in solubilizing P, and the diffusion of P back to the absorbing roots as well as away from them. The model was tested by comparing measured concentration profiles of P near roots with the predictions of the model made using independently measured parameter values. The agreement between the observed and predicted concentration profiles was very good, indicating that the theory is sound and the processes involved

well understood. A sensitivity analysis of the model showed that its predictions are sensitive to the rate of citrate decomposition. Thus any process that increases the longevity of the organic anions in the soil, such as the release of anti-microbial agents from the roots, will have a large effect on P solubilization and uptake.

For rice growing in anaerobic soil the solubilization is caused by root-induced acidification resulting from (a) Fe^{2+} oxidation by O_2 released from the roots, and (b) H^+ released from the roots to balance excess intake of cations over anions under NH_4^+ nutrition. A model of this process similar to that for solubilization by organic anion excretion has been developed, and IRRI scientists obtained similar good agreement between measured P depletion profiles near rice roots in flooded soil and those predicted by the model using independently measured parameter values.

These models have been used to study the effects of root geometry on P solubilization and the effect of excretion of a solubilizing agent being localized along the root axis. A comparison of cylindrical versus planar geometry showed that the ratio of P uptake to solubilizing agent excreted is smaller in cylindrical geometry than planar, a smaller proportion of the P solubilized being taken up. The importance of this effect depends on the relative rates of diffusion of P and the solubilizing agent in the soil. But in a system of many roots, neighbouring roots may benefit from P solubilized by each other. The situation is further complicated if excretion of the solubilizing agent is localized along the root axis rather than distributed uniformly. Localization can greatly increase the effectiveness of the solubilizing agent.

Scope for genetic manipulation of mineral nutrition in chickpea

M Y. Ali¹, L. Krishnamurthy¹, N.P. Saxena¹, O.P. Rupela², Jagdish Kumar¹, and C. Johansen²

1. *Genetic Resource and Enhancement Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India*
2. *Natural Resource Management Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India*

Nutrient acquisition in chickpea needs to be efficient, as this annual crop is largely grown rainfed in marginal soils. The extent of the root system and its efficiency in nutrient uptake are the plant factors that influence mineral nutrition. Recent research has explored in detail the root system of chickpea and its function in acquiring water and nutrients. This information is reviewed and synthesized so as to examine the scope for genetic enhancement of the ability of chickpea to acquire and efficiently use nutrients. Nutrient deficiencies cause yield losses of varying magnitude: for example, 40-48% are due to lack of iron (Fe), around 10% to sub-optimal nodulation, 28-49% to phosphorus (P) and up to 100% are due to lack of boron (B). There is a possibility of alleviating these losses by breeding for nutrient-efficient genotypes.

The prolificacy of root distribution in the soil is a first consideration in acquiring nutrients that are in scarce supply. Studies on chickpea root systems in relation to drought response have confirmed the vigorous and deep-rooting ability of this crop compared to other grain legume species of similar adaptation characteristics. Genotypic variation in rooting traits has been established for chickpea, albeit by laborious root extraction studies. In separate studies genotype CC 4958 was found to possess a more prolific root system than Annigeri or ICCV 10. Periodic irrigation was also found to encourage root growth and longer survival in the top 15cm of soil. The timing of root growth to maximize exploitation of the nutrients applied to the soil surface is another important consideration, as higher root activity, related to nutrient and water uptake is confined to moist soil. Drought-resistant genotypes, that root prolifically, can also acquire relatively more P during vegetative growth than non-resistant genotypes. However, implementation of a genetic enhancement program to enhance root prolificacy would need to rely on the use of molecular markers due to the overwhelming environmental influences, as compared to genetic effects

on root phenotype. Thus, plant-to-plant variation within a genotype needs to be addressed to effectively select for such traits. Considering the difficulty of reevaluating a large number of seedlings and plants for these traits, it would be advantageous to develop flanking molecular markers to select such quantitative trait loci (QTLs). This technology is rapidly progressing. Efforts are already being made to map some QTLs on the cultivated chickpea genome. If this is done, selection for QTLs could be relatively easy.

It has also been established that chickpea has a superior ability to excrete acid from its roots, thereby facilitating dissolution of otherwise unavailable but acid-soluble forms of P in the soil (e.g., calcium phosphates). This acid exudation also affects the availability of such other nutrients as iron (Fe). Recent studies in Japan have established genotypic differences in ability to use Fe and chickpea roots' ability to exude more carboxylic acids under Fe-deficient conditions. Such plant traits might be governed by polygenes (genes with small effects) that are also called QTLs. It should therefore also be possible to develop molecular markers for QTLs governing nutrient uptake and utilization in the near future. Thus there are now prospects of favorably manipulating the chemical composition of the rhizosphere through control of root exudation, to enhance mineral nutrition.

Like other legumes, chickpea can also meet at least 80% of its nitrogen (N) needs through biological nitrogen fixation (BNF). Genotypic variation for N₂-fixation traits has been established. In addition, the natural occurrence of large plant-to-plant differences in nodulation ability and N₂-fixation capacity within landraces (e.g., G 130) and bred cultivars (e.g., ICCV 91019) has been established. Some cultivars (e.g., ICCV 2) even have nonnodulating plants. It was therefore possible to identify high N₂-fixing selections from within high-yielding and agronomically accepted/acceptable cultivars for on-farm use.

Among crop plants, chickpea is relatively sensitive to salinity damage. Although genotypic variation in salinity tolerance of chickpea exists, any sources of substantial tolerance are yet to be identified. Such sources are a prerequisite to embarking on a genetic enhancement program for salinity resistance in chickpea. However, it is now becoming feasible to identify genes controlling salinity resistance mechanisms in other plant species and to transfer these to chickpea; but further fundamental research is required to overcome problems of the appropriate expression of transferred genes. Since sources of tolerance to Fe, B, and perhaps P have been identified, traditional breeding approaches such as rejection of susceptible types in segregating populations, as is practiced in disease-resistance breeding, could be effective in selecting for nutrient-efficient progeny. Enhancing salinity tolerance should be a long-term objective because of the unavailability of sources of tolerance/resistance useful in a breeding program. Molecular marker-aided selection, gene pyramiding, and transgenic approaches are worth applying to this difficult problem.

Recent studies have highlighted the importance of remobilization of nutrients in enhancing grain yield of chickpea, especially under stress conditions. There is scope for better understanding the extent of genotypic differences, the mechanisms involved, and their genetic control. Genetic manipulation of this process could substantially improve chickpea yield potential and stability in specific environments.

It is concluded that recent advances in understanding how chickpea acquires and uses water and nutrients in scarce supply, along with advances in molecular biology, have opened practical possibilities for the favorable manipulation of chickpea mineral nutrition.

Aluminium tolerance in nodulated N₂-fixing legume species native to two contrasting savanna sites

M-L Izaguirre-Mayoral¹, S. Flores², and T. Oropeza³

1. *Instituto Venezolano de Investigaciones Científicas (IVIC). Laboratorio de Biotecnología y Virología Vegetal, Centro de Microbiología y Biología Celular, Apartado Postal 21827, Caracas 1020-A, Venezuela*
2. *Centro de Ecología, IVIC*
3. *Universidad Experimental Simón Rodríguez, Caracas, Venezuela*

Tropical savannas are characterized by a strong seasonality in water availability, and by acid soils of extremely low fertility. Soil acidity, brought about by the high percentage of aluminium (Al) saturation, is known to hinder plant growth in many parts of the world and to constitute a main constraint to crop production in tropical areas. Aluminium toxicity occurs in more than 70% of the acid soils of tropical America, and nearly all these soils are phosphorus (P)-deficient or have a high P-fixing capacity. The percentage of exchangeable Al in soils is thus correlated with soil pH and plant growth.

Most commercial crops are unable to tolerate soil pH below 5.5 and levels of Al saturation above 25%. Nevertheless, in savanna soils containing high levels of Al the diversity of native legumes is wider than that of grasses, and nodulated legume species are able to fix N₂ at high rates. Knowledge of the degree of Al tolerance in tropical legumes has both scientific and practical significance, since Al-stressed environments are known to exert a selective pressure for species highly efficient in the exploitation of scarce nutrient resources.

The Al, calcium (Ca), and iron (Fe) contents in different plant parts of savanna legumes growing in soils with two contrasting Al levels were compared. Soil site 1 (S-1) was characterized by an Al content of 847.2 cmol kg⁻¹, whereas at soil site 2 (S-2) the Al content was 128.4 cmol kg⁻¹.

At S-1 the following species were harvested: *Galactia jussieuana*, *Chamaecrista flexuosa*, *Clitoria guianensis*, *Zornia curvata*, and *Stylosanthes elegans*. Individuals of the same species plus examples of *Centrosema pubescens*, *Chamaecrista tetraphylla*, and *Phaseolus gracilis* were harvested at S-2. Plants were divided into shoots, leaves, nodules, and lateral roots, and were dried and ground. Total Al, Fe, and Ca contents in digested samples were determined by atomic absorption spectrophotometry. The Al associated with organic matter was determined by atomic absorption spectrophotometry after extraction with 50 mL of 1N KCl or 1N CuCl₃.

Results indicate that legume species collected at S-1 can be categorized as Al-tolerant. However, species were divided into two groups; *G. jussieuana*, *C. flexuosa*, *C. guianensis*, and *Z. curvata* that accumulate high A1 concentrations in their root system, and *S. elegans* which accumulates A1 in the leaves. In the former group, the A1 content was higher in lateral roots>xylopodium>>> shoots>leaves>nodules. Whereas in *S. elegans* the A1 content was higher in leaves>shoots>>>lateral roots>xylopodium>nodules. On the other hand, the total absence of *C. puhescens*, *C. tetraphylla*, and *P. gracilis* in S-1 was considered to be an indicator of the non-tolerance of those species to levels of Al above 128.4 cmol kg⁻¹ of soil. Results also point out that for all legumes the Al contents were 9-13 fold higher in S-1 than in S-2 plants. Concomitantly, the Fe content was 3-4 fold higher in S-1 than in S-2 plants. It can therefore be postulated that in legumes species considered as root-A1 accumulators the high Fe content in the different plant organs might exert a counteracting effect on A1 toxicity. In contrast, Fe might not counteract the A1 content in leaf tissues of *S. elegans*. The Fe content did not differ between individuals of this species collected at S-1 and S-2. Rather, the abscission of leaves enriched with A1 might be the mechanism underlying the Al-tolerance in this species. For all A1-tolerant species there was a significant negative correlation between A1 and Ca contents in different plant organs. This finding could be explained by a displacement of Ca by A1. Therefore, the Ca/A1 ratio must be considered as an indicator of the capacity of different plant organs to tolerate and accumulate high levels of A1 rather than as an index of the magnitude of Al toxicity. This suggestion is based on the low significant values of Ca/A1 in all S-2 plants and in the organs of S-1 plants with low A1 contents.

Conclusions

1. The levels of Al in soils determine the biodiversity of legumes native to tropical savannas. Further, for all legume species tested in this investigation there seems to be a close relationship between the Al and Fe uptakes. This observation could be ascribed to the similar ionic form of both ions and to the concomitant presence of Fe and A1 in most savanna soils.
2. A number of native species can be considered promising germplasm sources for A1 tolerance. Those species identified as Al-tolerant could be used as a source of genes for future breeding programs. The accumulation of A1 mainly in roots and leaves, and the partial exclusion of A1 ions from nodules could be the mechanisms underlying the efficiency of the symbiotic system in the Al-tolerant legume species.
3. The inclusion of native nodulated, high N₂ fixing, legume species as associate crops could constitute a novel and low-input way to increase the sustainability of acid soils in developing countries.

Effect of rock phosphate and superphosphate fertilizer on the productivity of maize van Bisma

D. R. Lukiwati

Animal Science Faculty, Diponegoro University, Wisma UNDIP, Jalan Kagok 11/5, Semarang, Indonesia

Corn or maize is the most important crop after rice as a source of food and livestock feed in Indonesia where maize stalks are used for ruminant livestock feed. The Latosolic soil used for food crop production in Indonesia is characterized by low nutrient availability, particularly of nitrogen (N) and phosphorus (P), and low pH. Phosphorus fertilizer application is an important means of enhancing crop productivity in this soil.

Superphosphate (SP) fertilizers have been widely used to improve food crop production in poor soils in Indonesia. However, with the rapidly increasing cost of SP, farmers are now using cheaper and locally available rock phosphate (RP) fertilizers. In Indonesia, there are large deposits of RP in Tasikmalaya, Cirebon (West Java), and Gresik (East Java), but few studies have evaluated the agronomic potential of these locally available P sources.

A field experiment was conducted on acid Latosolic soil. A split-plot design with three blocks as replicates was used. The main plot consisted of two kinds of P fertilizer (RP and superphosphate SP-36). Four levels of P fertilizer (0, 66, 132, and 197 kg P ha⁻¹) were applied to the sub-plots at sowing. All plots received basal nitrogen (N) applications of 100 kg N ha⁻¹ as urea in 2 splits and 83 kg potassium (K) ha⁻¹ as KCl. Maize seeds var. Bisma were sown at a spacing of 70 cm x 40 cm. At harvest, the maize stalk was cut at ground level and analyzed for dry matter (DM) and crude protein (CP) content. The application of P fertilizer resulted in significantly higher maize grain yields, total stalk DM, and stalk CP contents than the control that did not receive P fertilizer. SP-36 treated crops produced significantly higher grain and total DM stalk yields than those that received applications of RP. Crude protein stalk contents of maize that received RP fertilizer were not significantly different from those in the SP-36 treatment. Rock phosphate fertilizer could not therefore be used as a substitute for SP-36 to improve the productivity of maize crops grown in Latosolic soils.

Phosphorus sources of low solubility such as RP frequently result in lower limiting yields, especially in annual crops than soluble P sources. Yield response to P generally declines or has no effect with increased P application.

Session 2 Interpretive Summary

Candidate mechanisms

J. J. Adu-Gyamfi

Introduction

Understanding nutrient efficient mechanisms is paramount for designing a simple, fast and effect screening technique that would be a cornerstone of future attempts to breed nutrient-efficient genotypes. It is well known that efficient genotypes grow and yield well on nutrient-deficient soils by exploring specific physiological mechanisms that allow them to gain access to sufficient quantities of nutrients and / or to more effectively utilize them (Rengel, 1999).

The papers presented in this Session covered a diverse range of topics on the candidate mechanisms of the adaptation of crop plants to low-nitrogen (N) and phosphorus (P) environments. We have attempted to group the presentations and extracted and highlighted the major points that were made. Three broad categories of mechanisms that exist in plants to increase the availability, uptake and utilization of N and P are:

1. Increase N and P uptake
2. More effectively utilize nutrients particularly N and P
3. Use the aluminium (Al) tolerance exhibited by native legume species.

However, reliable and well-targeted screening procedures using the appropriate parameters is a prerequisite to breeding for genotypes with enhanced tolerance to low-nutrient environments. Nakano et al., 2000 did a good job in screening 100 genotypes each of sorghum and pigeonpea on an Alfisol and a Vertisol and evaluating the morphological and ecophysiological characteristics associated with the adaptation to low-N and -P soils under field conditions. The genotypes were selected from a large collection of germplasm held in the ICRISAT genebank in Patancheru, India. Differences in shoot, grain, N, and P yields were reported among the genotypes. Dry matter was shown to be positively correlated to leaf size, leaf weight, and leaf / stem ratio but not to specific leaf weight. The conclusion that hybrids and improved varieties performed better than the local lines in low-N and -P soils should be quoted with caution.

There are many controversies on the performance of local landraces and farmer-selected local varieties compared to hybrids and newly improved varieties in low-nutrient soils. Biotic and abiotic factors are known to influence the adaptation of crop plants to low-nutrient environments. The data presented was based on single treatments at a single location. Future screening methods should

take into consideration the interaction of nutrients, water, the chemical and physical characteristics of the soil type, temperature and photoperiod, and the production system.

During the discussion it was suggested that future screening and selection of genotypes adapted to low-N and -P conditions for specific traits should be done in the target environment where the crop is widely cultivated before any physiological study is undertaken under controlled conditions.

Mechanisms to increase N and P availability and uptake

The mechanisms highlighted were mainly 1. the secretion or exudation of chemical compounds into the rhizosphere, 2. the association with microorganisms, and 3. the alteration of the geometry or architecture of the root system.

Ae et al., 1990 demonstrated that root exudates from pigeonpea contained piscidic acid that is effective in solubilizing Fe-P and releasing P from Alfisols. This finding, published in 'Science' was based on a single genotype of pigeonpea. Therefore Ishikawa et al., 2000 investigated the genotypic variation in the P-solubilizing activity of piscidic acid and other carboxylic anions from the root exudates of pigeonpea. They found that all the pigeonpea genotypes tested exuded piscidic acid from their roots and confirmed in vitro that piscidic acid can solubilize sparingly soluble P in Alfisols. However, they suggested the need to investigate more effective P-solubilizing mechanisms than piscidic acid exudation to explain genotypic variation in low-P availability of pigeonpea.

