รายงานวิจัยฉบับสมบูรณ์

โครงการกลไกทางสรีระเชิงนิเวศน์และพันธุกรรมที่ควบคุมการใช้ธาตุอาหารในพืช

(Ecophysiological processes and genetic controls relating to plant nutrition)

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สนับสนุนโดยสำนักงานกองทุนสนับสนุนการวิจัย

ชุดโครงการส่งเสริมกลุ่มวิจัย

Table of Contents

Executive summary i
Project outputs iv
Technical contents
Abstract
Thai viii
English xii
1. Boron nutrition 1
1.1 Plant adaptation to soils low in boron 1
1.1.1. Genotypic variation in adaptation to low boron soils 1
- Difference among crop species in adaptation to low B 2
- Adaptation to low B soils in wheat and related species as a means to overcome the problem of B deficiency in crop production. 2

1.1.2. Mechanisms for adaptation to low B soils 3
- Boron efficient vs inefficient vs very inefficient wheat 3
- Wheat vs other small grain cereals 4
- Relating adaptation to low B to adaptation to toxic levels B in wheat 5
- Phloem mobility 5

1.2 Function 6
1.2.1. Reproductive development 6
- Wheat and barley 6
- Maize and sorghum 7

1.2.2. Seed quality 7
- Nutrients and the keeping quality of bean sprout – a new connection 8

1.2.3. Sugar 8
1.3 Genetic controls 9
1.3.1. Screening for B efficiency 9
1.3.2. Source of B efficiency 9
1.3.3. Genetic controls 10
1.3.4. Breeding for B efficiency 11
1.4 From B physiology to crop management 11
1.4.1. Individual organs and processes The B limiting step 12
1.4.2. Whole plant response 12
2. Other nutrients in rice 13
2.1 Iron in rice grain 13
2.1.1. Factors affecting rice grain iron 13
2.1.2. Determination of iron in individual rice grain 14
2.1.3. Location and form of iron in rice grain 15
2.2 Other nutritional problems 15
2.2.1. Adaptation to wetland and dryland condition 16
2.2.2. N fixing endophytes 16
2.2.3. Rice quality 17
3. Agrodiversity 18
3.1 Agrodiversity and biodiversity management 18
3.2 Fallow enrichment and forest regeneration 18
References 20

EXECUTIVE SUMMARY

1. ความสำคัญและที่มาของปัญหา

ธาตุอาหารพืชเป็นปัจจัยจำกัดในการเพาะปลูกที่แพร่หลายที่สุดรองจากน้ำ การจัดการธาตุอาหารพืชอย่างมีประสิทธิภาพนอกจากช่วยเพิ่มผลตอบแทนจากการเพาะปลูกแล้ว ยังช่วยลดผลกระทบต่อสภาพแวดล้อมจากการใส่ปุ๋ย และอนุรักษ์ทรัพยากร ความเข้าใจกลไกทางสรีระเชิงนิเวศน์และพันธุกรรมควบคุมการใช้ธาตุอาหารในพืช เป็นพื้นฐานที่จะนำไปสู่ระบบการจัดการธาตุอาหารที่มีประสิทธิภาพในระดับฟาร์มและระบบนิเวศน์

2. วัตถุประสงค์

โครงการนี้มี 2 วัตถุประสงค์หลักคือ

1. สร้างกลุ่มนักวิจัยที่มีขีดความสามารถสร้างองค์ความรู้ใหม่ ที่เกี่ยวกับกลไกควบคุมการใช้ธาตุอาหารในพืช
2. สร้างองค์ความรู้ใหม่เกี่ยวกับกลไกทางสรีระเชิงนิเวศน์และพันธุกรรมที่ควบคุมการใช้ธาตุอาหารที่เป็นปัจจัยจำกัด ในพืชสำคัญ ในระบบเกษตรในประเทศไทย

3. ผลงาน (Output)

1. ได้เพิ่มขีดความสามารถแก่นักวิจัย 17 คน นักศึกษาปริญญาเอก 12 คน (สำเร็จ/กำลังจะสำเร็จการศึกษาในปี 2546 4 คน) นักศึกษาปริญญาโท 20 คน (สำเร็จการศึกษาแล้ว 9 คน) ผู้ร่วมโครงการได้เลื่อนตำแหน่งทางวิชาการเป็น รองศาสตราจารย์ 1 ราย
2. ได้ผลงานตีพิมพ์ในวารสารและหนังสือที่มี peer-review 26 เรื่อง เป็นวารสารและหนังสือที่มีกระบวนการตรวจสอบอย่างเข้มงวดเป็นที่ยอมรับในแวดวงวิชาการนานาชาติ 17 เรื่อง ได้ร่วมเป็นบรรณาธิการตีพิมพ์เผยแพร่หนังสือ 1 เล่ม บทความตีพิมพ์ได้รับรางวัลที่ 1 จาก United Nations University 1 เรื่อง
3. ได้องค์ความรู้ใหม่เกี่ยวกับกลไกทางสรีระเชิงนิเวศน์และพันธุกรรมที่ควบคุมการใช้ธาตุอาหาร ดังต่อไปนี้

   3.1 **ในด้านธาตุอาหารโบรอนในพืช** โครงการวิจัยได้ครอบคลุมถึงการปรับตัวต่อสภาพดินโบรอนต่ำ พันธุกรรมควบคุมการใช้โบรอน และบทบาทของโบรอนในกระบวนการทางชีวภาพในพืช ได้พบความหลากหลายในการปรับตัวต่อสภาพดินโบรอนต่ำของธัญพืชและถั่วที่สำคัญ และพบว่าสมรรถภาพการใช้โบรอนในพืชบางชนิดมีมากพอที่จะใช้แก้ปัญหาการขาดโบรอนในดินได้ ความเข้าใจในกลไกทางสรีระและพันธุกรรมที่เป็นพื้นฐานของการปรับตัวต่อการขาดโบรอนนี้ มีผลกระทบต่อการจัดการระบบการเพาะปลูก 3 ทาง คือ (ก) ช่วยเพิ่มประสิทธิภาพโครงการปรับปรุงพันธุ์ (ข) ช่วยเพิ่ม

ประสิทธิภาพการจัดการปุ๋ยโบรอน (ค) เสริมสร้างความเข้าใจและการศึกษากลไกพื้นฐานเพื่อการจัดการการเพาะปลูกในภาวะเครียด

- ภาวะเครียดสามารถมีอิทธิพลต่อกระบวนการชีวภาพหลายกระบวนการ และมีการศึกษาและรายงานไว้ทุกกระบวนการ หากแต่ละกระบวนการมิได้มีความสำคัญต่อการตอบสนองของพืชทั้งต้นตลอดจนการผลิตเท่ากัน กุญแจสำคัญของการศึกษากลไกพื้นฐานที่จะมีประโยชน์อย่างแท้จริงต่อการเพาะปลูกจึงจำเป็นต้องเน้นกระบวนการที่เป็นขั้นตอนที่จำกัดการตอบสนองของพืชทั้งต้น
- การสนองต่อภาวะเครียดในพืช เป็นระบบที่มีการเปลี่ยนแปลงตลอดเวลา ทั้งในภาวะเครียดและการตอบสนองของพืชที่เปลี่ยนไปตามอายุขัย การศึกษากลไกสรีระพื้นฐานที่จะนำไปสู่ความเข้าใจกลไกการปรับตัวของพืช ที่นำไปใช้ในการเพาะปลูกได้จึงจำเป็นต้อง (ก) แยกแยะการเปลี่ยนแปลงของภาวะเครียดตามกาลเวลาที่สอดคล้องกับอายุขัยของพืช และ (ข) การเปลี่ยนแปลงในลักษณะการตอบสนองต่อภาวะเครียดตามอายุขัยของพืช

3.2 **งานธาตุอาหารในข้าว** ประกอบด้วยงานเหล็กในเมล็ดข้าว ศึกษากลไกเกี่ยวกับประสิทธิภาพการใช้ธาตุอาหารเป็นหลัก งานที่ยังอยู่ในระยะแรกเริ่มได้แก่ประสิทธิภาพการใช้ฟอสฟอรัส ประสิทธิภาพการใช้เหล็ก และการทนกรด ซึ่งเน้นการพัฒนาระบบการทดสอบพันธุ์ (screening) และการบ่งชี้พันธุ์ข้าวไทยที่มีประสิทธิภาพสูง พันธุ์ทนกรดและอลูมิเนี่ยมเป็นพิษ ส่วนเรื่องที่มีความก้าวหน้าพอสมควรได้แก่ เรื่องเหล็กในเมล็ด การปรับตัวกับสภาพไร่ (ดินไม่ขังน้ำ) และแบคทีเรียเอ็นโดไฟต์ที่ตรึงไนโตรเจนในข้าว เรื่องเหล็กในเมล็ดข้าวได้องค์ความรู้ที่บอกว่าการปรับปรุงพันธุ์เป็นวิธีเพิ่มปริมาณเหล็กในเมล็ดที่มีศักยภาพดีที่สุด ได้พัฒนาวิธีการตรวจสอบปริมาณเหล็กในเมล็ดอย่างง่าย สามารถตรวจสอบได้ทีละเมล็ด ทำให้ได้พบความแตกต่างในปริมาณเหล็กในตัวอย่างเมล็ดข้าวของเกษตรกรที่ยังคงมีความหลากหลายทางพันธุกรรมอยู่ จึงคาดว่าอาจพบพันธุ์ข้าวที่มีเหล็กสูงกว่าที่พบอยู่ในปัจจุบัน วิธีการตรวจสอบเหล็กด้วยการย้อมสีนี้ยังจะมีประโยชน์ในการคัดเลือกพันธุ์เหล็กสูงในโครงการปรับปรุงพันธุ์ทั้งยังจะเป็นประโยชน์ในการศึกษาพันธุกรรมที่ควบคุมปริมาณเหล็กในเมล็ดด้วย

ได้ริเริ่มโครงการศึกษาการดูดธาตุอาหารของข้าวในสภาพไร่ และพบว่าข้าวมีลักษณะพื้นฐานเป็นพืชน้ำ คือเจริญเติบโตในสภาพนาที่มีน้ำขังได้ดีกว่าในสภาพไร่ที่น้ำไม่ขัง แต่ได้พบพันธุ์ข้าวไทยที่มีการปรับตัวต่อสภาพไร่ได้ดีกว่าข้าวนาสวนส่วนใหญ่ และเราได้พบว่าความสามารถนี้ส่วนหนึ่งขึ้นอยู่กับความสารถในการดูดอาหารจากดินไม่ขังน้ำ ข้อมูลการดูดอาหารเบื้องต้นชี้ว่าความสามารถนี้ขึ้นอยู่กับความสามารถในการสร้างรากในสภาพไร่ มากกว่าความสามารถในการดูดอาหารจำเพาะของราก (ต่อหน่วยน้ำหนักแห้งราก) กลุ่มผู้วิจัยคาดว่าความเข้าใจนี้จะนำไปสู่การปรับปรุงพันธุ์ให้มีการปรับตัวต่อสภาพไร่ ซึ่งรวมระบบการปลูกข้าวในระบบหว่านข้าวแห้งทั้งหมด

ได้พบแบคทีเรียที่ตรึงไนโตรเจนได้อาศัยอยู่ในราก ต้นและใบข้าวเป็นหมื่นตัว/กรัมน้ำหนักสด และพบทั้งในข้าวปลูกและข้าวป่า ซึ่งได้ยืนว่าเป็นแบคทีเรียที่ตรึงไนโตรเจนจากอากาศได้จริงโดยวิธี Acetylene Reduction แต่ความรู้นี้จะมีผลกระทบต่อการปลูกข้าวได้ก็ต่อเมื่อสามารถวัดได้ว่าแบคที่เรียเหล่านี้มีบทบาทอย่างไรต่อการใช้ธาตุอาหารไนโตรเจนในต้นข้าว ซึ่งในขณะนี้กำลังอยู่ในระหว่างการวัดอยู่

ธาตุอาหารไนโตรเจนยังอาจมีบทบาทต่อการผลิตข้าวอีกทางหนึ่งคือต่อคุณภาพการสี ได้พบว่าในการสีข้าว ข้าวที่มีปริมาณไนโตรเจนในเมล็ดสูง มีเมล็ดหักน้อยกว่าข้าวที่มีปริมาณไนโตรเจนในเมล็ดต่ำ นอกจากนี้พันธุ์ข้าวเมล็ดยาวของไทยมีความทนทานต่อการหักในระหว่างสีต่างกัน ขณะนี้ยังอยู่ในระหว่างการศึกษาลักษณะภายในด้วยกล้องจุลทัศน์ (แสง และอิเล็คตรอน) ว่ามีความแตกต่างกันอย่างไรตามระดับไนโตรเจนและพันธุ์

3.3 **งานด้านความหลากหลายในเกษตรนิเวศน์** (AGRODIVERSITY) ของกลุ่มได้เน้นการอนุรักษ์ความหลากหลายทางชีวภาพ และได้นำไปสู่การอนุรักษ์เชื้อพันธุ์ข้าวไทย[1] งานของโครงการทางด้าน AGRODIVERSITY ได้เน้นการค้นพบระบบองค์ความรู้ท้องถิ่นในการใช้พืชบำรุงดิน คือต้นปะดะ (*Macaranga denticulata* (Bl.) Muell. Arg.) ซึ่งพบว่าประกอบด้วย 2 องค์ประกอบที่สำคัญคือ (ก) ต้นปะดะ และ (ข) เชื้อราไมโคไรซ่า ระบบนี้สามารถรีไซเคิลธาตุอาหารอย่างมีประสิทธิภาพ สามารถทำให้เกษตรกรปลูกข้าวไร่ได้ผลผลิต 320 –640 กก/ไร่ ได้อย่างยั่งยืน และน่าจะมีบทบาทสำคัญในการฟื้นฟูป่าด้วย นอกจากนี้ยังพบว่าประชากรของเชื้อราไมโคไรซ่ามีความหลากหลายด้วย โดยพบถึง 29 species ใน 6 genera

สุดท้ายนี้สรุปได้ว่ากลุ่มวิจัยได้สร้างองค์ความรู้ใหม่มากมายภายในเวลา 3 ปี จากฐานงานเดิมที่มีอยู่ก่อนแล้ว การสนับสนุนกลุ่มวิจัยจาก สกว ได้เปิดโอกาสให้นำความสามารถทางวิชาการที่มีอยู่มาประยุกต์ใช้ และขยายงานไปครอบคลุมถึงปัญหาการเพาะปลูกในประเทศ ซึ่งคาดว่าขีดความสามารถในกลุ่ม โดยเฉพาะที่เกี่ยวกับสมรรถภาพการใช้ธาตุอาหารพืช และการปรับตัวเข้ากับภาวะเครียดจะสามารถนำไปสู่การปรับปรุงระบบการเพาะปลูกที่ได้ผล โดยเฉพาะในการปลูกข้าว

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[1] ซึ่งได้ขยายไปเป็นโครงการใหม่ "Agrodiversity for in situ Conservation and Management of Thailand's Native Rice Germplasm" ได้รับทุนสนับสนุนจาก Collaborative Crop Research Program ของมูลนิธิ McKnight โครงการ McKnight นี้ได้อาศัยองค์ความรู้และวิธีการต่าง ๆที่ได้พัฒนามาจากโครงการเมธีวิจัยอาวุโสนี้ แต่ APPLICATION เหล่านี้ยังมิได้รวมไว้ในรายงานฉบับนี้ด้วย

Project Outputs

(ดูรายละเอียดในรายงานภาคผนวก)

1. **Peer-reviewed papers published (ตีพิมพ์เผยแพร่แล้ว หรืออยู่ในระหว่างการตีพิมพ์)**

   1.1 Rerkasem B, Jamjod S, Niruntrayagul, S. Boron *In press.* Increasing boron efficiency in many international bread wheat, durum wheat, triticale and barley germplasm will boost production on soils low in boron. Field Crop Research

   1.2 Sansanee Jamjod, Sunisa Niruntrayagul & Benjavan Rerkasem. *In press.* Genetic control of boron efficiency in wheat (*Triticum aestivum* L.) Euphyitca

   1.3 Wongmo, J., Jamjod, S. and Rerkasem, B. *In press.* Contrasting responses to boron deficiency in barley and wheat. Plant and Soil

   1.4 Duangjai Nachiangmai, Bernie Dell, Richard Bell, Longbin Huang and Benjavan Rerkasem. *In press.* Genotypic variation in boron long distance transport into the reproductive organ of wheat. Plant and Soil

   1.5 Yimyam, N. Rerkasem, K and Rerkasem, B. 2003. Fallow enrichment with pada (*Macaranga denticulata* (Bl.) Muell. Arg.) trees in rotational shifting cultivation in Northern Thailand Agroforestry Systems 57: 79-86.

   1.6 M. Leesawatwong, S. Jamjod and B. Rerkasem. 2003 Determinants of a premium priced special quality rice. International Rice Research Notes. 28: 34

   1.7 C. Prom-u-thai and B. Rerkasem. 2003. The effect of nitrogen on rice grain iron. International Rice Research Notes. December 2003.

   1.8 Rerkasem K, Korsamphan C, Thong-ngam C, Yimyam N and Rerkasem B. 2002. Agrodiversity lessons in mountain land management. Mt. Res. Dev. 22: 4-9 (บทความได้รับรางวัลที่ 1 จาก United Nations University)

   1.9 C. Prom-u-thai, B. Dell, G. Thomson, B. Rerkasem. *In press.* Easy and rapid detection of iron in rice grain. ScienceAsia

   1.10 Rerkasem, B. and K. Rerkasem. 2002 Agrodiversity for *in situ* conservation of Thailand's native rice germplasm. CMU J. 1: 129-148.

   1.11 Rerkasem B and Jamjod S. 2001. Overcoming wheat sterility problem with boron efficiency. Dev. Plant Soil Sci. 92: 82-83.

   1.12 Prom-u-thai, C. and Rerkasem, B. 2001. Iron in Thai rice. Dev. Plant Soil Sci. 92: 350-351.

1.13 Benjavan Rerkasem. 2003. Biotechnology and Agriculture. An invited review, pp. 293-321, *in* Social Challenges for the Mekong Region, Mingsarn Kaosa-ard and John Dore (Eds.). White Lotus, Bangkok.

