根からみた作物の水ストレス耐性
Roles of Roots in Relation to Water Stress Tolerance of Crop

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要　約

作物の生産性を規定する主要因の一つは、水である。作物が栽培されている圃場においては、土壌環境は一定であることはむしろまれで、常に変動している。さらに空間的にも不均一である。このことは研究者の間ではっきりと認識されているとは言えず、水ストレス耐性と作物根系の発達と機能との関係を考える上では、たいへん重要な視点である。

作物が栽培されている圃場においては、栽培期間中、長期にわたって乾燥あるいは過湿ストレスが続く場合より、むしろ乾燥と過湿の間で土壌水分条件が変動することの方が実態に近いと考えられる。このような変動は、乾燥や過湿の単独のストレスに比べ、根の発育と機能にとってより厳しいストレス要因として働く可能性がある。

この問題をイネについて考えてみる。世界的にみるとイネ栽培地域の約半分が天水田（rainfed lowland rice field）で、灌漑設備が整っていない。この天水田における最大の収量制限要因は、水ストレスである。天水田には、深さ 20cm あたりに硬盤層という不透水層が存在し、そのため一時的に湛水状態となる場合がある。すなわち、硬盤層より下の心土は通常、湿潤状態であるが、硬盤層より上の作土は不定期な降雨によって嫌気的と好気的条件を繰り返し、その際に起こる水ストレスが生産性の低下を招く。このように、天水田における水ストレスは、畑状態で起こる単純な乾燥ストレスとは質的に異なるものである。さらには、世界的な水不足に対応して、潅漑設備が整っている水田においても、節水栽培技術の開発が急がれているが、ここでも共通の問題が存在する。

このような、時間的・空間的に不均一な土壌条件下で、イネ根系はどのような形質を具備すべきか？

環境条件に対して反応し、形態を変化させる能力を可塑性と呼ぶ。そこで、茎葉部より分配された光合成産物を効率よく利用して、変動する土壌環境、とくにストレス環境に応答して、個体の成長を安定させるような能力を有する、すなわち可塑性の大きい根系が、機能的に高いと考えることができる。しかし一方、この可塑性という形質は、遺伝学的にはたいへん扱いにくく、これをまともに取り上げるような育種プログラムもこれまでにはなかった。しかしこの形質は、作物のストレス耐性と密接に関連している可能性が高く、注目する必要がある。

本論文では、主として筆者らがこれまでに行ってきた研究成果をもとに、土壌環境の中で、とくに水ストレス耐性を中心に、作物根の発育や機能が果たす役割を、可塑性をキーワードに考えてみたい。

Roles of Roots in Relation to Water Stress Tolerance of Crop

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Abstract

Among the various soil conditions, the soil moisture effect is probably most commonly recognized. Soil environment is rarely constant but continues to change and is heterogeneous in space as well. These facts are quite important when the root development and function are analyzed in relation to their roles in water stress. During cropping period, it may be rather common that soil moisture conditions fluctuate between drought and excess in moisture than that the conditions continue to be either of them. It is important to note that such fluctuation can be more stressful as compared with singly consistent stress of either drought and excess in moisture on crop root development and function. In case of rice, more than a half of areas planted with rice is rainfed lowland field without irrigation. The most severe constraints to production there is water stress. Under rainfed lowland conditions, a hardpan that is water impermeable tends to be formed approximately 20 cm below soil surface, and thus waterlogged conditions can temporally appear. In other words, subsoil below the hardpan is usually wet while the topsoil above the hardpan is often exposed to frequent wet and dry cycles that are caused by irregular rainfall, and such water stress can cause substantial reduction in growth and yield of rice plants. As such, the water stress under rainfed lowland conditions is essentially different from the simple drought stress under upland conditions. Furthermore, global trend of water scarcity badly demands the development of water-saving rice production technology in irrigated rice fields, which however inherently contains the similar problem of water stress as rainfed lowlands. Then what kinds of root traits should rice plants possess under such heterogeneous soil environment in time and space? A root system of a crop plant is an integration of component roots with dissimilar morphology, anatomy and possibly physiological functions. They are different also in developmental responses to various environments. The ability of the plant to change its morphology as environmental conditions change is known as phenotypic plasticity. The root system that is high in function may be defined as that developmentally responds to environmental changes in a way that it stabilizes the whole plant growth, i.e., plastic root system. Such trait is difficult to be dealt with genetically and thus has been rarely incorporated in any breeding program. This paper aims to briefly review our research outputs with related areas on root system development and function in relation to the stress tolerance, especially that of water stress, of crop plants.

Key Words：
Aerobic rice, heterogeneity, irrigated lowland, plasticity, rainfed lowland, water saving production

Water stresses in rice fields and the roles of roots for plant adaptation

It is believed that roots play important roles in crop adaptation to various environments (Wang et al., 2006; Wang and Yamauchi, 2006; Yamauchi et al., 1996), but no practical rice variety has been developed based on root trait. It may be partially because the root traits responsible for the rice plant adaptation vary with the nature of the growing environment. For example, under upland conditions where soil moisture is available mainly in deep layer, the desirable traits may be simple and clear; deep and thick roots at least for vegetative growth. On the other hand, generally under field conditions, soil environment is rarely constant but continues to change and is heterogeneous in space. For example, the topsoil of rainfed lowlands is often exposed to frequent wet and dry cycles that are caused by irregular rainfall (Wade et al., 1999).

Irrigated rice fields with water-saving technology such as aerobic rice and alternate wetting and drying system (Bouman et al., 2005) also inherently contain the same nature of soil moisture environment as found in rainfed lowlands, that is, the fluctuating soil moisture but with less intensity and possibly more frequency. Although we need careful examination as to whether such fluctuations cause any 'drought' stress, we assume that moisture fluctuation alone can be stressful for root development and function. These may be understood if we address simple questions as follows; What would happen to the deep roots that developed in response to drought when the soil is suddenly waterlogged by rain or irrigation? What would happen to plants when droughted if the root system is shallow after being grown in waterlogged and O2 deficient soil? Then what kinds of root traits should rice plants possess under such heterogeneous soil environment in time and space?

Desirable root traits under water stress conditions

Root plasticity

A root system of a crop plant is an integration of component roots with dissimilar morphology, anatomy and possibly physiological functions. They are different also in developmental responses to various environments. The ability of the plant to change its morphology as environmental conditions change is known as phenotypic plasticity (O'Toole and Bland, 1987). The root system that is high in function may be defined as the one that developmentally responds to environmental changes in a way that it stabilizes the whole plant growth, which may be called as plastic root system.

Fig. 1 shows the root systems of Job's tears (adapted to excess moisture conditions), Japanese barnyard millet (adapted to both excess moisture and dry conditions), and Pearl millet (known to be drought resistant) grown under waterlogged, well-watered and droughted conditions. The root systems showed very sharp plasticity according to their adaptation ability to soil moisture conditions. For example, Job's tears showed promoted root system development under waterlogging and inhibited development under drought and pearl millet's root system was severely inhibited under waterlogging but especially fine branching was apparently promoted under drought, while the root system of Japanese barnyard millet relatively maintained the development under both extreme conditions (Galamay et al., 1992).

In this aspect, we have accumulated experimental evidences by comparing different crop species and varieties, which show that the response of root system to a certain soil environmental condition largely determines the plant's ability to adapt to the condition. Other examples include sorghum grown under high root-zone temperature (Pardales et al., 1991; 1992), waterlogging (Pardales et al., 1991), allelopatic influence (Pardales 1992), cassava under fluctuating soil moistures (Pardales et al., 1999; Pardale and Yamauchi, 2003; Subere et al., 2009), sweetpotato under high root-zone temperature (Pardales et al., 1999) and soil moisture fluctuations (Pardales et al., 2000), various food legumes under different soil moistures and temperature (Mia et al., 1996), maize under heterogenous N distribution (Tanaka et al., 2000) and rice under water stress (Bañoc et al., 2000a; b; Wang et al., 2009).

Fig. 2 shows the growth of rice varieties, Nipponbare and KDML 105 (rainfed lowland variety in North East Thailand) grown under soil moisture gradients from wet to dry. We identified KDML 105 as a variety that shows very sharp root developmental plasticity in response to changing soil moisture conditions (Bañoc et al., 2000a; b). This figure therefore strongly suggests that the root plasticity may play quite important roles in the plant growth in the wide range of soil moisture.

As such, the phenotypic plasticity, the ability of root traits to change developmentally and functionally in response to the changing conditions was suggested to be one of the most important traits for adaptation (Yamauchi et al. 1996). Such trait is difficult to be dealt with genetically and thus has been rarely incorporated in any breeding program.

We showed that in rice root system, the development of different component roots and their plastic responses to drought are under different QTL control. Such QTL were found also to differ with the intensities of water stress (Wang et al., 2005). We further showed that root osmotic adjustment is one of the physiological bases for the plasticity (Ogawa and Yamauchi, 2006). Especially, the sugar accumulation on root axes induced by water stress was found to be closely associated with plastic lateral root branching under the condition suggesting that such responses may be one of the physiological bases of the plasticity exhibited by the root system (Ogawa et al., 2005).

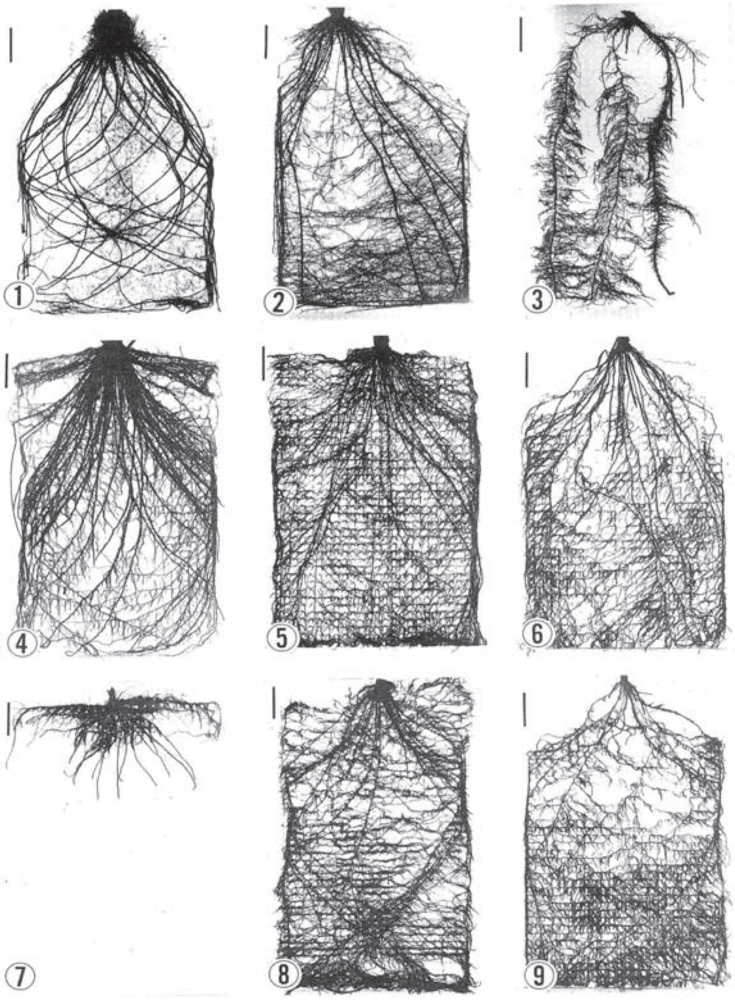

Fig. 1　Root system development of Job's tears (*Coix lacrima-jobi* L.) (upper, 1, 2, 3), Japanese barnyard millet (*Echinochloa utilis*) (middle, 4, 5, 6), Pearl millet (*Pennisetum typhoideum* L.) (bottom, 7, 8. 9) grown under waterlogged (left, 1, 4, 7), well-watered (center, 2, 5, 8) and droughted (right, 3, 6, 9) conditions. (Galamay et al., 1992)