Another important part of the work by Ishikawa et al., 2000 was the development of a rapid, simple, and easy technique for testing the solubilizing activity of root exudates. This method uses a simple filter paper and allows the screening of large samples of root exudates. Screening large numbers of crop genotypes for their ability to solubilize P has been hampered by lack of simple and relatively cheap techniques. This method, if improved, will help in-depth research into the genetic basis of qualitative and quantitative differences in root exudates from crop plants.

A new concept of "contact reaction" which focuses on the interaction between root surfaces and soil particles was presented by Ae and Shen, 2000 as a possible mechanism for the adaptation of pigeonpea and groundnut to low-P soils. It was shown that the better adaptation of groundnut and pigeonpea than sorghum and soybean to P-deficient soils might be explained by the higher solubilizing ability of their root cell walls. The author argued that one of the weaknesses of the "root exudate" theory is microbial degradation. It is shown that phenolic compounds (including piscidic acid) disappeared within 3-4 days after application because of microbial decomposition. Another weakness of the "root exudate" theory is the high amount of chelating chemicals in root exudates required to release of P. Participants expressed interest in the new concept.

Findenegg, 2000 emphasized that the phytase activity of roots is another mechanism of potential importance for the mobilization of phosphate from soils. Despite the report that the "root exudate" theory could not explain the ability of pigeonpea and groundnut to acquire P from soil, simulation models presented by Findenegg demonstrated the importance of citric acid excretion for the solubilization of both mineral and adsorbed P by plant roots. Such simulation models remained to be developed for the "contact reaction" mechanism.

Kirk, 2000 applied the theory of coupled diffusion processes in soil to quantify root-induced solubilization of nutrients. The fact that measured concentration profiles of P near roots coincided with the predictions of the model based on independently measured parameters, stressed the validity of the model and the importance of root exuded citric acid for P acquisition by roots in tropical soils. The conclusion that it is possible to model root-induced solubilization processes mechanistically would help in understanding and identifying the processes that are relevant in regulating nutrient and toxic dynamics. The author also attempted to use a mechanistic model to explain the alteration of geometry or architecture of the root system to the adaptation to low-P and -P soils. This is a major challenge to crop physiologists.

Nakamura et al., 2000 demonstrated that higher specific-N absorption rate per root mass (SRA) and per root length (SLRA) by hybrids than a local variety of sorghum in low-N conditions accounted for the better adaptation of hybrids to low-N conditions than the local variety.

It is well known that the association between roots and mycorrhizae allows plants to improve their access to soil-P pools. Gyaneshwar et al., 2000 reported the importance of phosphate solubilizing microorganisms (PSMs). The authors presented data on the successful isolation of a P-solubilizing *Enterobacter asburiae* that could release P from the soil. This finding was made under laboratory conditions, and there is a need to verify the results in the field. During discussions, some participants however, expressed the importance of isolating indigenous bacteria in low-P soils to solubilize P rather than using genetically engineered microorganisms.

Mechanism to more effectively utilize N and P

A study by Adu-Gyamfi et al., 2000 clearly demonstrate large significant difference in P utilization efficiency among pigeonpea and sorghum genotypes. An important trait observed in their study is the rapid and efficient translocation and remobilization of P from leaves and stem reserves to support crop growth and grain filling in P-stressed conditions. A ³²P study showed that in low-P conditions, P-efficient genotypes translocated more P from roots to the flag leaves. It was shown that the contribution from leaf and stem P offered powerful resources for grain filling for sorghum, and that hybrids and improved varieties were more

efficient in the translocation of P from roots to leaves, accounting for their relatively high adaptability to low-P conditions. The work by Fujita et al., 2000 showed that at low-P availability, there is increased partitioning of photo-assimilates to roots and decreased partitioning to the growing leaves. The synthesis of hemicellulose and cellulose in leaves is suppressed causing an inhibition in leaf area expansion. It was therefore concluded that the variability among crop plants in the translocation of photo-assimilates to leaves and the other growing parts at low-P availability provides scope for genetic manipulation of the trait to improve the adaptation of crops to low-P soils.

The long-term experiments by Bationo et al., 2000 showed that the rotation of cereals and legumes help increased the P use efficiency of crops. It was clearly shown that the P use efficiency of pearl millet increased from 46 kg grain kg fertilizer P⁻¹ in continuous rotation to 76 kg grain kg fertilizer P⁻¹ when rotated with cowpea. In the West African Sahel region, hill placement of small quantities of P fertilizer (4 kg P ha⁻¹) was shown to increase P use efficiency more than the recommended rate of 13 kg P broadcast ha⁻¹.

Bationo et al., 2000 showed that partially acidulated rock phosphate (PR) improved P use efficiency by crops, and that rainfall and soil acidity were the main determinants of the agronomic efficiency of different PR sources. For maize although superphosphate application gave a higher yield than RP, it is more economical for farmers to use RP (Lukiwati, 2000).

Mechanisms of aluminium tolerance by native legume species

The paper by Izaguirre-Mayoral et al., 2000 identified legumes species tolerant to aluminium (Al) toxicity. These native legume species can be considered promising germplasm sources for Al-tolerance and could be used as sources of genes for future breeding programs. Aluminium tolerance in transgenic plants by alteration of citrate synthesis has been reported earlier by de la Fuente et al., 1987.

References

- Adu-Gyamfi J J, Ishikawa S, Nakamura T and Nakano H 2000** Genotypic variability and physiological characteristics of crop plants adapted to low-nutrient environments. *In* Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00. Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Ae N and Shen R-F 2000** A proposed new phosphorus (P) uptake mechanism by groundnut and pigeonpea - P solubilizing reaction on the root surface. *In* Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00. Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).

- Ae N, Arihara J, Okada K, Yoshihara T and Johansen C 1990** Phosphorus uptake by pigeonpea and its role in cropping systems of the Indian subcontinent. *Science* 248, 477-480.
- Bationo A, Henao J and Anand Kumar K 2000** Phosphorus use efficiency as related to sources of P fertilizers, rainfall, soil, crop management, and genotypes in the West African semi-arid tropics. *In Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00.* Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- de la Fuente J M, Ramirez-Rodriguez V, Cabrera-Ponce J L and Herrera-Estrella L 1997** Aluminium tolerance in transgenic plants by alteration of citrate synthesis. *Science* 276, 1566-1568.
- Findenegg G R, 2000** Exploitation of plant genetic differences in solubilizing P from sparingly soluble sources. *In Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00.* Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Fujita K, Chaudhary M 1, Fujita A, Kai Y, Takayanagi M, El Sherry H and Adu-Gyamfi J J 2000** Photosynthesized carbon translocation and distribution of crops adapted to low-nutrient environments. *In Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00.* Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Gyaneshwar P, Naresh Kumar G, Parekh L J, and Poole P S 2000** Role of soil microorganisms in improving P nutrition of plants. *In Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00.* Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Ishikawa S, Adu-Gyamfi J J, Nakamura T, Yoshihara T and Wagatsuma T 2000** Genotypic variability in phosphorus solubilizing activity of root exudates by crops grown in low-nutrient environments. *In Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00.* Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Izaguirre-Mayoral M-L, Flores S and Oropeza T 2000** Aluminium tolerance in nodulated N₂-fixing legume species native to two contrasting savanna sites. *In Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00.* Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Kirk G J D 2000** Modelling root-induced solubilization of nutrients. *In Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00.* Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).

- Nakamura T, Adu-Gyamfi J J, Yamamoto A, Ishikawa S, Nakano H and Ito O 2000** Variability in rooting behavior and nutrient uptake of crop plants in low-nutrient environments. *In* Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00. Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Nakano H, Adu-Gyamfi J J and Nakamura T 2000** Genetic adaptation of crop plants to low-nutrient environments: Morphological and ecophysiological characteristics of adaptation. *In* Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00. Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Rengel Z 1999** Physiological mechanisms underlying differential nutrient efficiency of crop-genotypes. *In* Mineral Nutrition of Crops: Mechanisms and Implications. Ed Z Rengel. pp. 227-265. The Haworth Press, New York, USA.

Session 3

Methodology for genetic manipulation of nutrient availability

Assessing germplasm collections for traits useful in plant nutrition

P.J. Bramel-Cox

Genetic Resources and Enhancement Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India

In the past, empirical selection by breeders has been successful at changing such regulatory processes as the pattern of partitioning and the timing of development. It has done little to increase the efficiency of the major metabolic or assimilatory processes, such as photosynthesis or nutrient use efficiency. A number of possible agents of change to develop crop varieties that produce greater yield per unit of nutrient are available. A combination of enhanced use of limited nutrients and better extraction of available nutrients from the soil would likely result in the best possible option for crops grown under low-nutrient conditions. The unpredictable nature of such conditions will require plasticity to efficiently use a sustainable portion of the available nutrients, irrespective of the source.

The primary agent of change will be a source of genetic variation for the trait of interest. The two main options are intra-specific or inter-specific genetic variation. Intra-specific variation is more easily exploited by the plant breeder, but is less likely to exist, except in crops where the evolution has included significant production under very diverse marginal conditions. A more likely source of significant variation will be differences among species that have evolved under distinctly different environments, such as the wild relatives of the crop. The objective of this review is to explore the various agents of change required for enhanced nutrient use efficiency of such genetic variation. A number of studies have been undertaken in sorghum to assess the value of intra-specific and inter-specific variation as improved sources of drought tolerance and nutrient use efficiency. A number of accessions were identified based upon an assessment of the various components of these two traits within very diverse germplasm.

The key to progress in breeding nutrient use efficient cultivars will be in the enhanced utilization of genetic resources. Intra-specific strategies will concentrate on the use of landraces or farmer varieties and wild relatives in the primary gene pool. The use of these sources could be direct, but could involve backcrossing to minimize the impact of undesirable alleles. The secondary and tertiary gene pools might serve as very important sources of unique alleles. One option for the future will be the use of gene mapping and isolation. Once isolated and sequenced the gene can be directly introduced into the crop cultivars with

transformation. This same approach could be used in unrelated species where mechanisms are carefully evaluated using comparative approaches.

Root exudates as mediators of mineral acquisition in low-nutrient environments

F. D. Dakora¹ and D. A. Phillips²

1. Botany Department, University of Cape Town, Private Bag, Rondebosch 7701, Cape Town, South Africa
2. Department of Agronomy and Range Science, University of California, Davis, CA 95616, USA

Plant developmental processes are controlled by internal molecular signals that depend on the adequate supply of mineral nutrients by soil to roots. Thus the availability of nutrient elements can be a major constraint to plant growth in many environments of the world, especially in the tropics where soils are extremely low in nutrients. Plants take up most mineral nutrients through the rhizosphere where microorganisms interact with plant products in the root exudates. Thus root exudates have major effects on the acquisition of mineral nutrients that are required for plant growth. Phenolics and betaines exuded directly by roots of N₂-fixing legumes serve as major signals to *Rhizobiaceae* bacteria, which form root nodules where N₂ is reduced to ammonia. Some of the same compounds affect development of mycorrhizal fungi that are crucial for phosphate uptake. Plants growing in low-nutrient environments also employ root exudates in ways other than as symbiotic signals to soil microbes involved in nutrient procurement. Extracellular enzymes release phosphorus (P) from organic compounds and several types of molecules increase iron (Fe) availability through chelation. Organic acids form a major part of root exudates and can solubilize unavailable soil calcium (Ca), Fe, and aluminium (Al) phosphates. Plants growing on nitrate generally maintain electronic neutrality by releasing an excess of anions, including hydroxyl ions. Legumes, that can grow well without nitrate through the benefits of N₂ reduction in the root nodules, must release a net excess of protons. These protons can markedly lower rhizosphere pH and decrease both the availability of some mineral nutrients and the effective functioning of some soil bacteria, including the rhizobial bacteria themselves.

Thus environments that are naturally very acidic can pose a challenge to nutrient acquisition by plant roots, and even threaten the survival of many beneficial microbes including the roots themselves. A few plants, such as the Rooibos tea plant (*Aspalathus linearis*), actively modify their rhizosphere pH by extruding hydroxyl and bicarbonate ions to facilitate growth in low pH soils (pH 3-5) Whereas net alkalinization² of the rhizosphere by nitrate assimilation in

plants is understood, the mechanisms underlying rhizosphere alkalization by root exudates of *Aspalathus linearis* are only now being clarified. Current understanding of how plants can increase rhizosphere pH and the potential benefits associated with such processes are assessed.

Genetic control of root exudation

Z. Rengel

Soil Science and Plant Nutrition, Faculty of Agriculture, The University of Western Australia, Nedlands WA 6907, Australia

Literature on genotypic differences in the qualitative and quantitative composition of root exudates in crop and native plant species was critically assessed. Plants exude a large proportion of fixed carbon into the rhizosphere to change the chemical and biological properties of the immediate environment in which roots live. Such high energy and carbon cost should return increased adaptation to a particular environment.

The type of exudates plants release into the rhizosphere played a significant role in the distribution of plant species in various ecosystems. Calcicole plants exude mostly di- and tricarboxylic acids [with the former being good extractors of phosphorus (P) and the latter good extractors of iron (Fe) and manganese (Mn) from calcareous soils], while calcifuge plants exude mostly monocarboxylic acids (poor in mobilising P or Fe from calcareous soils).

In addition to genotypic differences among plant species, various genotypes exude a wide variety of compounds and in differing amounts. Genotypic variability within plant species exists for: 1. exudation of nodulation gene inducers by legumes to facilitate nodulation by rhizobia, 2. exudation of phytosiderophores under Fe and Zn deficiency (graminaceous monocotyledons), 3. exudation of protons by dicotyledons and non-graminaceous monocotyledons under Fe deficiency, 4. exudation of enzymes (e.g., phosphatase and phytase) and protons by plants subjected to P deficiency, 5. exudation of organic acids under deficiency of various nutrients and toxicity of aluminium (Al) and heavy metals, and 6. exudation of compounds that are stimulatory to reducing microflora and/or inhibitory to oxidising microflora in the rhizosphere of plants grown under Mn deficiency. In addition to the role of root exudates in tolerance to nutrient deficiency and/or ion toxicity, differential genotypic resistance to root pathogens also rely on the differential composition of root exudates; resistant genotypes exude compounds that inhibit pathogen growth, while susceptible genotypes frequently exude substances with a stimulatory effect on the pathogen growth.

Almost all the currently available literature deals with comparisons of the exudation profile of various genotypes (frequently only two genotypes with contrasting response to the environmental condition tested). Little is known about the variability in larger samples of the germplasm of any species, or about the actual genetics behind differential qualitative and quantitative composition of

root exudates. This lack of knowledge makes manipulation of plant capacity to exude specific compounds difficult. In principle, manipulation of the exudation profile of a given genotype could be achieved by manipulating the biosynthetic capacity (in terms of the rate of certain reactions and/or cell compartment where these reactions take place) and by increasing the capacity of the plasma membrane to transport the specific compound out into the rhizosphere (e.g., number and/or capacity of anion channels in the case of carboxylate anions). In addition, introducing genes that code for enzymes facilitating the biosynthesis and exudation of a compound that a specific plant species/genotype cannot otherwise produce is a possibility, but clearly a more difficult one to achieve successfully.

Exudation of citrate is beneficial under a range of nutrient deficiencies (most notably P) and ion toxicities (e.g., Al). Overexpression of the citrate synthase — gene in the cytoplasm resulted in the exudation of large quantities of citrate into the rhizosphere and alleviation of the Al-toxicity stress. The similar strategy of transforming plants with the citrate synthase gene is being tried as a way to improve plant capacity to extract P and other nutrients from soils with notoriously low nutrient availability.

Screening various adapted plant species and a large number of genotypes of some plant species could yield a source of genes important in controlling root exudation. A screening system can be devised that would estimate genotypic differences among various cultivars and/or breeding lines in response to limiting environments by measuring the relative rate of root exudation of specific compounds.

In conclusion, understanding the genetic control of root exudates, followed by manipulation of qualitative and quantitative composition of root exudates, will result in better adaptation of plants to environmental conditions and increase crop yields.

Transporter genes to enhance nutrient uptake: Opportunities and challenges

J. Dunlop and T. Phung

*AgResearch, Grasslands Research Centre, Private Bag 11008, Palmerston North,
New Zealand*

During the past decade knowledge of the membrane processes involved in the acquisition of mineral nutrients by plants has advanced dramatically. Much more detailed information about the molecular structures involved in influx into cells, efflux from cells, and movement from cell to cell through the plasmodesmata is now available. Genes that code for transporter proteins for all major inorganic nutrients and some of the minor nutrients have been cloned from plants. The properties of ion channels through which efflux occurs have been studied incisively, and in a few cases the genes involved have been cloned. The intricacies of movement through plasmodesmata have been demonstrated and some of the associated genes have been cloned.

These transporter genes are being viewed as a potential means to develop plants that are better equipped to cope with soils that are deficient in nutrients or that reduce the requirement for fertilizer in developed agricultural systems. However an understanding of how these genes are controlled and their function integrated with other processes involved in mineral nutrition is still insufficient to permit the informed design of plants better suited to cope with nutrient deficiency. However, these genetic resources provide powerful new tools to develop some of the understanding necessary for the effective design of plants with improved mineral nutrition.