1.14 Kanok Rerkasem. 2003. Uplands Land Use. An invited review, pp. 323-346, *in* Social Challenges for the Mekong Region, Mingsarn Kaosa-ard and John Dore (Eds.). White Lotus, Bangkok.

1.15 Rerkasem, B. 2002. Crop responses to boron and genotypic variations. An invited review, pp. 269-280, *in* All Aspects of Plant and Animal Boron Nutrition, Eds: H. E. Goldbach, B. Rerkasem, M. A. Wimmer, P. H. Brown, M. Thellier and R.W. Bell. Kluwer and Plenum Academic Publishers

1.16 Ahmed M, Jaihiruddin M, Jamjod S and Rerkasem B. 2002. Boron efficiency in a wheat germplasm from Bangladesh. Pp. 299-303, *in* All Aspects of Plant and Animal Boron Nutrition, Eds: H. E. Goldbach, B. Rerkasem, M. A. Wimmer, P. H. Brown, M. Thellier and R.W. Bell. Kluwer and Plenum Academic Publishers.

1.17 NaChiangmai D, Dell B, Huang L, Bell R and Rerkasem B. 2002. The effect of boron on pollen development in two wheat cultivars (*Triticum aestivum* L.). Pp. 181-185, *in* All Aspects of Plant and Animal Boron Nutrition, Eds: H. E. Goldbach, B. Rerkasem, M. A. Wimmer, P. H. Brown, M. Thellier and R.W. Bell. Kluwer and Plenum Academic Publishers.

1.18 Rerkasem K, Thong-ngam C, Korsamphan C, Yimyam N and Rerkasem B. 2002. Pp. 200-232, *in*: Land Use Changes in the Highlands of Northern Thailand. An invited review paper in 'Cultivating Biodiversity' Eds. H Brookfield, C Padoch, H Parson and M Stocking. ITDG Publishers, London and United Nations University, Tokyo.

1.19 เนตรนภา อินสลุด Richard W. Bell และเบญจวรรณ ฤกษ์เกษม 2546 การตอบสนองของพันธุ์ข้าวไร่และข้าวนาสวนต่อสภาพดินขังน้ำและดินระบายน้ำดี วารสารเกษตร (มช) ACCEPTED

1.20 จำเนียร วงษ์โม้, ศันสนีย์ จำจด และ เบญจวรรณ ฤกษ์เกษม 2546 เปรียบเทียบการตอบสนองต่อการขาดธาตุโบรอนในข้าวบาร์เลย์และข้าวสาลี วารสารเกษตร (มช) ACCEPTED

1.21 ทินกร ศรีวิชัย ศันสนีย์ จำจด และ เบญจวรรรณ ฤกษ์เกษม 2546 การตอบสนองต่อโบรอนในถั่วพุ่ม วารสารเกษตร (มช) ACCEPTED

1.22 นริศ ยิ้มแย้ม สิทธิชัย ลอดแก้ว เบญจวรรณ ฤกษ์เกษม และ กนก ฤกษ์เกษม 2546 การจัดการความหลากหลายของต้นปะดะในไร่หมุนเวียนของกะเหรี่ยงโปว์ ในภาคเหนือของประเทศไทย วารสารเกษตร (มช) ACCEPTED

1.23 รัตญา ยานะพันธุ์ และ เบญจวรรณ ฤกษ์เกษม 2546 การคัดเลือกพันธุ์ข้าวไทยภายใต้สภาพขาดธาตุเหล็กโดยวัดปริมาณคลอโรฟิลล์ในใบ วารสารเกษตร (มช) ACCEPTED

1.24 การเคลื่อนย้ายโบรอนในถั่วเขียว 2546 สาวิกา กอนแสง และเบญจวรรณ ฤกษ์เกษม วารสารเกษตร (มช) ACCEPTED

1.25 สุพรรณิการ์ พันชนะ ศันสนีย์ จำจด และเบญจวรรณ ฤกษ์เกษม 2546 การตอบสนองต่อความเป็นพิษของโบรอนในข้าวสาลีสามพันธุ์ที่มีระดับความทนทานต่อการขาดโบรอนแตกต่างกัน วารสารเกษตร (มช) ACCEPTED

1.26 อยุธย์ คงปั้น ศันสนีย์ จำจด และ เบญจวรรณ ฤกษ์เกษม 2546 อิทธิพลของโบรอนต่อคุณภาพเมล็ดในถั่วเขียวต่างพันธุ์ วารสารเกษตร (มช) ACCEPTED

2. **Papers submitted for publication in peer-reviewed journals**

2.1 Somchit Youpensuk, Benjavan Rerkasem, Bernie Dell and Saisamorm Lumyong. Arbuscular mycorrhizal fungi from the rhizosphere of a fallow enriching tree, *Macaranga denticulata* Muell. Arg. and their effect on the host plant. Submitted to Agroforestry Systems (January 2003).

2.2 C. Prom-u-thai, B. Dell, G. Thomson, B. Rerkasem. Distribution and structure of protein and phytin bodies in seed of four rice genotypes. Submitted to Canadian Journal of

3. **Papers in preparation, submission expected by end of 2003**

3.1 Ayut Kongpan, Sansanee Jamjod and Benjavan Rerkasem. Boron efficient germplasm identified in *Vigna mungo* (L.) Hepper and *Vigna radiation* (L.) Wilczek. For submission to Plant and Soil or Field Crop Research.

3.2 Supannika Punchana, Sansanee Jamjod and Benjavan Rerkasem. Are boron efficient wheat always susceptible to boron toxicity? For submission to Euphytica.

3.3 Chanakan Prom-u-thai and Benjavan Rerkasem. Iron in the Grain of High and Low Iron Density Rice Grown in Different Water Regimes.

3.4 Supawadee Ngorian, Sansanee Jamjod and Benjavan Rerkasem. Response of F_2 population derived from boron efficient (Fang 60) x boron inefficiency

(Bonza) wheat (*Triticum aestivum* L.) genotypes to boron levels. For submission to Euphytica or J. Plant Breeding.

3.5 Benjavan Rerkasem and Sansanee Jamjod. Boron Deficiency in Wheat: a Review Submitted to Field Crop Reserch

4. Book edited

4.1 Goldbach, H.E., Rerkasem, B., Wimmer, M.A., Brown, P.H., Thellier M. and Bell, R.W. 2002. All aspects of Plant and Animal Boron Nutrition, Kluwer and Plenum Academic Publishers

บทคัดย่อ

โครงการได้สร้างองค์ความรู้ใหม่ใน 3 เรื่อง คือ ธาตุอาหารโบรอน ธาตุอาหารอื่นในข้าว และเรื่องความหลากหลายในระบบการเพาะปลูก

ในด้านธาตุอาหารโบรอนในพืช โครงการวิจัยได้ครอบคลุมถึงการปรับตัวต่อสภาพดินโบรอนต่ำ พันธุกรรมควบคุมการใช้โบรอน และบทบาทของโบรอนในกระบวนการทางชีวภาพในพืช ได้พบความหลากหลายในการปรับตัวต่อสภาพดินโบรอนต่ำของธัญพืชและถั่วที่สำคัญ ข้าวนับว่าปรับตัวต่อได้ดินโบรอนต่ำได้ดีที่สุดเพราะไม่เคยพบว่าขาดเลย ข้าวสาลี ข้าวสาลีดูรัม ข้าวบาร์เลย์ และทริติคาเลย์ ไม่ทนทานต่อการขาดโบรอนในดินมากที่สุด ข้าวโพดถือว่าทนได้ปานกลาง การขาดโบรอนมีผลต่อธัญพืชในระบบการเจริญพันธุ์ แต่มีข้อแตกต่างตรงที่ข้าวสาลีมีปัญหาที่เกสรตัวผู้แต่ข้าวโพดมีปัญหาเกสรตัวเมีย

แม้ข้าวสาลีโดยทั่วไปจะปรับตัวต่อดินโบรอนต่ำได้ไม่ดี แต่มีข้อยกเว้นในบางพันธุ์ที่สามารถปรับตัวต่อดินโบรอนต่ำได้ดี และได้พบว่าพันธุกรรมที่เกี่ยวข้องไม่สลับซับซ้อน จึงเป็นทางนำไปสู่การแก้ปัญหาการผลิตในพื้นที่โบรอนต่ำได้ไม่ยากนัก ในโครงการได้พัฒนาวิธีการคัดเลือกที่ใช้ตรวจสอบการปรับตัวต่อดินโบรอนต่ำของสายพันธุ์ข้าวสาลีจำนวนมากเป็นพันๆสายพันธุ์และใช้ในโครงการปรับปรุงพันธุ์ได้

องค์ความรู้ที่สร้างความเข้าใจเกี่ยวกับการปรับตัวต่อภาวะเครียดของพืช อีกทั้งจะช่วยให้ได้ประโยชน์จากความสามารถปรับตัวของพืชในการเพาะปลูกในสภาพดินโบรอนต่ำอีกทางหนึ่งคือกลไกที่เกี่ยวข้อง เราได้พบว่าพันธุ์ที่ปรับตัวได้ดีมากเช่น ฝาง 60 สามารถดูดโบรอนจากดินได้อย่างมีประสิทธิภาพมากกว่า พันธุ์ที่อ่อนแอที่สุด เช่น บอนซ่า และ แทตเทียร่า แต่ความสามารถดูดโบรอนจากดินนี้ไม่สามารถอธิบายความแตกต่างระหว่างระหว่าง ฝาง 60 กับพันธุ์ที่อ่อนแอปานกลางเช่น SW41 ได้ ความแตกต่างนี้อธิบายได้ด้วยการทดลองที่สามารถแยกโบรอนที่ดูดขึ้นมาในเวลาต่างกันด้วยไอโซโทป ^{10}B กับ ^{11}B การวัดปริมาณโบรอนที่สะสมในรวงได้อย่างแม่นยำทันเวลาที่ต้องการในการสร้างละอองเรณูพอดี และการวัดผลของการขาดโบรอนในละอองเรณูที่มีชีวิต ซึ่งได้พบว่าถึงแม้โบรอนที่รากดูดได้จะมีปริมาณลดลง ฝาง 60 ยังสามารถตอบสนองความต้องการโบรอนที่ใช้สร้างละอองเรณู (ซึ่งต้องการโบรอนมากกว่าเนื้อเยื่อ somatic เช่นต้น ใบ ราก และกลีบดอก ถึง 7-8 เท่า) ได้ดีโดยการลำเลียงโบรอนโดยตรงจากราก ในขณะที่ SW41 มีปัญหาในการขาดโบรอนที่จะนำไปสร้างละอองเรณู จึงทำให้มีละอองเรณูที่ตายไปถึง 40-70% เพราะไม่สามารถสนองความต้องการโบรอนในกระบวนการสำคัญนี้ได้

เราได้พิสูจน์อย่างชัดเจนว่ากระบวนการรีไซเคิลโบรอนไม่มีความสำคัญในข้าวสาลี แต่ได้พบว่าการรีไซเคิลโบรอน ซึ่งเกี่ยวข้องกับความสามารถในการลำเลียงโบรอนในโฟลเอ็ม อาจมีความสำคัญในการปรับตัวต่อสภาพขาดโบรอนในพืชสำคัญของไทย 6 ชนิดคือ ต้นสัก มะละกอ ฝรั่ง มังคุด ขนุน และกาแฟ เพราะลักษณะของการกระจายโบรอนตามอายุใบของพืชเหล่านี้คล้ายกับการกระจายของโปแตสเซียมซึ่งเป็นธาตุที่มีการลำเลียงได้ดีในโฟลเอ็มและมีการรีไซเคิลอยู่ตลอดเวลา พืชสำคัญอีก 6 ชนิดคือ มะนาว มันสำปะหลัง มะม่วง มะม่วงหิมพานต์ น้อยหน่า และเสาวรส น่าจะไม่สามารถรีไซเคิลโบรอนได้ เพราะมีลักษณะของการกระจายโบรอนตามอายุใบคล้ายกับการกระจายของแคลเซียมซึ่งเป็นธาตุที่รีไซเคิลไม่ได้ เพราะไม่มีการลำเลียงเลยในโฟลเอ็ม

ความเข้าใจพื้นฐานเหล่านี้ได้นำไปสู่กฎเกณฑ์ 2 ข้อ ในการศึกษาการตอบสนองและปรับตัวต่อการขาดโบรอนในพืช ซึ่งน่าจะใช้ได้ในการศึกษาการตอบสนองและปรับตัวต่อภาวะเครียดอื่นๆ ได้ด้วย ดังต่อไปนี้ คือ

1. ภาวะเครียดสามารถมีอิทธิพลต่อกระบวนการชีวภาพหลายกระบวนการ และมีการศึกษาและรายงานไว้ทุกกระบวนการ หากแต่ละกระบวนการมิได้มีความสำคัญต่อการตอบสนองของพืชทั้งต้นตลอดจนการผลิตเท่ากัน กุญแจสำคัญของการศึกษากลพื้นฐานที่จะมีประโยชน์อย่างแท้จริงต่อการเพาะปลูกจึงจำเป็นต้องเน้นกระบวนการที่เป็นขั้นตอนที่จำกัดการตอบสนองของพืชทั้งต้น
2. การสนองต่อภาวะเครียดในพืช เป็นระบบที่มีการเปลี่ยนแปลงตลอดเวลา ทั้งในภาวะเครียดและการตอบสนองของพืชที่เปลี่ยนไปตามอายุขัย การศึกษากลไกสรีระพื้นฐานที่จะนำไปสู่ความเข้าใจกลไกการปรับตัวของพืช ที่นำไปใช้ในการเพาะปลูกได้จึงจำเป็นต้อง (ก) แยกแยะการเปลี่ยนแปลงของภาวะเครียดตามกาลเวลาที่สอดคล้องกับอายุขัยของพืช และ (ข) การเปลี่ยนแปลงในลักษณะการตอบสนองต่อภาวะเครียดตามอายุขัยของพืช

นอกเหนือไปจากการเจริญพันธุ์ อีกกระบวนการหนึ่งที่พบว่ามีผลต่อการปรับตัวต่อการขาดโบรอนคือความงอกและการเจริญเติบโตของต้นอ่อน ซึ่งเราได้พบว่าเมล็ดถั่วที่ผลิตในดินโบรอนต่ำปานกลาง (ไม่มีผลต่อผลผลิต) อาจมีปริมาณโบรอนในเมล็ดต่ำซึ่งมีผลต่อการงอกและการเจริญเติบโตของต้นอ่อน และเนื่องจากมีรายงานว่าโบรอนอาจมีบทบาทในการสังเคราะห์ฟีนอลล์ อีกทั้งอาจเกี่ยวข้องกับการสร้าง oxygen free radicals จึงเป็นที่น่าสงสัยว่าโบรอนอาจมีบทบาทเกี่ยวข้องกับคุณภาพการเก็บรักษาของถั่วงอกด้วย

ภายใต้การสนับสนุนในโครงการนี้ ทางกลุ่มวิจัยได้ริเริ่มงานธาตุอาหารในข้าว โดยเน้นเรื่องกลไกเกี่ยวกับประสิทธิภาพการใช้ธาตุอาหารเป็นหลัก งานที่ยังอยู่ในระยะแรกเริ่มได้แก่ประสิทธิภาพการใช้ฟอสฟอรัส ประสิทธิภาพการใช้เหล็ก และการทนกรด ซึ่งเน้นการพัฒนาระบบการ

ทดสอบพันธุ์ (screening) และการบ่งชี้พันธุ์ข้าวไทยที่มีประสิทธิภาพสูง พันธุ์ทนกรดและอลูมิเนี่ยมเป็นพิษ ได้แก่พันธุ์ บือหมื่อตาบ้อง บือกัว บือปอแล พันธุ์พิษณุโลก 1 มีประสิทธิภาพในการใช้เหล็กสูง เป็นต้น ส่วนเรื่องที่มีความก้าวหน้าพอสมควรได้แก่ เรื่องเหล็กในเมล็ด การปรับตัวกับสภาพไร่ (ดินไม่ขังน้ำ) และแบคทีเรียเอ็นโดไฟต์ที่ตรึงไนโตรเจนในข้าว

หลังจากที่ได้สร้างฐานข้อมูลเหล็กในเมล็ดข้าวไทยว่า ขาวดอกมะลิ 105 กข6 กข 15 และข้าวพันธุ์มาตรฐานอื่นๆและพันธุ์ปรับปรุงใหม่ทุกพันธุ์มีปริมาณเหล็กต่ำ เราได้พบว่ามีข้าวพันธุ์พื้นเมืองบางพันธุ์ที่มีเหล็กสูงกว่าเป็น 2 เท่า เราได้พบว่าสภาพแวดล้อมภายนอก (น้ำขัง ดินกรด/ด่าง ฯลฯ) มีผลต่อการดูดเหล็กเข้าไปในต้นข้าวแต่มีผลเพียงเล็กน้อยต่อการสะสมเหล็กในเมล็ด (ไม่นับเปลือก) ปริมาณเหล็กในเมล็ดตั้งแต่ข้าวกล้องเป็นต้นไป นับว่าควบคุมโดยพันธุกรรมเป็นส่วนใหญ่ จึงนับว่ามีโอกาสสูงที่จะปรับปรุงพันธุ์ให้มีปริมาณเหล็กสูงขึ้น

โครงการได้พัฒนาวิธีการตรวจสอบปริมาณเหล็กในเมล็ดอย่างง่ายและรวดเร็วโดยการย้อมสี (Perls' Prussian blue หรือ "น้ำเงิน PP") สามารถตรวจสอบได้ทีละเมล็ด (การวิเคราะห์ทางเคมีใช้เมล็ดถึงร้อยเมล็ดต่อหนึ่งตัวอย่าง) ทำให้ได้พบความแตกต่างในปริมาณเหล็กในตัวอย่างเมล็ดข้าวของเกษตรกรที่ยังคงมีความหลากหลายทางพันธุกรรมอยู่ จึงคาดว่าอาจพบพันธุ์ข้าวที่มีเหล็กสูงกว่าที่พบอยู่ในปัจจุบัน การย้อมสี น้ำเงิน PP นี้ยังจะมีประโยชน์ในการคัดเลือกพันธุ์เหล็กสูงในโครงการปรับปรุงพันธุ์ทั้งยังจะเป็นประโยชน์ในการศึกษาพันธุกรรมที่ควบคุมปริมาณเหล็กในเมล็ดด้วย