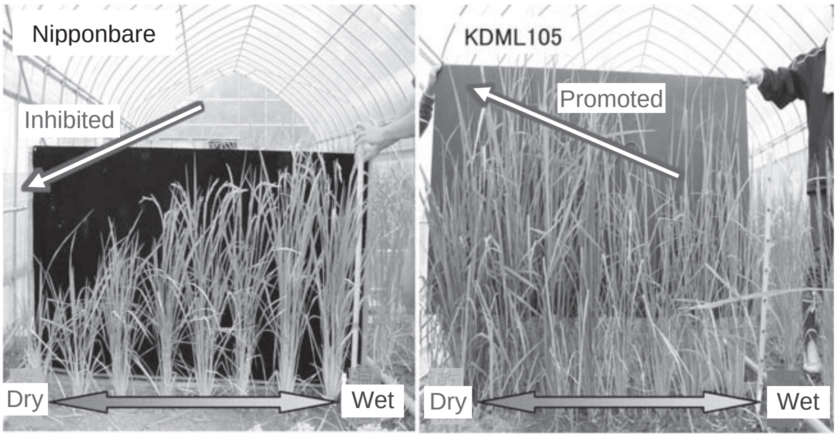

Fig. 2　Growth of rice varieties, Nipponbare (left) and KDML 105 (rainfed lowland variety in North East Thailand) (right) grown under soil moisture gradients from wet to dry.

With this paper, therefore, we propose that the plasticity is one of the key root traits that are required for rice plants to adapt to various environments with soil moisture fluctuation including rainfed lowlands and irrigated lowlands with water-saving production systems.

Identification of key root traits in rice

Our recent studies have been aiming at evaluating the genetic variations in responses in dry matter production, shoot growth and root system development to constant drought stress and transient moisture stress conditions (drought and O_2 deficiency) to identify key root traits that contribute to plant adaptation to various intensities of drought stress and fluctuating soil moisture stresses.

Constant drought stress

Fifty-four chromosome segment substitution lines (CSSLs) derived from Nipponbare and Kasalath parents provided by the Rice Genome Research Center of the National Institute of Agrobiological Sciences, Japan were used in the field experiments for three years. We used a watertight experimental bed installed with line source sprinkler system, which creates and maintained various intensities of soil moisture stresses as shown in Fig. 3. Results showed that these CSSLs generally showed reduced plant height, tillering and dry matter productions as the drought intensified in both years, which were associated with reduced photosynthesis and transpiration, and stomatal conductance. However, compared with Nipponbare, CSSL45 and 50 relatively maintained dry matter production with increasing drought stress due to their ability to maintain or promote root elongation and branching under the conditions. Specifically, their growth in shoot and roots were not different from Nipponbare at 40% and above in soil moisture content (SMC), while the dry matter production and total root length in those CSSLs peaked around 30-35 % of SMC. Under severe drought at 10 % of SMC or below, the extent of shoot and root growth reductions were similar to those of Nipponbare (Kanou et al., 2007; Yamauchi et al., 2008). These results strongly suggest that plastic root responses of rice genotypes may be one of the key traits that contribute to plant adaptation to various intensities of water stress.

Fig. 3 Watertight experimental bed installed with line source sprinkler system, which creates and maintained various intensities of soil moisture stresses.

Transient moisture stress

Two aerobic genotypes (UPLRi7 and NSICRc9), one irrigated lowland (PSBRc82), Kasalath (*indica*) and Nipponbare (*japonica*) CSSLs parents were grown under transient moisture stress in a growth chamber for 2 weeks (one week under each moisture stress) (Suralta and Yamauchi, 2008). The transient moisture stress treatments were drought to O_2 deficient (stagnant) and stagnant to drought conditions. Then, the 54 CSSLs were also evaluated in similar manners.

Consistent genotypic differences were found between aerobic and irrigated lowland genotypes in lateral root production responses to transient moisture stresses (Suralta et al., 2008b). Under transient stagnant to drought condition, the root trait that mainly determined the genotypic differences was the ability to maintain seminal root elongation and branching of lateral roots along seminal root axis, nodal root production and elongation. Under transient drought to stagnant condition, the differences were mainly determined by greater ability in maintaining seminal root elongation and nodal root production, which were exhibited by aerobic genotype. The seminal roots of aerobic genotypes had the ability to enhance root aerenchyma formation when subjected to stagnant condition while the irrigated lowland genotype completely lost such ability once droughted. Kasalath showed much greater ability in lateral root production under both transient moisture stresses than Nipponbare. This indicates the potential utilization of their CSSLs for precise identification of desirable root traits with reduced effects of genetic confounding (Suralta et al., 2008b).

Among the 54 CSSLs, Line 47 was identified to show no significant differences in shoot and root growth with the recurrent parent Nipponbare under non-stressed conditions but consistently exhibit greater lateral root production under both transient conditions. Using this line in comparison with Nipponbare, the key root traits observed with genetically diverse rice cultivars and the CSSL as shown above were confirmed to contribute to better adaptation through enhanced water uptake, stomatal conductance, photosynthesis and dry matter production when grown in soil with fluctuating moistures (Suralta et al., In press). Some of the traits were found to be common with those identified for aerobic and irrigated lowland genotypes grown under constant drought and waterlogged conditions (Suralta and Yamauchi, 2008).

The selected CSSLs under constant drought and transient moisture stresses are being used for further production of near isogenic lines on the QTLs to examine quantitatively the physiological function of the root plasticity for plant adaptation under constant drought and transient moisture stresses as well as its genetic regulation.

Conclusion

Roots undoubtedly play one of the key roles for crop plants to grow and adapt to environments with abiotic stresses such as water stress. It is primarily important to characterize to understand the environment and the nature of the stresses of the target area so that desirable traits required for the growth and adaptation can be specifically identified. One typical example is the difference between simple drought and soil moisture fluctuations under various rice production ecosystem. One of the key traits we have so far identified is the developmental plasticity of root system. We still need to accumulate direct evidence on roles of root plasticity in whole plant growth by producing near isogenic line, chromosome segment substitution line, which can also be useful for QTL analysis. For developing varieties that can be practically grown in the field, evaluation on genotypes (QTL) x environmental interaction is essential in the target ecosystems.

References

Bañoc, D. M., Yamauchi, A., Kamoshita, A., Wade, L. J. and Pardales, Jr. J. R. 2000a. Dry matter production and root system development of rice cultivars under fluctuating soil moisture. Plant Production Science 3 (2): 197-207.

Bañoc, D. M., Yamauchi, A., Kamoshita, A., Wade, L. J. and Pardales, Jr. J. R. 2000b. Genotypic variations in response of lateral root development to fluctuating soil moisture in rice. Plant Production Science 3(3): 335-343.

Bouman, B.A.M., Peng, S., Castañeda, A.R., Visperas, R.M., 2005. Yield and water use of irrigated tropical aerobic rice systems. Agric. Water. Manage. 74, 87-105.

Galamay, T. O., A. Yamauchi, T. Nonoyama and Y. Kono. 1992. Acropetal lignification in cereal nodal root axes as affected by different soil moisture conditions. Japanese Journal of Crop Science. 61:511-517.

Kanou, M., Y. Inukai, H. Kitano and A. Yamauchi. 2007. Identification of key root traits for adaptation of rice genotypes to various intensities of water stress. In the Proceedings of The 2nd International Conference on Rice for the Future, 5-9 November 2007, Bangkok, Thailand. pp. 216-220.

Mia, M. W., Yamauchi, A. and Kono, Y. 1996. Plasticity in taproot elongation of several food legume species. Japanese Journal of Crop Science. 65:368-378.

Ogawa, A., C. Kawashima and A. Yamauchi 2005. Sugar accumulation along the seminal root axis, as affected by osmotic stress in maize:a possible physiological basis for plastic lateral root development. Plant Prod. Sci. 8 : 173-180.

Ogawa, A. and A. Yamauchi 2006. Root Osmotic Adjustment under Osmotic Stress Conditions in Maize Seedlings. 1. Transient response of growth and water relations in roots to osmotic stress. Plant Prod. Sci. 9 : 27-38.

O'Toole, J. C. and W. L. Bland. 1987. Genotypic variation in crop plant root systems. Advance in Agronomy. 41: 91-145.

Pardales Jr., J. R., Bañoc, D. M., Yamauchi, A., Iijima M. and Kono, Y. 1999. Root system development of cassava and sweetpotato during early growth stage as affected by high root zone temperature. Plant Production Science. 2 (4): 247-251.

Pardales Jr. J. R., Bañoc, D. M., Yamauchi, A., Iijima M., and Esquibel, C. B. 2000 The Effect of Soil Moisture Fluctuation on Root Development During the Establishment Phase of Sweetpotato. Plant Production Science 3(2): 134-139.

Pardales, J. R. Jr, Y. Kono and A. Yamauchi. 1991. Response of the different root system components of sorghum to incidence of waterlogging. Environmental and Experimental Botany. 31:107-115.

Pardales, J. R. Jr, Y. Kono and A. Yamauchi. 1992. Epidermal cell elongation in sorghum seminal roots exposed to high root-zone temperature. Plant Science. 81:143-146.

Pardales, J. R. Jr, A. Yamauchi and Y. Kono. 1991. Growth and development of sorghum roots after exposure to different periods of a hot root-zone temperature. Environmental and Experimental Botany. 31:397-403.

Pardales, J. R. Jr, Y. Kono, A. Yamauchi and M. Iijima. 1992. Seminal root growth in sorghum (*Sorghum bicolor*) under allelopatic influences from residues of taro (*Colocasia esculenta*). Annals of Botany. 69:493-496.

Pardales Jr., J. R. and A. Yamauchi 2003. Regulation of root development in sweetpotato and cassava by soil moisture during their establishment period. Plant and Soil. 255: 201-208.