The promoters which control the expression of transporter proteins are likely to be an important component in the design of the desired plants. Identification, cloning, and characterization of promoters are lagging behind the corresponding work on transporters. The practical use of transporter genes would benefit from more rapid progress in this area, as it would facilitate a more sophisticated understanding of the control of nutrient acquisition and utilization. Promoters may also be essential components in the genetic modifications necessary to develop plants more suited to nutrient-deficient soils.

Recent data for mechanisms involved in the acquisition of phosphate can be used to illustrate some processes that require further study. Net acquisition of phosphate by roots is the difference between influx and efflux. Influx and efflux of phosphate from roots was measured simultaneously by double labeling with ^{32}P and ^{33}P . The experiments involved ryegrass and white clover plants grown in

both phosphorus (P) adequate and deficient conditions. When grown together in a pasture, white clover is the weaker competitor for phosphate. The rates of efflux and influx were both affected by the P status of the plants. Influx increased and efflux decreased when phosphates supply was inadequate. The rates of phosphate influx showed some tendency to be higher for ryegrass than white clover but the most prominent and consistent differences between species were in the rates of efflux. These were approximately three times greater for white clover, than the corresponding values for ryegrass. These results suggest that gains in net acquisition obtained by increasing influx may be limited by an increase in efflux associated with improved P status. It also suggests that lowering the rate of phosphate efflux might be another strategy for increasing P acquisition.

The fact that efflux in P-sufficient roots was an order of magnitude higher than in P-deficient roots suggests that efflux is not simply a result of dysfunctional membranes. Using patch clamp methods protoplasts isolated from roots of ryegrass, white clover, and *Arabidopsis thaliana* were examined for ion channels permeable to phosphate. A variety of such channels that oscillate between open and closed states were observed. Opening is controlled by voltage. It appears that there are different channels for H_2PO_4 and HPO_4^{2-} ions. The data also suggest that when the normal cytoplasmic contents are replaced by a simple solution containing salts and ATP, the frequency of channel openings decreases. Thus, phosphate efflux involves specific protein structures (ion channels) that are controlled by cytoplasmic conditions. The presence of phosphate-specific ion channels in the vacuole membrane has also been demonstrated. In this case their location would allow them to contribute to phosphate movement between the cytoplasm and vacuole.

These studies, like the majority of experiments on nutrient acquisition by roots, have been conducted in hydroponics and the extrapolation of the results to roots growing in soil must be made with caution. A tacit assumption that nutrient absorption is uniform along the length of the root, which is implicit in many commentaries, implies a situation where phosphate lost by efflux may be reabsorbed. However absorption is not uniformly distributed along the root and the sites of influx and efflux may be spatially separated with the consequence that roots might not be efficient in reabsorbing phosphate moving out of the root by efflux. Current attempts to define the variation of nutrient transport properties along roots with greater spatial resolution are in progress. Initial results point to further complexities in phosphate absorption that could be important in developing a model that is sufficiently accurate to provide a base for genetic engineering decisions.

In addition to information and insights from molecular and cellular studies, the genetic engineering of plants for mineral-deficient soils also requires an ability to integrate mineral nutrition processes with such other major plant functions as

photosynthesis and water relations. There is a lack of models that can be used to do this. The synthesis of information needed will require collaboration between molecular biologists, plant physiologists, agronomists, soil scientists, and plant breeders. In the area of mineral nutrition, such collaboration has been rare, but it is likely to be crucial to the success of any endeavor to develop better plants for nutrient-deficient soils.

The phosphate uptake mechanism

F. W. Smith

Commonwealth Scientific and Industrial Research Organization CSIRO Tropical Agriculture, Cunningham Laboratory, 306 Carmody Road, St Lucia,, Queensland 4067 Australia

The slow rate of diffusion of phosphate in soil results in a zone of depletion of phosphate ions in solution around the roots of plants in low-phosphate soils. Transfer of phosphate to the site of uptake into the root symplasm limits phosphate uptake in such soils. This transfer involves movement across the depletion zone and through the root apoplasm. The apoplasm is made up of the cell walls of epidermal and cortical cells, together with the associated intercellular spaces. Although the pores in the open latticework of these cell walls permit movement of nutrients around cells they increase the path length across which phosphate ions have to diffuse. The structural components and net negative charges of the cell walls also influence the effective concentrations of phosphate in the apoplasm. This concentration may be further modified by excreted organic compounds around cell walls and by the presence of microorganisms that use such compounds as carbon sources.

The plasma membrane on the inner surface of the cell wall separates the apoplasm from the symplasm. Uptake of nutrients into the root symplasm occurs through transporter proteins embedded in the plasma membrane. Our understanding of the mechanisms by which phosphate is transported across the plasmalemma into the plant symplasm has advanced considerably over the past 4 years due to the application of molecular techniques. Genes encoding the transporters involved in this process have been isolated from a number of plant species. These transporters belong to a family of membrane proteins characterized by having 12 membrane-spanning domains arranged in a '6+6' configuration. H_2PO_4^- ions, together with protons, are transported through this protein. This transport process is driven by the potential across the membrane maintained by the action of a H^+ -ATPase, the 'proton pump', which extrudes protons to the outer surface of the membrane.

The expression of genes encoding high-affinity root phosphate transporters is regulated by the phosphorus status of the plant. The transduction pathway involved in this regulation is not known at present. It is a systemic response rather than a localized response however, the overall phosphate status of the plant being the controlling factor. Under phosphate stress the expression of genes encoding these phosphate transporters is up-regulated. This results in a greater

number of transporter proteins in the plasmalemma and enhanced phosphate uptake rates if phosphate is available at the membrane surface. This uptake occurs around the root tip, into epidermal cells with their associated root hairs and into cells in the outer layers of the root cortex. Further back along the root axis phosphate can also be taken up by transfer from mycorrhizal fungi to root cortical cells.

Strategies for increasing nutrient uptake by overexpressing genes encoding high-affinity phosphate transporters are likely to be mainly applicable to situations where a reasonable phosphate concentration can be maintained at the outer surface of the plasmalemma. Maintaining such a concentration is a major problem in the phosphate-deficient soils of the semi-arid tropics, so emphasis in these soils is on strategies to improve the movement of phosphate to the surface of the plasmalemma. There may be scope however, for manipulating the expression of genes involved in the internal mobilisation of phosphate within the plant, thereby improving phosphate utilization.

Breeding for better symbioses

Z . Rengel

Soil Science and Plant Nutrition, Faculty of Agriculture, The University of Western Australia, Nedlands WA 6907, Australia

The present review gives a critical assessment of the literature dealing with symbiotic relationships between plants and microflora: dinitrogen fixation in the rhizobia-legume symbiosis, and vesicular arbuscular mycorrhizae (VAM) and ectomycorrhizal symbioses between fungi and most plants. Since associative diazotroph bacteria depend on the organic compounds exuded by plant roots, associative nitrogen (N₂) fixation (even though strictly speaking not a symbiotic relationship) does have some characteristics of such a relationship due to the mutualistic dependence and usefulness of the relationship, and is therefore covered here.

Dinitrogen fixation provides more N to agricultural ecosystems worldwide than the total fertilizer N applied. However, a significant potential exists to improve symbiotic and associative N₂ fixation by breeding genotypes with a greater capacity to sustain these symbioses.

The current knowledge of the signalling process involved in the rhizobia-legume symbiosis is fragmented and hampered by the complexity of the plant-soil-microbe interactions that exist in agricultural ecosystems. Improved understanding of the signalling process will allow more targeted breeding efforts toward improving the symbiosis.

Initial nodulation may be limited by an insufficient amount of the nod-gene inducers released from seed and/or roots. However, there is genotypic variation in the germplasm of legume species in all components of the signalling pathway, suggesting both a need for, and a prospect of, improving nodulation by selecting and/or transforming legume genotypes for increased exudation of flavonoids.

Thorough knowledge on the localization of *nod*, *nif*, and other genes important in development of the symbiotic relationship will create new avenues in using molecular biology tools to manipulate the existence and expression of these genes to enhance the symbiotic relationship.

There is considerable genotypic variability in the legume germplasm for efficiency of the symbiotic relationship. Similar genetic variability also exists within nodule bacteria germplasm, and needs to be taken into account when creating a breeding program for better symbioses. Such genotypic variability clearly indicates a potential for greatly increasing efficacy of symbiotic N₂ fixation by selecting the best combination of plant genotype and nodule bacteria.

In addition, screening for increased activities of glutamine synthetase and glutamate synthase might be used in a breeding program to increase the symbiotic efficiency of legume genotypes. Including VAM inoculum together with the rhizobial inoculum in the host-legume breeding program should be considered.

Considerable effort over the years has been directed toward selecting the optimal combination of rhizobial inoculum and the legume genotype for acidic or saline soils. These selection efforts are presently expanding into nutritionally limited environments (e.g., phosphorus (P) deficiency). It would also be particularly important to develop genotypes that maintain high efficiency of N₂ fixation in the presence of small or moderate levels of nitrate.

While there are several avenues for increasing the effectiveness of the naturally occurring symbiotic relationships (e.g., *Rhizobium-legume*), it still appears quite difficult to create conditions conducive to symbiosis between non-host plants and rhizobia (clearly rice and wheat are the most interesting species in that respect).

As flavonoids exuded by legume seedlings may not only be nod-gene inducers, but also stimulants for hyphal growth of the VAM fungi, selecting and/or transforming plants to increase exudation of these flavonoids could result in double benefits for mycorrhizal legumes. Introducing factors that stimulate VAM colonization into non-host plants via genetic transformation might contribute to extending the VAM host range. Mutants unable to sustain mycorrhizal colonization will be instrumental in increasing knowledge of the colonization process, which may ultimately pay off in attempts to breed for the more effective symbiosis.

There appears to be a strong role for beneficial rhizosphere bacteria in increasing adaptation to environmental stresses by certain plant genotypes capable of producing root exudates of a specific qualitative and quantitative composition. Further research on designing suitable screening methods to select and breed crop cultivars with desirable responses to beneficial rhizosphere bacteria is warranted, but little work has been done so far.

In conclusion, targeted efforts to breed genotypes for improved symbiotic and/or associative N₂ fixation and for mycorrhizal symbiosis and the capacity to support beneficial rhizobacteria will bring benefits in increased yields of crop plants under a wide range of environmental conditions and will contribute toward sustainability of agricultural ecosystems in which soil-plant-microbe interactions will be better exploited.

Session 3 Interpretive Summary

Genetic approaches for manipulating crop plants to enhance root exudation and access low nutrients in the rhizosphere

F. D. Dakora, and T. R. Sinclair

Introduction

Opportunities exist for promoting plant nutrient uptake through genetic manipulation of rhizosphere processes. An assessment of the genotypic differences in plants such as in the excretion of nod-gene inducers by symbiotic legumes, the release of protons and phytosiderophores by crop varieties suffering from iron (Fe) and zinc (Zn) deficiencies, the extrusion of organic acid anions under aluminium (Al) and phosphorus (P) stress, and the release of root border cells and/or enzymes (phosphatases and phytases) concerned with P nutrition, is essential for identifying crop cultivars adapted to low-nutrient conditions. Approaches for creating nutrient-efficient crops suitable for low-nutrient environments include: 1. the screening of adapted landraces for a better understanding of the genetic basis of root exudation, 2. the selection of plants with enhanced symbiotic performance when infected with stem/root nodule bacteria (rhizobia) and/or vesicular arbuscular (VA) mycorrhizae, 3. increased experimentation on ion-channels, transporter genes and the promoters controlling their expression, and 4. the use of molecular markers to select useful plant traits. Additionally, we need to understand the operational relationship of these various genes to other processes involved with mineral nutrition, and to integrate the latter with such whole-plant processes as photosynthesis in order to obtain higher crop yields in low-nutrient environments. But the real challenge with these low-nutrient environments lies in the production of food crops with clinically acceptable levels of nutrients and vitamins that, when consumed by humans, do not cause malnutrition. Breeding for micro-nutrient enriched crops could be one way to produce foods that meet the dietary requirements of human nutrition. This summary presents the tools currently available for manipulating rhizosphere processes and plant genes for increased nutrient uptake and assimilation in low-nutrient environments.

To promote nutrient uptake and increase yields of crop plants in low-nutrient environments requires a multi-pronged approach, involving selection and breeding for useful nutrition-related biological traits, genetic manipulation of cellular processes involved with nutrient uptake and assimilation, a deeper

understanding of how plants growing in very low-nutrient soils actually optimize growth and productivity in ecosystems that would otherwise not support growth and yield of conventional crop varieties, and a costing of carbon and other inputs that enhance nutrient uptake and its use efficiency.

Assessing germplasm collections for traits useful in plant nutrition

The key to progress in breeding nutrient use efficient cultivars will be in the enhanced utilization of genetic resources. Intra-specific strategies will concentrate on the use of landraces or farmer varieties and wild relatives in the primary gene pool. The use of these sources could be direct, but could involve backcrossing to minimize the impact of undesirable alleles. The secondary and tertiary gene pools might serve as very important sources of unique alleles, but there will be a limit to the crossability and direct introgression from these accessions. One option for the future will be the use of gene mapping and isolation. Once isolated and sequenced, the gene can be directly introduced into the crop cultivars with transformation. This same approach could be used in unrelated species where mechanisms are carefully evaluated using comparative approaches (Bramel-Cox, 2000).

Plant selection for low-nutrient environments

Large differences exist among plant cultivars, species, and genotypes in their tolerance of low nutrients, and this is due largely to genetic variation in root characteristics and nutrient acquisition. An understanding of these biological differences could help develop crop plants that enhance growth from efficient uptake and utilization of nutrients in low-nutrient environments (Zhu et al., 2000). The use of classical plant breeding techniques has contributed significantly to the development of high-yielding disease-, drought-, and pest-resistant crop varieties, and can similarly be applied to the selection of crop plants that grow well in low-nutrient situations. Selection criteria based on root architecture, cluster root formation, massiveness of root hair development, and VA mycorrhizal infection which all enhance the absorptive surface are important in addition to the use of suitable bioassays (Zhu et al., 2000).

Some plants have evolved effective mechanisms for attaining good growth under low-nutrient conditions. These include release of root exudates which modify the rhizosphere for increased nutrient uptake and for the establishment of symbiotic interactions that enhance nutrient acquisition (Rengel, 2000a; Dakora and Phillips, 2000). Plants growing in low-nutrient environments employ root exudates as symbiotic signals to such soil microbes as rhizobium bacteria and VA fungi (Phillips, 1992), that are involved in nutrient procurement. Selecting cultivars that are enhanced in the biosynthesis and release of these signal molecules is likely to produce crop plants with the ability to increase nutrient

acquisition from symbiotic interactions in nutrient-poor soils (Rengel, 2000b; Dakora and Phillips, 2000). Root exudation of organic acids, phenolics, amino acids, and extracellular enzymes by plants adapted to low-nutrient environments serves to improve nutrient uptake from direct modification of the rhizosphere. Cereal plants use phytosiderophores in root exudates to promote iron acquisition, while organic acids and phenolics chelate and solubilize sparingly soluble Fe, calcium (Ca), and Al phosphates. The selection of cultivars and species that can produce quality exudates would be crucial for promoting plant growth for higher yields in low-nutrient environments.

But to increase plant growth also requires higher photosynthetic rates in addition to efficient nutrient uptake and utilization. It is known that plants grown under elevated CO₂ generally show greater biomass accumulation than ambient controls; and this occurs under conditions of increased photosynthetic activity and lowered levels of nutrients (e.g., N) in tissues (Drake et al., 1997). Thus, with the rising CO₂ concentration in the atmosphere, it is to be expected that plant species will respond naturally, and perhaps gradually, by increasing their photosynthetic rates even in low-nutrient environments. In fact, plant species that photosynthesize efficiently in low-N regimes have been identified. Some sorghum cultivars grow well under highly limiting soil-N conditions by maintaining high rates of photosynthesis via a sustained increase in the activity of PEP carboxylase enzyme (Maranville and Madhavan, 2000). Such plants are characterized by a low concentration of chlorophyll in their tissues, which in itself is an adaptive mechanism, and therefore offers scope for selecting species under low-nutrient conditions. While achieving high productivity in crop plants is therefore feasible in low-nutrient environments, food quality becomes a problem in terms of dietary balance of nutrients in the edible grain. So although plants growing in low-nutrient conditions can increase their biomass from an efficient PEP carboxylase enzyme system that leads to increased grain yield, the challenge is how to maintain clinically acceptable levels of nutrients and vitamins in the grain of such plants (Welch and Graham, 2000). No doubt, conventional breeding techniques can improve the protein and micronutrient contents of food crops especially cereals, but the task becomes the more difficult if the plants are growing in low-nutrient environments.