ทางกลุ่มได้ริเริ่มโครงการศึกษาการดูดธาตุอาหารของข้าวในสภาพไร่ และพบว่าข้าวมีลักษณะพื้นฐานเป็นพืชน้ำ คือเจริญเติบโตในสภาพนาที่มีน้ำขังได้ดีกว่าในสภาพไร่ที่น้ำไม่ขัง แต่ได้พบพันธุ์ข้าวไทยที่มีการปรับตัวต่อสภาพไร่ได้ดีกว่าข้าวนาสวนส่วนใหญ่ และเราได้พบว่าความสามารถนี้ส่วนหนึ่งขึ้นอยู่กับความสามารถในการดูดอาหารจากดินไม่ขังน้ำ ข้อมูลการดูดอาหารเบื้องต้นชี้ว่าความสามารถนี้ขึ้นอยู่กับความสามารถในการสร้างรากในสภาพไร่ มากกว่าความสามารถในการดูดอาหารจำเพาะของราก (ต่อหน่วย น้ำหนักแห้งราก) กลุ่มผู้วิจัยคาดว่าความเข้าใจนี้จะนำไปสู่การปรับปรุงพันธุ์ให้มีการปรับตัวต่อสภาพไร่ ซึ่งรวมระบบการปลูกข้าวในระบบหว่านข้าวแห้งทั้งหมด

อีกธาตุอาหารหนึ่งที่สำคัญต่อการปลูกข้าวคือไนโตรเจน เราได้พบแบคทีเรียที่ตรึงไนโตรเจนได้อาศัยอยู่ในราก ต้นและใบข้าวเป็นหมื่นตัว/กรัมน้ำหนักสด และพบทั้งในข้าวปลูกและข้าวป่า ซึ่งได้ยืนว่าเป็นแบคทีเรียที่ตรึงไนโตรเจนจากอากาศได้จริงโดยวิธี acetylene reduction แต่ความรู้นี้จะมีผลกระทบต่อการปลูกข้าวได้ก็ต่อเมื่อสามารถวัดได้ว่าแบคที่เรียเหล่านี้มีบทบาทอย่างไรต่อการใช้ธาตุอาหารไนโตรเจนในต้นข้าว ซึ่งในขณะนี้กำลังอยู่ในระหว่างการวัด

ธาตุอาหารไนโตรเจนยังอาจมีบทบาทต่อการผลิตข้าวอีกทางหนึ่งคือต่อคุณภาพการสี ได้พบว่าในการสีข้าว ข้าวที่มีปริมาณไนโตรเจนในเมล็ดสูง มีเมล็ดหักน้อยกว่าข้าวที่มีปริมาณไนโตรเจนในเมล็ด นอกจากนี้พันธุ์ข้าวเมล็ดยาวของไทยมีความทนทานต่อการหักในระหว่างสีต่างกัน ขณะนี้ยังอยู่ในระหว่างการศึกษาลักษณะภายในด้วยกล้องจุลทัศน์ (แสง และอิเล็คตรอน) ว่ามีความแตกต่างกันอย่างไรตามระดับไนโตรเจน และพันธุ์

งานด้านความหลากหลายในเกษตรนิเวศน์ (agrodiversity) ของกลุ่มได้เน้นการอนุรักษ์ความหลากหลายทางชีวภาพ และได้นำไปสู่การอนุรักษ์เชื้อพันธุ์ข้าวไทย[1]

งานของโครงการทางด้าน agrodiversity ได้เน้นการค้นพบระบบองค์ความรู้ท้องถิ่นในการใช้พืชบำรุงดิน คือต้นปะดะ (*Macaranga denticulata* (Bl.) Muell. Arg.) ซึ่งพบว่าประกอบด้วย 2 องค์ประกอบที่สำคัญคือ (ก) ต้นปะดะ และ (ข) เชื้อราไมโคไรซ่า ระบบนี้สามารถรีไซเคิลธาตุอาหารอย่างมีประสิทธิภาพ สามารถทำให้เกษตรกรปลูกข้าวไร่ได้ผลผลิต 320 –640 กก/ไร่ ได้อย่างยั่งยืน และน่าจะมีบทบาทสำคัญในการฟื้นฟูป่าด้วย ต้นปะดะสามารถหมุนเวียนธาตุอาหารกลับไปยังรากและดินได้ในปริมาณสูง คาดว่าจะเป็นสาเหตุหนึ่งที่ที่ปะดะมีเชื้อราไมโคไรซ่าในบริเวณรากมากว่าต้นไม้อื่นในบริเวณเดียวกัน นอกจากนี้ยังพบว่าประชากรของเชื้อราไมโคไรซ่ามีความหลากหลายด้วย โดยพบถึง 29 species ใน 6 genera

ในท้ายนี้กลุ่มวิจัยได้สร้างองค์ความรู้ใหม่มากมายภายในเวลา 3 ปี โดยสร้างจากฐานงานเดิมที่มีอยู่ก่อนแล้ว การสนับสนุนกลุ่มวิจัยจาก สกว. ได้เปิดโอกาสให้นำความสามารถทางวิชาการที่มีอยู่มาประยุกต์ใช้ และขยายงานไปครอบคลุมถึงปัญหาการเพาะปลูกในประเทศ ซึ่งคาดว่าขีดความสามารถในกลุ่ม โดยเฉพาะที่เกี่ยวกับสมรรถภาพการใช้ธาตุอาหารพืช และการปรับตัวเข้ากับภาวะเครียดจะสามารถนำไปสู่การปรับปรุงระบบการเพาะปลูกที่ได้ผล

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[1] ซึ่งได้ขยายไปเป็นโครงการใหม่ "Agrodiversity for in situ Conservation and Management of Thailand's Native Rice Germplasm" ได้รับทุนสนับสนุนจาก Collaborative Crop Research Program ของมูลนิธิ McKnight โครงการ McKnight นี้ได้อาศัยองค์ความรู้และวิธีการต่าง ๆที่ได้พัฒนามาจากโครงการเมธีวิจัยอาวุโสนี้ แต่ application เหล่านี้ยังมิได้รวมไว้ในรายงานฉบับนี้ด้วย

ABSTRACT

Advances have been made in three areas, namely, boron (B) nutrition, other nutritional problems in rice and agrodiversity.

For B nutrition of plants, the areas covered included adaptation to low B soils, genetic control of B efficiency and function of B in plant processes. Genotypic variation in adaptation to low boron soils has been established among major crop species and within some important cereals and grain legumes. Rice is the most well adapted to low B soils, it has never been found to be deficient. Bread wheat, along with durum wheat, barley and triticale, is the most sensitive to B deficiency. Maize is intermediate between these two extremes. Wheat and its Triticeae relatives are affected by B deficiency in a different way from maize. Bread and durum wheat and barley and triticale are all affected by B deficiency primarily through the development of the male gametes, the pollen. Maize, on the other hand, is affected first through the function of the style of the female flower, commonly known as silk , during pollen germination.

The range of genotypic variation in adaptation to low B is very large in wheat. Boron efficiency genotypes will set grain normally in the same soils in which B inefficient genotypes fail completely. We have also found that the international wheat germplasm used to improve production by most developing countries is largely B inefficient. Wheat production on the world' wheat growing areas on low B soils, hundreds of thousand of hectares already identified in Asia, can be greatly boosted by increasing B efficiency in these international germplasm. This should be relatively easy. Some advanced breeding lines, even only a few, in the international germplasm are already B efficient. The genetics of B efficiency has been proved to be relatively simple, involving two dominant genes. We have developed a simple screening that may be used to evaluated very large germplasm with thousands of entries as well as to select segregating materials. The other Triticeae cereals, durum wheat, barley and triticale, have somewhat more complex response to low B. They should nevertheless also benefit from similar increase in B efficiency.

One key issue in B nutrition in this project is the mechanism by which B efficient genotypes become adapted to low B soils. For wheat, B efficient Fang 60 and very inefficient genotypes such as Bonza and Tatiara are distinguished by their B uptake. This, however, does not explain the difference between B efficient Fang 60 or Sonora 64 with moderately inefficient genotypes such as SW41. The differential mechanism was demonstrated with the use of ^{10}B and ^{11}B and more precise methods for evaluating pollen viability. Fang 60 has the ability to maintain the B supply line from the root to the developing ear and so meeting demand for microsporogenesis even while external supply was interrupted. The inefficient SW41 cannot do this. It was also clearly established that phloem mobility and recycling of B did not play a part. On the other hand, we found some evidence that phloem mobility and the ability to recycle B may be very important in the adaptation to low B of some tropical species, including coffee, guava, jackfruit, mangosteen, papaya and teak. In custard apple, cashew, mango, lime, passion fruit, and cassava, B appeared to be as immobile as calcium.

We have established 2 simple rules to study adaptation with implications to crop management in low B soils that may be applied to the study of whole plant responses to any stress factor.

1. While adverse effects of a stress factor of so many processes may be of interest to physiologists, not all of them are equally important to whole plant response and so relevant to crop adaptation and production. Physiological studies with agronomic aims should always try to identify those processes that are most sensitive and are likely to adversely affect whole plant response.
2. Physiological studies of plant under stress must always take into account all possible dynamics of (a) changes in the stress condition over time, (b) changes in the plant's various responses over different growth and developmental stages.

In addition to the reproductive response, which appears to be the key whole plant response in many crop species, germination and seedling growth have been identified as a possible limiting step in the production of grain legumes on low B soils. Low B concentration in the seed may depress germination and affect the growth of seedlings when grown on low B soils. Phenol metabolism and the production of oxygen free radicals have both been suggested to involve B. Keeping quality of bean sprouts is therefore another effect of low B that should be further investigated in sprout making species such as mungbean, black gram and soybean.

Our research group has initiated nutritional work in rice in several areas under this project. Many of the study areas that are still in the preliminary stage include phosphorus efficiency, iron efficiency and tolerance to soil acidity. Progress has been made in development of screening methods and identifying efficient and tolerant genotypes from Thailand's native rice germplasm. Areas in which considerable progress has been made are in iron (Fe) in rice grain, adaptation to wetland (water logging) and dryland (aerated) condition and nitrogen fixing endophytes of rice.

For grain Fe, we have earlier established the baseline of grain Fe contents of Thailand's many important varieties, including KDML105, RD6 and RD15 and some new improved varieties and advanced breeding lines. These are generally low, about 10 mg Fe/kg in brown rice. We have also identified genotypes with almost twice as much Fe among local varieties. Some GxE effects on grain Fe have been found, but largely on whole plant Fe uptake. The grain Fe is a relatively small fraction of the whole plant uptake. The grain Fe, especially after the husk is removed, appears to be controlled largely by genetics. This makes genetic improvement promising as a means to increase grain Fe.

A rapid and simple method for assessing Fe in individual rice grains has been developed by using a dye called Perls' Prussian blue (PP blue) for staining localized Fe on the grain. The PP blue has enabled us to discover a relatively large range of grain Fe-content in farmers' normally heterogeneous seed lots. Thus we are now optimistic in find genotypes with even higher grain Fe. The PP blue should also be useful in selection and breeding programs aiming to increase grain Fe, as well as to study the controlling genetics.

In the newly initiated program on nutrient uptake efficiency of rice in dryland, we are finding that rice is basically a 'water' plant. It generally grows better when waterlogged in the wetland condition than in the aerated soil of the dryland condition.

Among Thailand's native rice germplasm, however, we are finding varieties that are better adapted to dryland than others. Part of this adaptation is an ability to take up nutrients in dryland. Preliminary nutrient uptake data show that this ability may be related to the ability to continue to grow more roots in aerated soil rather than the specific ability of the roots to take up nutrients from dry soil per unit root dry weight. This is expected to be an area of understanding that can make significant contribution to rice breeding for Thailand's largely rainfed growing condition. The program now focuses on nutrient uptake efficiency in intermittently waterlogged and aerated soil, in acidic soil and with a special focus on phosphorus, one of the most limiting nutrients in dryland condition.

Nitrogen (N) was another important nutrient covered by the project. We have found large numbers of N fixing endophytic bacteria inside the rice plant, from the roots, stems and leaves. They were found in both crop rice and wild rice. Their N fixing ability has been confirmed by acetylene reduction assays. Practical implications of these findings require measurement of the impact on rice growth and N use. The methodology for doing this is now under investigation. Another aspect of N nutrition is the negative relationship between grain N concentration and grain breakage during milling. Different rice varieties with similar long grained type have also been found with different tolerance to grain breakage. The internal structure of the rice grain is now being studied under light and electron microscopy to determine the effect of grain N concentration and variety.

The group's research on agrodiversity on biodiversity management has led to its application on the conservation of Thailand's native rice germplasm[1]. The other area was in forest regeneration and fallow enrichment. We found a system of local knowledge system involving a small pioneer tree called pada (*Macaranga denticulata* (Bl.) Muell. Arg.). The system has a most impressive capacity to recycle nutrients that has proved to be effective in keeping upland rice yield at respectable levels of 2-4 t/ha that should also be useful in forest regeneration. Furthermore, we have found that the system has two key elements. First is a highly diverse population of arbuscular mycorrhizal (AM) fungi in the pada roots, which greatly enhanced nutrient uptake by the tree. Second is the tree itself which recycle a very large proportion of the nutrients back to the roots and soil. This second point may explain why the AM fungi are much more abundant in the rhizosphere of pada than other local tree species.

In conclusion, the group has made much progress in the 3 years of support from TRF. We have built on the work that had already been ongoing before August 2000. The TRF funding has enabled to group to embark on new areas, which are expected to have more impact on Thailand's agriculture. The group's technical capacity in nutrient efficiency should be particularly relevant particularly for understanding adaptation of rice and having real impact in improving production difficult growing conditions.

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[1] This further evolved into the project "Agrodiversity for in situ Conservation and Management of Thailand's Native Rice Germplasm", which has received substantial funding from the Collaborative Crop Research Program of the McKnight Foundation. The McKnight project has been built on key findings and methodologies developed in this TRF project. However, findings on Thai rice germplasm from that project have largely been kept out of this report.

Ecophysiological processes and genetic controls relating to plant nutrition

1. BORON NUTRITION

Advances have been made in three areas of boron (B) nutrition in plants, namely, adaptation to low B soils, genetic control of B efficiency and function of B in plant processes. Adaptation studies explored differential ability to grow and yield in low B soils of different plant species and genotypes from the same species. This body of knowledge is useful to crop production on low B soils, by helping to identify adapted species and genotypes of plants that will not be constrained by B deficiency. Results of genetic studies help in the manipulation of the B efficiency trait, i.e. to increase B efficiency in agricultural germplasm through breeding and selection. Understanding the mechanism for B efficiency and physiological roles of B will reinforce genetic manipulation and crop management.

1.1 Plant adaptation to soils low in boron

Among the micronutrients, B deficiency is the most widespread and most frequently encountered in world crop production (Shorrocks, 1997; Sillanpaa, 1982). In Thailand, soils low enough in B to be a constraint to commercial crop production are common in the North and Northeast. Based on the idea of 'nutrient efficiency' suggested by Graham (1984), we have pioneered the use of 'B efficiency trait' to evaluate and identify plants that are adapted to low B soils without the need to specify the key mechanism(s) of that adaptation. A plant is more B efficient if it can grow and yield normally in a soil that is deficient in B for another plant. Thus any plant may be experimentally evaluated for B efficiency simply by growing them along side standard checks with known B adaptation ranges. This may be done in the soil that is naturally low in B, availability of soil B lowered by liming, or biologically available soil B depressed by an application of lime. We have also developed and adapted special culture media that can be used for the purpose, including solution culture, sand culture and B-buffered solution (*Sithichai Lordkaew*[1]). A set of standard B efficiency check genotypes have also been established, ranging from very B inefficient (extremely poorly adapted to low B soil) to B efficient (well adapted to low B soil).

1.1.1. Genotypic variation in adaptation to low boron soils

We have evaluated germplasm from 11 crop species, including important cereals and grain legumes, for adaptation to low B, totaling more than 5,000 entries (Table 1). The emphasis was placed on the Triticeae cereals, which included bread and durum wheat, barley and triticale, for three reasons. Firstly, these were found to be much more sensitive to B deficiency than previously believed and documented (e.g. see Lamb, 1967; Marten and Westermann, 1991). Secondly, a very large range of adaptation to low B has been identified, especially among bread wheat. Thirdly, bread wheat and barley together offer a unique system on which a model for studying B efficiency may be built (see sections on genetics and mechanisms below). Two main findings have resulted from this evaluation of germplasm for adaptation to low B: (i) relative tolerance to low B soils among the species of cereals and legumes; (ii) the value of adaptation to low B soils, based on studies of wheat and related species.

[1] Researcher or graduate student responsible for the work

Difference among crop species in adaptation to low B. Among all of the crops evaluated, rice was found to be the most tolerant to low external B supplies. It never exhibited any sign of B deficiency in soil with 0.1 mg hot water soluble (HWS) B kg^{-1}, in solution or sand culture to which no B had been added. Rice can be made B deficient only when B contamination in the water and chemicals used in experimentation is removed with the aid of B-specific resin (IRA-743, Sigma Chemical Co.). The next group of crops following rice includes soybean, maize, sorghum, green gram and cowpea. These are occasionally affected by B deficiency in the field, but can be made B deficient in sand or solution culture to which B had been omitted. The group of crops which may be considered least well adapted to low B soils, include the Triticeae cereals, bread and durum wheat, barley and triticale, and black gram. These have been shown to become deficient in B on the lighter soils of Northern Thailand, e.g. Sansai or Lampang series, with about 0.1 mg HWS B kg^{-1}. The poor adaptation to low B soils of wheat and other small grain cereals compared with dicots such as soybean or green gram, in spite of their relatively lower functional requirement for B, is explained in the section on mechanisms below. Genotypic variation in adaptation to low B soils was found in soybean (*Nattawut Sukcumpa*[1]), cowpea (*Tinnakorn Srivichai*[1]) and mungbeans, i.e. both green and black gram (*Ayut Kongpan*[1]). The range of variation, however, was greatest in wheat and related species of Triticeae cereals.