Subere, J. O. Q., Bolatete, D, Bergantin, R., Pardales, A., Belmonte, J. J., Mariscal, A., Sebidos, R. and Yamauchi, A. 2009. Genotypic Variation in Responses of Cassava (*Manihot esculenta* Crantz) to Drought and Rewatering. I. Root System Development. Plant Production Science 12 (4): 462-474.

Suralta, R. R. and Yamauchi, A. 2008. Root growth, aerenchyma development, and oxygen transport in rice genotypes subjected to drought and waterlogging. Environmental and Experimental Botany 64:75–82.

Suralta. R. R., Inukai, Y. and Yamauchi, A. 2008a. Genotypic variations in responses of lateral root development to transient moisture stresses in rice cultivars. Plant Production Science. 11: 324-335.

Suralta, R. R., Inukai Y. and Yamauchi, A. 2008b. Utilizing chromosome segment substitution lines (CSSLs) for evaluation of root responses under transient moisture stresses in rice. Plant Production Science 11: 457-465.

Suralta, R. R., Inukai, Y. and Yamauchi, A. Dry matter production in relation to root plastic development, oxygen transport and water uptake of rice under transient soil moisture stresses. Plant and Soil (In Press)

Tanaka, S., Yamauchi, A., Yano K., Iijima, M. and Tatsumi, J. 2000. Functional significance of root developmental plasticity in nitrogen acquisition in maize. Root Research 9: 167-171. (In Japanese)

Wade, L. J., Fukai, S., Samson, B.K., Ali, A. and Mazid, M.A. 1999. Rainfed lowland rice: Physical environment and cultivar requirements. Field Crops Res. 64: 3-12.

Wang, H., Y. Inukai, A. Kamoshita, L. J. Wade, J. D. L. C. Siopongco, H. Nguyen and A. Yamauchi. 2005. QTL analysis on plasticity in lateral root development in response to water stress in the rice plant. In The Proceedings of the World Rice Research Conference. Tsukuba, Japan. Toriyama, K., K. L. Heong and B. Hardy (eds.) Rice is life: scientific perspectives for the 21st century. pp. 464-469.

Wang, H., Y. Inukai and A. Yamauchi. 2006. Root Development and Nutrient Uptake. Critical Reviews in Plant Sciences. 25:279–301.

Wang, H., Siopongco, J. D. L. C, Wade, L. J. and Yamauchi, A. 2009. Fractal Analysis on Root Systems of Rice Plants in Response to Drought Stress. Environmental and Experimental Botany. 65: 338-344.

Wang, H., and Yamauchi, A. 2006. Growth and function of roots under abiotic stress soils. In B. Huang ed., Plant-Environment Interactions 3rd ed. CRC Press, Taylor and Francis Group, LLC, New York. 271-320.

Yamauchi, A., Pardales Jr, J. R. and Kono, Y. 1996. Root system structure and its relation to stress tolerance. In Dynamics of roots and nitrogen in cropping systems of semi-arid tropics (eds. Ito, O. et al.). pp. 211-233. Japan International Research Center for Agricultural Sciences, Tsukuba.

Yamauchi, A., Inukai, Y., Kano, M., Suralta, R., Ogawa, A., Kobayashi K. and R. Serraj. 2008. Role of roots for stabilizing rice production under water stress conditions. In The Proceedings of the 5th International Crop Science Congress, April 13-18, 2008, Jeju, Korea.

Roles of roots in relation to water stress tolerance of crop

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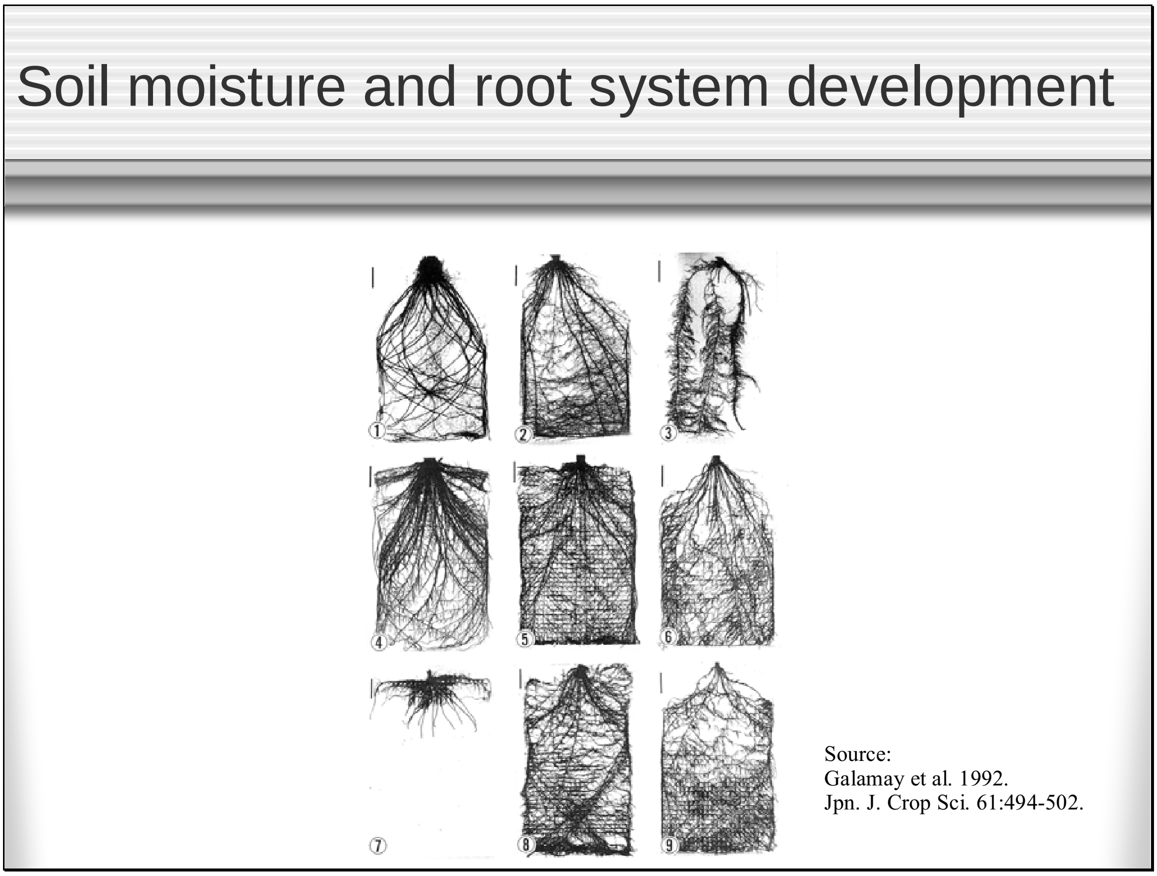
Characteristics of crop-grown fields

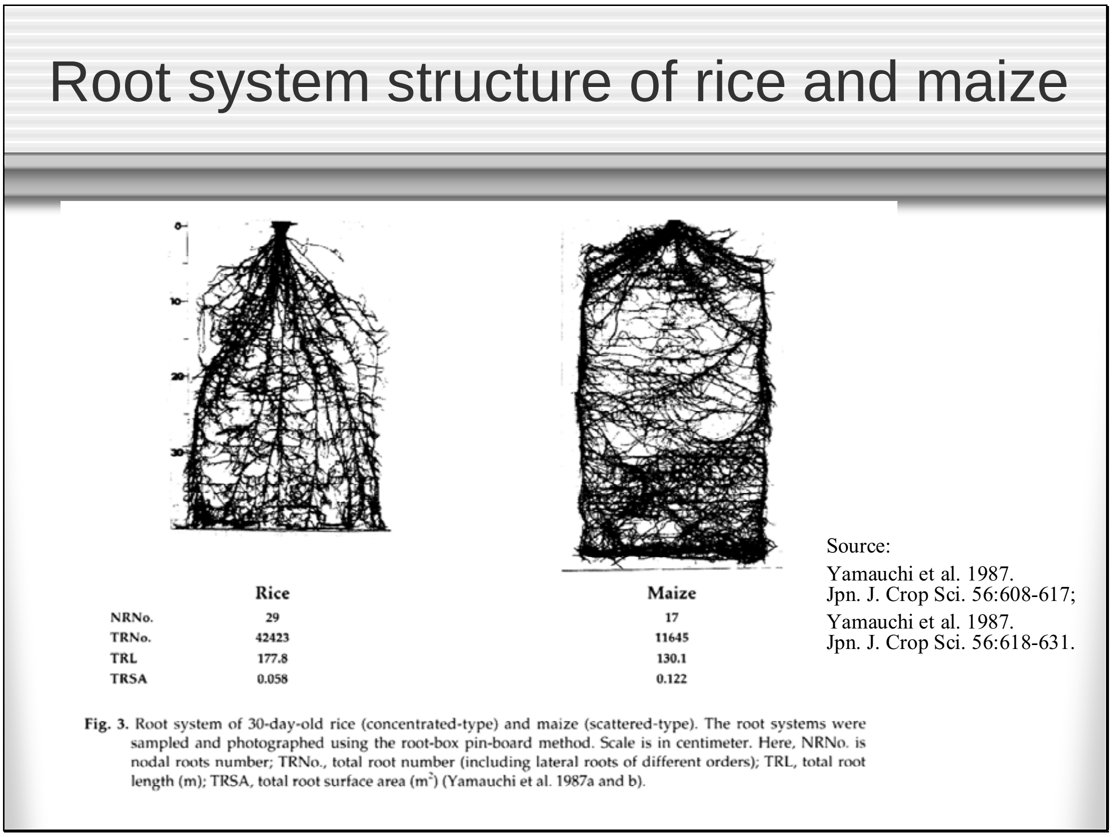
Heterogeneity

- in space
  - resource distribution
- in time
  - moisture fluctuation



Soil moisture and root system development

Source:
Galamay et al. 1992.
Jpn. J. Crop Sci. 61:494-502.