Manipulation of plant genes for enhanced nutrient acquisition

Nutrient uptake and assimilation involves transport across root hair membranes, loading into xylem, and transport across the membranes that occur between sources, sinks, and such storage units as vacuoles. Absorbed nutrients are generally partitioned between a metabolically active cytoplasmic pool and a vacuolar storage pool, with the former being maintained at relatively constant concentration at the expense of the latter. When nutrient supply is limited, as in

low-nutrient environments, plants grow more roots, increase uptake rates from the soil, retranslocate from older leaves, and deplete vacuolar pools for use in new metabolic processes. So, given the multitude of cellular membranes that must be traversed by nutrient ions during uptake and translocation, the movement of any single mineral nutrient from root hairs to storage depots and metabolic sinks must involve many different membrane-embedded transport proteins. In the case of P, an increase in its uptake rates following P-starvation of the roots has been observed in many plant species, with the enhanced uptake being attributed to increased synthesis of P-transporter proteins in response to the P starvation.

Modern biology has afforded us ample opportunities for gene manipulation in plants, and these tools can be applied by plant breeders and geneticists to — promote nutrient acquisition in crops (Johansen et al., 1995). Molecular markers such as isozymes, restriction fragment length polymorphism (RFLP), and random amplified polymorphic DNA (RAPD) are routinely used to map genes concerned with plant functions. They can similarly be used to map genes controlling root development and nutrient uptake, and in so doing identify and characterize each quantitative trait loci. Genetic maps revealing quantitative trait loci for water use efficiency and tolerance of P-stress in tomato have been developed (Johansen et al., 1995) using RFLP techniques. These can be applied to the screening of new cultivars and new germplasm collections for nutrient use efficiency.

In addition to manipulating native genes in plants, there are many successful gene transfer programs that offer opportunities to produce and screen clones for such specific traits as tolerance of low nutrients. Through the use of these techniques, some important genes controlling the synthesis of transporter proteins have been cloned from plants for a number of essential mineral nutrients (Chrispeels et al., 1999). The recent cloning and characterization of potassium (K), selenium (Se), P, magnesium (Mg), Ca, and N transporters support the existence of both high-affinity and low-affinity ion transport components in plants (Dunlop and Phung, 2000). The expression of some of those genes specifically in roots (the organs involved in nutrient acquisition by plants) suggests their involvement in mineral nutrient uptake. However, some of these transporter genes are not root-specific, and can be located in shoot, leaves, and flowers (Dunlop and Phung, 2000). Such transporter genes are probably concerned with routine nutrient translocation between organs of a plant, and not direct uptake from soil. While P-deficient rape typically releases malic acid near its root tips or at the site of contact with insoluble rock phosphate, P-starved hedge mustard, in contrast, does not secrete organic acids; and this has been attributed to problems associated with synthesis and transport across membranes (Hoffland et al., 1992). Clearly, the manipulation of these transporter genes has potential for "creating" crop plants capable of producing high yields from improved mineral nutrition,

especially in low-nutrient environments. However, to achieve this, requires an equally deeper understanding of the ion channels that control the influx and efflux of mineral nutrients. In general, influx increases and efflux decreases under conditions of nutrient deficiency, while with nutrient sufficiency efflux increases to avoid the nutrient accumulating to toxic levels. While the tools of modern biology have started to provide an insight into our current understanding of plant nutrition, a multidisciplinary approach is needed if results are to be translated into crop yields of field plants.

Insights from nutrient acquisition by novel plant systems

A new study (Ae and Shen, 2000) has shown that the root cell walls of groundnut are capable of solubilizing insoluble Fe-P and Al-P for uptake by the species. In contrast, the root cell walls of soybean and sorghum are ineffective in mobilizing P from sparingly insoluble forms. Although the trait might be genotype-specific, it clearly indicates the diversity of strategies employed by plants to improve mineral nutrition. Root border cells are pioneers in the rhizosphere of plants, and their quality and quantity control many rhizosphere processes including the release of extracellular enzymes, proteins, antibiotics, mucilage, and molecular signals concerned with symbiotic establishment (Hawes et al., 1998). It is therefore likely that future research may find that root border cells play a major role in nutrient acquisition, especially in nutrient-poor environments.

Another recent study (Dakora et al., 1999) has also provided very puzzling data on the N nutrition of a desert legume. The African marama bean (*Tylosema esculentum* L.) is a non-nodulating legume that grows in very nutrient-poor sandy soils including those of the Kalahari desert. However it can accumulate up to 3% N in leaves, tubers and seeds; N-concentrations comparable to those found in effective N₂-fixing nodules. As with the groundnut (Ae and Shen, 2000), the marama bean must have a special mechanism for enhancing its N nutrition in these nutrient-poor soils. Additionally, a few plants, such as Rooibos tea (*Aspalathus linearis*), which grows in naturally very acidic sands of the Western Cape in South Africa, can actively modify their rhizosphere pH to enhance nutrient uptake in the low pH soils (pH 3-5). They do so by extruding OH⁻ and HCO₃⁻ to increase the rhizosphere pH, and thus make nutrients more available (Dakora and Phillips, 2000).

These three examples, involving the nutrient-solubilizing ability of groundnut root cell walls, the high N-acquiring capacity of marama bean plants in nutrient-poor soils, and the active modification of rhizosphere pH for enhanced nutrient uptake by *Aspalathus linearis* plants, together offer an opportunity for increased understanding of mineral nutrition in low-nutrient environments. So, in addition to selecting crop varieties for root exudation and nutrient use efficiency, future studies should consider wild landraces that are naturally adapted to low-nutrient

environments. That way, the chance of creating or identifying crop plants with the ability to increase growth and provide higher yields under low-nutrient conditions would be greater.

Future Research

This synthesis has identified four key areas for future research: 1. screening large collections of genotypes, cultivars, and their wild relatives for tolerance of low-nutrient conditions, 2. development of simple bioassays for quantifying root exudation of organic acid anions, phenolics and phytosiderophores, followed by an assessment of their respective roles in solubilizing unavailable nutrients (e.g., P, Fe, etc.) in low-nutrient environments, 3. increased experimentation on symbiotic systems involving rhizobia and VA fungi that enhance N and P supply to crop plants in nutrient-poor soils, and 4. an aggressive application of molecular tools to increase our knowledge of ion channels, transporter genes, and their promoters of gene expression in order to enhance root exudation and promote nutrient uptake through gene transfer and genetic manipulation in plants.

References

- Ae N and Shen R-F 2000** A proposed new phosphorus (P) uptake mechanism by groundnut and pigeonpea - P solubilizing reaction on the root surface. *In* Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00. Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Bramel-Cox P J 2000** Assessing germplasm collections for traits useful in plant nutrition. *In* Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00. Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Chrispeels M, Crawford N M, and Schroeder J 1999** Proteins for transport of water and mineral nutrients across the membranes of plant cells. *Plant Cell* 11, 661-675.
- Dakora F D, Lawlor D W and Sibuga K P 1999** Assessment of symbiotic nitrogen nutrition in marama bean (*Tylosema esculentum* L.), a tuber-producing underutilized grain legume. *Symbiosis*, (in press).
- Dakora F D and Phillips D A 2000** Root exudates as mediators of mineral acquisition in low nutrient environments. *In* Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India. Developments in Plant and Soil Sciences volume 00. Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Drake B G, Gonzalez-Meier M A and Long S P 1997** More efficient plants: a consequence of rising atmospheric CO₂? *Annu. Rev. Plant Physiol. Mol. Biol.* 48, 609-639.
- Dunlop J and Phung T 2000** Transporter genes to enhance nutrient uptake: opportunities and challenges. *In* Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru,

- India. Developments in Plant and Soil Sciences volume 00. Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Fox T C and Guerinot M L 1998** Molecular biology of cation transport in plants. *Ann. Rev. Plant Physiol. Plant Mol.* 49, 669-696.
- Hawes M C, Brigham L A, Wen F, Woo H H and Zhu Y 1998** Functions of root border cells in plant health: pioneers in the rhizosphere. *Ann. Rev. Phytopathol.* 36, 311-327.
- Hoffland E, van den Boogaard R, Nelemans J and Findenegg G 1992** Biosynthesis and root exudation of citric and malic acids in phosphate-starved rape plants. *New Phytol.* 122, 675-680.
- Johansen C, Subbarao G V, Lee K K and Sharma K K 1995** Genetic manipulation of crop plants to enhance integrated nutrient management in cropping systems - the case of phosphorus. *In Genetic Manipulation of Crop Plants to Enhance Integrated Nutrient Management in Cropping Systems - 1. Phosphorus.* Eds C Johansen, KK Lee, KK Sharma, GV Subbarao and EA Kueneman. pp 9-29. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh, India.
- Maranville J W and Madhavan S 2000** Physiological adaptations for nitrogen use efficiency in sorghum. *In Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India.* Developments in Plant and Soil Sciences volume 00. Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Phillips D A 1992** Flavonoids: Plant signals to soil microbes. *In Phenolic Metabolism in Plants.* Eds H A Stafford and R K Ibrahim. Plenum Press, New York. *Rec. Adv. Phytochem.* 26, 201-231.
- Rengel Z 2000a** Breeding for better symbiosis. *In Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India.* Developments in Plant and Soil Sciences volume 00. Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Rengel Z 2000b** Genetic control of root exudation. *In Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India.* Developments in Plant and Soil Sciences volume 00. Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Welch R M and Graham R D 2000** Breeding crops for enhanced nutrient content. *In Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India.* Developments in Plant and Soil Sciences volume 00. Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).
- Zhu Y-G, Chuang C, Howes N K and Smith S E 2000** Breeding for low-nutrient environments. *In Food Security in Nutrient-Stressed Environments: Exploiting Plants' Genetic Capabilities, Proceedings of an International Workshop 27-30 September 1999, Patancheru, India.* Developments in Plant and Soil Sciences volume 00. Ed J J Adu-Gyamfi. Kluwer Academic Publishers, Dordrecht, The Netherlands, (in press).

Session 4

**Combining genetic improvement
with natural resource management**

Breeding crops for enhanced nutrient content

R.M. Welch¹ and R.D. Graham²

1. *United States Department of Agriculture-Agricultural Research Service (USDA-ARS), U.S. Plant, Soil, and Nutrition Laboratory, Cornell University, Ithaca, New York, NY 14853-2901, USA*
2. *Department of Plant Sciences, Waite Campus, University of Adelaide, Glenn Osmond, SA 5064 Australia*

Deficiencies of dietary energy (i.e., calories) and protein currently affect more than 800 million people in food-insecure regions; incredibly, micronutrient malnutrition, i.e., "hidden hunger" afflicts over 40% (>2 billion) of the World's people especially poor women, infants, and children in the developing world. The numbers of micronutrient-malnourished individuals are still increasing at an alarming rate. Today, deficiencies of iron (Fe), vitamin A, and iodine are of most concern although other nutrient deficiencies, including zinc (Zn), selenium (Se), calcium (Ca), magnesium (Mg), and such other vitamins as vitamin C, vitamin E, and folic acid, may be prevalent in some regions. The consequences of malnutrition create immense economic and societal costs to nations. Malnutrition results in greatly increased mortality and morbidity rates, diminishes cognitive abilities of children and lowers their educational attainment, reduces labor productivity, stagnates national development efforts, contributes to continued high population growth rates, and reduces the livelihood and quality of life for all those affected.

Past programs to combat micronutrient malnutrition have relied primarily on interventions directed at food fortification or nutrient supplementation programs. Unfortunately, these approaches have not proved to be sustainable for various reasons, and do not reach all the people at the highest risk of developing micronutrient malnutrition. Remarkably, the nutrition community has never embraced agriculture as an important tool to use in fighting hidden hunger. Nor has the agricultural industry viewed agricultural systems as playing an important and explicit role in human nutrition. Their efforts have been primarily focused on productivity, efficiency, and profit margin issues to drive research and national agricultural programs without regard to either the nutritional quality of the products produced, or the adequacy of such systems to meet all the nutritional needs of humans. Furthermore, institutional and governmental programs have not attempted to closely link agricultural production to human nutrition and health concerns although current knowledge and logic suggest that this should be a high priority.

Within the agricultural community, plant-breeding efforts greatly contributed to advances in staple plant food productivity (mostly cereal crops) that resulted in the Green Revolution. During the last four decades, such breeding efforts succeeded in providing enough calories and protein to stave off the threatening massive starvation and famines predicted in the early 1960s in many developing countries. Importantly, plant breeding can again be used as a tool to address hidden hunger. Breeding for micronutrient-enriched staple plant foods is a possibility that should be pursued. Success in such a breeding effort would target those groups of people most at risk of developing micronutrient malnutrition because these sectors of society are dependent on such staple foods for their sustenance. Furthermore, a plant breeding approach is sustainable; once micronutrient-dense lines of staple plant foods are produced there is no additional cost to continue their lineage in ongoing breeding programs.

A collaborative effort is currently being conducted by four Consultative Group on International Agricultural Research (CGIAR) centers; Centra Internacional de Agricultura Tropical (CIAT), Centra Internacional de Mejoramiento de Maiz y Trigo (CIMMYT), International Food Policy Research Institute (IFPRI), and International Rice Research Institute (IRRI), the University of Adelaide, Waite Campus, and the USDA-ARS, U.S. Plant, Soil, and Nutrition Laboratory in Ithaca, New York. This project is being carried out to determine the magnitude of genomic changes possible in the concentrations of Fe, Zn, and provitamin A carotenoids in the edible portions of several staple food crops including rice, wheat, maize, beans, and cassava. Results to date indicate wide ranges in concentrations of these micronutrients exist in the genomes of these staple foods. Thus, it appears possible to breed for micronutrient-enriched staple foods. Indeed, scientists at IRRI have already identified a high-yielding, highly disease-resistant line of rice that is significantly enriched in Fe and Zn, and after polishing much of the Fe accumulated in the grain is retained in the edible product. Furthermore, experiments using both rat and human caco-2 cell culture models, have demonstrated that the Fe in the grain of this enriched line has greater bioavailability than that found in currently available high-yielding IRRI rice varieties.

To date, the accumulating results from this collaborative effort are demonstrating that a new tool to use in the fight against hidden hunger is at hand. Plant breeding can be used to improve the micronutrient content of staple plant foods. What is now needed is a commitment from the world agricultural and nutrition communities to use this new tool. Not doing so will defy logic and will prolong the societal costs and suffering resulting from deficiencies of these nutrients among the world's poor.

Appropriate farm management practices for low-nutrient soils

P. C. Smithson¹ and K. E. Giller²

1. *International Centre for Research in Agroforestry (ICRAF), PO Box 30677, Nairobi, Kenya*
2. *University of Zimbabwe, Box MP 167, Mount Pleasant, Harare, Zimbabwe*

Tropical regions currently have the highest population growth rates in the world, and at the same time suffer from relatively larger areas of infertile soils than the temperate zones. Tropical soils are as diverse as those in the temperate zone, as all USDA soil orders are found in the tropics, but the relatively infertile Oxisols and Ultisols occupy about 43% of the tropics and only 7% of the temperate zone, while fertile Mollisols account for only 2% of the tropics but 11% of temperate regions. Most Oxisols and Ultisols suffer from acid infertility, especially aluminium (Al) toxicity, and the often-related problems of phosphorus (P) deficiency and high P fixation. In addition, large areas of formerly moderately fertile soils in sub-Saharan Africa (Alfisols and eutric Oxisols) have become depleted as a result of continuous low-input cropping. Finally, one can assume nitrogen (N) deficiencies for almost any cropping system, that does not receive external N inputs. Infertile or depleted soils can be made productive by use of chemical inputs; however, small land holdings, poorly developed transport and market infrastructures, and lack of credit facilities all militate against higher use of mineral fertilizers by tropical smallholders. Lower cost options are therefore necessary in order to achieve the critically needed increases in agricultural production. Some options for several of the most widespread nutrient problems are summarized.

Nitrogen

It is very difficult to build large reserves of soil N (unless in recalcitrant, poorly available forms), so a nearly continual supply of N is necessary. This can be achieved through green manuring, legume rotations, or fallowing with leguminous shrubs or trees. Legume rotations are common, but since most involve a harvest offtake in grain or fodder, net N additions are low or even negative. Partial exceptions that give both edible yield and non-trivial soil-N additions are pigeonpea and cowpea. Green manure crops can supply the needed N, but involve the loss of one or more season's marketable harvest. Tree legumes fix similar quantities of N to herbaceous legumes, and agroforestry options are indicated in some cases. Simultaneous agroforestry systems such as alley cropping often

suffer from excessive competition, especially in nutrient-poor soils and in drier areas. The early hopes for alley cropping as a solution for N deficiencies have not been realized, and sequential systems such as relay cropping or 1- to 3 - year leguminous fallows now receive greater attention. Nitrogen accumulation and crop yield increases are related to the duration of the fallow, and longer fallows require a surplus of land, that is not available in many areas. Mineral-N additions are indicated in many cases, but failing this, marginal lands currently not cropped could be used to grow legumes, and the biomass harvested as fodder or transferred to crop fields.