Adaptation to low B soils in wheat and related species as a means to overcome the problem of B deficiency in crop production. Boron deficiency depresses the yield of wheat, barley and triticale by depressing grain set. Adaptation to low B soils of germplasm of bread and durum wheat, barley and triticale was evaluated by means of the grain set index (GSI, percentage grain set in the first two florets of 10 central spikelets, Rerkasem and Loneragan, 1994). This was conducted on the international germplasm received from CIMMYT each year. They included mainly bread wheat (High Temperature Wheat Yield Trial; Elite Selection Wheat Yield Trial; Semi-Arid Areas Wheat Screening Nursery; International Bread Wheat Screening Nursery) and some durum wheat (International Durum Yield Nursery), barley (International Barley Observation Nursery) and triticale (International Triticale Yield Nursery; International Triticale Screening Nursery).

The International Maize and Wheat Improvement Center (CIMMYT) is the world's single most important source of wheat germplasm. Each year thousands of lines and breeding populations from CIMMYT are introduced into countries throughout the world. In the last four years alone, more than 160 bread wheat, durum wheat, triticale, and barley varieties derived from CIMMYT germplasm have been released by more than 30 countries (www.cimmyt.org/Research/wheat). About 55 million hectares of spring bread wheat, nearly 80% of annual spring wheat area in the developing world excluding China, are now sown each year with varieties developed from the CIMMYT germplasm. Results from the 2000/01 germplasm illustrated the typical range of adaptation to low B found in this international germplasm (Table 2). Two important findings came out of this evaluation. Firstly, the germplasm is dominantly B inefficient, but a few B efficient wheat genotypes were also present in each year. Secondly, the most B efficient genotypes were bread wheat, none of the barley, durum and triticale were as well adapted to low B soils as Fang 60.

The high frequency of B inefficiency in this international germplasm is a cause for concern. In areas prone to B deficiency, the genetic yield potential of this introduced germplasm cannot be fully utilized because of the B deficiency constraint. Furthermore, new improved varieties selected from these on research stations where B fertilizer has been applied can be expected to fail commercially, unless advanced breeding lines are assessed for B efficiency before they reach on-farm trials. The remarkable adaptation to low B soils conferred by the B efficiency trait, on the other hand, can prevent grain set failure and yield losses, by ensuring B efficiency in germplasm destined for areas prone to B deficiency. Boron efficient genotypes identified in the CIMMYT germplasm include advanced breeding lines that have already incorporated desirable modern characteristics for high yield and disease resistance (Table 3). National breeding programs can choose to release these where they prove to be also adapted to local environment. They can also be used as sources for B efficiency genes, which may be easily incorporated into new cultivars (see section on genetics).

These findings have direct implications for the world wheat growing areas on low B soils. Wheat germplasm from Bangladesh have been found to be largely B inefficient (Ahmed et al., 2002) (Table 4). Increasing B efficiency will boost wheat production on soils low in B which are found in many of the world's major growing areas (Rerkasem et al., *in* press). Valuable lessons for the management of other crop species in soils low in other nutrients (see 2.2, below).

1.1.2. Mechanisms for adaptation to low B soils

Physiological studies attempted to identify the mechanism(s) governing adaptation to low B soils, to compare B efficient Fang 60 with inefficient SW41 (*Duangjai Na Chiangmai*[1]), very inefficient Bonza (*Jumnien Wongmo*[1]), between B efficient and inefficient barley (*Tamarong Pasook*[1]), between wheat and barley (*Jumnien Wongmo*[1]), and between bread and durum wheat and barley and triticale. In order to prevent inadvertently selecting for genotypes are poorly adapted to toxic levels B while searching to increase B efficiency we attempted to relate adaptation to low B to adaptation to toxic levels B in wheat (*Supannika Panchana*[1]). Also explored were differences between the B efficient green gram and B inefficient black gram (*Ayut Kongpan*[1]) and the ability of different tropical species to recycle B from older tissues (*Sawika Konsaeng*[1]).

Boron efficient vs inefficient vs very inefficient wheat The effect of B deficiency on grain set in wheat and other small grains may be detected in fertility or sterility of the male gametes, the pollen grain. The iodine (KI/I2) test, which indicates starch accumulation, is very effective in determining dead pollen but was found to be somewhat imprecise in determining live pollen. That is, dead pollen does not normally accumulate starch, but those pollen that accumulate starch are not always viable. Two other methods for examining pollen viability were adapted for use on wheat pollen, the fluorochromatic (FCR) test, presence or absence of nuclei by the DNA-specific fluorochrome (DAPI) (*Duangjai Na Chiangmai*[1]). These two new tests were used to evaluate pollen viability and found to be much more sensitive than the iodine test (Nachiangmai et al., 2001). Withholding B for 5 days during the microsporogenesis was found to depress pollen viability in the B inefficient wheat genotype SW41 by 40-70% but had no effect on the B efficient Fang 60. This effect,

however, was detectable only with the FCR and DAPI tests, but not by the iodine test. All pollen accumulated starch and stained black with iodine, including those of SW41, which were no longer viable due to short term B deficiency.

This improved precision in determining the effect of B deficiency on pollen viability enabled the effect of B deficiency on B efficient Fang 60 and B inefficient SW41 to be compared more rigorously (Nachiangmai et al., *in press*). Following this finding of the effect of short term B deficiency on B inefficient SW41 and not on B efficient Fang 60, we were able to detect the greater ability of Fang 60 to continue to accumulate B in its developing ear even while external supply is interrupted. By labeling B with ^{10}B and ^{11}B, it was further found that the continuing B supply to the ear of Fang 60 (i) had not been recycled from previously taken up B, but (ii) had come from its ability to keep sending B to the ear for pollen development even from the greatly diminished external supply to the roots. Furthermore, we found that Fang 60 can accumulate more B in the ear than SW41 when external supply is limited. This, however, is detectable only at the crucial moment, around microsporogenesis. In the past, others have failed to pinpoint this difference (Rerkasem and Loneragan, 1994; Subedi et al, 1999) because ear samples were collected long after this time, e.g. at ear emergence or anthesis. The somatic ear tissues, the lemma, palea and rachis, can continue to accumulate B long after the damage has already been done to pollen development. This taught a valuable lesson about the often highly dynamic nature of plant responses to a stress factor.

We have previously ranked wheat genotypes according to their adaptation to low B soils in into 5 classses, efficient (E), moderately efficient (ME), moderately inefficient (MI), inefficient (I) and very inefficient (VI) (Rerkasem and Jamjod, 1997). Different adaptation mechanisms have been found associated with some classes. The difference in adaptation to low B soil between Fang 60 (E) and SW41 (MI) was detectable only in this ability to keep sending B from a much diminished supply in the root to the ear, and not in the specific B uptake capacity of their roots (mg B per unit root dry weight) or the partitioning of B to different plant parts (Subedi et al, 1999). In contrast, in the case of the VI group, B uptake and partitioning may be the key to their poor adaptation to low B soils. Genotypes such as Tatiara and Bonza set virtually no grain in soils with 0.1 mg HWS B kg^{-1} or in sand culture without added B are also found to accumulate much less B in their leaves and ears (Wongmo et al., *in press*).

Wheat vs other small grain cereals Adverse effects of B deficiency on barley and triticale are more complex than those observed on wheat (*Jumnien Wongmo*[1]; *Tamarong Pasook*[1]). In addition to male sterility, B deficiency has been found to depress terminal spikelet development in some barley and triticale genotypes. In these genotypes the number of spikelets per ear may be reduced by half to 1/5 of its normal size by B deficiency (Table 5). These two effects of B deficiency, the grain set response and ear size response, do not appear to be linked. Relative response to B in grain set correlated very weakly with the relative B responses in number of tillers per plant, ears per plant and spikelets per eat. Unlike wheat, in which adaptation to low B may be measured by just one single measure of the grain set index (GSI), barley and triticale may also affected through spikelets and ear development. Delayed ear emergence was another adverse effect of B deficiency were observed in barley. Examination of primordial at floral initiation found that B deficiency did not affect

the onset of floral initiation. Delayed ear emergence in B deficient barley appeared to have resulted from suppressed elongation of the peduncle instead.

Relating adaptation to low B to adaptation to toxic levels B in wheat Since 'exclusion', i.e. the ability to keep B out of the roots, has been found to be one of the primary mechanisms for adaptation to soils with toxic level B in wheat (Nable et al., 1997), our finding that B toxicity tolerant wheat varieties such as Bonza, Halberd and Schomburgk are generally very inefficient is a cause for concern for selection and breeding wheat for soils where toxic and deficient levels B may occur in close proximity such as Pakistan (Rashid et al., 2002) or the Anatolia in Turkey (Gezgin et al. 2002), or anywhere B fertilizer has just been applied. Should the mechanisms for adaptation to toxic level B turns out to be the mirror image of adaptation to low B soils, any attempt to increase B efficiency by selection and breeding would inadvertently results in genotypes that accumulate B and so are susceptible to B toxicity.

We have found that the relationship between adaptation to low and toxic levels B in wheat may be classified into 4 groups (Table 6). In the first group is Fang 60 which is B efficient, adapted to low B soils but poorly adapted to high B soils because it accumulates B in its leaves. In the second group are most CIMMYT materials that are B inefficient and poorly adapted to low B soils and at the same time have potential to be susceptible to B toxicity because they also accumulate B. In the third group are Bonza and Turkey 1473 which are very well adapted to soils with toxic levels B but are not so well adapted to low B soils because they are very inefficient. Theoretically there should be a fourth group, which is adapted to both toxic levels and low B. No genotype in existence has yet been found in this group. Existence of wheat genotypes in this group may be proved by testing lines already developed from crosses between Fang 60 of group 1 and Bonza of group 3.

Phloem mobility Since B has been found to be mobile in the phloem of certain temperate crop species, phloem mobility is seen a mechanism for adaptation to low B soils. In those species with phloem mobility, B may be recycled from old tissues to young growing points when external supply runs out. We took up the study of mobility of B in the phloem as a new direction to understand B efficiency in tropical species (*Sawika Konsaeng*[1]). First B concentration was examined in the leaf of mangosteen (*Garcinia mangostana*) collected monthly at the age of 3 to 7 months. The trend in B concentration was compared with that of Ca (phloem immobile) and K (phloem mobile). Calcium concentration in the mangosteen leaf increased linearly with leaf age, from less than 1.2% at 3 months to 1.35% at 7 months. This is typical of the accumulation of a phloem immobile nutrient. Potassium, on the other hand, showed the typical trend of non-accumulation of a phloem mobile nutrient. Its concentration remained constant at about 0.47% from 3 to 7 months. Leaf B in mangosteen showed a trend similar to phloem mobile K, i.e. was constant around 34 mg B kg^{-1} from 3 to 7 months. Leaf samples from 11 other species were collected and analyzed for B, K and Ca. They included coffee, custard apple, guava, jackfruit, cashew, mango, lime, papaya, passion fruit, teak and cassava. Concentration gradient between young and old leaves in six species, namely, custard apple, cashew, mango, lime, passion fruit, and cassava, suggested phloem immobility of B. Boron concentration in these species showed the same trend as phloem immobile Ca, i.e. increasing with leaf age. Five species, coffee, guava, jackfruit, papaya and teak,

showed concentration gradient of B between old and young leaf that was similar to the phloem mobile K. It is likely that these five species, along with mangosteen, represent tropical species, which are more efficient in their use of B by being able to recycle it from older tissues (Table 7). Direct determination of phloem mobility of B in some of these species will be made with the use of B isotopes, ^{10}B and ^{11}B. Mechanism for B transportation in the phloem may be explored with B transport molecules such as sugar alcohols.

1.2 Function

We have established that the key limiting step through which B deficiency may adversely affect productivity of many crops is reproductive development. For grain legumes, namely, green gram, black gram and cowpea, B deficiency, which may or may not be expressed in yield loss, may also affect seed quality. Since many authors have reported the involvement of B in sugar transport, we have also explored the possibility of direct effect of B deficiency on sugar accumulation in sugarcane and yam bean.

1.2.1. Reproductive development

In addition to wheat and barley (*Duangjai Nachiangmai; Jumnien Wongmo; Tamarong Pasook*[1]) we have examined the role of B in reproductive development of maize and sorghum (*Sithihai Lordkaew*[1]).

Wheat and barley We have established that functional B requirement that is specific to reproductive development in wheat is 7-8 times the amount needed for vegetative growth, including somatic tissues of the secondary sex organs such as the lemma, palea and rachis. There is a critical stage for this B requirement at about five days from premeiotic interphase stage to the young microspore stage. Interrupting B supply to the anthers during this crucial 5 days proved to be detrimental to pollen development (Nachiangmai et al, in press).

Maize and sorghum Similar to wheat and barley, B deficiency has been found to affect reproductive development in maize and sorghum much more than their vegetative development (*Sithichai Lordkaew*[1]). When grown in sand culture, omission of B from the nutrient solution depressed seed set and seed yield in both maize and sorghum while having no adverse effect on their shoot dry weight (Table 8). Although the adverse effect of B deficiency was not measurable in shoot dry weight, typical symptoms of B deficiency were observed in maize leaves. Appearing all over the upper leaves were thin (0.5-1 mm) longitudinal streaks of dead, papery white tissues, that may be short (3-4 cm) or long, running along the whole length of the leaf blade.

The effect of B deficiency on reproductive development was most strong in maize, which was later confirmed (Table 9). Boron concentration at 4-5 mg B/kg appeared to be more than sufficient to meet the requirement for vegetative growth. The reproductive organs, both male (the tassels, anthers and pollen) and female (baby corn and silk), required more B per unit dry weight. Measurable effects of B efficiency on the male flower are small. Occasionally the whole tassel or florets on a few branches will appear to be poorly developed, the lemma and palea are white and

papery. Inside these dead and white florets, the anthers are much smaller (3-4 mm Vs. 5-6 mm) or thinner (0.2-0.3 mm Vs. 1.2-1.5 mm) than those with sufficient B, or they may be absent altogether. These anthers may contain no or very few pollen grains. On the whole there were only a few of these poorly developed tassel branches. About the same amount of pollen were harvested from B0 and B20 plants by shaking the tassels over a receptacle (Table 9c). The harvested pollen from both B0 and B20 stained positive with iodine in KI/I_2 solution. However, detection of viable pollen was more precise with the fluorochromatic (FCR) test, using autoclaved pollen as control. In this way it was possible to detect the effect on B deficiency on pollen viability in maize.

The role of B in reproductive development of maize is, however, very different from that in wheat and the small grains. The adverse effect of B deficiency was much more pronounced on the female flower, i.e. the ear, which includes the baby corn and silk. The next sign of B deficiency that was observed after the papery streaks on leaves was that there were multiple, 2-3, ears in B0 compared with the normal single ear at the ear node. Externally these appeared just like normal maize ears covered with husk. However, when the husk was removed they do not look like normal babycorn, but have the appearance of branching panicle more close resembling the tassel. Those female flowers that developed normally in B0 into babycorn were smaller, having only one quarter of the dry weight on those in B20. Boron deficiency also clearly depressed development of the style or silk. The silk on the maize ear in B0 was much shorter and had only about half of the dry weight as that on the ear in B20.

In addition to development of the male and female flowers, B deficiency also had adverse effects on the function of various reproductive parts of the flowers. We assessed this by experimentally crossing male and female flowers with different B status (Table 10). The role of B in the function of pollen and style was clearly seen in the success of the crosses. Clearly, the effect of B deficiency in maize is much more severe on the development and function of the female flower. This includes (a) development of babycorn and the silk, and (b) the function of the silk during fertilization (presumably through the B supply for germinating pollen in the silk – this is now under investigation by *Sithichai Lordkaew*[1]).

Rice, wheat and maize – a new challenge. It is very curious that the world's three most important food grains should have uniquely different adaptation to low B. Rice is so highly insensitive to low B, it hardly ever is B deficient. Maize is affected through the female flower, which may depress fertilization, or B deficiency may 'switch' the reproductive primordia from female into male. Wheat, on the other hand, is affected primarily through development of the male gametes. Understanding these differences, and also genotypic variation within each, will enable us to control the reproductive process of three important species. This will have implications not only for the production of these crops on low B soils but also in the control of their breeding systems such as in hybrid seed production.

1.2.2. Seed quality

We have known for a long time that grain legumes growing on low B soils may produce seed of low quality even when there is no adverse effect of deficiency

on plant growth or seed yield. The seed quality may be affected into two ways, (1) in germination, and (2) in subsequent growth of seedlings produced from the seed. We set out to examine how genotypes differ in their ability to accumulate B in the seed, and how black gram and mungbean differ in this respect (*Ayut Kongpun*[1]). When grown on the same low B condition, genotypes may accumulate B differently (Table 11). The seed B, however, may be confounded by the dilution factor of how growth and seed yield is affected by B deficiency (Table 12). The genotype CPI79563, for example, had the highest seed B concentration in B0 mainly because it set only a few seeds and yielded only a fraction of the other genotypes while its root system showed on only a slight effect of B deficiency (Table 13). In total CPI179563 accumulated only 2 μg B/pot compared with 80-100 μg B/pot accumulated by M1, KPS1 and VC2755. Regur and VC1163 did not differ from M1 and KPS1 in the seed B concentration in B0. They, however, accumulated less B in the seed simply because of their significantly lower seed yield. The poorer ability to accumulate B in the seed of Regur and CPI179563 was also measurable as significantly lower seed B content per unit root dry weight at both B0 and B0.5.

The effects of low B on seed yield and seed B accumulation together produced different seed B concentrations in different genotypes. The seed B concentration in turn affected % germination and seedling growth. The low seed B at 5-7 mg B/kg appeared to depress germination slightly (10-20%) in some genotypes (M1, Regur and KPS1) but not in others (VC2755 and VC1163). This seed with the low B concentration produced abnormal seedlings when germinated and allowed to grow in low external B supply. The percentage of seedlings that were affected in this way varied from 54% in M1, 66% in VC2755, 81% in VC1163 to 90-100% in Regur, CPI79563 and KPS1. Abnormal seedlings all disappeared when germination and seedling growth was supplied with B, except in CPI79563 (4.6 mg B/kg) and VC2755 (5.3 mg B/kg) which still exhibited some 20% of abnormal seedlings.