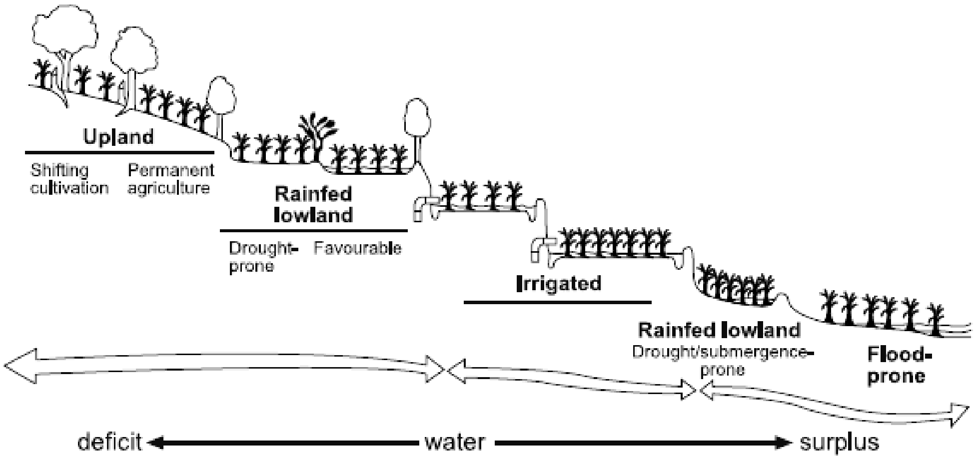
Root system structure of rice and maize

	Rice	Maize
NRNo.	29	17
TRNo.	42423	11645
TRL	177.8	130.1
TRSA	0.058	0.122

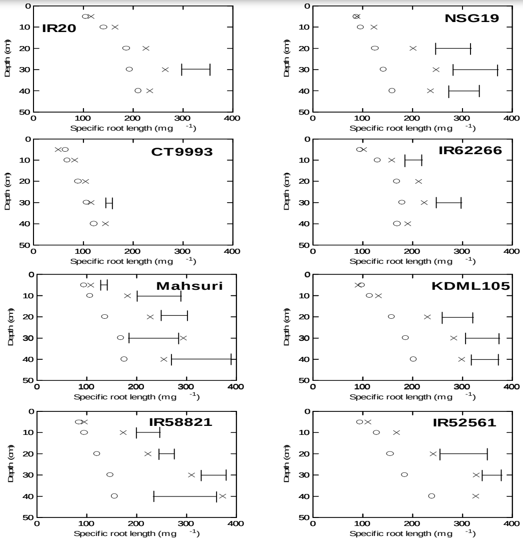
Fig. 3. Root system of 30-day-old rice (concentrated-type) and maize (scattered-type). The root systems were sampled and photographed using the root-box pin-board method. Scale is in centimeter. Here, NRNo. is nodal roots number; TRNo., total root number (including lateral roots of different orders); TRL, total root length (m); TRSA, total root surface area (m^2) (Yamauchi et al. 1987a and b).

Source:
Yamauchi et al. 1987.
Jpn. J. Crop Sci. 56:608-617;
Yamauchi et al. 1987.
Jpn. J. Crop Sci. 56:618-631.

Characteristics of rice ecosystem



Rice roots response to soil moisture fluctuation



Source: Azhiri-Sigari et al. 2000. Plant Prod. Sci. 3, 180-188.

Soil moisture fluctuations and root elongation

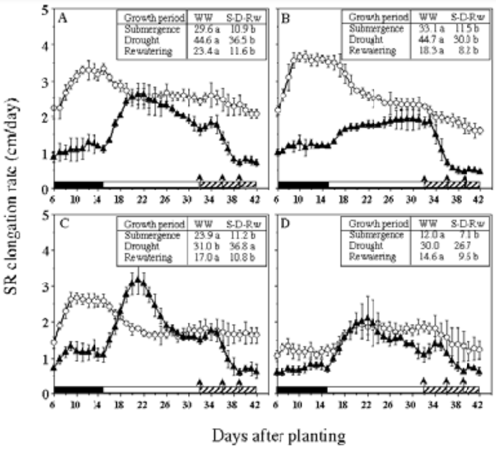


Fig. 2. Daily seminal root elongation rate of four rice cultivars, IRAT109 (A), Dular (B), KDML105 (C), and Honenwase (D) under well-watered (WW) and soil submerged-droughted-rewatered (S-D-Rw) conditions in Exp. 2.

Numbers inside the graph indicate the SR length (cm) in each growth period; drought and rewatering periods under WW and D-Rw conditions. Arrows indicate the time of rewatering was administered. Columns denote mean and standard deviation of three replicates. SR length values with different letters are not significantly different at 5% level of significance based on Duncan Multiple Range Test.

Symbols : (—○—) well-watered conditions, (—▲—) submerged-droughted-rewatered conditions, (■) soil submergence period, (□) drought period and (▨) rewatering period.

Source:
Bañoc et al. 2000.
Plant Prod. Sci. 3 (2): 197-207.

Soil moisture fluctuation and lateral root development

Table 4. Branching density of lateral roots in four rice cultivars grown under well-watered and soil submerged-droughted-rewatered conditions (Exp. 2).

Cultivars/	Growth Period								
Growing	Soil Submergence			Drought			Rewatering		
Conditions/	Branching Density of 1OLRs			Branching Density of 1OLRs			Branching Density of 1OLRs		
% of Control	Total (cm-1)	L-type (cm-1)	S-type (cm-1)	Total (cm-1)	L-type (cm-1)	S-type (cm-1)	Total (cm-1)	L-type (cm-1)	S-type (cm-1)
IRAT109:									
WW	13.1	3.6	9.5	12.4	3.4	9	12.9	3.5 a	9.4 b
S-D-Rw	14.3	3.2	11.1	13.5	2.9	10.6	14.7	1.4 b	13.3 a
% of Control	109.2 ns	88.9 ns	116.8 ns	108.9 ns	85.3 ns	117.8 ns	114.0 ns	40.0*	141.5*
Dular:									
WW	16	4	12	13.2	2.2	11	8.3 b	0.64 b	7.7 b
S-D-Rw	17.2	3.2	14	14.7	1.8	12.9	19.7 a	1.6 a	18.1 a
% of Control	107.5 ns	80.0 ns	116.7 ns	111.4 ns	81.8 ns	117.3 ns	237.3*	250.0**	235.1**
KDML105:									
WW	13.8 b	2.6	11.2 b	10.3	1.1 b	9.2	9.8	0.33 b	9.5
S-D-Rw	18.5 a	2.7	15.8 a	10.3	2.5 a	7.8	10.7	1.3 a	9.4
% of Control	134.0*	103.8 ns	141.1*	100.0 ns	227.3**	84.8 ns	109.2 ns	393.9**	98.9 ns
Honenwase:									
WW	15.6	3.0 b	12.6	14.5	2.6 a	11.9	8.9 b	0.62 b	8.3 b
S-D-Rw	17.2	4.4 a	12.8	11.2	1.6 b	9.6	14.0 a	1.7 a	12.3 a
% of Control	110.2 ns	146.7*	101.6 ns	77.2 ns	61.5*	80.7 ns	157.3*	274.2**	148.2*

For abbreviations, legend and statistical significance, see Tables 1 and 3 for details.

Source:Bañoc et al. 2000. Plant Prod. Sci. 3(3): 335-343.

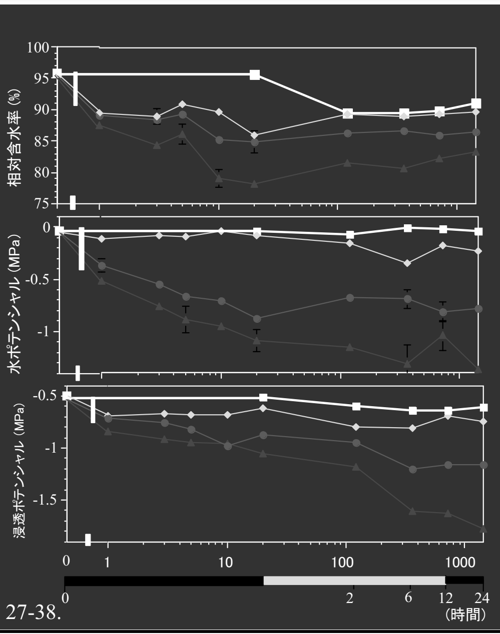
Phenotypic Plasticity; dynamic aspects of root system sturucture

Ability of a genotype to alter phenotype in response to environment

- Soil moisture → lack, excess, fluctuate
- Soil temperature
- Chemical substances
- Nutrient distribution
- Microorganism

Root osmotic adjustment 1

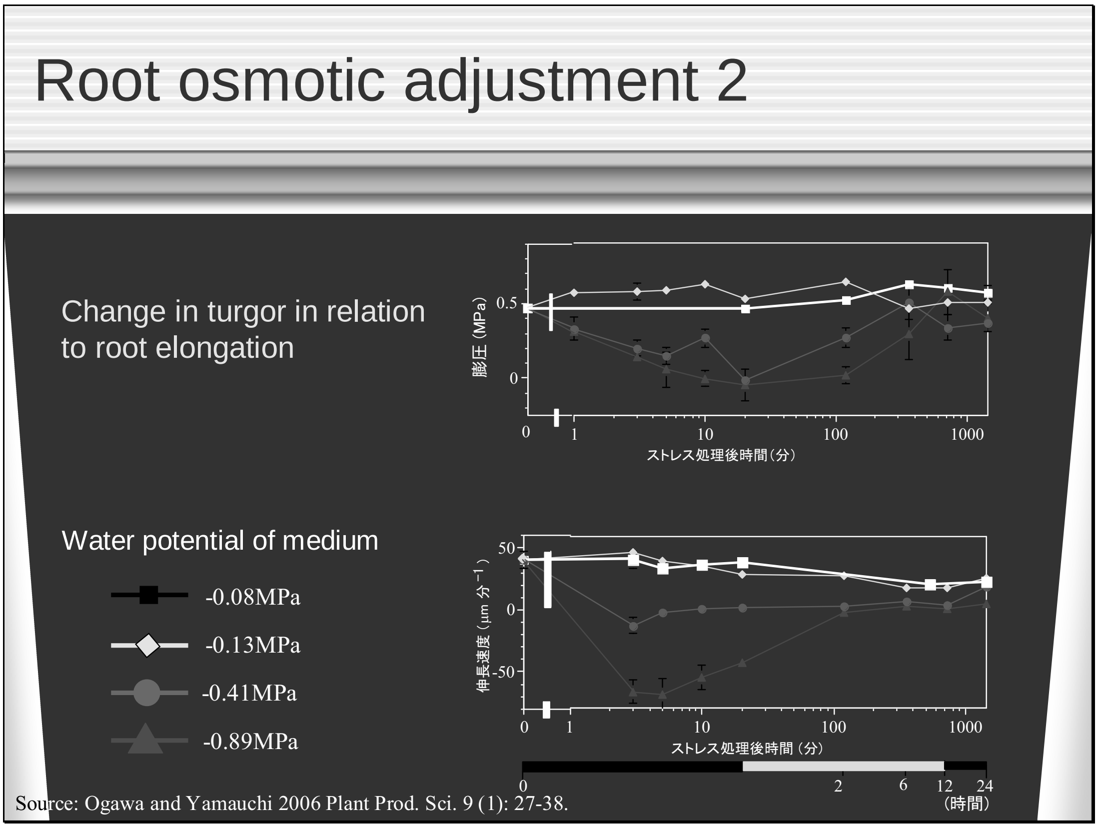
Water relation of elongation portions of seminal root (maize)



Water potential of medium

- ■ -0.08MPa
- ◇ -0.13MPa
- ● -0.41MPa
- ▲ -0.89MPa

Source: Ogawa and Yamauchi 2006 Plant Prod. Sci. 9 (1): 27-38.