Phosphorus

Phosphorus concentration in plants is too low to provide the necessary amounts of P, so additions of inorganic P are almost essential. Some crops, such as pigeonpea or groundnut can access poorly soluble sources of soil-P, and other crops have substantial genetic variability in growth potential under low-P conditions. This potential could be exploited in plant breeding efforts. These can be considered only as temporary measures, as they exploit the limited capital store of soil-P and cannot be sustained. Heating the soil during the burning of forest or fallow vegetation appears to provide increased P availability above that expected from the ash alone, an effect which often lasts for several years. Again, this is a temporary solution, presumably resulting from the release of recalcitrant soil organic P compounds, but involving only offtake with no additions. Manure from animals grazed off-farm offers a net P input at the farm level, but at the expense of decreased P capital in surrounding areas. Given the eventual necessity of inorganic P additions, the question is whether to use processed fertilizers or indigenous phosphate rocks (PRs). The decision is an economic one, based on the relative agronomic effectiveness and the relative price of PRs compared to soluble fertilizers. In cases where use of PR is dictated regardless of the economics, there are several options. Moderately soluble PRs are often effective in acid soils with moderate P fixation, and may often be applied directly. Poorly soluble PRs must either be processed or used in such extensive systems as perennial crops or permanent pasture where rapid P release is not required. Processing options include local processing of superphosphates, partial acidulation, or microbial solubilization. Superphosphate production requires both industrial capacity and relatively high-grade ores, the combination of which is rare in the developing world. Partial acidulation can tolerate low-grade ores, but again requires often non-existent industrial capacity. Microbial processing may be amenable to community-scale operations, using locally available materials, but to date has only been tested on a laboratory scale under controlled conditions. Alternatively, the few annual crops, able to access the poorly soluble PR, could be grown, and crop wastes recycled to slowly improve soil P status. For other

crops, microbial P solubilizers may be useful as seed inoculants, though apparently not as broadcast soil amendments such as the so-called "phosphobacterin" tested in the past. Microbial seed inoculants have enjoyed modest success in temperate agriculture, and should be tested in tropical agriculture.

Aluminium toxicity

As with other mineral deficiencies or toxicities, Al toxicity is amenable to a chemical solution. Lime deposits are fairly common in the tropics, and the materials cost is generally low. Transport cost is usually prohibitive, however, given the usual need for lime additions of up to several t ha⁻¹. Given these constraints, organic additions or plant-based solutions are probably the best short-term alternative. Organic additions in green manure or cleared fallow vegetation can complex the Al³⁺ ion and render it less toxic, though the effect is temporary, lasting only one or two seasons. The greatest promise is probably in plant breeding for Al-tolerant varieties. Species differences in Al tolerance are well known, and within crop varieties there is also often-substantial variation in tolerance, that can be exploited in breeding programs. Unconscious selection due to inherent soil properties at breeding stations delayed progress in some crops such as maize, most varieties of which were developed on high base status soils. In contrast, upland rice has long been grown in acid soils, so suitably tolerant germplasm was available early. Early efforts were often simply based on selection of tolerant crops and varieties, but later breeding programs have succeeded in developing Al-tolerant varieties of maize and other staple crops, while maintaining acceptable yield and culinary qualities. While liming to ameliorate Al toxicity is an eventual goal, proper crop selection offers a sustainable alternative in the interim.

In conclusion, there are no magic solutions to soil nutrient deficiencies or toxicities. The examples given represent perhaps the most widespread problems in the tropics. In the case of P certainly, and N most probably, fertilizer additions should be seen as necessary. An organic-based system, coupled with judicious use of moderate doses of inorganic fertilizers, probably offers the best path to increased agricultural productivity in the tropics.

Farmer preferences for crop varieties in low-nutrient environments

S. S. Snapp¹ and S.N. Silim²

1. *Natural Resource Management Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Matopos Research Station, PO Box 776, Bulawayo, Zimbabwe*
2. *Genetic Resources and Management Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), PO Box 39063, Nairobi, Kenya*

Low-fertility soils and limited resources are barriers to improved cropping system productivity throughout the developing world. In risky environments farmers are reluctant to invest in fertilizers because they are not sure of the returns on investments made. Further, farmers may not have access to or resources to invest in fertilizers. Crops adapted to nutrient deficiency can improve food security among these poorest farmers. However, the development literature documents the limited adoption of many improved varieties and agronomic practices. If research is to achieve impact, understanding farmer preferences and addressing multiple selection criteria must be high on the agenda. Investigation of farmer decision-making is an important complement to research on the genetic basis of plant adaptation to low soil fertility. Strategies to reduce risk and meet farmers' criteria include cropping system design and intercropping of long-duration (LD) and short-duration (SD) genotypes. The purposeful combination of low-nutrient tolerant varieties to build cropping systems that meet multiple farmer objectives is discussed. The question remains, what are the long-term environmental consequences of widespread adoption of low-nutrient adapted varieties and cropping systems? Preliminary nutrient budget data from on-farm trials are discussed. It is suggested that intensification of cropping systems with low-nutrient adapted, LD leguminous species can improve the natural resource base.

Smallholder farmers have historically benefited from research investments in genetic improvement of crops with high tolerance of nutrient-deficient soils. These crops include sorghum, pigeonpea, cowpea, and cassava. Crops that are adapted to poor soils are generally able to access nutrients that are in relatively unavailable forms, and are able to efficiently use nutrients thus acquired. Legume species form a distinct group of low-nutrient adapted crops, as they can biologically fix nitrogen (N), and thus improve the N status of nutrient-deficient soils. A trade-off is often apparent between adaptation to low nutrients and yield potential, as crops tolerant of deficiency tend to have low yield potential. The challenge researchers face is to improve tolerance to nutrient stress for a wide range of genotypes, and to improve yield potential. Simultaneously, researchers

must keep in mind other criteria of smallholder farmers, e.g., low labor requirements, grain quality, and the secondary benefits from leaf consumption, i.e., stover for livestock feed and soil fertility enhancement.

Farmer preference is determined by perceptions of constraints, probable returns, and investment risk. Farmer participatory research on genetic improvement of common bean in East Africa has shown that yield is usually the first priority criteria, whereas tolerance to edaphic stress (low nutrients and drought) is a lesser priority. Farmers in West Africa were much less interested in improving tolerance to low-nutrient soils in cowpea. This may be due to the general adaptation of cowpea to low fertility. The participatory breeding literature also indicates that labor requirement is a criterion that cannot be overlooked. This is particularly true in Africa, where labor constraints are high.

A case study of legume-intensification systems and farmer preference in Malawi is presented. Tradeoffs were found among yield, labor requirements, and tolerance of low soil fertility. A matrix of grain yields versus adaptation to nutrient deficiency was developed for Malawi SD and LD grain legumes. The matrix reflected the relationship between growth period and yield, where high yields were associated with LD crops that have a long period of time to biologically fix N, acquire nutrients, photosynthesize, and fill grain, compared to SD crops. The exception was LD pigeonpea, that has a very low harvest index. A survey indicated farmers are willing to accept low yields of LD pigeonpea because of its low labor demand and secondary benefits, e.g., soil fertility improvement and fuel wood. A matrix was also used to investigate the relationship between labor requirement and tolerance of low nutrients. A close association was found between high yield potential and labor demand. For example, bush beans which are SD and determinant have low yield potential in poor soils, yet they tend to require minimum labor; whereas LD climbing beans have high yield potential in nutrient-deficient soils, yet require high labor inputs.

It is a challenge to develop crops that perform well under nutrient stress and have low labor requirements. *Mucuna* spp. is unusual in this respect. *Mucuna* suppresses weeds and produces high biomass and seed yields in poor environments, addressing both yield and low labor criteria; however, its grain toxicity generally limits its use to green manure and cover crops. In order to meet farmer criteria for consistent yields, low labor demands, and tolerance to poor soils, intercrop systems were designed. This systems approach, in conjunction with genetic improvement is one way forward. Purposeful combination of species and growth duration in an intercropping system allowed effective exploitation of resources; e.g., deep-rooted LD genotypes interplanted with SD shallow-rooted genotypes. Risk of crop failure in poor quality soils was moderated by intercropping genotypes with tolerance of nutrient deficiency with more nutrient-demanding crops.

Intercrops were investigated through 200 on-farm trials in Malawi, using a satellite trial design where researcher evaluation of system performance was crosschecked with farmer assessment. Promising intercrops included LD pigeonpea (LDP) with a SD groundnut variety (SDG), and LDP with soybean varieties. The SDG/LDP system combined SDG high yield potential and low labor demand (compared to spreading type groundnut varieties) with LDP "bonus" grain crop and soil-enhancing residues. The SDG met farmer criteria for early harvest, increased food security, exploitation of a market niche, and minimal labor requirements. However, SDG yields were erratic in poor soils, a risk moderated by intercropping with LDP. Early growth above ground by LDP was very slow, which minimized competition with the SDG, and exploited nutrients below the groundnut root system. In addition, LDP grew into the dry — season and recycled nutrients lost in a SDG monoculture. Results from farmer participatory research indicated that "doubling up" SDG and LDP had consistently high land area equivalent ratios. Comparisons demonstrated marked farmer interest in SDG/LDP intercrops grown in rotation with maize, and other LD/SD intercrops. Women farmers in particular preferred "doubling up legume systems" to their current cropping systems. The labor-efficiency of weeding doubled-up legume systems was ranked high by farmers. Farmer selection criteria also highlighted problems; primarily, concerns about high cost and the unavailability of legume seeds.

Questions have been raised about the sustainability of crop varieties that effectively exploit nutrients in a low-nutrient environment. Will these varieties mine soils? Preliminary data from on-farm measurements of nutrient input and outputs in the intercrop systems indicate a more complex picture. Phosphorus and N budgets suggested that intercropping with LD pigeonpea can enhance soil coverage, reduce erosion, and significantly improve the nutrient balance, with little or no fertilizer inputs, compared to maize monocultures. Apparently, more effective mining can be balanced by reduced erosion and retention of nutrients in plant-available forms.

Nutrient balances - a guide to improving the management of sorghum- and groundnut-based dryland cropping systems in semi-arid tropical India

T. J. Rego, B. Seeling, V. Nageswara Rao, G. Pardhasaradhi, J.V.D.K Kumar Rao, R.J.K Myers, and C. Johansen

Natural Resource Management Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India

Nutrient balance studies have shown that the depletion of soil nutrients is one of the most important problems for sustainable agriculture in sub-Saharan Africa. Information on nutrient depletion in India is surprisingly scarce. Nutrient balances are generally estimated on various scales, e.g., at national or regional level, on farms of a particular farming system, or in fields of a particular cropping system. Much of the published data on nutrient balances in India is at the national and regional level and deals only with mineral fertilizer inputs and estimates of crop nutrient uptake. These studies ignored major differences which existed between dryland and irrigated systems in terms of fertilizer and FYM inputs.

Methodology

In order to obtain reliable data on nutrient mining in dryland farming systems of the Indian semi-arid tropics (SAT), nutrient balance studies were conducted in farmers' fields. After a survey of dryland cropping systems on Alfisols in the Indian SAT, two cropping systems (a sorghum-based system in Mahaboobnagar district and a groundnut based system in Ananthapur district) that were of primary importance were selected. The nutrient balance study was limited to these systems and to three major nutrients; nitrogen (N), phosphorus (P), and potassium (K).

Initial survey and selection of the villages

The basic cropping systems on Alfisols in SAT India were determined and delineated through the use of crop statistics and geographic information systems (GIS). The sorghum- and the groundnut-based systems were selected because they are the most important dryland cropping systems in this area. Based on the initial survey, the villages Nusikottala and Krishnamreddypally in Anantapur district and Bhootpur mandal in Mahboobnagar district, were selected as locations for the nutrient balance study. The farmer sample was stratified according to farm size (small < 2 ha, medium 2 - 10 ha, and large > 10 ha) and farmers from each group were selected for the nutrient balance study in the two areas. Fields

of the 45 farmers were selected according to crop distribution in the first season. The nutrient balance of the same field was determined in the second season regardless of the crop grown. In addition to these criteria, access to irrigated land was considered important for the nutrient management of the dryland crops. The same proportion of farmers with access to irrigated land was maintained in the sample group. The selection of farmers and fields was similar in the groundnut-based system.

Nutrient balance

In 1995/96 and 1996/97 an attempt was made to establish a nutrient balance for N, P, and K for the two cropping systems. Of the 5 identified inputs (mineral fertilizers, organic manure, atmospheric deposition, biological N₂ fixation, and sedimentation), and 5 outputs (harvested product, residue removal, leaching, gaseous losses, and water erosion), it was possible to determine the nutrient application with mineral fertilizers and organic manure, and the nutrient removal with harvested products and residue removal. The amount of fertilizer and organic manure applied was determined through farmer interviews. An initial soil sampling through full profile depth was only made in selected fields. In the second year, all the fields were sampled to the depth of the murram layer (semi-weathered stratum). The soil samples were analyzed for mineral N content, available P content, and exchangeable K.

Results

From the results, overall nutrient balances were estimated in a few of the cropping systems. In a sorghum-castor rotation, the N input was 87 kg ha⁻¹, as against an output of 77 kg N ha⁻¹, and this indicated a net annual gain of + 10 kg ha⁻¹. As N losses were not estimated in this study, and they may have been quite significant, the +10 kg N ha⁻¹ may not indicate the correct N balance. For P and K that are less susceptible to loss, the estimates clearly reveal the positive P and negative K balances in the cropping system. With an improved sorghum/pigeonpea-castor system, the nutrient balances of N (+24), P (+26), and K (-16) kg ha⁻¹ were estimated. The positive balance for N does not include an estimate for biological nitrogen fixation (BNF) of pigeonpea, which, if included might increase the positive N balance. Nutrient balances for the mirror images of the two systems namely castor-sorghum (+45 kg N, +35 kg P, +1 kg K ha⁻¹), and castor-sorghum/pigeonpea (+58 kg N, +44 kg P, +32 kg K ha⁻¹) cropping systems were positive. Over a longer period, similar nutrient balances in a long-term cropping systems experiment at ICRISAT were observed. A continuous cropping system of sole groundnut was on average positive for P (+37 kg ha⁻¹) and negative for K (-20 kg ha⁻¹). For N when an estimate of BNF was not included the balance was negative (-111kg ha⁻¹). If it is assumed that 50% of groundnut N uptake is from

BNF, then the balance is also negative (-30 kg ha^{-1}). However, observations of farmers' fields indicate that BNF is 53%, averaged from 20 farmers' fields and ranged between 41% and 65%. In order to have a positive N balance the BNF value would need to be $>68\%$. The soil analysis data from these farmers' fields indicate scant accumulation of soil N in spite of groundnut monocropping for more than 40 years. The low BNF in the farmers' fields may be one of the causes for poor accumulation of soil N.

Conclusions

This study provides factual information on nutrient balances specifically for different cropping systems in farmers' fields, that can be generalized for the region. Poor BNF in groundnut monocropping over a long period suggests that more efficient BNF rhizobium strains need to be inoculated in that region. Measuring N losses precisely, with different cropping systems in farmers' fields by applying isotope ^{15}N would help in understanding the N dynamics in this environment. Phosphorus inputs met the crop requirements in most of the cropping systems that were studied, but K application needs to be recommended along with N inputs in dryland cropping systems, either through FYM or fertilizer inputs to reduce nutrient mining. Positive nutrient balances in maize- and cotton-based cropping systems can be attributed to farmers' preference for fertilizer application to commercial crops.

Preplant moisture and fertility conditions as indicators of high and stable yields in rainfed cropping systems

C.F. Yamoah¹, G. E. Varvel², and J. J. Adu-Gyamfi³

1. *Soil Research Institute, Council for Scientific and Industrial Research (CSIR), Academy Post Office, Kwadaso, Kumasi, Ghana*
2. *Department of Agronomy, University of Nebraska, Lincoln, N E 68583-0949, USA*
3. *Natural Resource Management Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India*

Rainfed cropping systems are vulnerable to weather fluctuations. Corn (maize) or sorghum-soybean rotations are commonplace in the Corn Belt in Nebraska, USA. Long-term studies ranging from 12-20 years have been conducted in Nebraska to compare rotations to continuous cropping systems. Empirical analyses of these studies showed that rotations were more high-yielding, relatively stable, and profitable than monocultural systems.

Data from a long-term crop rotation experiment conducted at the University of Nebraska from 1984 to 1998, was analyzed to determine the effect of preplant moisture condition on yields of maize, sorghum, and soybean. The experimental design was a split-plot design with four replications. The main cropping system treatments were; 1. monocultures of maize, sorghum, or soybean, 2. 2-year soybean-maize or soybean-sorghum rotation, 3. 4-year soybean-sorghum-oat+clover-maize rotations, and 4. 4-year oat + clover-sorghum-soybean-maize rotations. Subplots were N levels of 0, 90, or 180 kg ha⁻¹ for maize and sorghum, and N levels of 0, 34, or 68 kg ha⁻¹ for soybean and clover. This report is based only on the monoculture and 2-year rotation systems.