Nutrients and the keeping quality of bean sprout – a new connection During discussion with grain legume users at Prof. Peerasak Srinives's second phase project meeting at TRF in early July 2003 the problem of damages and keeping quality of bean sprout was raised. This suggests a possibility to open up a new direction of research on nutrition and metabolism of germinating seeds. Boron is a strong candidate because of its major structural role in the cell wall (Matoh, 1997) plus reports of the involvement of B in phenol metabolism and formation of oxygen free radicals leading to cell damages (Cakmak and Rőmheld, 1997). Research into the effect of nutrient deficiency on metabolism of germinating seed could be very useful. This may be studied both internally through nutrition of the mother plant and externally through supply to the germinating seed. This could be lead to new understanding of the role of nutrients in phenol metabolism and production of oxygen radicals as well as providing useful tips in the production of bean sprout. Exploring genotypic variation in the adaptation within the mungbean and black gram germplasm could be very profitable, since it is well known that black gram has a much greater keeping quality than mungbean.

1.2.3. Sugar transport

While some metabolic roles of B have been clearly defined in the last decade, some that have been reported are still in dispute. It has been proposed that B plays a

key role in sugar transport in plants (Dugger, 1983). In two preliminary experiments, we explored the possibility of the direct role of B in sugar accumulation in sugarcane (*Prateep Oupkaew*[1]) and yam bean (*Saicome Pintasen*[1]).

Yam bean (*Pachyrhizus erosus* (L.) Urban) and sugarcane (cv. Supanburi 50) were grown in sand culture with 3 levels of B (0, 0.5, 10 μM B) added to the otherwise complete nutrient solution. Dry matter yield and tuber yield of yambean increased with added B to 0.5 μM, increasing the added B to 10 μM had no further effect. We found no effect of B on the tuber sugar content. Similarly in sugarcane was adversely affected by B deficiency when no B was added to the nutrient solution. The effects observed included transparent longitudinal streaks on the upper leaf blades, and depressed fresh and dry weight of the cane and leaves and reduced leaf area. No effect of B on sugar content was found.

1.3 Genetic controls and breeding

Large range of adaptation to low B was found in many crop species, especially bread wheat and barley. Mechanisms of adaptation to low B soil are much more understood by physiological and agronomical studies (see section 1.1). In this part we described genetic controlling B efficiency in these two crops. Understanding genetic control will help in set up breeding and selection strategies to incorporate B efficiency into new cultivars.

1.3.1 Screening for B efficiency

For genetic study, two systems were used in screening for B efficiency. The first was to grow plant in a soil with low B (0.1 mg B kg^{-1}) at the Agronomy Department's field. Control plots were added by applied B into the soil (defined as plus B (B+)) togenether with growing genotypes with a range of known levels of B efficiency along as check genotypes. The second system was to grow plant in sand culture and water with an otherwise complete nutrient solution with (B+) or without (B0) B added to the solution. Check genotypes were always included. As B deficiency depressed grain set in wheat plants were measured for GSI only. In barley, B deficiency not only depressed grain set, it also reduced number of spikelet $spike^{-1}$ and promote number of late tillering $plant^{-1}$. Therefore, for barley plants were measured for GSI, spikelet $spike^{-1}$ and tillers $plant^{-1}$ at maturity.

1.3.2 Source of B efficiency

Genetypic variation for B efficiency exists for wheat, barley, mungbean and blackgram. High levels of efficiency are available in an elite, well adapted germplasm for example, Fang 60 wheat (Jamjod et al., 1992), BRB 9604 and BRB 9624 barley (Jamjod and Rerkasem, 1999) some advanced lines of wheat in CIMMYT nurseries (Rerkasem et al. *in press*), KPS1 mungbean (Kongpahan et al., *in press*). These sources of B efficiency were chosen and use as donor parents for a backcrossing program to transfer B efficiency gene(s) into local varieties.

In genetic study, the most B efficient wheat (Fang 60, E) was intercrossed to moderately inefficient (CMU 88-9, ME), moderately inefficient (SW 41, MI) and inefficient (Bonza, I) genotypes. By the same way, the most B efficient barley (BRB

9604, E) was crossed to moderately efficient (BRB 9, ME), moderately inefficient (BCMU 96-9, MI) and inefficient (SMGBL 91002, I) genotypes. Response of F_1 from all cross and F_3 from selected crosses were evaluated and described in the next section.

1.3.3 Genetic control

Mode of gene expression for B efficiency was studied by comparing response of F_1 hybrids and parents from different combinations in solution culture with four levels of applied B (0, 0.1, 1 and 10 μM B). In wheat, GSI of F_1 hybrids between the most efficient (E) parents Fang 60 and other genotypes in low B were similar to Fang 60 parent. This indicates that B efficiency in wheat was expresses as a completely dominant trait. In contrast, gene actions for B efficiency in barley were varied with cross combinations and B levels. Complete dominant gene action for B efficiency in term of GSI was found only for the E x ME cross. The GSI of (E x MI) and (E x I) of barley were close to more inefficient parents when grown in B0 and B0.1, indicating partially to complete dominance gene actions of B inefficiency (Table 14).

In barley, as B deficiency increased number of late tillerings plant^{-1} and decreased spikelets spike^{-1} of inefficient genotypes. Response of parents in terms of number of late tillers plant^{-1} and spikelets spike^{-1} could be classified as; efficient (BRB 9604), moderately inefficient (SMGBL 91002 and BRB 9) and inefficient (BCMU 96-9) (Table 15 and 16). Crosses between BRB 9604 x SMGBL 91002 and BRB 9604 x BRB 9 were similar to the more efficient parent (BRB 9604) and therefore expressed as a dominant gene action. F_1 hybrids from BRB 9604 x BCMU 96-9 were intermediate between parents for both characters suggesting additive gene action.

Expression of B efficiency was varied according to cross combination and B concentrations (Jamjod et al., *in press*; *Napat Somkuan*[1]). The nature of expression of B efficiency will influence the level of the treatments selected for screening each segregating population and method of selection in a breeding programme. The B level should be deficient for homozygous inefficient rather than homozygous for a backcrossing programme, whereas the level should be deficient to heterozygotes but not the homozygous efficient genotypes in screening an F_2 or other segregating population. In the case of Fang 60 in which B efficiency express as dominant trait, selection must be postponed to another generation, or progeny test, to separate homozygous efficient from heterozygotes (*Supawadee Ngorian*[1]).

In order to determine number of gene controlling B efficiency, three parents were intercrossed and the F_2-derived F_3 populations were evaluated for segregation in sand culture without added B. Characters measured were the same as described in F_1 study. Segregation patterns for GSI of F_3 are reported below. Those of number of spikelets spike^{-1} and tillers plant^{-1} are under investigation (*Panomwan Boonchuay*[1]).

In wheat, the segregating patterns of the F_2-derived F_3 families from parents having contrasting levels of B efficiency were consistent with B efficiency being under the control of major genes (Table 17). The full response range of the three parents was shown to be controlled by two major independent loci, with the efficient Fang 60 having efficiency alleles at both loci and the moderately inefficient SW 41

having efficiency alleles at one locus. The B inefficient Bonza is expected to have alleles for inefficiency at both loci. If the gene symbol *Bo$_d$* is assigned to the loci controlling B efficiency, the proposed genotypes of these parental lines were as follow:

Fang 60 –Efficient-	*Bo$_d$1Bo$_d$1 Bo$_d$2Bo$_d$2,*
SW 41 –Moderately inefficient-	*bo$_d$1bo$_d$1 Bo$_d$2Bo$_d$2*
Bonza –Inefficient	*bo$_d$1bo$_d$1 bo$_d$2bo$_d$2.*

In barley, response to B measured by GSI was a under simple genetic controlled as found in wheat. No different between reciprocal crosses was observed. Digenic segregation were found in crosses between (E x I) and (ME x I). Therefore, B efficiency was controlled by at least two major genes. However, transgressive segregation was observed between (E x ME) lines (Table 18), suggesting these two lines might possess alternate loci. Proposed genotypes of the parental lines of barley were:

BRB 9604 –Efficient-	*Bo$_d$1Bo$_d$1 Bo$_d$2Bo$_d$2 bo$_d$3bo$_d$3*
BRB 9 –Moderately efficient-	*bo$_d$1bo$_d$1 Bo$_d$2Bo$_d$2 Bo$_d$Bo$_d$3*
BCMU 96-9 –Inefficient	*bo$_d$1bo$_d$1 bo$_d$2bo$_d$2. bo$_d$3bo$_d$3*

To test this hypothesis the derived lines from (E x ME) cross exhibited highest and lowest GSI were developed and will be tested in low B. They will be backcrossed to both parents and analysed for segregating patterns in F_2 generation.

1.3.4 Breeding for B efficiency

As B efficiency in wheat was simply inherited, backcross method is the most efficient way to transferring this character into inefficient varieties. The first backcross population was made for Bonza (I) x SW 41 (MI) using Bonza as a recurrent parent in order to transfer *Bod2* from SW 41 to Bonza (*bod2*) background. The backcross population was grown in sand culture without added B and assessed for GSI. It was found that the backcross population segregated at a ratio of Bonza type:heterozygote = 1: 1 as expected ($\chi 2 = 1.17$, p =0.5945) (Jamjod et al., *in press*). This result confirmed that B efficiency in wheat can be easily transferred by backcross breeding method. Backcross-derived lines between SW 41 (*Bo$_d$2*) as the donor parent and Bonza as the recurrent parent are now being developed at Chiang Mai University and will be evaluated for yield advantage in the next growing season. The Bonza derivatives carrying *Bo$_d$2* will be selected and following further crosses with Fang 60 as a donor parent, lines carrying *Bo$_d$1* and *Bo$_d$2* will be developed for evaluation under low B conditions.

1.4 From B physiology to managing crop production on low B soils

Adverse effects of boron (B) deficiency on physiological processes are associated with both vegetative growth and reproductive growth. The vegetative processes reportedly affected by B deficiency are root and leaf growth, vascular differentiation and assimilate partitioning; reproductive ones include flower and gametes development, fertilization and fruit growth. However, not all of the physiological responses to low B documented in the literature are encountered in field grown crops on low B soils. Boron responses of crops in farmers' fields can be very different from those that interest plant nutritionists and physiologists. The synthesis

of our studies of B nutrition suggests that not all of these various responses observed and reported are equally important to whole plant response and so productivity. This section summarizes the synthesis of B physiology studies in our group, with a specific focus on how it may be applied to crop management on low B soils.

1.4.1. Individual organs and processes

The most rapid response to B deficiency in higher plants is the cessation of root elongation (Dugger, 1983; Marschner, 1995; Shelp, 1993; Dell and Huang, 1997), but this has rarely been seen in wheat. Boron deficiency in early vegetative growth is much less readily inducible in wheat than in dicots. In earlier studies, B deficiency was induced in vegetative growth in wheat only after B in the nutrient solution had been depleted by plant uptake. Characteristic symptoms in young wheat plants made B deficient in this way include a longitudinal splitting of the newer leaves close to the midrib and the development of a saw tooth effect on young leaves reflecting abnormal cellular development (Snowball and Robson, 1983). None of the effects of low B on early vegetative growth cited above has ever been observed in the field. An exception is the longitudinal split along the mid-rib observed in solution culture (Snowball and Robson, 1983) which is common in the field in Thailand, Bangladesh and Nepal (Rerkasem unpublished). In the field, however, the symptom is extremely ubiquitous and not restricted only to fields or plants that are otherwise proved to be B deficient.

1.4.2. Whole plant response

We have established 2 simple rules to study adaptation with implications to crop management in low B soils that may be applied to the study of whole plant responses to any stress factor.

1. While adverse effects of a stress factor of so many processes may be of interest to physiologists, not all of them are equally important to whole plant response and so relevant to crop adaptation and production. Physiological studies with agronomic aims should always try to identify those processes that are most sensitive and are likely to translate to adverse effects on whole plant response.
2. Physiological studies of plant under stress must always take into account all possible dynamics of (a) changes in the stress condition over time, (b) changes in the plant's various responses over the different growth and developmental stages.

To understand whole plant response to a nutrient deficiency, and thus to apply the understanding to field grown crops, it is necessary to consider responses of different growth processes in relation to one another as well as the response of individual processes. The relationship may be in the chronological order in which the processes occur in the life cycle of the plant, and in their relative sensitivity to the deficiency. Irreversible adverse effects that occur earlier may over-ride effects on more sensitive processes or organs that occur later. Boron deficiency causes flower buds to shed in some species, e.g. in apple (*Malus domestica*) (Dong et al., 1997); black gram (Noppakoonwong et al., 1997) and sunflower (Blamey, 1987). In such cases it may be irrelevant if the development of the male and female gametes are more sensitive to B deficiency if the flower buds had been lost even before meiosis. On the other hand, a greater sensitivity of the development the stamen or carpel or the fertilization process may make one of them the limiting-step if the B deficiency is not

severe enough cause prior irreversible damages. The key to understanding B deficiency and so to manage production on low B soils appears to be the relative sensitivity of its reproductive process.

With wheat and maize we have established an understanding on the key role of B in reproductive development, which is similar in one respect and very different in another. The similarity is that both crops require more B for reproduction than for vegetative growth, so that B deficiency becomes a constraint to production primarily through the failure of flower development and grain set. The difference is that the limiting step in maize is the development and function of the female flower, whereas in wheat the limiting step is in male fertility.

For the wheat, maize and grain legumes that we have studied, the key to an understanding of their adaptation to low B is the sensitivity of their reproductive process. Of all the physiological responses to low B reported in the literature, reproductive development is the only response observed in field grown crops. Greater functional B requirement for reproduction than any other physiological processes is another of our main findings. With maize and wheat we have shown that the difference may be refined further within the reproductive process. The most sensitive step is wheat is in the development of the male gametes, i.e. the pollen, while for the maize it is in fertilization process, in which pollen germination is governed by B concentration of the style or silk.

Understanding the role of B in reproductive development of the world's three major food grain species, rice maize and wheat, including genotypic variation within each, will provide an insight into whole plant responses and adaptation that would integrate physiological processes, morphological changes as well as molecular genetic control.

2. OTHER NUTRIENTS AND RELATED PROCESSES

2.1 Iron in rice grain

Increasing grain iron (Fe) content in rice is now believed to be one way to improve Fe intake in rice eaters, especially in Asia. For Thailand, it could also mean value adding to high quality rice such as the Thai Jasmine. At the beginning of this project information on grain Fe content of Thai rice was extremely limited. We set out to examine the range of Fe concentration in Thai rice, how it is influenced by rice genotype, and the external environment (*Chanakan Prom-u-thai*[1]). In order to gain an understanding into how bioavailable Fe may be affected by milling and cooking we also look at the location and forms of Fe in the rice grain. Bioavailability of rice with different grain Fe content, different varieties and different parts of the grain, and the relationship between bioavailability and phytate content are currently under exploration.

2.1.1. Factors affecting rice grain iron

We grew 38 varieties of Thai rice under wetland and dryland condition and found that grain Fe concentrations in brown rice ranged from 7-15 mg Fe/kg when grown in wetland condition and 8-16 mg Fe/kg when grown in dryland condition

(Table 19). Standard Thai rice varieties (e.g. KDML 105, RD 6, RD15 and RD10) and newly developed rice varieties from the Thai Rice Research Institute are all among the lowest in grain Fe (Table 20). The environment in which the rice is grown may affect grain Fe, but the effects were small compared with differences between genotypes (Table 21). Similarly, nitrogen fertilizer also had relatively small effects on rice grain Fe (Table 22). The rice plant can take up quite a lot of Fe, as we may see hundreds mg Fe/kg dry weight in rice leaves, stems and leaf sheaths (Table 23). The roots can accumulate thousands of mg Fe/kg DW and even tens of thousand when the rice plant is grown in waterlogged soil. Only a fraction of this Fe, however, gets into the grain. External environmental condition that strongly affects availability of Fe in the soil such as water regime or liming can significantly influence Fe uptake by the rice plant. However, the effect on grain Fe is relatively very small. For example, we saw that water logging about doubled Fe concentration in leaves, stems and leaf sheaths of KDML105, and increased Fe concentration in the roots by a factor of 10 or more (Table 23). However, its grain Fe concentration was increased from about 8-9 to 10 mg Fe/kg. A lot more of Fe is already taken up into the plant and is present in the leaves, stems, leaf sheaths and even the husk in much larger concentration than in the grain (Table 23). Any attempt to increase rice grain Fe should therefore focus on how to allow just a little more of this Fe already in the plant into the grain, instead of increasing the Fe taken up from the soil into the plant.

2.1.2. Location and forms of iron in rice grain

Of the total Fe content of the whole rice grain, some two third to three quarters is in the husk and is removed in milling (Table 23). Only one quarter to one third is left in brown rice. In many varieties considerable Fe is concentrated in the bran, so grain Fe concentration decreases after polishing. These included RD6, Ubon 2, Hom Nangfah and Basmati. Interestingly, the Fe concentration of brown rice and 30 seconds white rice (normal polishing time in mills) did not differ in low grain Fe KDML 105 and high grain Fe IR68144. Further polishing for 30 more seconds decrease Fe concentration KDML105 but not in IR68144.

Electron microscopy of the internal structure of the rice grain showed that Fe in rice is associated with inclusion in protein bodies that look like phytate.
In thin sections, endosperm cells of all genotypes had about a quarter of the number of protein bodies than cells in the embryo and aleurone layer. Protein bodies were spherical, rod-shaped or irregular in outline and diameters ranged from <1 to 4 μm. The relative distribution and density of protein bodies were similar for the four genotypes. Some of the protein bodies in the non-endospermic part of the seed contained crystalline inclusions. From their histochemistry and FEGTEM-EDX-analysis, showing enrichment in P, Mg, K, Mn, Fe, and Zn, it was concluded that the inclusions were phytin bodies. The phytin bodies ranged from <1 to 2 μm in diameter, and were round, oval or irregular in shape. Phytin bodies were more abundant in the embryo and aleurone layer of the high Fe (IR68144, CMU122) than the low Fe genotypes (KDML105, UBON2). Seed with more abundant phytin bodies also contained higher concentrations of Cu, Mn, Mg, K and P. Analyses are currently being conducted to determine bioavailable Fe and phytate contents of different rice varieties and different portions of the grain, with high and low Fe concentration.