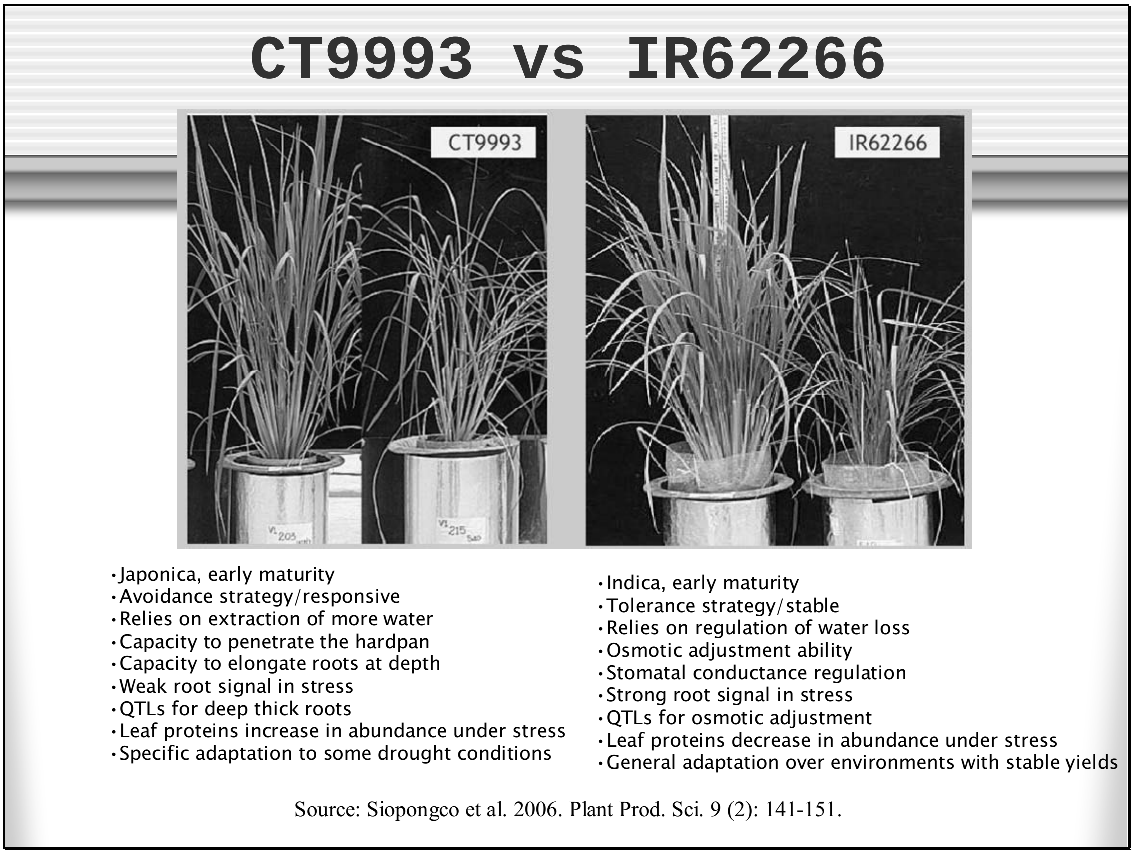
Root osmotic adjustment 2

Change in turgor in relation to root elongation

Water potential of medium

- -0.08MPa
- -0.13MPa
- -0.41MPa
- -0.89MPa

Source: Ogawa and Yamauchi 2006 Plant Prod. Sci. 9 (1): 27-38.



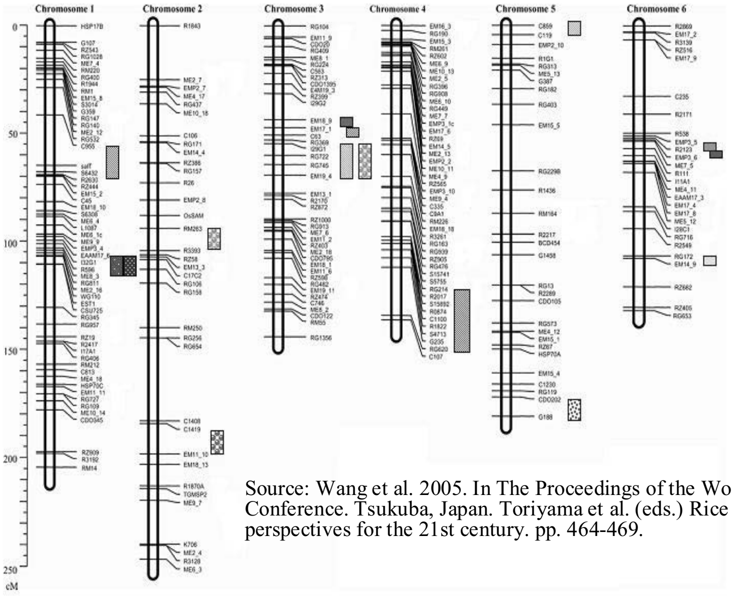
CT9993 vs IR62266

- Japonica, early maturity
- Avoidance strategy/responsive
- Relies on extraction of more water
- Capacity to penetrate the hardpan
- Capacity to elongate roots at depth
- Weak root signal in stress
- QTLs for deep thick roots
- Leaf proteins increase in abundance under stress
- Specific adaptation to some drought conditions

- Indica, early maturity
- Tolerance strategy/stable
- Relies on regulation of water loss
- Osmotic adjustment ability
- Stomatal conductance regulation
- Strong root signal in stress
- QTLs for osmotic adjustment
- Leaf proteins decrease in abundance under stress
- General adaptation over environments with stable yields

Source: Siopongco et al. 2006. Plant Prod. Sci. 9 (2): 141-151.

Genetic background for plasticity *(QTL)*



Source: Wang et al. 2005. In The Proceedings of the World Rice Research Conference. Tsukuba, Japan. Toriyama et al. (eds.) Rice is life: scientific perspectives for the 21st century. pp. 464-469.

QTL identified for root plasticity traits

▨ **ALLL: Average L type lateral root length under well-watered condition**

□ **TLLL: Total L type lateral root length under well-watered condition**

▨ **LLLL: The longest L type lateral root length under well-watered condition**

■ **TLLL: The longest L type lateral root length under water stress condition**

▨ **AMLL: Average M type lateral root length under well-watered condition**

▨ **AMLL: Average M type lateral root length under water stress condition**

▨ **TMLL: Total M type lateral root length under well-watered condition**

■ **TMLL: Total M type lateral root length under water stress condition**

□ **LMLL: The longest M type lateral root length under well- watered condition**

□ **SMLL: The shortest M type lateral root length under water stress condition**

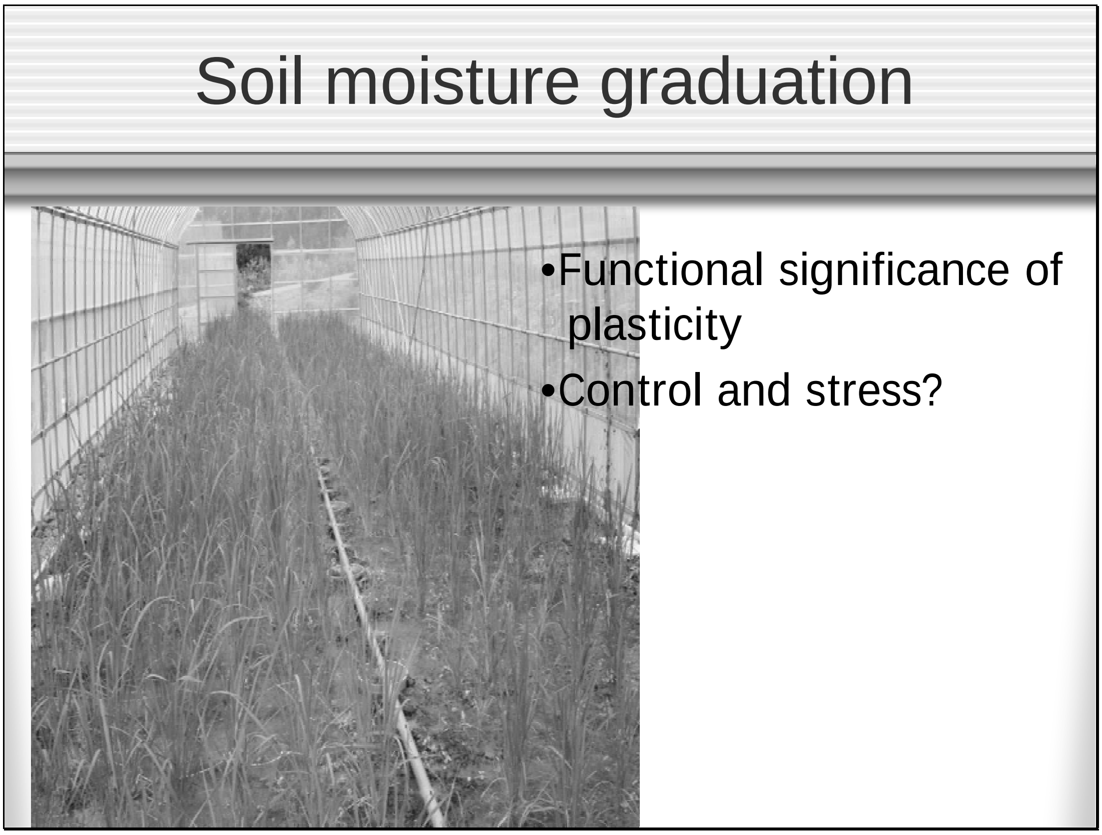
▒ **LN: The lateral root number per cm seminal root axis under well-watered condition**

■ **LN: The lateral root number per cm seminal root axis under water stress condition**

▒ **LLN: The L type lateral root number per cm seminal root axis under well-watered condition**