Preplant moisture condition was calculated as the Standardized Precipitation Index (SPI) which is a measure of drought. The April 8-month SPI was used to capture the moisture status from September to April. The crops were largely rainfed, therefore crop water use was entirely dependent on precipitation. An SPI value of zero indicates average conditions, and values of greater than +2 or less than -2 generally indicate extreme conditions associated with events that occur only 5 % of the time. Furthermore, long-term climatic records in Nebraska demonstrate that there is moisture recharge and surplus from September to May and a deficit during the summer months from June to August. Crops are sown in May and early June and usually attain physiological maturity by October. Therefore, it was hypothesized that favorable preplant moisture conditions could increase microbial activity, and result in early crop establishment and high yields. This thesis stemmed from the concept of drought elaborated by Wilhite and Glantz in *Water Int.* 10, 1985.

Results showed that maize and soybean yields in years with moist April 8-month SPI were higher ($P < 0.05$) than those that were dry. Sorghum did not respond to preplant moisture conditions ($P > 0.05$). Nitrogen fertilizer significantly ($P < 0.02$) increased yields of monoculture sorghum, not in rotation with soybean ($P = 0.20$). Maize responded to N fertilizer in both monocrop and rotation with soybean, but soybean did not ($P < 0.008$ to $P < 0.02$). Maize yields in monoculture and rotation were increased by 17 % at the high-N rate when preplant conditions were moist. Maize normally responds to fertilizer under good moisture conditions, but sorghum yields were reduced by 2 to 8 % in moist preplant conditions.

Regression models have been used to predict crop yields from standardized and non-standardized weather variables in North America. The main weather variables implicated in the above studies were precipitation and temperature. In the present study, a second order regression equation using preplant April 8-month SPI as independent variables and subsequent crop yields as dependent variables from 1984 to 1995, described maize and soybean yields in rotation fairly well. Preplant April 8-month SPI accounted for up to 85 % of variability in maize yields and 81 % in soybean. Sorghum yields were indifferent to preplant moisture conditions. The resilience of sorghum to adverse weather is attributed to its peculiar anatomical features. There was a reasonable agreement between actual maize yields and yields predicted by the regression models using the April 8-month SPI values from 1996 to 1998. The results from this study could be used as indicators to warn farmers and policy makers against impending droughts in order to prepare for strategies to mitigate their effects.

Role of modelling in improving nutrient efficiency in cropping systems

P. S. Carberry¹, M. E. Probert², J. P. Dimes³, B. A. Keating², and R. L. McCown¹

1. Commonwealth Scientific and Industrial Research Organization (CSIRO), Tropical Agriculture, Agricultural Production Systems Research Unit (APSRU), PO Box 102, Toowoomba, Queensland 4350, Australia
2. Commonwealth Scientific and Industrial Research Organization (CSIRO), Tropical Agriculture, Agricultural Production Systems Research Unit (APSRU), Carmody Road, St Lucia, Queensland 4067, Australia
3. Natural Resource Management Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Matopos Research Station, PO Box 776, Bulawayo, Zimbabwe

A 10-year research effort in utilizing experimental research and simulation modelling in attempting to identify a development path for subsistence agriculture in semi-arid Kenya is reported. It concludes that a strategy of augmenting traditional soil enrichment practices, based on manure and legumes, with modest amounts of fertilizer is economically feasible for many farmers and provides the best prospects for food security in this climatic zone. The work provided strong argument that the use of the simulation model permitted the assessment of fertilizer use in a way that would not have been possible using traditional field experimentation alone. Subsequent research has confirmed both the apparent attractiveness of fertilizer use in Kenya and the applicability of models to address such research questions. However, the implementation of apparently advantageous changes to current farming practice remains an intractable problem.

In reflecting on the work in Kenya, it was suggested that there were six lines of research that were worthy of further exploration in addressing soil fertility decline in Africa:

1. Find more efficient ways of capturing, storing, and using manure on crops,
2. Test various Fertilizer-Augmented Soil Enrichment (FASE) strategies for combining applications of chemical fertilizer with manure and crop residues
3. Extrapolate research results on legumes in systems
4. Research the economics of FASE strategies for different price-cost scenarios
5. Input into national policies on commodities, food security, and fertilizers
6. Keep fertilizer on the policy agenda.

While the application of simulation models were explicitly recommended in the second and third areas, one could easily imagine that modelling analyses

could readily contribute to other of these recommended areas of future activity, particularly as inputs into economic and policy analyses.

The recommendations address both research activities to broaden understanding of the biophysical system under study and operations research that uses current understanding to predict likely outcomes for alternative management strategies that may be imposed on the farming system. Also included is possible intervention via policy actions. However, important questions are whether intervention directly with farmers is possible, and whether simulation models can contribute beyond the research phase to assist in achieving improved farming practices? While not suggesting close analogy between developed and subsistence agriculture, it is relevant in the present context to refer to recent experiences in Australia that demonstrated that simulation models can contribute to farmer exploration and acceptance of practice change.

Clearly, there has been significant past research effort into utilizing modelling to explore management strategies in nutrient-stressed environments. The present objectives are firstly to provide some case study examples of how models can contribute to research on nutrient efficiency in cropping systems and, secondly, to address the question of whether these models can assist the research community in contributing to purposeful change in farming practice.

In fulfilling these stated objectives, the opportunity is taken to report on the current status of the systems model, Agricultural Production Systems Simulator (APSIM), particularly in regard to current capabilities in addressing the issues raised. Accordingly, applications addressing the use of manure and the incorporation of legumes in cropping systems are explored. And finally, some attention is given to model assistance in identifying how plants' genetic capabilities may be exploited in low-nutrient farming systems.

Session 4 Interpretive Summary

Combining genetic improvement with natural resource management

R.M. Welch and C. Johansen

Introduction

Ultimate success in exploiting the genetic capabilities of plants to grow in nutrient-stressed environments of the semi-arid tropics (SAT) requires a holistic view of food systems to ensure that genetic selections for improved yields on nutrient-poor soils will actually be adopted by farmers. This session focused on using existing knowledge of soil fertility and plant nutrition to develop farming technologies that could increase crop productivity on the nutrient-depleted soils of small-farm holders in the SAT. Knowledge gaps were identified for future research opportunities in low-nutrient input farming systems. Additionally, the important role that simulation models can play in synthesizing existing knowledge, determining future research and development needs, and in providing information applicable to policy and economic decision-making was discussed. Brief overviews of the papers presented during this session follow.

Appropriate farm management practices for low-nutrient soils

Because of poorly developed transportation and market infrastructures, limited access to credit facilities and the small size of land holdings, frequent and adequate use of mineral fertilizers in the tropics is not an option for most farmers. Thus, lower cost options supplying essential nutrients need to be developed if smallholder farmers are to achieve increased crop productivity on infertile soils. Some potential options for improved nitrogen (N) and phosphorus (P) availability and the control of aluminium (Al) toxicity in acid soils in the region were presented.

Nitrogen

Various cropping techniques have been employed to increase available-N in soils such as green manures, legume rotations, or incorporating leguminous shrubs or trees in fallow land. Because of the harvest offtake of grain or fodder legumes, most of these rotations do not significantly increase net soil-N. Most effective of the grain legumes tested were pigeonpea and cowpea. The use of green manure crops contributes significant quantities of N to subsequent crops but causes farmers to forego one or more marketable crops. Tree legumes, herbaceous

legumes, and agroforestry options can provide net increases in soil-N under some circumstances. However, simultaneous agroforestry systems, including alley cropping techniques, may result in excessive competition with adjacent seasonal crops especially in nutrient-poor soils under low moisture conditions. More attention should now be given to sequential cropping systems (e.g., relay cropping, 1- to 3-year leguminous fallows). Fallow duration is an important factor but requires more land so is not an option for typical smallholders in regions of increasing human population. Therefore, N fertilizers are necessary in many cases. Possibly, marginal lands not currently cropped (if available) should be planted with legumes and the biomass produced used as fodder or as organic matter for soil enrichment.

Phosphorus

Infertile Oxisols and Ultisols do not contain enough soil-available P to allow maximum production of available crop varieties in the SAT. Thus, additions of inorganic sources of P are essential to good soil fertility. Crops such as pigeonpea and groundnut are capable of accessing poorly available P in the soils of these regions. There is also substantial genetic diversity in P use efficiency among most cultivated crops grown in these regions that has not been exploited fully. However, selecting for P-efficient crops will not sustain crop productivity indefinitely. Mining of the soil-P by P-efficient crops will ultimately deplete the available soil-P stores and exacerbate the nutrition for less P-efficient ones. Burning forests can increase available soil-P levels for several years, but this technique is not sustainable because successive crops will eventually deplete native P supplies in the soil. Phosphorus-rich manures from off-farm sources can also contribute to soil-P fertility but this is often impracticable for smallholder farmers and causes a transfer of P from surrounding, perhaps more fertile, areas.

Ultimately, sources of inorganic P must be applied to maintain or increase soil-P fertility. Choosing to use either processed P fertilizers or indigenous phosphate rocks is an economic decision based on both relative agronomic effectiveness and the cost of phosphate sources. If processed P fertilizers are not an option, then moderately soluble indigenous phosphate rock sources can be used if applied to acidic soils. However, poorly soluble rock sources must either be processed or used exclusively in perennial crop or permanent pasture systems where slow P release is desirable. Options for processing P-rock sources include local processing of superphosphate, partial acidulation, and microbial solubilization. Production of superphosphate requires some industrial capacity and relatively high-grade P-ores that are not normally available in many regions. Low-grade P-ores can be partially acidulated but this also requires some industrial capacity. Microbial processing has yet to be demonstrated as effective in field experiments using community-scale operations. Better recycling of crop residues

from P-efficient annual crops could be an option worth pursuing. Possibly, the use of microbial-P solubilizers as seed inoculants could be developed for tropical agricultural systems because modest success using this technique in temperate agricultural regions has been reported.

Aluminium toxicity

Liming soils is seen as the ultimate solution to Al toxicity in acid soils. The high cost of transporting lime to farmers fields from lime deposits is seen as the major constraint in treating acid soils in the tropics. Increasing soil organic matter status, permitting chelation of free Al, is an option worthy of further investigation in the tropics. Breeding for Al tolerance has not been a major goal in plant breeding efforts in this region. Recent evidence suggests that it may be possible to genetically transform crop plants such that they exude greater quantities of organic acids which neutralize the effects of Al toxicity. Such approaches would indeed better adapt crop plants to acid soil conditions, but would not necessarily improve the soil condition itself (except perhaps by allowing greater biomass production and consequent return of organic matter to the soil). While genetic enhancement of crop productivity constraints offer prospects for the medium term, the long-term goal of improving the soil condition, by lime or organic matter addition, must remain.

The paper points out the problems associated with low-nutrient status and Al toxicity in tropical regions will not be solved easily. Ultimately, locally available and affordable sources of both P and N fertilizer must be developed. The use of organic-based agricultural systems together with efficient use of moderate levels of inorganic fertilizers offers the most promising means of dealing with soil fertility constraints in the tropics.

Farmer preferences for crop varieties in low-nutrient environments

Both low soil fertility and inadequate resources are primary limitations to improving crop productivity in the developing world. Integrating farmer preferences with cropping system approaches were viewed as effective means of attaining sustainable and acceptable production levels on nutrient-poor soils. Understanding farmer preferences and multiple selection criteria are seen as very important factors in achieving farmer acceptance of new technologies. Farmer decision-making processes should be studied along with genetic improvements in crops adapted to nutrient-poor environments to maximize impact. To meet multiple farmer objectives a purposeful combination of nutrient-efficient crops and improved cropping system designs (including long-duration and short-duration genotypes) were employed in a case study in Malawi.

Important interactions were shown to exist between crop yield, labor requirements, and crop tolerance to infertile soils in legume-intensification

systems. Using a matrix of grain yields versus adaptation to nutrient-deficient conditions, it was shown that farmers could accept lower yields if labor demands were low enough and if secondary benefits were high enough (e.g., significant improvements in soil nutrient status and availability of fuel wood). There was a close association between high yield potential and labor demand.

Mucuna spp. can suppress weeds and produce high biomass and seed yields when grown on relatively nutrient-poor soils; its propagation requires relatively low labor demands. However, because *Mucuna* grain is toxic it is only useful as a green manure or in cover-crop rotations. Intercrop systems were designed to meet farmer criteria for consistent yields, low labor demands, and tolerance to nutrient-poor soils. Combined with genetic improvements, this approach appears to have many advantages because purposeful combination of species and growth duration in intercropping system maximizes resource exploitation and reduces risk of crop failure.

Other studies in Malawi in on-farm trials were carried out using a satellite trial design where system performance (evaluated by researchers) was compared to farmer assessment. Intercrops showing promise included long-duration pigeonpea genotypes with either short-duration groundnut genotypes or short-duration soybean genotypes. Farmers showed great interest in short-duration groundnut/long-duration pigeonpea intercrops. Limitations to farmer acceptance included concerns for the high cost and short supply of legume seeds.

The soil "mining" issue associated with nutrient-efficient genotypes was addressed. Intercropping with long-duration pigeonpea can reduce soil erosion and significantly improve nutrient balance with little or no fertilizer additions. Both P and N budgets obtained from on-farm measurements suggest that soil "mining" of nutrients by crops can be effectively balanced by reducing soil erosion and improving retention of available nutrients. It was concluded that intensification of cropping systems with low-nutrient adapted, long-duration leguminous species will improve the natural resource base.

Nutrient balances - a guide to improving the management of sorghum- and groundnut-based dryland cropping systems in semi-arid tropical India

Nutrient balances (N, P, and K) for farmers fields in two dryland cropping systems (sorghum-based and groundnut-based) on Alfisols were carried out in an Indian SAT region using geographical information system (GIS) analysis and crop statistics. Determinations were made for mineral fertilizer and organic manure inputs from farmer interviews. In addition, nutrient removal was also determined from harvested products and residue removal. Soil samples from farmers fields were analyzed for mineral N, available P, and exchangeable K content.

Overall nutrient balances were calculated for a few cropping systems. In a sorghum-castor bean rotation, N balance was positive with a net annual gain of

10 kg ha⁻¹. However, N losses were not determined in this study and they may have been significant. Balances of P and K were also estimated as showing a positive P and a negative K balance for the cropping system. In an improved sorghum/pigeonpea-castor bean system, N and P were in positive balance while K was estimated to be in negative balance. The positive N balance did not include biological N fixation that could have contributed significant amounts of N. Other cropping systems were also investigated.

Similar nutrient balances were seen in a long-term cropping systems experiment at ICRISAT. In a continuously cropped groundnut system, positive P and negative K balances were noted. If biologically fixed N were not included in the balance calculations, negative N balances resulted. If only 50% of the groundnut N uptake came from fixed N, the N balance was also negative. In farmers' field trials (20 field sites) biologically fixed N ranged from 41% to 65%, averaging 53%. Positive N balance would require that >68% of the N come from biological N fixation. After 40 years of continuous groundnut monocropping, no significant N accumulation in the soils was found. Low soil biological N-fixation rates may be one reason contributing to the poor accumulation of soil-N in the region. Thus, more efficient N-fixing rhizobium strains need to be used for legume root inoculation in this region.

The use of the stable isotope, ¹⁵N, should be expanded in research to determine N losses precisely in different cropping systems in farmers' fields. Doing so would provide valuable data needed to understand the dynamics of N balance in these cropping systems. The use of P fertilizer inputs apparently meets the crop requirements in most cropping systems studied, but K and N inputs need to be increased in dryland cropping systems to offset losses from nutrient mining. In maize and cotton systems, positive nutrient balances were attributed to farmers' preferences for fertilizer application to these high-value crops.

The reported studies gave only a broad estimate of micronutrient balance. The study pinpointed the various knowledge gaps in sources of gain or loss of nutrients, which will require further component research to quantify. Further, such balances provide only a static picture of the situation. It is desirable to understand the long-term dynamics of nutrient flows in the target systems. This is now becoming more feasible to attempt with the advent of more user-friendly crop and nutrient models.

Preplant moisture and fertility conditions as indicators of high and stable yields in rain-fed cropping systems

Cropping systems dependent on rain are vulnerable to weather fluctuations. Data was collected from experiments on long-term maize, sorghum and soybean rotations (monoculture and 2-year rotations) in the Corn Belt of Nebraska in the USA.

Standard Precipitation Indices (SPI), indicative of preplant moisture, were calculated and used to quantify yearly drought conditions. Moisture status was determined by using 8-month (September to April) SPI values. A SPI value of zero indicated average conditions while positive values greater than or less than 2 indicated extreme conditions associated with weather events that occurred only 5% of the time. Hypothetically, favorable preplant moisture conditions could be responsible for increased soil microbial activity resulting in early crop establishment and higher yields.