2.1.3. Determination of iron in individual rice grain

In the course of the microscopy study to locate Fe on the rice grain, a rapid method for detection of Fe on rice grain has been identified (Prom-u-thai, in press). We show how a preliminary determination of grain Fe in rice may be made with reaction to Perls' Prussian blue, a stain for Fe (III). Differential localization of Fe in parts of the grain is indicated by intensity of reaction of tissue Fe to the dye. The blue colour reaction was most intense in the embryo, weak in the aleurone layer of the pericarp and invisible in the endosperm. The staining intensity varied with region of the embryo, generally being strongest in the scutellum, intermediate in the coleorhiza and weakest in the coleoptile. Variation in the reaction to Perls' Prussian blue was observed among eleven rice cultivars with varying grain Fe contents. The intensity of the blue colour reaction in the embryo of different rice cultivars was indicative of their grain Fe contents for both brown and white (polished) rice. Those with high grain Fe, >14 mg Fe kg-1, were clearly distinguishable from those with <10 mg Fe kg-1 with Perls' Prussian blue. This simple staining procedure may be used to quickly screen for high Fe contents in large germplasms containing hundreds of entries, using reactions in genotypes with known grain contents as standards. The method is now being used to find variation in grain Fe content within landraces and to identify genotypes with exceptionally high Fe that are present at relatively low frequencies in individual seed lots (*Chanakan Prom-u-thai and Saicome Pintasen*[1]). We are thus optimistic at identification of genotypes with higher grain. Furthermore, because of the localized nature of the staining, Perls' Prussian blue may be used to verify whether contamination from FeO_3 is responsible for very high Fe analysis values of some rice samples. Contamination would show up in irregular smudges of very high intensity whereas naturally high Fe concentration would stain uniformly and vary only according to Fe concentration of individual tissues, i.e. highest in embryo, weak in the aleurone layer and invisible in the endosperm.

2.2 Other nutrients in rice

Other nutritional problems in rice that we are looking into all focus on growing rice in aerated soils. Currently these include nutrient uptake efficiency in rice in intermittently wet and dry soil (*Nednapa Insalud*[1]), adaptation to acid soil (*Natthinee Pattarakul*[1]), efficiency in phosphorus (P) (*Chumnien Wongmo*[1]), nitrogen (N) (*Chanikarn Kumnok and Ayut Kongpun*[1]) and Fe (*Rataya Yanapan*[1]). Of these, the work on P efficiency has only been originated in the last 3-4 months (PhD programme to commence October 2003), so results will not be reported here. The work on acidity has progressed to identification of genotypes tolerant to aluminium toxicity from local rice germplasm (e.g. Bue Mue Tabong) at the village of Tee Cha in Sob Moei District of Mae Hong Son Province farmers' rice varieties can yield reasonably well on soil with pH 3.8-4.2 (Yimyam et al., 2003). The method for screening for acid tolerance, however, is still being finetuned. We have developed a method for screening for Fe efficiency with chlorophyll meter. Phitsanulok 1 has been identified as Fe efficient. We are now attempting to identify the mechanism for this efficiency by evaluating for phytosiderophores in the roots in comparison with less efficient genotypes (Chainat 1, KDML105) and wheat, a known phytosiderophores producer.

2.2.1. Adaptation to wetland and dryland condition

Availability and uptake of many nutrients are greatly enhanced in rice grown rice in flooded, waterlogged, wetland condition. However, only 25% of Thailand's rice area are irrigated. In the remaining 75% rice must grow in aerated soil or dryland condition for some of the time during the growing season. Some of these include upland rice, which is grown in the highlands and dry seeded rice in rainfed areas and deepwater rice before the arrival of the flood. With rising labour cost, transplanted rice is being increasingly replaced by dry seeded rice in rainfed areas in the North and Northeast. Basic understanding of adaptation of rice to aerated soil or dryland condition, particularly during the first 6-8 weeks, should contribute towards rice production in this country[2]. To serve this purpose we have initiated a program on nutrient uptake efficiency in dryland.

Early results have shown that rice cultivars are generally better adapted to wetland condition than to dryland condition, but upland rice tend to perform better in dryland relative to wetland (from now on referred to as 'relative dryland performance' or RDP and defined as performance in dryland as % of performance in wetland) than wetland varieties (Table 24). This difference was reflected in nutrient uptake, especially for P (Table 25). Upland varieties Kae Noi and Sew Mae Jan took up as much and sometimes more nutrient in dryland than in wetland, whereas Chainat 1 took up a lot less nutrient in dryland than in wetland. This difference was clearly not associated with greater specific uptake ability of the roots (mg nutrient taken up per unit root dry weight). We are now attempting to prove a hypothesis that adaptation to dryland condition of some rice genotypes (e.g. upland rice) is associated with the ability to grow more roots in dryland. If proofed to be valid, this will have implication on the way in which the adaptation of rice to dryland condition is studied, the way in which selection for adapted genotypes may be carried out and also how genotypes are evaluated for adaptation to intermittent wetland/dryland condition.

2.2.2. N fixing endophytes

Nitrogen fixing endophytic bacteria have been found and isolated from leaves, stems and roots of cultivated and wild rice (Table 26). Isolated on N-free medium, their nitrogen fixing ability was confirmed with acetylene reduction assays. The bacteria have been identified by morphological and physiological characteristics into 4 genera, namely, *Azospirillum, Herbaspirillum, Beijerinckia and Pseudomonas* (Table 27). In three varieties of crop rice investigated, the nitrogen fixing endophytes were found in the leaves, stems and roots in numbers that ranged from 100s to 10,000s bacteria per g fresh weight of the rice tissue at 30 days (Table 28). The number of bacteria generally increased with time to 100,000s bacteria per g FW of tissue at 60 days. Even greater numbers of nitrogen fixing endophytes were found in wild rice (Table 29). The practical significance of these bacteria would be in the effect they have on nitrogen nutrition of the rice plant. We are now attempting to do this (*Ayut Kongpun*[1]).

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[2]Adaptation to drought stress would be another important area, but a very large international research program on this is already on-going in collaboration with the Thai Rice Research Institute at Ubon Rice Research Centre.

2.3 Rice quality

We set out to define the measurable characteristics of 'high quality' rice that would bring premium prices to farmers, and to identify those that could be managed on-farm (*Manop Leesawatwong*[1]). With the help of a commercial rice buyer (Chiangmai Chaiwiwat Ricemill Co., LTD), we determined the price range paid to farmers by the mill for 'Hom Mali' rice, and assessed the characteristics used for price determination (Leesawatwong et al., *in press*). Just as the milled Hom Mali rice in shops may range in price from 12 to 25 *baht*/kg, paddy grown from KDML105 was found to fetch prices ranging from 5,000 to more than 7,000 *baht*/kg. Samples from Nakhon Sawan were much more variable in quality and price than those from Chiang Mai. Only 10% of the samples from Nakhon Sawan were judged to be of premium quality and priced at more than 7,000 bath per ton, and 40% were priced at less than 5,500 bath per ton. Grain moisture was all under the required standard of not exceeding 14% in all of the samples. Prices of Nakhon Sawan samples were determined by 4 major characteristics, namely, percent head rice (X_1), aroma (X_2), vitreousness (X_3) and translucency (X_4). The primary determinants were aroma and vitreousness scores, with translucency and percentage head rice having relatively minor effects:

$$P = 3259.7 + 28.8X_1 + 403.5X_2 + 357.1X_3 + 71.9X_4$$
$$r^2 = 0.94,\ p < 0.001$$

All samples from Chiang Mai received the full score for vitreousness, translucency and aroma. Price was determined by one quality characteristic only, the percentage head rice (X_1):

$$P = 69.4 + 11.3X1$$
$$r^2 = 0.94,\ p < .001$$

(Leesawatwong et al., 2003)

This study was expanded with an on-farm survey in the growing season 2002 with a larger number of samples, to cover a wider range of growing conditions (e.g. Sanpatong, Sankamphaeng, Prao, Mae Chan, Phan, Lampoon), more rice varieties (glutinous rice RD6 as well as nonglutinous Hom Mali rice) and involving price determination by different rice mills.

In addition to the time of harvest, which affects grain moisture content, we have determined experimentally that % head rice increased with increasing grain N concentration. To understand the role of N in strengthening the rice grain against breakage during milling, and how varieties differ in this respect, should contribute towards management of the rice crop for better milling quality and price. We have found that in general % head rice is inversely related to grain shape (length to width), the longer and more slender grain tends to break much more easily, as would normally be expected (Manop Leesawatwong, Unpublished). Thus medium grained rice, with length/width ratio of < 2.8, (e.g. Hom Nangfah, Niaw Muang Pai, Bue Gua, Bue Polo, Kao Luang, Bue Pa Toh, Bue Meo, Dawk Prao) tend to be very resistant to breakage. Grain breakage tends to increase with increasing length/width ratio beyond 3. Within this general trend, however, some significant variation has been found in % head rice of varieties with about the same grain shape. Interestingly, glutinous rice tends to break less than nonglutinous varieties. For example RD6 breaks less than KDML105, and all of those varieties that were more resistant to breakage were

glutinous, i.e. the new Sanpatong 1, Niaw Sanpatong, RD 6, RD 10 and Hom Sakhon. The internal structure of the grain of these different varieties and with different N concentration is now being investigated with electron and light microscopy at the Centre for Microscopy and Microanalysis University of Western Australia and Murdoch University (*Manop Leesawatwong*[1]).

3. AGRODIVERSITY

3.1 Agrodiversity and biodiversity management

Agrodiversity has been defined as "the dynamic variation in cropping systems, output and management practice that occurs within and between agroecosystems. It arises from biophysical differences, and from the many and changing ways in which farmers manage diverse genetic resources and natural variability, and organize their management in dynamic social and economic contexts. It has four main elements through which it may be analyzed:

- Agricultural biodiversity, the diversity of genetic material employed;
- Management diversity, the way in which plants and the land are managed;
- Biophysical diversity, the diversity of the land, wild biota and atmospheric conditions;
- Organizational diversity, the manner in which farm, human and capital resources are managed, and the large social, economic and political context in which this takes place". (Brookfield 2000).

Through the UNU's project on People, Land Management and Environmental Change, we were first involved in applying this idea to the conservation of natural biodiversity in the mountains of Northern Thailand (*Kanok Rerkasem, Narit Yimyam*[1]). In this TRF project we have adapted and applied the idea of agrodiversity to the conservation and management of domesticated species germplasm, especially rice (Rerkasem and Rerkasem, 2002). This further evolved into the project "Agrodiversity for *in situ* Conservation and Management of Thailand's Native Rice Germplasm", which has received substantial funding from the Collaborative Crop Research Program of the McKnight Foundation. The McKnight project has been built on key findings and methodologies developed in this TRF project. However, findings on Thai rice germplasm from that project have largely been kept out of this report. This section will focus on forest regeneration and nutrient cycling.

3.2 Nutrient cycling and forest regeneration

Rotational shifting cultivation has been shown to be a productive and sustainable form of land use in mountainous areas where land is sufficiently plentiful to allow 10-20 years fallow (Kunstadter, 1978). Population pressure combined with increasing demand for conservation (from watersheds, erosion control, carbon squestration to biodiversity) by society at large, however, have made certain that this luxury of very long fallows is now no longer an option for most shifting cultivators in Southeast Asia and elsewhere. Considerable interest therefore has arisen in approaches that might maintain crop productivity with shorter fallow. Numerous efforts, especially in Africa, have gone into identification of trees and other plants as fallow enriching species. We have identified a local system with rapid regeneration of the fallow forest that can be cropped every 7th year and upland rice yield

maintained at reasonable levels of 2 to 4 Mg ha^{-1} on a seven years rotation (*Narit Yimyam*[1]).

The key to this rapid forest regeneration is a small tree called pada (*Macaranga denticulata* (Bl.) Muell. Arg.). Pada is well known for its fallow enriching property amongst the various ethnic groups who make a living on rotational shifting cultivation in northern Thailand. It is known as Teen Tao amongst the Khamu and H'tin who populate the northeastern mountains, on the border with Laos. Pada is the name in Skaw Karen (Thailand's largest minority group, now concentrated along the western border with Myanmar), while the Pwo Karen calls it Letha. The Lua (who are believed to have been the dominant group in the region until about a thousand years ago) calls it Tong Coab. Loom Piah is its name amongst the Akha (a group not known to practice rotational shifting cultivation in Thailand). Amongst lowland Thai it is variously called Tong Taeb, Tong Tao, Tao Maew, Por Khee Haed or Bai Hoo Chang. Pada is a small evergreen tree of the Euphorbiaceae family, that can reach 19 m in height and up to 40 cm diameter at breast height. Macaranga is a relatively large genus of pioneer species. Some 80 species have been identified in Africa and 200 in the Eastern Tropics, although not all are pioneer speices. In the study village of Haui Tee Cha, there are also *M. gigantea* and *M. kurzii* but according to farmers pada is the only species with the fallow improving property. The presence of pada in the fallow is believed to be responsible for maintaining productivity of upland rice in the shorter rotation.

Dense pada patches in 7-year-old fallow averaged 43 tons ha^{-1} of above ground biomass, 20 % more than sparse patches. The biomass in dense pada contained 536 kg N, 38 kg P, 253 kg K, 132 kg Ca and 46 kg Mg ha^{-1}, 34 %, 92 %, 80% and 107 % more, respectively, than in sparse pada patches (Yimyam et al., 2003). Slashing and burning 7-year-old fallow with dense pada produced rice yield that was three time those with sparse pada or dense pada that was cropped after 3 years.

There was a much greater abundance of arbuscular mycorrhizal fungi in the rhizosphere of pada than in another other native tree species of the area (Table 30). Pada roots were found to be heavily colonized by micorhizal fungi. In the wet season, root colonization exceeded 80% and the rhizoshpere soil contained more than 30 spores g^{-1}. (Table 31). In addition to the abundance, the mycorrhizal fungi population in pada rhizosphere was also highly diverse, with some 30 species in 6 genera (Table 32). *Glomus* was the most common, with 17 species. The effective nutrient cycle in pada appeared to be associated with two primary mechanisms. The mycorrhizal fungi help to increase nutrient accumulation by the tree. The nutrients are then partitioned by the tree to its roots and are thus returned to the soil. Mycorrhizal inoculation doubled the uptake of nutrients by pada when P was limiting but N was not. Pada was found to send 23% of its N, 32% P, 44% K, 33% Ca and 50% Mg to the roots. This nutrient recycling is very important to N supply to the upland rice crop in this shifting cultivation system as most of the N accumulated in the above ground biomass that is slashed and burned is volatilized in the fire.

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Table 1. Crop species evaluated for adaptation to low B

Species	Number of genotypes	Researchers/graduate students responsible
Vigna radiata (Green gram)	70	*Ayut Kongpan; Nattawut*
Vigna mungo (Black gram)	16	*Sukcumpa*
Glycine max (Soybean)	3	
Vigna unguiculata (Cowpea)	6	*Tinnakorn Srivichai*
Zea mays (Maize)	8	*Sithichai Lordkaew*
Sorghum bicolor (Sorghum)	7	
Oryza sativa (Rice)	15	*Benjavan Rerkasem*
Triticum aestivum (Wheat)	3,000	*Benjavan Rerkasem; Sansanee*
Triticum durum (Durum)	500	*Jamjod; Sunisa Niratrayagul;*
x*Triticosecale* (Triticale)	850	*Jumnien Wongmo; Tamarong*
Hordeum vulgare (Barley)	650	*Pasook, Mohuddin Ahmed*
Total	5,125	

Table 2. Frequency distribution (%) of boron efficiency classes in selected sets of CIMMYT 2000/01 international germplasm grown in soil with 0.1 mg HWS B kg^{-1}.

Grain set	Bread wheat		Barley	Durum	Triticale	Whole
index	33IBS-	18SA-	28IBON†	wheat	33ITSN	germplasm
class	WYN	WSN		33IDYN		
%	Frequency (%)					
< 20	36.4	23.0	37.0	34.7	42.8	35.4
20-49	25.0	23.0	39.0	51.0	25.5	29.2
50-74	8.0	28.7	24.0	14.3	27.5	19.5
75-90	20.6	17.2	0.0	0.0	4.1	11.0
>90	10.1	8.0	0.0	0.0	0.0	4.9
Total	388	190	265	49	216	1108
SW41	71.1±7.4	71.6±5.5	60.5±6.6‡	82.8±1.0	70.1±4.3	
Fang 60	97.2±0.8	96.8±1.2	84.3±2.3§	99.3±0.1	96.5±0.8	
GSI of B efficiency checks (%, with standard deviation in brackets)						

† From CIMMYT/ICARDA
‡ BCMU96-9 and § BRB9604
33IBWSN, 33rd International Bread Wheat Screening Nursery.
18SAWSN, 18th Semi-Arid Areas Wheat Screening Nursery
28IBON, 28th International Barley Observation Nursery
33IDYN, 33rd International Durum Yield Nursery
33ITSN, 33rd International Triticale Screening Nursery

Table 3. Grain set index (GSI) of various boron efficient and inefficient bread wheat lines in a soil low in B (0.1 mg HWS B kg^{-1}, B0.1) and sand culture without added B, B0). (Each GSI number is mean of two replicates, ±standard deviation)

Boron condition for screening		Soil (B0.1)	Sand (B0)
Nursery, entry no., variety or cross		Grain set index (%±SD)	
4HTWYT			
1	Fang 60	94.3±1.7	95.0±7.1
4	MOCHIS T 88	29.3±8.8	38.8±14.5
5	FASAN	3.6±12.0	8.3±18.0
12	PAT10/ALD//PAT72300/3/PVN/4/BOW	92.7±2.4	89.4±1.9
13	PAT10/ALD//PAT72300/3/PVN/4/BOW	85.8±0.4	91.6±3.4
15	TRAP#1/BOW	83.5±15.6	85.3±2.1
20	PRINIA	0±0.0	15.8±0.0
30	TIA.1	85.0±4.2	82.4±7.1
17ESWYT			
1	Fang 60	85.5±14.1	nd[†]
6	WEAVER	2.8±3.2	nd
7	CHIL/2*STAR	89.0±0.6	nd
9	TURACO/CHIL	17.8±1.8	nd
28	CHEN/AEGILOPS SQUARROSA(TAUS)//BCN	5.3±0.4	nd
31	STAR//KAUZ/PVN	87.0±1.4	nd
43	KAUZ*2//SAP/MON/3/KAUZ	88.3±11.0	nd
47	CPAN 3004	86.0±16.3	nd

[†]nd = no data

Table 4. Frequency distribution of boron efficiency in a wheat germplasm from Bangladesh.