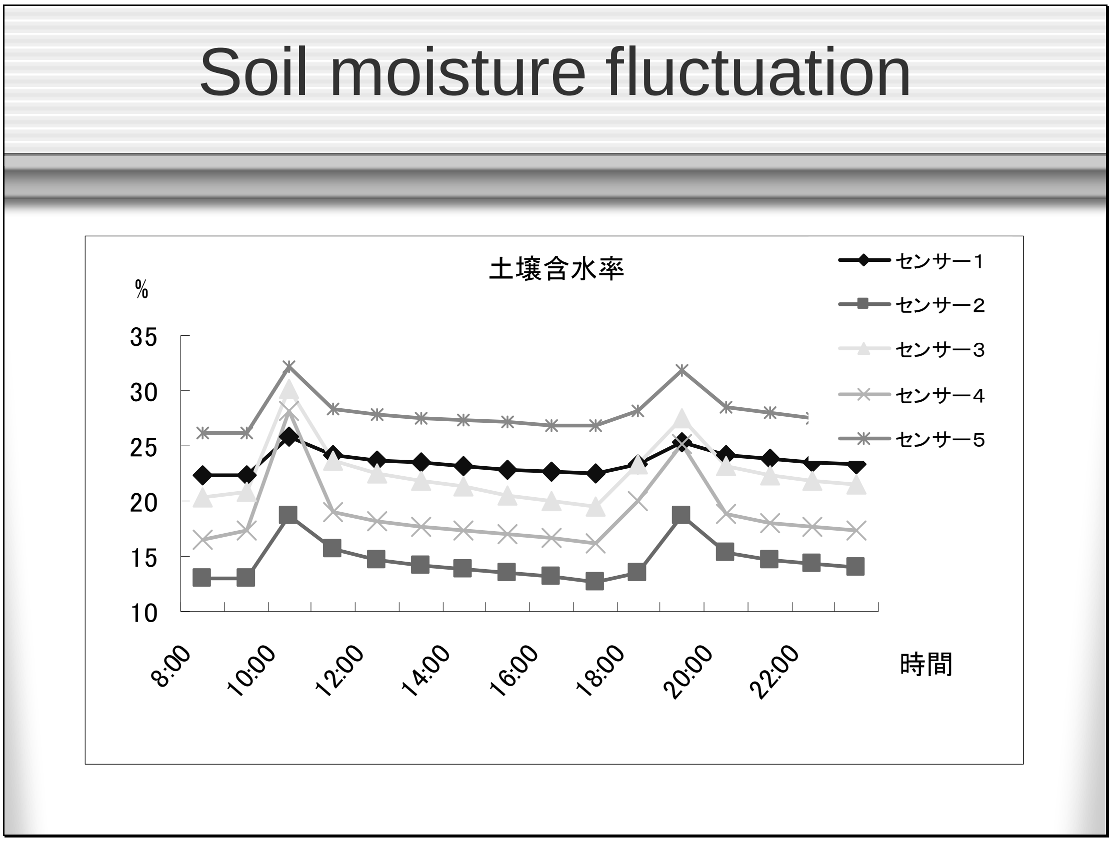
▒ **MLN: The M type lateral root number per cm seminal root axis under well-watered condition**

■ **SLN: The S type lateral root number per cm seminal root axis under water stress condition**



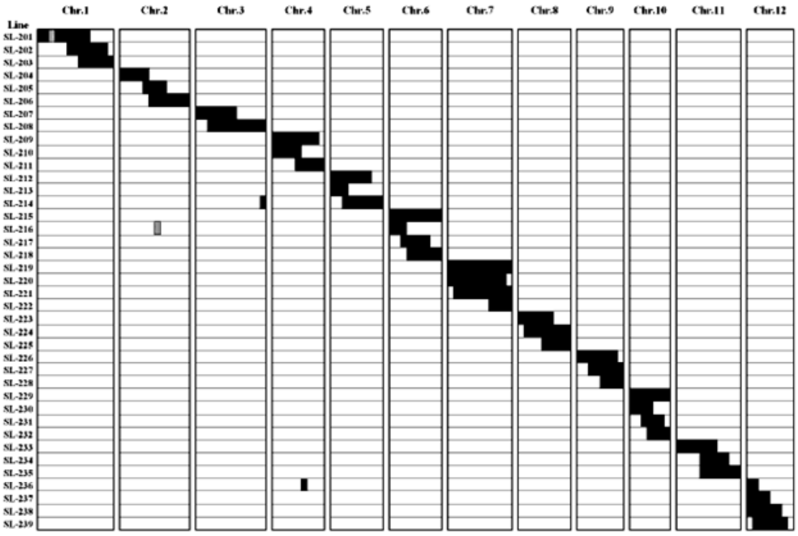
Soil moisture graduation

- Functional significance of plasticity
- Control and stress?



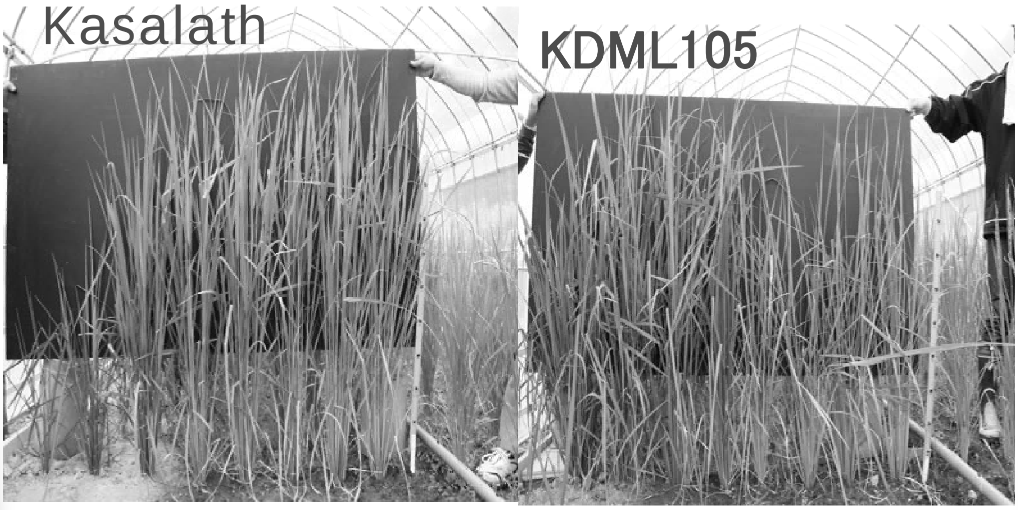
Soil moisture fluctuation

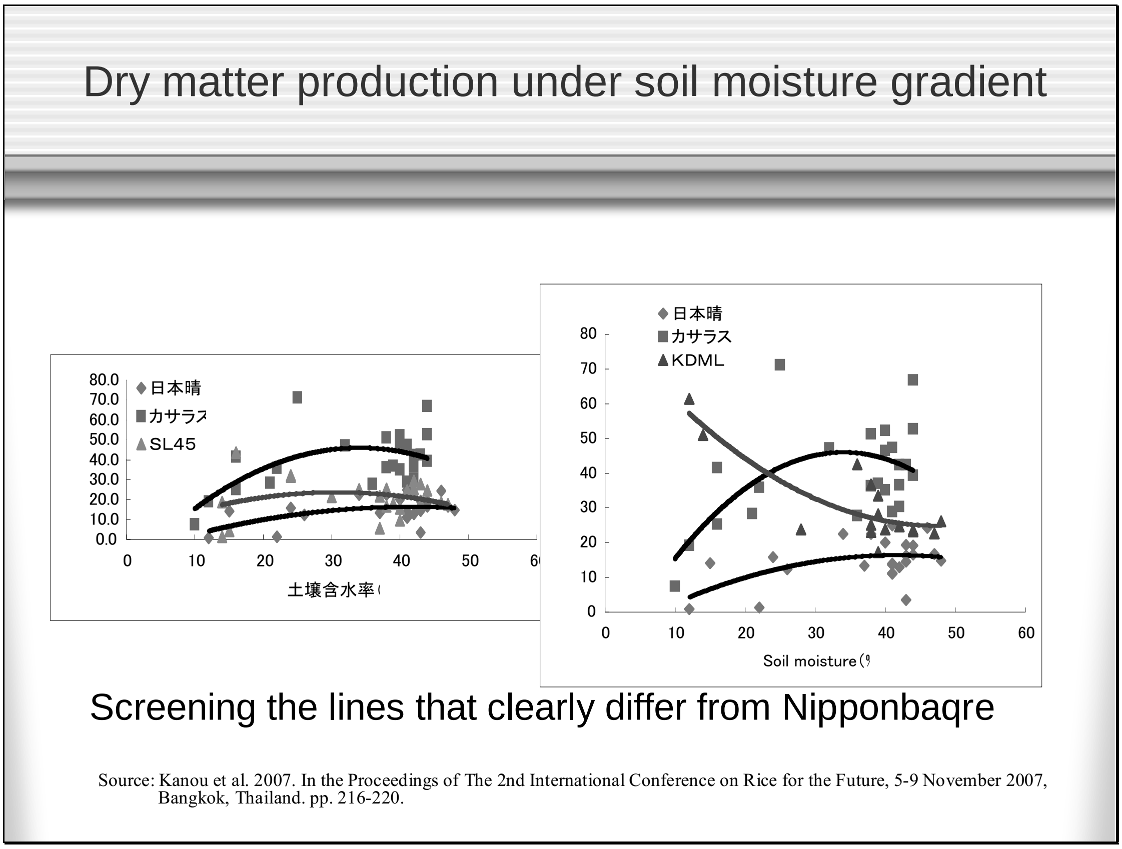
Chromosome segment substitution lines for rice



Source: Rice Genome Resource Center, National Institute of Bioagricultural Science