Maize and soybean yields were sensitive to preplant soil water content with moist soil producing higher yields. However, sorghum did not respond to preplant moisture conditions. Nitrogen fertilizer effects varied with crop and with preplant moisture conditions. Yields of sorghum in monoculture (and not in rotation with soybeans) increased in response to N fertilizer additions while maize responded to N fertilizers in both monoculture and in rotation with soybean. Soybeans did not respond to N fertilizers. Maize yield normally increases in response to N application under moist preplant conditions. However, sorghum yields usually were reduced by 2 to 8% when soil moisture was high before sowing.

Regression models were constructed to predict crop yields from weather data. The most important weather data used included precipitation and temperature. A second-order regression equation that included preplant SPIs as independent variables and subsequent crop yields as dependent variables, described maize and soybean yields in rotation satisfactorily. Sorghum yields were not affected by preplant moisture conditions. The resilience of sorghum to adverse weather conditions may be the result of certain peculiar anatomical characteristics of the plant. The regression model provided reasonable predictions between actual maize yields and predicted yields. Possibly, the utility of the model constructed from this study could be applied to provide warnings to farmers and policy makers of impending droughts so that strategies could be implemented to mitigate their adverse effects.

Role of modeling in improving nutrient efficiency in cropping systems

Simulation modeling in conjunction with experimental research was used to identify a development path for subsistence agriculture in the semi-arid region of Kenya. Manure- and legume-based strategies to augment traditional soil enrichment practices along with modest amounts of fertilizer inputs was judged economically feasible for many farmers. Possibly, this approach provides the best prospects for food security in this region. Simulation modeling allowed for the assessment of fertilizer use in a way that was not possible using only traditional field experiments. Research confirmed the value of fertilizer use in Kenya and

the applicability of the models to address such research questions. Unfortunately, using these findings to actually change current farming practices has not yet been possible. Considerable follow-up with extension-oriented projects is required.

Future research areas identified for focus by the models included:

- Develop more efficient means of utilizing manure on crops (including capturing, storing, and using).
- Determine which Fertilizer-Augmented Soil Enrichment (FASE) strategies should be used to improve the efficiency of use of chemical fertilizers combined with manure and crop residue applications.
- Transfer results obtained through research to legume systems
- Carry out research to determine the most economical applications of FASE strategies for different price-cost scenarios.
- Contribute input into national policies on commodities, food security and fertilizers.
- Make sure that fertilizer investments remain on the policy agenda.

The models developed could be used not only in the areas of identifying future research activities but also as a source of inputs into economic and policy analyses. Both research activities to understand the biophysical system and operations research (using current understanding) to predict likely outcomes for alternative management farming system strategies can be addressed using the models.

Interventions via policy action could also be developed by using simulation modeling. Whether or not direct interventions with farmers are possible, or if simulation models can contribute beyond the research phase to improve farming practices are unknown. In Australia, simulation models have contributed to farmer exploration and to their acceptance of practice change. The challenge is to determine if this can be applied to resource-poor smallholder farmers.

The current systems model, Agricultural Production Systems Simulator (APSIM) was described particularly in regard to current capabilities in addressing important issues. Plans are being made to explore the worth of APSIM in addressing the use of manure and legumes in cropping systems. Some attention will also be given to using the model to identify how plants' genetic potential might be exploited to improve yields in low-nutrient input farming systems.

Conclusion

In the short term, the use of legume crops in rotations with staple food crops, improved utilization of manure and crop residues, and genetic improvement in crop nutrient efficiencies can all help improve N and P balances for crop production in the SAT. However, in the long term these technologies will not provide the needed P and other nutrient inputs required to sustain production for

the distant future. Thus, there is a great need to develop more affordable, locally available sources of N, P, and K fertilizer for farmers in the SAT.

Clearly, more emphasis should be given to transferring technology obtained from basic research and applied research findings to farmers if sustainable ways to improve food security in this region are to be found. This will require closer cooperation between agricultural researchers and other experts studying food system functionality. Getting farmers to adopt new technologies directed at improving nutrient-use efficiency in crops and more sustainable low-input agricultural practices must consider the food system in its entirety. Without farmer participation and technology adoption, research findings will go untried. More holistic food system approaches should be encouraged whereby agricultural scientists interact with other specialists (such as sociologists, economists, and policy makers) to ensure that their recommendations are practical and adopted by farmers. These new practices need to have a sustainable impact on improving food security for these regions of the world with minimum adverse impact on the environment.

Closing Session

Closing Remarks

T Hamazaki

Director, Environmental Resources Division, Japan International Research Center for Agricultural Sciences (JIRCAS), 1-2 Ohwashi, Tsukuba, Ibaraki 305-8686, Japan

On behalf of the Director General of the Japan International Research Center for Agricultural Sciences (JIRCAS), and the Ministry of Agriculture, Forestry and Fisheries (MAFF), I would like to thank all the participants of the workshop for their contributions. I am also delighted that Dr L D Swindale, who helped initiate the Project in 1984 and who today is at ICRISAT as the Director General, was able to be with us to open the meeting.

As you are all aware, this workshop was held to culminate the activities of the Government of Japan Special Project at ICRISAT. Many of the scientists who were involved with the Project are here today and join me in thanking the Management of ICRISAT for their unflinching support to them and their families whilst they were here in India.

During the 15 years of the Project its scientists conducted strategic and basic research aimed at improving crop nutrient and water uptake and utilization efficiencies through field management practices, and/or by exploiting morphological and physio-genetic systems to improve the adaptation of ICRISAT mandate crops to the low-nutrient and low-moisture environments of the semi-arid tropics (SAT). The Project also trained Research Fellows, Visiting Scientists, and Scholars and improved the creativity and job competence of its support staff.

The valuable research achievements of the Project from 1984 to 1999 have been highlighted in their presentations by the Project scientists. Among these achievements, the discovery that piscidic acid is exuded by pigeonpea and that this compound enhances pigeonpea's ability to take up more phosphorus (P) from iron phosphates in the soil is highly significant. As a follow-up to Phase I, further studies to examine genotypic variability in the solubilizing activity of root exudates were conducted here at ICRISAT and at the National Institute of Agro-Environmental Sciences (NIEAS) in Japan. These led to Dr Ae proposing the new concept of "contact reaction" which postulates the role of root cell walls in nutrient acquisition by groundnuts and pigeonpea.

I am delighted that during Phase III, there was an effort to identify physiological and agronomic traits to help improve the efficiency of nutrient uptake and use by ICRISAT mandate crops. Because crop productivity in the SAT is often limited by the lack of available nutrients (particularly P), enhancing

the efficiency of crops' ability to exploit sparingly available nutrients from the soil will eventually accelerate the adoption of improved cultivars by farmers, thus improving productivity in these harsh environments where agriculture is such an unpredictable enterprise.

Being a pedologist, I had little previous knowledge of nutrient physiology, soil fertility, or water management, but I have learned a lot since I took over as the Coordinator of GoJ Special Projects at ICRISAT and the International Rice Research Institute (IRRI). I am glad to know that ICRISAT has started to work on cross-program projects that aim to exploit the joint research application of genetically based, statistical, crop-physiological models to overcome the current limitations to breeding for low-nutrient environments.

The current workshop solicited a range of scientists' views on whether it is socio-economically viable, and environmentally sustainable to breed for enhanced crop productivity for low-nutrient environments. Questions have been raised about the sustainability of crop varieties that effectively exploit nutrients in low-nutrient environments. Will these varieties mine the soils and further exacerbate land degradation? This question has been well addressed during the meeting.

Major breakthroughs have been achieved in breeding for resistances to pests, diseases, and drought. It is now time to seriously consider breeding for nutrient acquisition and use efficiency. Recent studies by Drs Wissuwa, Yano, and Ae reported in *Theoretical and Applied Genetics*, 1998 on mapping quantitative trait loci (QTLs) for P-deficiency tolerance in rice provide evidence that could have application in helping to enhance P-use efficiency in ICRISAT mandate crops. This potential is encouraging in the light of the use of modern molecular biological tools to enhance P-use efficiency as demonstrated by other workshop participants.

Apart from improving nutrient use efficiencies through genetic manipulation, there is also an urgent need to fine-tune the technologies available for improving field management practices to enhance crop yields. Soil fertility management and enhancement are vital to food security in the western and southern Africa. Pigeonpea was identified as a unique crop capable of increasing the pool of available P in the cropping systems in which it is grown. Besides, it is documented that pigeonpea leaf fall contributes to 4-7 kg P ha⁻¹ during the cropping season. There is a need to quantify the advantages of pigeonpea over indigenous and such introduced leguminous crops as cowpea, groundnuts, and mungbean in relation to soil fertility replenishment. The deep-rooting ability of pigeonpea allows the crop to exploit water from lower soil layers. But, the problem of ensuring that efficient crops reach smallholder farmers who need them is a key bottleneck that remains to be addressed.

Clearly, despite the advances made by this Project during the past 15 years, there is a need for more research into the decomposition of piscidic acid in

Alfisols and the biochemical and molecular mechanisms of P acquisition, along the lines of the work on mugineic acid by Professors Takagi and Mori at the University of Tokyo. Though Phase III identified physiological traits responsible for P uptake and use efficiency, there is still a need to develop mapping populations, or to identify previously existing mapping populations, based on pairs of adapted parents of each crop that differ greatly in P uptake ability and/or use efficiency. Such pairs could be used to map the QTLs that contribute to components of these traits.

An important feature of the GoJ Project work was its interdisciplinary approach, the result of joint efforts by Drs Arihara and Ito. During all three Phases the team members were chosen for their appropriate blend of disciplines. What we need to do now is to build on the solid foundation they laid. The GoJ would have continued to fund the Project, taking into consideration its achievements and their implications in improving the productivity of dryland agriculture in the SAT. But, as all of you may be aware, because of the economic crisis in Japan, the Government decided to reduce its Overseas Development Assistance (ODA). I therefore encourage other donors to now support the excellent work and achievements by the scientists, so that it may continue.

In conclusion, the GoJ Project based at Patancheru helped to enhance the productivity of upland crops in the SAT through research, and enhanced our knowledge base of mechanisms of P and N acquisition by crops. The Project also helped to strengthen interdisciplinary efforts among scientists from Japan and their counterparts in ICRISAT. Once again, on behalf of MAFF, and the Director General of JIRCAS, Dr Maeno, I would like to thank ICRISAT's Management and Staff for their cooperation and support to the Project scientists. I thank all the Project Scientists, Drs Arihara, Ae, Okada, Ito, Matsunaga, Katayama, Tobita, Nakamura, and Nakano for their dedication and hard work. I thank the Organizing Committee for their efforts to ensure high standards of presentation and discussions. I wish to express my sincere thanks to all the workshop participants for the kindness with which they shared their knowledge and experience with us. Thanks are also due to Drs Adu-Gyamfi and Ishikawa, who coordinated this culmination of 15 years' successful work. My special thanks to those who assisted the Japanese teams in the field and laboratories; without their help it would have been impossible to attain the results presented in the three Project workshops. And Dr Johansen, I thank you especially for the important role you played to ensuring the excellent research results throughout the Project. I trust that these achievements highlighted in the commemorative publication that it was our pleasure to release this week, will not be an end, but a means to an end.

Future research needs, priorities, and strategies

During the final workshop discussion sessions it was agreed that optimizing phosphorus (P) nutrition of sorghum, pigeonpea, groundnut, and cowpea is a high priority area that requires immediate attention. Whereas considerable progress has been made in breeding for pest and disease resistant cultivars of crops, little has been achieved in breeding for nutrient uptake and use by crops. In the low-P, adverse rainfall regions of the semi-arid tropics (SAT), no improved cultivar has a reasonable chance of achieving substantial and sustainable yield levels in farmers' fields unless the critical constraint of P deficiency is addressed by adapting crops to the existing soil conditions.

Consequently, the following research needs were identified by participants as priorities. These research needs build on achievements of the 15-years' research activities of the Government of Japan Project at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Patancheru, India.

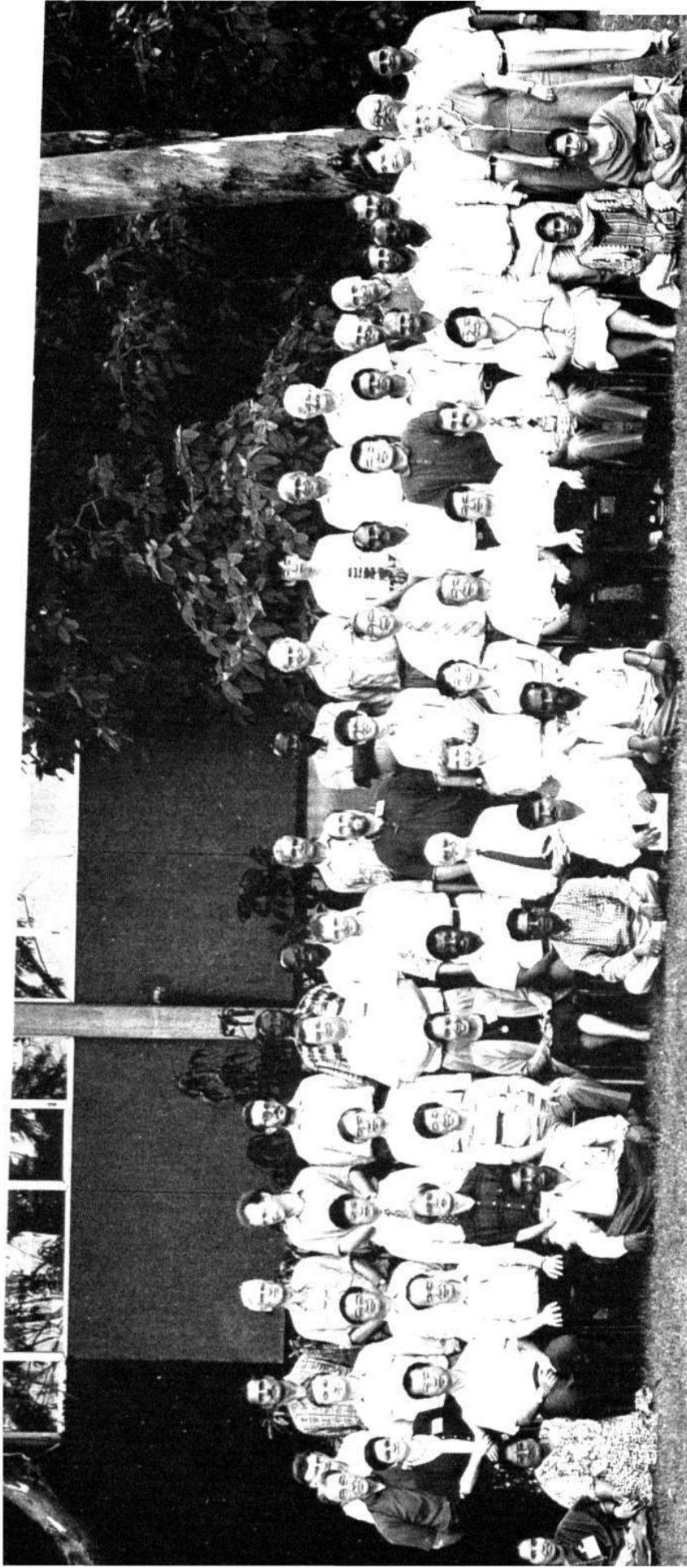
Researchable issues

- The need to exploit mechanisms by which wild species of some of ICRISAT's mandate crops are adapted to low-P conditions. Screening for adaptation of crops to low-P soils has been done on-station rather than in the target environments where P bioavailability is low. It was recommended that future projects should screen and select from large collections of genotypes (including wild relatives) of pigeonpea, groundnuts, cowpea, and sorghum for their capacity to produce high yields in both P-sufficient and P-deficient field conditions in the Sahel and Guinea Savanna zones.
- Carboxylic anions from root exudates play a critical role in enabling desert grasses or wild relative species to survive in low-P environments. The current methodology used to screen large number of germplasm accessions for their P- solubilizing ability is laborious and requires sophisticated and expensive equipment. It was therefore recommended that future projects focus on developing rapid, simple, and easy screening systems to quantify the P solubilizing activity of carboxylic anions from the root exudates of a large number of genotypes. Such prospects should examine genotypic variability in the mechanisms by which these crops solubilize P from rock phosphates. The degradation of carboxylic and piscidic acids in soils needs to be studied in detail. Their physical properties and metal stability constants, genetic variability in their synthesis or excretion, and its quantification in the rhizosphere all need to be established.