Boron efficiency class	Number of entries	B0	B10	B-field
		Mean GSI (%) in each class		
Very inefficient	7	9.8	84.5	28.2
Inefficient	27	31.7	83.5	47.0
Moderately inefficient	3	53.7	88.4	62.0
Moderate efficient	0	ne	ne	ne
Efficient	0	ne	ne	ne
Total	37			
GSI (%) of B efficiency checks				
Efficient	Fang 60	82.5	97.1	84.3
Inefficient	SW 41	29.9	85.5	33.8
Very inefficient	E-12	16.8	85.5	38.8

ne = no entry in this class
Source Ahmed et al. (2001)

Table 5. Relative boron responses (B0 as % of B10) for tillers, ears, spikelets and Grain Set Index (GSI) in barley and wheat grown in sand culture.

Species/ genotype	Tillers plant^{-1}	Ears plant^{-1}	Spikelets ear^{-1}	GSI (%)
Two-row barley				
BRB 9604	103.0ab	84.7b	45.1b	70.8c
BRB 9	204.0cd	94.5b	27.9a	60.7c
BCMU 96-9	260.7d	10.8a	24.9a	34.0b
Stirling	110.9ab	11.6a	35.2ab	0.0a
Six-row barley				
FNBL 8309	119.7ab	55.6ab	76.9c	72.0c
LARTC 9408	237.7d	55.6ab	45.6b	34.4b
BRB 2	186.7cd	74.2b	36.8ab	10.4a
Bread wheat				
Fang 60	103.0ab	98.0b	95.0d	93.3d
Flycatcher	82.4a	67.6b	87.8cd	97.6d
SW 41	109.4ab	98.0b	88.1cd	66.3c
Bonza	95.8ab	79.7b	90.6cd	1.3a
Tatiara	151.9bc	154.7c	97.8d	0.0a
Effects	F-test			
Boron	**	**	**	**
Genotype	**	**	**	**
BXG	**	*	**	**

Differences (by LSD $p < 0.05$) in the same row are indicated by different lowercase letters and in the same column by different uppercase letters.
** significant at $P < 0.01$

Table 6. Relating adaptation to toxic levels and low boron in wheat genotypes

Group	Adaptation to		Genotypes
	Boron toxicity	Low boron	
1.	Sensitive	Efficient	Fang 60
2.	Sensitive	Inefficient	CMU88-9†, SW41, most lines from the 18thSAWSN
3.	Tolerant	Inefficient	Bonza, Turkey 1473
4.	Tolerant	Efficient	No genotype found so far

† Originated from CIMMYT

Supunnika Panchana (2003)

Table 7. Boron mobility in some tropical crops

Crop	Family	Possible boron mobility in phloem
Mangosteen (*Garcinia mangostana*)	*Guttiferae*	Yes
Coffee (*Coffee arabica*)	*Rubiaceae*	Yes
Custard apple (*Annona squamosa*)	Annonaceae	No
Guava (*Psidium guajava*)	Myrtaceae	Yes
Jackfruit (*Artocarpus heterophyllus*)	Moraceae	Yes
Cashew (*Anacardium occidentale*)	Anacardiaceae	No
Mango (*Mangifera indica*)	Anacardiaceae	No
Lime (*Citrus aurantifolia*)	Rutaceae	No
Papaya (*Carica papaya*)	Caricaceae	Yes
Passion fruit (*Passiflora edulis*)	Passifloraceae	No
Teak (*Tectona grandis*)	Labiatae	Yes
Cassava (*Manihot esculenta*)	Euphorbiaceae	No

Source: Sawika Konsaeng, Unpublished

Table 8. Effects of boron levels on vegetative and reproductive yield of maize and sorghum.

Boron level (μM B)	0	10	RRB†	0	10	RRB
Plant response	Maize (cv. NS72)			Sorghum (cv. Uthong)		
Straw yield (g/plant)	87.1	75.8	114.91	41.65	39.78	104.70
Grain yield (g/plant)	0.62	71.83	0.86	18.73	23.89	78.40
Number of grains/plant	0.58	377	0.15	595	755	78.81

† Relative response to boron, performance in B0, as percentage of performance in B10

Source: Sithichai Lordkaew, Unpublished

Table 9. Effect of B on vegetative and reproductive growth of maize cv. NS72.

Boron level (μM B)	0	20	Significant difference
(a) 5 leaf stage			
Dry weight (g/plant)			
Tops	2.78	3.69	NS ($P < 0.05$)
Roots	1.01	1.28	NS ($P < 0.05$)
Total	3.79	4.97	NS ($P < 0.05$)
B concentration (mg B/kg)			
Youngest emerged blade (YEB)	4.7	18.1	$P < 0.01$
YEB-1	3.8	16.6	$P < 0.01$
YEB+1	5.1	17.9	$P < 0.01$
Whole top	4.5	16.8	$P < 0.01$
Roots	6.1	10.3	$P < 0.01$
(b) Tasselling stage			
Dry weight (g/plant)			
Tassel	3.7	5.8	NS ($P < 0.05$)
Baby corn	0.1	0.2	NS ($P < 0.05$)
Whole tops	52.4	49.1	NS ($P < 0.05$)
Roots	23.8	22.1	NS ($P < 0.05$)
B concentration (mg B/kg)			
Tassel	3.9	8.1	$P < 0.01$
Baby corn	6.8	13.7	$P < 0.05$
Ear leaf	5.1	9.8	$P < 0.05$
Roots	7.4	7.8	NS ($P < 0.05$)
(c) Silking stage			
Dry weight (g/plant)			
Anthers, panicle axis	0.24	0.28	NS ($P < 0.05$)
Anthers, primary branches	0.10	0.18	NS ($P < 0.05$)
Chaff, panicle axis	0.12	0.14	NS ($P < 0.05$)
Chaff, primary branches	0.08	0.12	NS ($P < 0.05$)
Pollen	0.05	0.04	NS ($P < 0.05$)
Baby corn	1.16	4.50	$P < 0.05$
Silk	0.52	0.93	$P < 0.01$
B concentration (mg B/kg)			
Anthers, panicle axis	2.9	6.4	$P < 0.05$
Anthers, primary branches	3.5	7.4	$P < 0.05$
Chaff, panicle axis	3.4	5.2	$P < 0.05$
Chaff, primary branches	3.6	5.2	$P < 0.01$
Pollen	4.4	9.0	$P < 0.01$
Baby corn	2.8	5.2	$P < 0.05$
Silk	4.4	11.3	$P < 0.01$

Table 9. Conitnued

Boron level (μM B)	0	20	Significant difference
(d) Maturity			
Dry weight (g/plant)			
Straw	89.8	91.4	NS ($P < 0.05$)
Grain	0.4	72.3	$P < 0.001$
Husk	11.1	14.6	NS ($P < 0.05$)
Cob	7.3	14.9	$P < 0.01$
Total	108.6	193.2	$P < 0.01$
Number grains/plant	0.4	410	$P < 0.001$

Source: Sithichai Lordkaew, Unpublished.

Table 10. Effect of B deficiency on the function of the male and female flower on grain set in maize

Boron status				Grain set		Straw
Supply (μM B)		Tissue B (mg B/kg)		Number	%	yield†
Female	Male	Silk	Anther	grains	Grain set	(g/plant)
20	20	15.9	9.0	452	100	83.9
0	20	4.5	9.0	0	0	82.4
20	0	14.5	4.4	169	37.4	73.6
0	0	4.2	4.4	2	0.4	80.3

† of the female plant
Source: Sithichai Lordkaew, Unpublished.

Table 11. Boron concentration in the youngest fully expanded leaf (YFEL) at R3 (beginning of podset) of of mungbean and black gram genotypes grown at different B levels.

Genotype	Boron level (μM)			
	0	0.5	3	5
Black gram				
M1	16.7	26.9	42.9	43.0
Regur	10.0	21.1	38.9	42.0
CPI179563	8.3	14.5	38.3	45.0
Mungbean				
KPS1	6.4	16.2	41.5	47.4
VC2755	8.7	12.7	39.6	41.4
VC1163	8.8	16.4	28.8	36.1
F-test	Genotype**	Boron**	GxB**	
$LSD_{0.05}$	3.0	2.4	6.0	

** Significant at $P < 0.01$

Source: Ayut Kongpun (2002)

Table 12. Boron concentration in the mature seed of mungbean and black gram genotypes grown at different B levels.

Genotype	Boron level (μM)			
	0	0.5	3	5
Black gram				
M1	6.2	13.8	18.0	17.4
Regur	4.9	9.4	17.6	17.1
CPI179563	24.3	4.6	18.1	18.5
Mungbean				
KPS1	4.3	11.0	17.7	20.7
VC2755	5.3	11.0	22.0	22.4
VC1163	6.9	11.1	17.2	18.2
F-test	Genotype**	Boron**	GxB**	
$LSD_{0.05}$	1.2	1.0	2.3	

** Significant at $P < 0.01$

Source: Ayut Kongpun (2002)

Table 13. Effects of B levels on growth and yield of mungbean and black gram genotypes grown at different B levels.

Genotype	Boron level (μM)			
	0	0.5	3	5
(a) Above ground dry weight at maturity (g/pot)				
Black gram				
M1	60.1	29.2	12.5	16.4
Regur	30.9	41.2	38.0	61.5
CPI179563	47.4	89.2	84.6	100.4
Mungbean				
KPS1	46.2	40.2	39.9	18.1
VC2755	42.6	45.3	54.0	33.2
VC1163	16.9	40.1	21.2	28.1
F-test	Genotype**	Boron($NS_{0.05}$)	GxB**	
$LSD_{0.05}$	13.0	-	25.9	
(b) Root dry weight at maturity (g/pot)				
Black gram				
M1	4.5	2.5	1.4	1.9
Regur	5.4	5.5	5.3	6.4
CPI179563	19.1	25.9	11.4	10.9
Mungbean				
KPS1	5.5	3.3	3.3	0.2
VC2755	5.4	5.2	5.9	3.5
VC1163	1.8	1.8	1.7	2.2
F-test	Genotype**	Boron**	GxB**	
$LSD_{0.05}$	1.9	1.5	3.7	
(c) Mature seed yield (g/pot), with relative yield (% maximun) in brackets				
Black gram				
M1	15.7(90.2)	17.4(100)	7.7(44.6)	9.1(52.3)
Regur	2.2(9.0)	14.1(58.7)	24.0(100)	22.0(91.7)
CPI179563	0.1(0.3)	18.4(38.5)	41.5(86.9)	47.8(100)
Mungbean				
KPS1	18.7(89.2)	19.6(93.6)	21.0(100)	7.0(33.3)
VC2755	16.8(61.6)	22.2(81.3)	27.4(100)	13.3(48.5)
VC1163	5.5(32.2)	14.3(100)	10.8(75.6)	13.2(92.0)
F-test†	$Genotype^{(NS)}$	Boron**	GxB**	
$LSD_{0.05}$†	-	21.9	46.6	

† Analysis of variance and LSD for relative yields
NS at $P < 0.05$ ** Significant at $P < 0.01$
Source: Ayut Kongpun (2002)

Table 14. GSI (%) of parents and F_1 hybrids of wheat and barley grown in sand culture with four levels of applied B.

Crop/Genotype	B treatment[a] (M)			
	0	0.1	1	10
Wheat				
Fang 60 (E)	88.0 c	90.4 c	91.1 c	91.8 bc
CMU 88-9 (ME)	43.4 b	46.8 b	69.7 b	67.5 ab
SW 41 (MI)	54.1 b	46.5 b	85.8 bc	76.6 b
Bonza (I)	8.2 a	10.8 a	51.8 a	50.4 a
(E x ME)F_1	85.1 c	86.6 c	87.7 c	91.1 bc
(E x MI)F_1	79.9 c	88.2 c	92.5 c	93.8 c
(E x I)F_1	82.0 c	93.0 c	83.6 c	86.9 bc
F-test B, G*, BxG**				
Barley				
BRB 9604 (E)	77.5 c	80.9 d	88.9 c	87.0 b
BRB 9 (ME)	59.7 b	65.6 c	84.5 c	77.8 b
BCMU 96-9 (MI)	2.8 a	7.1 a	21.9 ab	50.1 a
SMGBL 91002 (I)	7.9 a	24.2 b	36.0 b	52.8 a
(E x ME)F_1	80.6 c	78.1 d	88.8 c	78.2 b
(E x MI)F_1	3.4 a	8.2 a	19.1 a	47.8 a
(E x I)F_1	11.0 a	18.4 ab	33.1 b	42.7 a
F-test B, G*, BxG**				

* Significant at 0.05 probability levels.

[a] Mean within a column for each crop with the same letter do not differ significantly at 5% level with LSD. To compare mean within a row LSD for wheat = 16.9 and LSD for barley = 12.0.

Source: Napat Somkuan (2003)

Table 15. Number of tillers plant^{-1} at maturity of parents and F_1 hybrids of wheat and barley grown in sand culture with four levels of applied B.

Crop/Genotype	B treatment[a] (μM)				% increase
	0	0.1	1	10	(B0/B10)
Wheat					
Fang 60 (E)	9.4	9.6	10.3	9.9	
CMU 88-9 (ME)	6.2	6.8	7.6	7.1	
SW 41 (MI)	10.1	10.1	10.4	7.7	
Bonza (I)	14.3	19.2	15.4	13.0	
(E x ME)F_1	8.9	10.4	9.2	10.8	
(E x MI)F_1	10.3	9.4	9.7	9.9	
(E x I)F_1	13.2	12.1	16.5	11.8	
F-test B^{ns}, G^{*}, BxG^{ns}					
Barley					
BRB 9604	15.9 a	15.3 a	14.5 a	14.5 a	9.8 ^{ns}
BRB 9	23.8 b	25.1 bc	17.1 a	15.4 a	54.4 *
BCMU 96-9	37.5 c	36.8 c	22.4 b	17.9 ab	109.3 *
SMGBL 91002	31.8 c	24.0 b	23.6 b	23.7 b	34.0 *
(BRB 9604 x BRB 9)F_1	15.8 a	16.9 a	12.9 a	13.7 a	15.6 ^{ns}
(BRB 9604 x BCMU 96-9)F_1	32.4 c	36.4 c	24.3 b	19.6 ab	65.3 *
(BRB 9604 x SMGBL 9100I)F_1	31.7 c	31.5 c	23.5 b	24.7 b	28.5 *
F-test B^{*}, G^{*}, BxG^{*}					

* Significant at 0.05 probability levels, ns not significant.

[a] Mean within a column for barley with the same letter do not differ significantly at 5% level with LSD. To compare mean within a row LSD for barley = 7.4.

Source: Napat Somkuan (2003)

Table 16. Number of spikelets spike^{-1} of parents and F_1 hybrids of wheat and barley grown in sand culture with four levels of applied B.

Crop/Genotype	B treatment[a] (M)				% decrease
	0	0.1	1	10	B0/B10
Wheat					
Fang 60 (E)	15.6	16.1	15.8	15.9	
CMU 88-9 (ME)	15.1	16.2	16.3	16.2	
SW 41 (MI)	18.3	19.4	18.4	15.9	
Bonza (I)	13.4	12.5	14.2	14.9	
(E x ME)F_1	15.8	16.5	16.5	16.4	
(E x MI)F_1	15.9	16.3	16.8	16.8	
(E x I)F_1	17.6	18.6	17.0	18.2	
F-test B^{ns}, G^{*}, BxG^{ns}					
Barley					
BRB 9604	11.3 b	12.2 b	13.2 a	12.5 a	9.6^{ns}
BRB 9	8.7 a	9.6 a	12.3 a	11.8 a	26.3^{*}
BCMU 96-9	13.3 c	18.5 c	21.7 c	23.7 c	43.9^{*}
SMGBL 91002	18.3 d	18.7 cd	19.7 b	24.2 c	24.4^{*}
(BRB 9604 x BRB 9)F_1	11.3 b	11.7 b	11.9 a	11.5 a	1.7^{ns}
(BRB 9604 x BCMU 96-9)F_1	18.4 d	19.4 cd	22.2 c	23.3 c	21.0^{*}
(BRB 9604 x SMGBL 9100I)F_1	19.8 d	20.5 d	21.6 bc	21.0 b	5.7^{ns}
F-test B^{*}, G^{*}, BxG^{*}					

* Significant at 0.05 probability levels, ns not significant.

[a] Mean within a column for barley with the same letter do not differ significantly at 5% level with LSD. To compare mean within a row LSD for barley = 2.0.

Source: Napat Somkuan (2003)

Table 17. Chi-square analysis for responses to B of F_2-derived F_3 families from three wheat crosses grown in sand culture without added B.

Cross	Model		Number of families			χ^2	P
			I	Seg.+MI			
Bonza (I) x SW 41 (MI)	1:3	Exp.	21.25	63.75		0.18	0.6611
	1:15	Exp.	5.31	79.66		18.62	<0.001
		Obs.					
				Seg.+MI	E		
SW 41 (MI) x Fang 60 (E)	1:3	Exp.		69	23	1.06	0.3355
	1:15	Exp.		86.25	5.75	11.65	<0.001
		Obs.		73	19		
			I	Seg.+MI	E		
Bonza (I) x Fang 60 (E)	1:3	Exp.	28.5	57	28.5	61.34	<0.001
	1:15	Exp.	7.125	99.75	7.125	5.26	0.078
		Obs.	12	92	10		

[a] Exp. – expected ratio; Obs. – observed ratio.

[b] E = homozygous efficient, MI = homozygous moderately inefficient, I = homozygous inefficient, Seg = segregating, Int. = homozygous intermediate.

Source: Jamjod et al. *in press*

Table 18. Chi-square analysis for response to B of F_2-derived F_3 families from five crosses of barley grown in sand culture without added B.