Kasalath and KDML 105

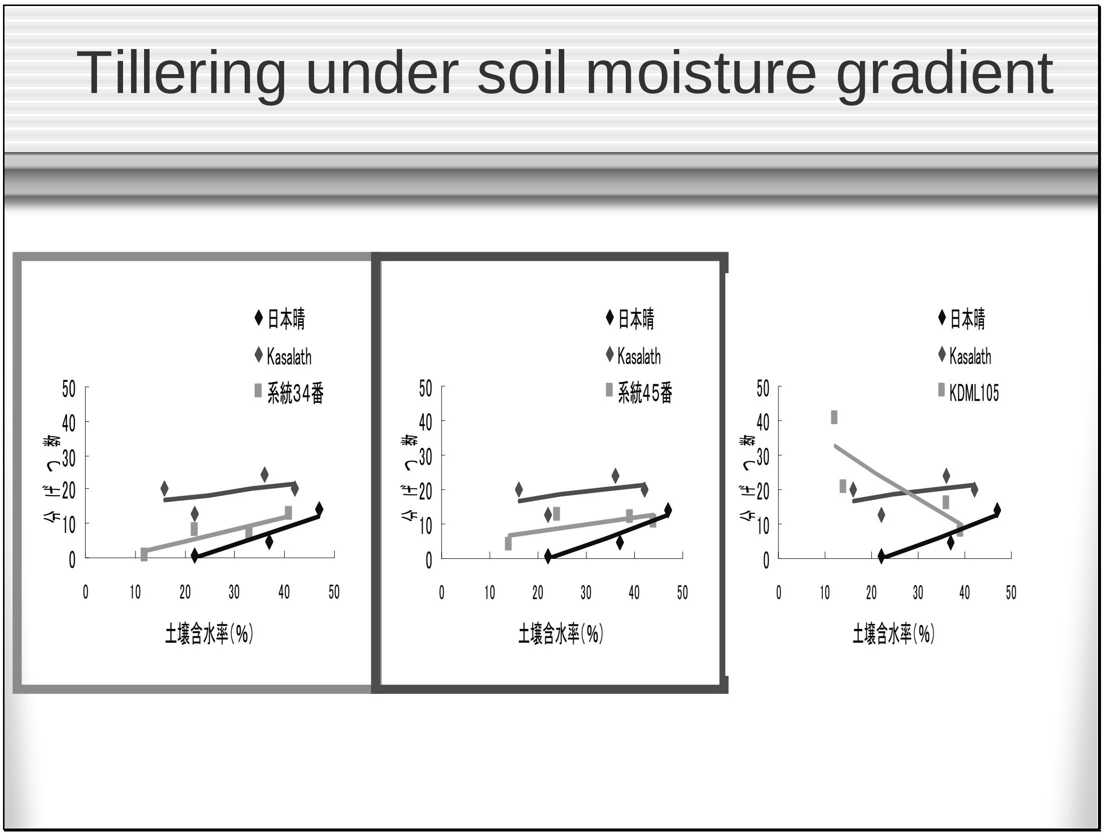




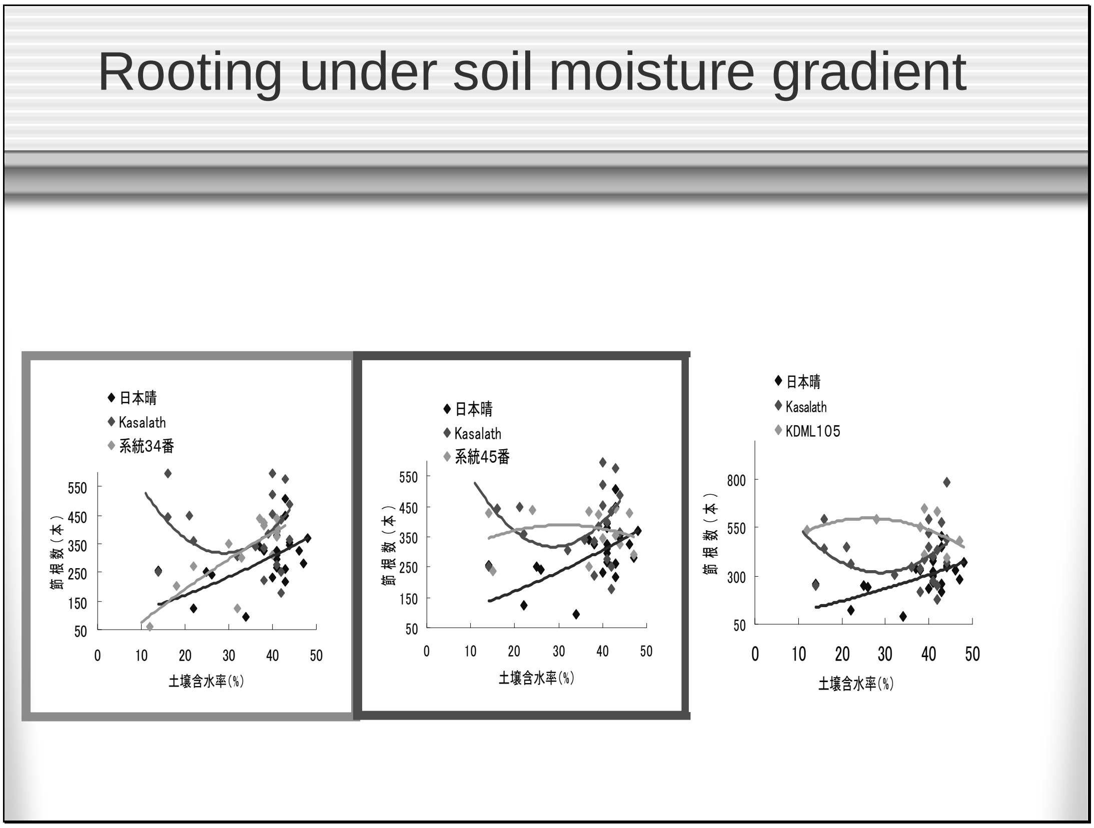
Dry matter production under soil moisture gradient

Screening the lines that clearly differ from Nipponbaqre

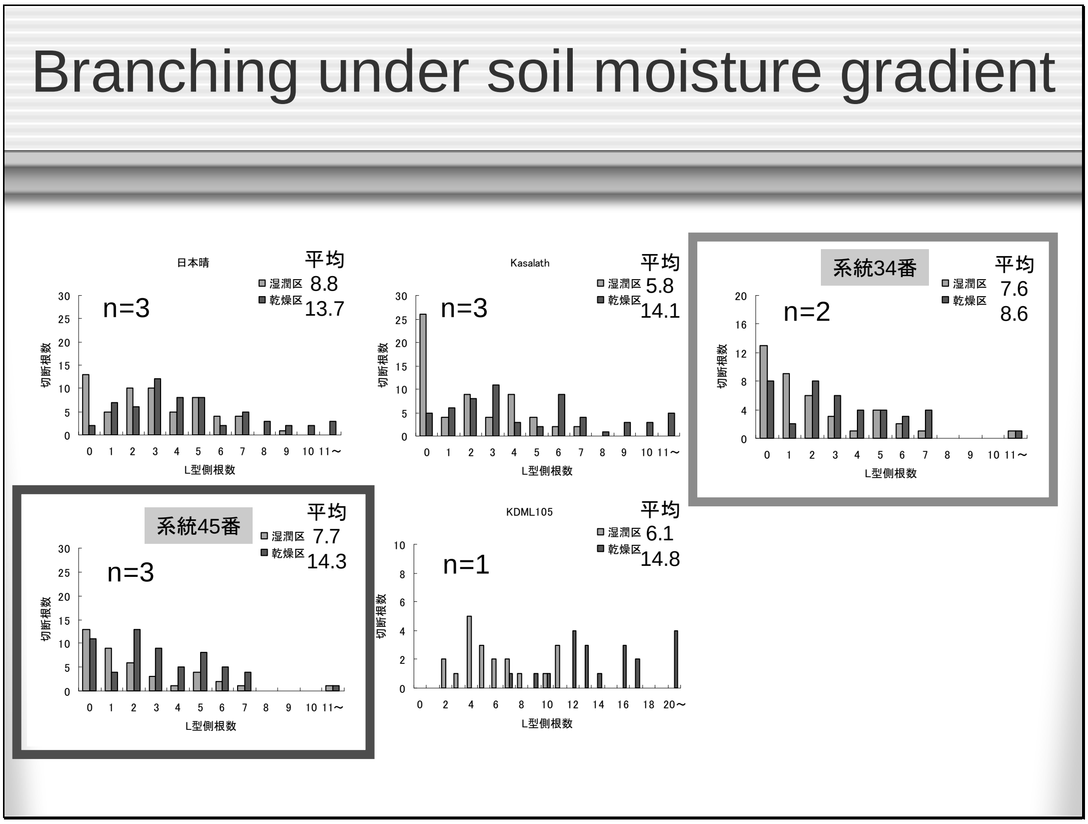
Source: Kanou et al. 2007. In the Proceedings of The 2nd International Conference on Rice for the Future, 5-9 November 2007, Bangkok, Thailand. pp. 216-220.