- With the evolution of new molecular biotechnological tools the need to create transgenic plants that over-express enzymes of the biosynthetic pathway for organic acid anions, and to test their exudation pattern was identified. Particular genes can then be mapped to a genome of the crops in question as future molecular markers.
- Pigeonpea has been shown to increase the pool of available P in the cropping systems in which it is grown. It is documented that the leaf fall contributes to 4-6 kg P ha⁻¹ during the cropping season. Quantifying the advantages of pigeonpea over indigenous and introduced leguminous crops (e.g., cowpea, groundnuts) in relation to soil fertility replenishment was identified as a researchable area.
- The advantage of pigeonpea over other crop species in its ability to utilize iron-bound P and/or locally available P sources of rock phosphate in cropping systems under field conditions needs to be quantitatively evaluated. This would involve quantifying and documenting the nutrient content of fallen leaves, and measuring the rate of decomposition of the fallen litter, and the amount of nutrients (N and P) released into the soil.
- The development of a simple and easy screening system for target traits that would improve the N-fixation ability of leguminous crops, and permit quantification of their nitrogen-fixing abilities in cropping systems in on-farm conditions was identified as another area for future research.
- On-farm experimentation using a farmer participatory approach to the intensification of pigeonpea from the view point of biologically cycled P in cereal/legume cropping systems in order to improve the available P in such systems was highlighted.
- Socio-economic and risk analysis of pigeonpea-based technologies and identification of the critical factors influencing farmers' preference of pigeonpea varieties were identified as worthy of attention.

The target regions for the proposed research are western and southern Africa. Delegates endorsed the suggestion that a project proposal that builds on the achievements of the Government of Japan Project, and on the intensive discussions during the workshop, be developed and submitted for funding to a range of donors.

Participants



Workshop participants at the International Crops Research Institute for the Semi-Arid Tropics
Patancheru, Andhra Pradesh, India, 29 September 1999.

Participants

N Ae

Division of Soil Sciences
National Institute of Agro-Environmental
Sciences (NIAES)
3-1-1 Kannondai
Tsukuba, Ibaraki 305-8604
Japan
Tel 81 298 38 8271
Fax 81 298 38 8271
E-mail noriae@niaes.affrc.go.jp

M Y Ali

Bangladesh Agricultural Research
Institute (BARI)
On-Farm Research Division
Barind Station
Rajshahi 6000
Bangladesh

J Arihara

Department of Crop Physiology and
Quality
National Agricultural Research Center
(NARC)
3-1-1 Kannondai
Tsukuba, Ibaraki 305-8666
Japan
Tel 81 298 38 8392
Fax 81 298 38 8392
E-mail arihara@narc.affrc.go.jp

P S Carberry

Commonwealth Scientific and Industrial
Research Organisation (CSIRO)
Tropical Agriculture
Agricultural Production Systems
Research Unit (APSRU)
PO Box 102
Toowoomba, Queensland 4350
Australia
Tel 61 7 4688 1377
Fax 61 7 4688 1193
E-mail peter.carberry@tag.csiro.au

F D Dakora

Botany Department
University of Cape Town
Private Bag Rondebosch 7701
Cape Town
South Africa
Tel 21 650 2964
Fax 21 650 4041
E-mail dakora@botzoo.uct.ac.za

J Dunlop

AgResearch
Grasslands Research Centre
Private Bag 11008
Palmerston North
New Zealand
Fax 64 6 351 8032
E-mail dunlopj@agresearchxri.nz

G R Findenegg

Wageningen Agricultural University
Broekemalaan 18
6703 GM Wageningen
The Netherlands
Tel 31 317 412034
Fax 31 317 425675
E-mail g.findenegg@diva.nl

K Fujita

Faculty of Applied Biological Science
Hiroshima University
1-4-4 Kagamiyama
Higashi-Hiroshima 739-8528
Japan
Fax 81 824 24 0791.
E-mail fujiko@ipc.hiroshima-u.ac.jp

Gyaneshwar P

Soil and Water Sciences Division,
International Rice Research Institute
(IRRI)

MCPO Box 3127

1271 Makati City

Philippines

Tel 63 2 845 0563

Fax 63 2 891 1292

E-mail g.prasad@cgiar.org

S D Hainsworth

Editorial and Publishing Services

Plot 200, Road 14

Jubilee Hills

Hyderabad 500 033

Andhra Pradesh

India

Tel 91 40 3544367

E-mail suehains@hd2.vsnl.net.in

T Hamazaki

Environmental Resources Division

Japan International Research Center for
Agricultural Sciences (JIRCAS)

I-2 Ohwashi

Tsukuba, Ibaraki 305-0851

Japan

Tel 81298 38 6306

Fax 81 298 38 6651

E-mail hamazaki@jircas.affrc.go.jp

O Ito

Japan International Research Center for
Agricultural Sciences (JIRCAS)

1-2 Ohwashi

Tsukuba, Ibaraki 305-0851

Japan

Tel 81298 38 6306

Fax 81 298 38 6651

E-mail osamuito@jircas.affrc.go.jp

M-L Izaguirre-Mayoral

Instituto Venezolano de Investigaciones
Cientificas (IVIC)

Laboratorio de Biotecnología y Virología
Vegetal

Centro de Microbiología y

Biología Celular

Apartado Postal 21827

Caracas 1020-A

Venezuela

Tel 58 2 5041189

Fax 58 2 5041382

E-mail mizaguir@pasteurJvic.ve

H H Jensen

Department of Agricultural Sciences

KvL Thorvaldsensvej 40

DK 1871 Copenhagen

Denmark

Tel 45 35283391

E-mail hhj@kvldk

G J D Kirk

Soil and Water Sciences Division

International Rice Research Institute
(IRRI)

MCPO Box 3127

1271 Makati City

Philippines

Tel 63 2 845 0563

Fax 63 2 845 0606

E-mail g.kirk@cgiar.org

D R Lukiwati

Animal Science Faculty

Diponegoro University

Wisma UNDIP, Jalan Kagok II/5

Semarang

Indonesia

Tel 62 24 411053

Fax 62 24 50074

E-mail wr-

luki@semarang.wasantara.netid

S Madhavan

Department of Biochemistry
PO Box 880 664
University of Nebraska
Lincoln, NE 68588-0817
USA
Tel 1 402 472 2932
Fax 1 402 472 7842
E-mail msoundar@unlnotes.unl.edu

T Nakamura

Japan International Research Center for
Agricultural Sciences (JIRCAS)
1-2 Ohwashi
Tsukuba, Ibaraki 305-8686
Japan
Tel 0298 38 6313
Fax 0298 38 6316
E-mail takuwan@jircas.affrc.go.jp

H Nakano

Hokkaido National Agriculture
Experiment Station (HNAES)
Shinsei, Memuro, Kasaigun
Hokkaido 082-0071
Japan
Tel 81 155 62 9297
Fax 81 155 62 2926
E-mail nakanohi@mmr.affrc.go.jp

J M Peacock

International Center for Agricultural
Research in the Dry Areas (ICARDA)
Arabian Peninsula Regional Program
(APRP)
PO Box 13979
Dubai
United Arab Emirates
Tel 971 4 2957338
Fax 971 4 2958216
E-mail j.peacock-t@cgiar.org

Z Rengel

Soil Science and Plant Nutrition,
Faculty of Agriculture
The University of Western Australia
Nedlands WA 6907
Australia
Tel 618 9380 2557
Fax 61 8 9380 1050
E-mail zengel@agric.uwa.edu.au

T R Sinclair

United States Department of
Agriculture - Agricultural Research
Service (USDA-ARS)
Agronomy, Physiology, and Genetics
Laboratory,
University of Florida
PO Box 11095
Gainesville, FL 32611-0965
USA
Tel 352-392-6180
Fax 352-392-6139
E-mail trsincl@gnv.ifas.ufl.edu

F W Smith

Commonwealth Scientific and Industrial
Research Organization (CSIRO)
Tropical Agriculture
Cunningham Laboratory,
306 Carmody Road
St Lucia, Queensland 4067
Australia
Tel 07 3214 2288
Fax 07 3378 3214
E-mail frank.smith@tag.csiro.au

P C Smithson

International Centre for Research in
Agroforestry (ICRAF)
PO Box 30677
Nairobi
Kenya
Tel 254 2 521450
Fax 254 2 521001
E-mail p.smithson@cgiar.org

S P Srivastava

Agricultural Research Station
Rampur Chitwan
Nepal
Tel 97 756 29301
Fax 97 715 21197

C Sudha Rani

Regional Agricultural Research Station
Nandyal
Kurnool 518 501
Andhra Pradesh
India
E-mail sudhac@hotmail.com

T Tadano

Faculty of Agriculture
Hokkaido University
Kita-9, Nishi-9, Kita-ku
Sapporo 060-8589
Japan
Tel 81 11 706 3846
Fax 81 11 706 3846
E-mail
tadano@chem.agr.hokudai.ac.jp

R M Welch

United States Department of
Agriculture - Agricultural Research
Service (USDA-ARS)
US Plant, Soil, and Nutrition Laboratory
Cornell University
Ithaca, New York
NY 14853-2901
USA
Tel 1 607 255 5434
Fax 1607 255 1132
E-mail rmwl@cornell.edu

A Yamamoto

Experimental Farm of Tohoku University
Tohoku University
Miyagi 989-67
Japan
Tel 81 229 84 7311
Fax 81 22 251 1341
E-mail ayama@bios.tohoku.ac.jp

C F Yamoah

Soil Research Institute
Council for Scientific and Industrial
Research (CSIR)
Academy Post Office
Kwadaso, Kumasi
Ghana
Tel 233 51 50353
Fax 233 5150308
E-mail soils@africaonline.com.gh

T Yoneyama

National Agricultural Research Center
(NARC)
3-1-1 Kannondai
Tsukuba, Ibaraki 305-8666
Japan
Tel 81 298 38 8392
Fax 81 29838 8392
E-mail yoneyama@narc.afrc.go.jp

T Yoshihara

Laboratory of Bioscience and Chemistry
Hokkaido University
Graduate School of Agriculture
Kita -9, Nishi- 9, Kita-ku
Sapporo 060-8589
Japan
Tel 81 11 706 2505
Fax 81 11 706 2505
E-mail yosihara@chem.agr.hokudai.ac.jp

Y-GZhu

Department of Soil and Water,
Collabrative Research Centre for
Molecular Plant Breeding,
Centre for Plant Symbioses
Waite Campus
The University of Adelaide
Glen Osmond, SA 5064
Australia
Tel 61 8 83037436
Fax 61 8 83036511
E-mail yongguan.zhu@adelaide.edu.au

**International Crops Research
Institute for the Semi-Arid Tropics
(ICRISAT)**

Patancheru 502 324
Andhra Pradesh
India
Tel 91 40 3296161
Fax 91 40 241239

Administration**L D Swindaie**

E-mail l.swindale@cgiar.org

**Natural Resource Management
Program****J J Adu-Gyamfi**

E-mail j.j.adugyamfi@cgiar.org

A Bationo

International Fertilizer Development
Center / International Crops Research
Institute for the Semi-Arid Tropics
(IFDC / ICRISAT)
BP 12404
Niamey
Niger
Tel 227 72259
Fax 227 734329
E-mail a.bationo@cgiar.org

S Ishikawa

E-mail s.ishikawa@cgiar.org

C Johansen

E-mail c.johansen@cgiar.org

Sailaja Koti

E-mail sailakoti@hotmail.com

T J Rego

E-mail t.rego@cgiar.org

O P Rupela

E-mail o.rupela@cgiar.org

B I Shapiro

B P 320
Bamako
Mali
Tel 223 223375
Fax 223 228683
E-mail b.shapiro@cgiar.org

S S Snapp

Matopos Research Station
PO Box 776
Bulawayo
Zimbabwe
Tel 263 83 8311
Fax 263 83 8253
E-mail s.snapp@cgiar.org

**Genetic Resources and Enhancement
Program****P Bramel-Cox**

E-mail p.bramel-cox@cgiar.org

C T Hash Jr

E-mail c.t.hash@cgiar.org
cth8@cornell.edu

Jagadish Kumar

E-mail j.kumar@cgiar.org

L Krishnamurthy

E-mail l.krishnamurthy@cgiar.org

R Ortiz

E-mail r.ortiz@cgiar.org

N P Saxena

E-mail n.saxena@cgiar.org

**Partnerships and Information
Management Division**

M D Winslow

E-mail m.winslow@cgiar.org

About ICRISAT

The semi-arid tropics (SAT) encompasses parts of 48 developing countries including most of India, parts of southeast Asia, a swathe across sub-Saharan Africa, much of southern and eastern Africa, and parts of Latin America. Many of these countries are among the poorest in the world. Approximately one-sixth of the world's population lives in the SAT, which is typified by unpredictable weather, limited and erratic rainfall, and nutrient-poor soils.

ICRISAT's mandate crops are sorghum, pearl millet, finger millet, chickpea, pigeonpea, and groundnut; these six crops are vital to life for the ever-increasing populations of the SAT. ICRISAT's mission is to conduct research which can lead to enhanced sustainable production of these crops and to improved management of the limited natural resources of the SAT. ICRISAT communicates information on technologies as they are developed through workshops, networks, training, library services, and publishing.

ICRISAT was established in 1972. It is one of 16 nonprofit, research and training centers funded through the Consultative Group on International Agricultural Research (CGIAR). The CGIAR is an informal association of approximately 50 public and private sector donors; it is co-sponsored by the Food and Agriculture Organization of the United Nations (FAO), the United Nations Development Programme (UNDP), the United Nations Environment Programme (UNEP), and the World Bank.

ICRISAT について

半乾燥地はインドの大半、東南アジアの一部、サブサハラアフリカ周辺、南アフリカと東アフリカの多くの国、ラテンアメリカの一部、を含む48の発展途上国を取り巻いています。これらの多数の国は、世界で最も貧困な地域です。世界の人口の約6分の1が、半乾燥地帯に居住し、その地域は予測の難しい天候、限られた一定しない降雨、そして貧栄養土壌によって象徴されています。

ICRISATでの主要な作物はソルガム、トウジンビエ、シコクビエ、ヒヨコマメ、キマメ、ラッカセイです。これら6つの作物は、常に増加している半乾燥地域の人口を維持するため、きわめて重要です。ICRISATの使命は、これら作物の持続的な生産増大と半乾燥地における限られた生物資源の有効利用を導くための調査を行うことです。ICRISATは、ワークショップ、ネットワーク、トレーニング、図書、サービス、出版物を通して、発展させた科学技術に関する情報を伝えます。

ICRISATは、1972年に設立されました。国際農業研究協議グループ(CGIAR)の拠出金による非営利的研究・トレーニングセンターは16ありますが、ICRISATはその中の1つです。

CGIARは、国連食糧農業機関(FAO)、国連開発計画(UNDP)、国連環境計画(UNEP)、世界銀行、をはじめとする約50の公的または私的機関の資金提供による非公式な組織です。

About the Government of Japan Project

The Government of Japan (GoJ) Project is a restricted-funding, agreed-agenda project within the Natural Resource Management Program of ICRISAT's research portfolio. Initiated in November 1984, it is one of the external projects supported by the Japanese Ministry of Agriculture, Forestry and Fisheries (MAFF) and managed by the Japan International Research Center for Agricultural Sciences (JIRCAS). The GoJ Project currently has 15 staff, and an annual budget of about US \$ 286,000.

The mission and focus of the GoJ Project is to conduct strategic and basic research aimed at improving nutrient and water uptake and utilization efficiencies through field management practices and/or through exploiting morphological and physio-genetic systems for improving the adaptation of ICRISAT mandate crops to the low-nutrient and low-moisture environments of the semi-arid tropics (SAT). The Project addresses the issue of an effective combination of genetics and management to improve productivity and the economic well-being of the smallholder farmer making a living on degraded soils in the SAT.

The Project staff are based at Patancheru, India, but communicate with ICRISAT scientists working in the same or similar disciplines at ICRISAT African locations. The Project is co-managed by Director of the Environmental Resource Division, the JIRCAS and a Project Team Leader appointed by ICRISAT in consultation with the GoJ.

日本政府プロジェクト (GoJ) について

GoJ プロジェクトは、制約された資金のもと、ICRISAT の生物資源利用プログラムと協定を結んでいます。本プロジェクトは農林水産省 (MAFF)、国際農林水産業研究センター (JIRCAS) の支援による対外的なプロジェクトの1つであり、1984年に開始されました。本プロジェクトは最近15名のスタッフと年間約US\$286,000の予算のもと運営されています。

本プロジェクトの使命と目的は、有効な養水分の低い半乾燥地において、ICRISATの主要作物 (ソルガム、ミレット、ラッカセイ、ヒヨコマメ、キマメ) の適応性の改善に向けた形態学的な、生理遺伝的システムの開拓、さらに農地経営の実践を通しての養水分吸収とその効率的な利用を改善することを目標にした基礎戦略的調査を行うことでもあります。本プロジェクトは、半乾燥地の荒廃した土壌で生計を立てている小作農民による作物生産性と収入の向上を目指した経営と作物遺伝子の有効な組み合わせの観点について取りかかっている。

プロジェクトスタッフは、インドのパタンチェルを本拠地としていますが、ICRISATのアフリカ支部にいる同分野の研究者とも交流を深めています。本プロジェクトは、日本政府の配下のもと、ICRISATによって任命されたプロジェクトチームリーダーとJIRCASの研究所長によって共同運営されています。



Japan International Research Center for Agricultural Sciences (JIRCAS)
1-2 Ohwashi, Tsukuba, Ibaraki 305-8686, Japan



International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)
Patancheru 502 324, Andhra Pradesh, India