Cross	Model		Number of families			$\chi 2$	P
			E	Seg+Int.	I		
(a) BRB 9604 (E) x BRB 9 (ME)	1:2:1	Exp.	18.25	36.5	18.25		
	1:14:1	Exp.	4.6	63.8	4.6		
		Obs.	Transgressive segregation observed				
(b) BRB 9 (ME) x BRB 9604 (E)	1:2:1	Exp.	22.75	45.5	22.75		
	1:14:1	Exp.	5.7	79.6	5.7		
		Obs.	Transgressive segregation observed				
(c) BRB 9 (ME) x BCMU 96-9 (I)	1:2:1	Exp.	11.5	23.0	11.5	14.69	<0.001
	1:14:1	Exp.	2.9	40.2	2.9	3.59	0.166
		Obs.	5	36	5		
(d) BCMU 96-9 (I) x BRB 9 (ME)	1:2:1	Exp.	10.5	21.0	10.5	12.28	0.002
	1:14:1	Exp.	2.6	36.7	2.6	7.95	0.019
		Obs.	3	32	7		
(e) BCMU 96-9 (I) x BRB 9604 (E)	1:2:1	Exp.	12.75	25.5	12.75	17.47	<0.001
	1:14:1	Exp.	3.2	44.6	3.2	7.75	0.021
		Obs.	3	40	8		

Expected ratio for single gene was homozygous efficient : segregating : homozygous inefficient = 1:2:1 and for two genes was homozygous efficient : segregating + homozygous intermediate : homozygous inefficient = 1:14:1.
E = homozygous efficient, I = homozygous inefficient, Seg. = segregating, Int. = homozygous intermediate

Table 19. Number of rice genotypes with various grain Fe concentration in unhusked rice and brown rice under wetland and dryland conditions.

mg Fe/kg	Number of rice genotypes			
	Wetland condition		Dryland conditoion	
	Unhusked	Brown	Unhusked	Brown
< 10	0	27	0	15
10.1-13.0	6	8	0	14
13.1-16.0	25	3	5	18
16.1-19.0	6	0	14	1
19.1-22.0	0	0	17	0
> 22	1	0	2	0
Total	38	38	38	38
Mean ± SD	14.7 ± 1.9	8.7 ± 1.7	14.7 ± 1.9	8.7 ± 1.7
Range	12-23	7-15	14-24	8-19

Source: Chankan Prom-u-thai, Unpublished

Table 20. Iron concentration (mg Fe/kg) in selected Thai rice genotypes grown under wetland and dryland conditions

Genotype	Iron concentration in brown rice (mg Fe/kg)	
	Wetland condition	Dryland condition
DOA 2 (U)	15.2 a	14.6 a
CMU123 (U)	13.7 a	15.8 b
CMU124 (U)	13.2 a	16.1 b
CMU122 (U)	11.7 a	18.9 b
DOA 1 (W)	10.7 a	12.7 b
SPT 84051 (W)	10.2 a	11.8 b
KDML105 (W)	10.0 a	9.3 a
Phrae 1 (W)	9.9 a	11.0 a
Ubon 2 (W)	9.7 a	13.4 b
Hom Supan (W)	9.2 a	11.7 b
NSP (W)	9.1 a	11.1 b
RD6 (W)	9.1 a	8.9 a
RD15 (W)	9.0 a	8.6 a
Lueng11 (W)	8.7 a	8.4 a
RD10 (W)	8.4 a	9.5 a
KL1 (W)	8.0 a	10.5 b
Chiangsaen (W)	7.6 a	10.5 b

Analysis of variance

P (Genotypes)	< 0.01
P (Water)	< 0.01
P (Genotypes X Water)	< 0.01
LSD (0.05)	1.17

Different letters following the numbers indicate significant ($P < 0.05$) effect of water condition

W=Wetland rice U=upland rice

Source: Chankan Prom-u-thai, Unpublished

Table 21. Grain Fe concentration in three rice genotypes grown with 2 levels of water (aerated, waterlogged) and lime (L0, L+)

Genotypes	Soil condition		Fe concentration (mg Fe/kg)	
	Water	Lime	Unhusked	Brown rice
IR68144	Aerated	0	22.3 b	18.9 b
	Aerated	+	18.5 a	15.6 a
	waterlogged	0	20.9 b	16.7 a
	waterlogged	+	18.9 a	16.5 a
Basmati 370	Aerated	0	17.1 b	13.8 ab
	Aerated	+	14.8 a	12.3 a
	waterlogged	0	15.1 a	14.3 b
	waterlogged	+	15.5 a	13.2 ab
KDML105	Aerated	0	13.8 a	8.3 a
	Aerated	+	14.8 ab	9.8 ab
	waterlogged	0	16.3 b	10.0 ab
	waterlogged	+	16.8 b	10.3 b
Analysis of variance	*P* (Genotypes)		< 0.01	
	P (Soil condition		< 0.01	
	P (G X S)		< 0.05	
	$LSD_{0.05}$		1.59	1.71

Source: Chankan Prom-u-thai, Unpublished

Table 22. The Fe concentration in unhusked, brown rice, white rice (polished for 30 and 60 seconds) and the husk of six rice genotypes grown under three levels of N (0, 60, 120 kg N/ha)

Genotype	N (kg/ha)	Iron concentration (mg Fe/kg)				
		Unhusked rice	Brown rice	White (30 sec)	White (60 sec)	Husk
KDML105	0	13.0 a	7.8 a	7.9 a	5.6 a	36.0 a
	60	14.6 ab	8.2 a	7.2 a	6.5 a	32.6 a
	120	16.1 b	8.8 a	7.3 a	6.8 a	37.4 a
IR68144	0	15.8 a	13.5 a	12.3 b	12.3 a	37.9 a
	60	17.2 a	13.0 a	13.6 b	10.3 a	38.3 a
	120	21.1 b	13.1 a	10.0 a	11.6 a	48.6 a
Hom	0	12.5 a	8.4 a	5.9 a	4.4 a	35.3 a
Nangfah	60	12.5 a	9.0 ab	6.0 a	5.2 a	35.2 a
	120	15.9 b	10.3 b	nd	nd	48.4 b
Ubon 2	0	13.8 a	9.3 a	4.6 a	4.7 a	42.7 a
	60	13.6 a	8.1 a	10.1 b	7.0 a	44.8 a
	120	13.5 a	8.3 a	6.5 a	7.0 a	48.5 a
RD6	0	15.2 a	8.2 a	5.1 a	4.9 a	39.8 a
	60	15.8 a	8.3 a	10.3 b	6.6 ab	51.3 a
	120	18.3 a	9.0 a	8.2 b	8.6 b	44.2 a
Basmati	0	15.6 a	10.8 a	7.6 a	7.0 a	35.8 a
	60	16.3 a	12.1 ab	6.5 a	6.1 a	37.5 a
	120	18.3 b	12.4 b	10.2 b	8.0 a	47.3 b
Analysis of variance						
	P (Genotype)	<0.01	<0.01	<0.01	<0.01	<0.01
	P (Nitrogen)	<0.01	NS	<0.05	<0.01	<0.05
	P (G x N)	<0.05	<0.05	<0.01	NS	<0.05
	$LSD_{0.05}$	2.6	1.5	2.3	3.4	11.5

Source: Chankan Prom-u-thai, Unpublished

Table 23. The Fe concentration in some parts of KDML105 grown under 2 levels of lime and water

Soil condition		Iron concentration (mg Fe/kg)			
Water	Lime	Brown rice	Leaves	Stem+leafsheath	Roots
Aerated	0	8.3	221.7	142.8	2,757
Aerated	+	9.8	237.3	140.9	1,592
Waterlogged	0	10.0	361.4	284.1	27,195
Waterlogged	+	10.3	356.9	280.4	26,623

Source: Chankan Prom-u-thai, Unpublished

Table 24. Relative dryland performance in shoot and root growth of some wetland and upland rice varieties at 8 weeks.

	Growing condition	Sew Mae Jan	Kae Noi	Chainat 1	KDML 105	G x W ($LSD_{0.05}$)
Root DW (g/pot)	Wetland	3.86	3.46	5.53	3.92	$P<0.05$
	Dryland	2.07	3.32	1.26	2.16	0.94
	RDP†	53.63	95.95	22.78	55.10	
Shoot DW (g/pot)	Wetland	13.0	8.9	15.6	17.5	$P<0.05$
	Dryland	11.7	11.2	8.9	11.1	4.3
	RDP	90.0	125.8	57.1	63.4	
Total DW (g/pot)	Wetland	16.86	12.36	21.13	21.42	
	Dryland	13.77	14.52	10.16	13.26	
	RDP	81.7	117.5	48.1	61.9	
Root volume (ml)	Wetland	36.3	52.2	58.0	36.3	$NS_{0.05}$
	Dryland	24.0	35.0	20.7	12.3	
	RDP	66.1	67.0	35.7	33.9	
Root length (cm)	Wetland	36.0	41.8	44.1	43.2	$NS_{0.05}$
	Dryland	37.4	44.0	33.2	39.1	
	RDP	103.9	105.3	75.3	90.5	
Shoot length (cm)	Wetland	80.6	73.2	60.3	92.2	$P<0.05$
	Dryland	68.4	67.9	51.9	63.3	6.0
	RDP	84.9	92.8	86.1	68.7	

† Relative dryland performance, performance in dryland as % of performance in wetland

Source: Nednapa Insalud, Unpublished

Table 25. Relative dryland performance in nutrient uptake of some wetland and upland rice varieties at 8 weeks.

Nutrient uptake	Growing condition	Sew Mae Jan	Kae Noi	Chainat 1	KDML 105	G x W ($LSD_{0.05}$)
Nitrogen (mg/pot)	Wetland	2.01	1.72	2.20	2.72	$NS_{0.05}$
	Dryland	1.78	2.19	1.13	1.43	
	RDP†	88.6	127.3	51.4	52.6	
Nitrogen (mg/g root DW)	Wetland	0.52	0.50	0.40	0.69	
	Dryland	0.86	0.66	0.90	0.66	
	RDP	165.4	132.0	225.0	95.7	
Phosphorus (mg/pot)	Wetland	2.48	2.28	3.38	3.52	$P<0.05$
	Dryland	1.54	1.82	1.10	1.54	0.96
	RDP	62.1	79.8	32.5	43.8	
Phosphorus (mg/g root DW)	Wetland	0.64	0.66	0.61	0.90	
	Dryland	0.74	0.55	0.87	0.71	
	RDP	115.6	83.3	142.6	78.9	
Potassium (mg/pot)	Wetland	2.79	2.21	3.14	3.64	$NS_{0.05}$
	Dryland	2.54	2.38	1.82	2.38	
	RDP	91.0	107.7	58.0	65.4	
Potassium (mg/g root DW)	Wetland	0.72	0.64	0.57	0.93	
	Dryland	1.23	0.72	1.44	1.10	
	RDP	170.8	112.5	252.6	118.3	

† Relative dryland performance, performance in dryland as % of performance in wetland

Source: Nednapa Insalud, Unpublished

Table 26. Diazotrophic bacteria isolated from various tissues of cultivated rice and wild rice

Plant	Tissue	Isolate code†	Total
Cultivated rice (*O. sativa*)			
Khao Dawk Mali 105	Stem	AS1, AS2, AS3	3
	Leaf	AL	1
	Root	AR1, AR2	2
Purple Glutinous Rice	Stem	BS1, BS2, BS3	3
	Leaf	BL	1
	Root	BR1, BR2, BR3	3
Karieng	Stem	CS1, CS2	2
	Leaf	CL	1
	Root	CR1, CR2	2
Wild rice			
O. granulata	Stem	DS1, DS2, DS3	3
	Leaf	DL	1
	Root	DR1, DR2,	3
O. rufipogon	Stem	ES1, ES2,	3
	Leaf	EL	1
		Total	29

†Codes	Source species/genotype	†Codes	Source tissue
A	*Oryza sativa*, cv. KDML 105	L	Leaf
B	*Oryza sativa*, cv. Kam Doisaket	S	Stem
C	*Oryza sativa*, cv. Karieng	R	Root
D	*Oryza granulata*		
E	*Oryza rufipogon*, Lampoon population		
F	*Oryza rufipogon*, accession number 18883‡		
G	*Oryza nivara*, accession number 18852‡		

‡ Seed from National Genebank, grown at Agronomy Department, Chiang Mai University

Source: Chanikarn Koomnok, Unpublished.

Table 27. Identification and characterization of diazotrophic bacteria isolated from various tissues of cultivated and wild rice.

Group§	Source†	Characteristic	Genus
I (17)	AS1, AR1, BS1, BR1, CS1, CR1, DS1, DR1, ES1, ER1, EL1 FS1, FR1, FL1 GS1, GR1, GL1	Gram negative, rod or vibrioid, motile, oxidase & catalase positive, large white colony and slimy on N-free medium, pink colony on PDA	*Azospirillum*
II (15)	AS2, AR2, BS2, BR2, CS2, DS2, DR2, ES2, ER2, EL2, FS2, FR2, GS2, GR2, GL2	Gram negative, short curve rod, motile, oxidase & catalase positive, small white colony and slimy on N-free medium, brown colony on PDA	*Herbaspirillum*
III (6)	ES3, ER3 FS3, FR3 GS2, GR2	Gram negative, short curve rod, motile, oxidase & catalase positive, copious tenacious and elastic slime and giant colony on N-free medium	*Beijerinckia*
IV (6)	AL, BL, CL, CR2, DL, EL	Gram negative, straight rod, , oxidase & catalase positive, Cannot growth on N-free semi-medium, small white colony on CCM	*Pseudomonas*

†CODES	Source species/genotype	†CODES	Source tissue
A	*Oryza sativa,* cv. KDML 105	L	Leaf
B	*Oryza sativa*, cv. Kam Doisaket	S	Stem
C	*Oryza sativa*, cv. Karieng	R	Root
D	*Oryza granulata*		
E	*Oryza rufipogon,* Lampoon population		
F	*Oryza rufipogon,* accession number 18883‡		
G	*Oryza nivara,* accession number 18852‡		

§ Number of isolates in each group in brackets

‡ Seed from National Genebank, grown at Agronomy Department, Chiang Mai University

Source: Chanikarn Koomnok, Unpublished.

Table 28. Most probable number (MPN) of endophytic diazotrophic bacteria per gram (fresh weight) of various tissues of three cultivated rice varieties.

Variety	Tissue	Number of bacteria per g fresh weight			
Days from transplanting		30	45	60	75
KDML105	Leaf	$3.0x10^2$	$4.0x10^4$	$2.1x10^5$	$2.0x10^4$
	Stem	$3.0x10^2$	$4.0x10^4$	$2.1x10^5$	$2.0x10^4$
	Root	$4.0x10^4$	$3.0x10^4$	$2.3x10^5$	$9.0x10^3$
Kam Doisaket	Leaf	$1.5x10^4$	$7.0x10^3$	$4.0x10^4$	$9.0x10^3$
	Stem	$7.0x10^3$	$7.0x10^4$	$1.1x10^6$	$9.0x10^3$
	Root	$2.3x10^4$	$7.0x10^4$	$5.0x10^5$	$9.0x10^3$
Karieng	Leaf	$3.0x10^2$	$4.0x10^3$	$2.0x10^4$	$2.0x10^3$
	Stem	$4.0x10^4$	$2.1x10^4$	$2.1x10^5$	$2.0x10^4$
	Root	$4.0x10^4$	$3.0x10^4$	$2.3x10^5$	$9.0x10^3$

Source: Chanikarn Koomnok, Unpublished.

Table 29. Population of endophytic bacteria from various tissuses of wild rice before and after transplanting one month.

Wild rice	Tissue	Number of bacteria by MPN (cells/ g fresh weight)			
		Before transplanting		One month after	
		Diazotroph	Heterotroph	Diazotroph	Heterotroph
O. rufipogon	Leaf	$4.0x10^3$	$3.4x10^3$	$6.7x10^3$	$3.5x10^3$
Population from	Stem	$5.0x10^5$	$4.4x10^5$	$4.1x10^5$	$2.0x10^5$
Lampoon	Root	$7.0x10^6$	$5.2x10^6$	$1.7x10^6$	$1.4x10^6$
O. rufipogon	Leaf	$6.8x10^3$	$3.4x10^3$	$6.0x10^3$	$2.1x10^3$
Acc. No. 18883†	Stem	$1.7x10^5$	$1.4x10^5$	$9.1x10^4$	$6.8x10^4$
	Root	$1.2x10^6$	$6.8x10^5$	$1.0x10^6$	$3.6x10^5$
O.nivara	Leaf	$5.5x10^3$	$2.5x10^3$	$3.7x10^3$	$1.6x10^3$
Acc. No. 18852†	Stem	$9.1x10^4$	$6.0x10^4$	$4.3x10^4$	$3.5x10^4$
	Root	$8.9x10^5$	$6.3x10^5$	$5.6x10^5$	$2.3x10^5$

†Seed from National Genebank, grown at Agronomy Department, Chiang Mai University

Source: Chanikarn Koomnok, Unpublished.

Table 30. Comparing abundance of arbuscular mycorrhizal (AM) fungi in the rhizosphere of various tree species in a rotational shifting cultivation field.

Tree species	AM spore density (spores/g of soil)
Cratoxylum formosum	2
Dipterocarpus tuberculatus	1
Gluta usitata	1
Lithocarpus elegans	3
Xylia xylacarpa	3
Macaranga denticulata	15-22

Source: Somchit Youpensuk, Unpublished.

Table 31. Variation by season of the abundance of arbuscular mycorrhizal (AM) fungi in pada rhizosphere.

	Abundance of arbuscular mycorrhizal (AM) fungi			
Season†	Root colonization (%)		Spores/ g rhizosphere soil	
Pada density‡	Dense	Sparse	Dense	Sparse
Wet	83.3a	81.8a	32a	37a
Cool	74.3b	74.5b	19b	19b
Hot	64.0c	59.5c	7c	9c

†Effects of seasons are significant at $P < 0.01$, and are indicated by different letters in the same column

‡Effects of pada density are not significant ($P < 0.05$)

Source: Somchit Youpensuk, Unpublished.

Table 32. Species of arbuscular mycorrhizal (AM) fungi associated with pada

Genus	Number of species
Acaulospora	6
Archaeospora	1
Gigaspora	2
Glomus	17
Paraglomus	1
Scutellospora	2
Total	29

Source: Somchit Youpensuk, Unpublished.