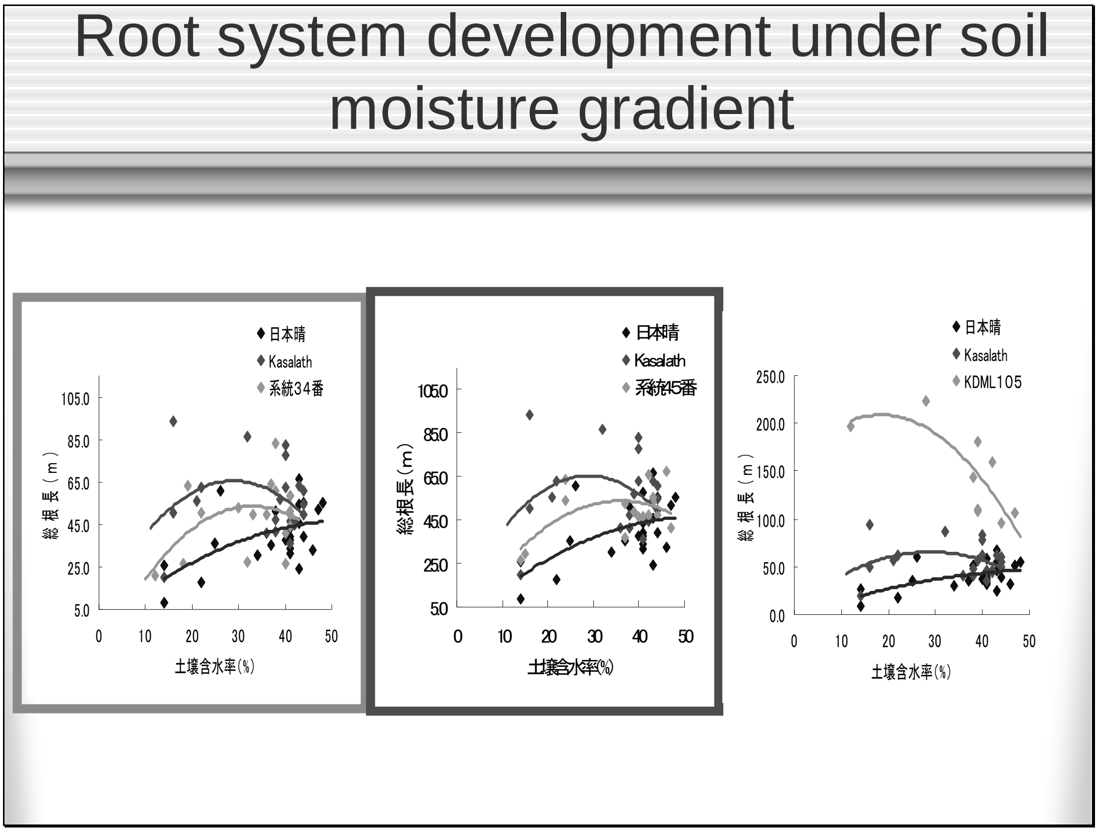
Tillering under soil moisture gradient



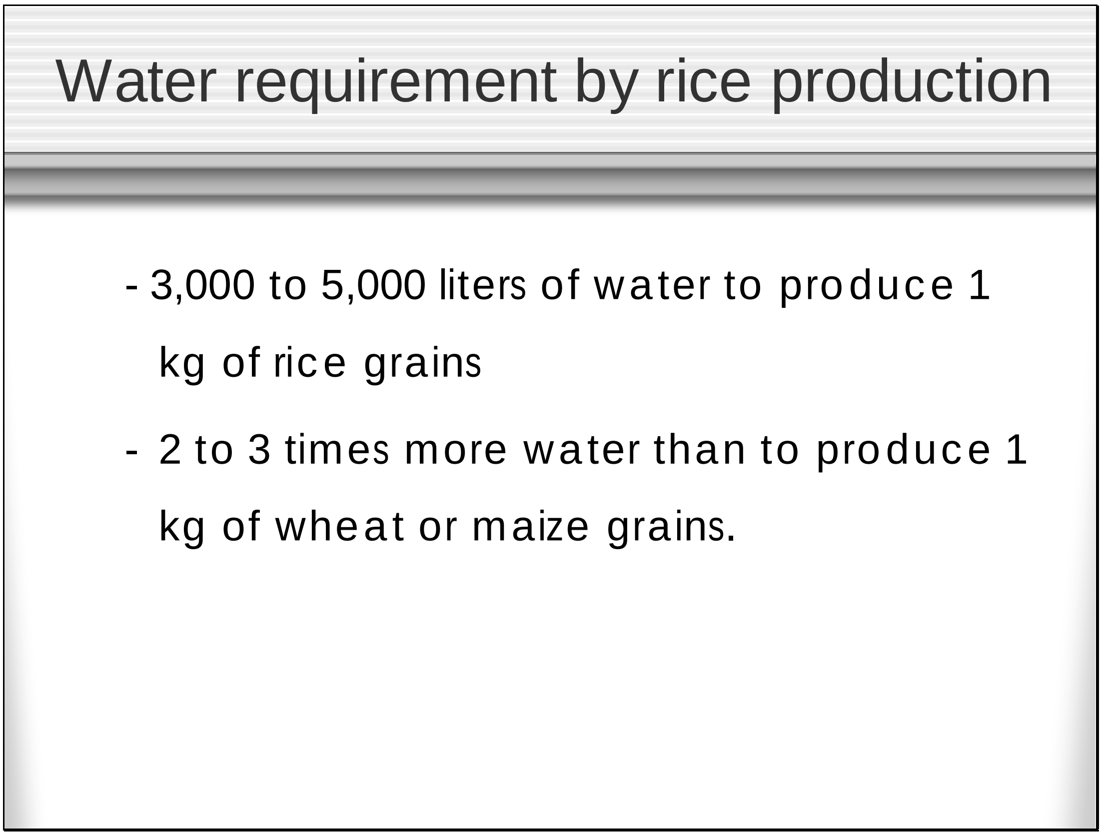
Rooting under soil moisture gradient



Branching under soil moisture gradient



Root system development under soil moisture gradient



Water requirement by rice production

- 3,000 to 5,000 liters of water to produce 1 kg of rice grains
- 2 to 3 times more water than to produce 1 kg of wheat or maize grains.

Water saving rice production

- ☐ Saturated soil culture (SSC)

  Soil is kept as close to saturation as possible by shallow irrigation to obtain about 1-cm floodwater depth a day after the disappearance of standing water

- ☐ Alternate wetting and drying (AWD) system

  Irrigation water is applied to obtain 2-5 cm floodwater depth after a certain number of days (ranging 2-7 days)

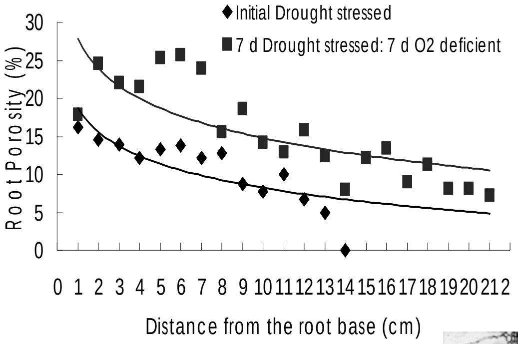
- ☐ Thin-water-layer irrigation and draining depending on the development of rice

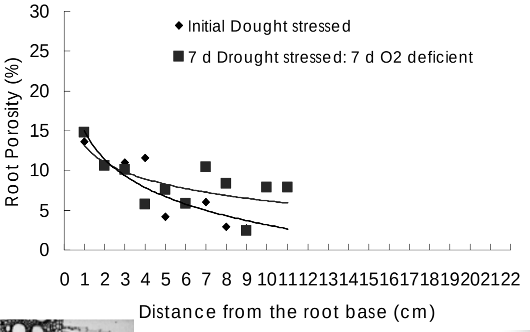
  A thin standing water layer exists throughout the growing season, except for transplanting, end of effective tillering, and at heading (flowering) stage

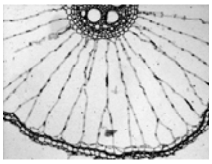
- ☐ Aerobic rice

  To grow rice like an irrigated upland crop such as wheat or maize , that is on non-puddled, aerobic soil without standing water

Aerenchyma development under soil moisture fluctuations

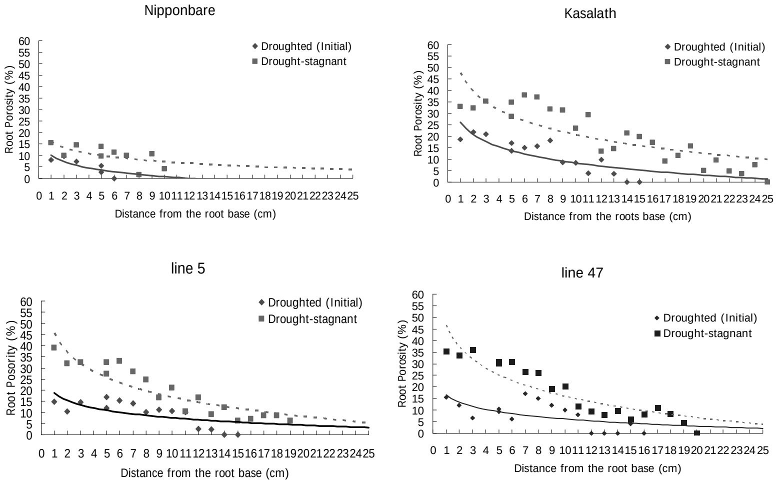






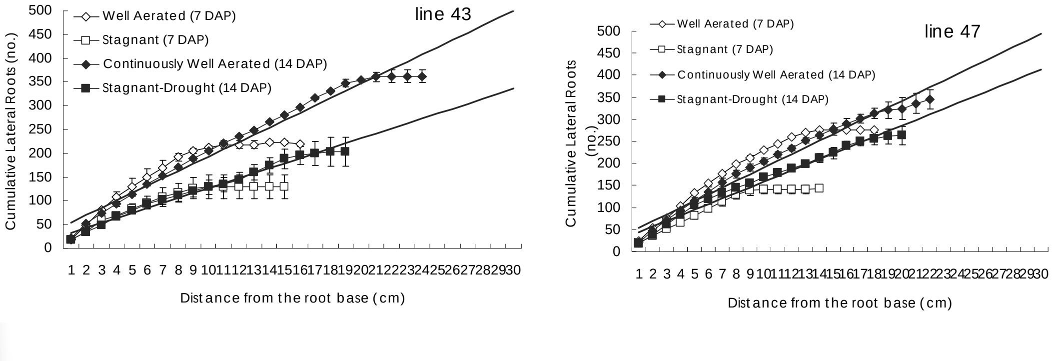
Source:
Suralta and Yamauchi 2008.
Environ Exp Bot 64:75–82.

Aerenchyma development: genotypic difference



Root porosity along seminal root axis selected lines and parents under transient drought stressed-stagnant conditions.

Lateral root development

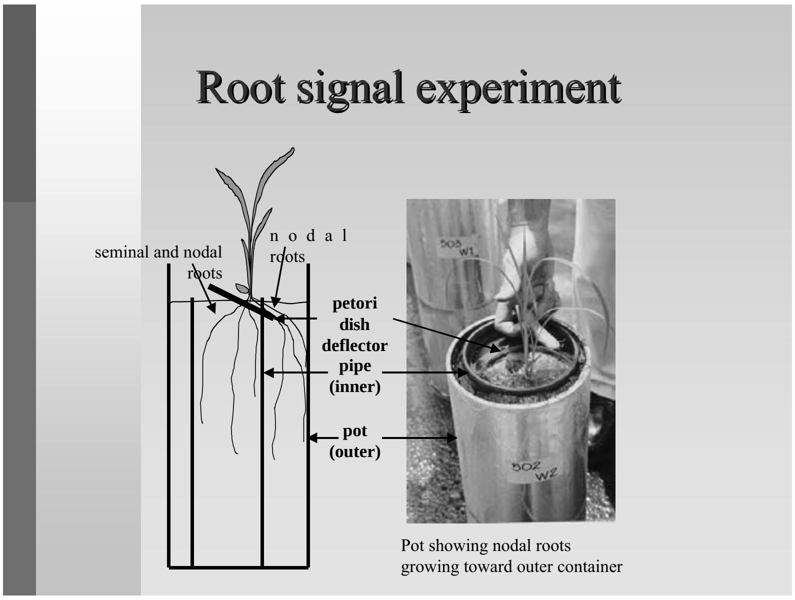


Lateral root development along seminal root axis of selected lines and parents under transient stagnant-drought stressed conditions.

Source: Suralta et al. 2008. Plant Prod. Sci. 11: 457-465.

Experiment on drought responses at IRRI

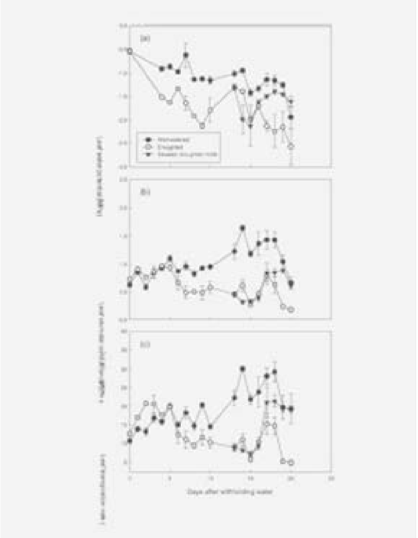
Soil heterogeneity-root signal



Root signal experiment

Pot showing nodal roots growing toward outer container

Stomatal response to soil drought

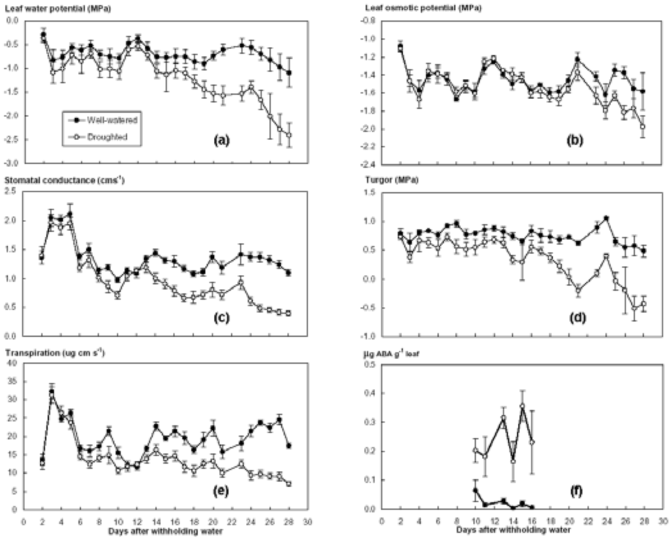


Source:

Siopongco et al. 2008.
Plant Prod. Sci. 11: 28-41.

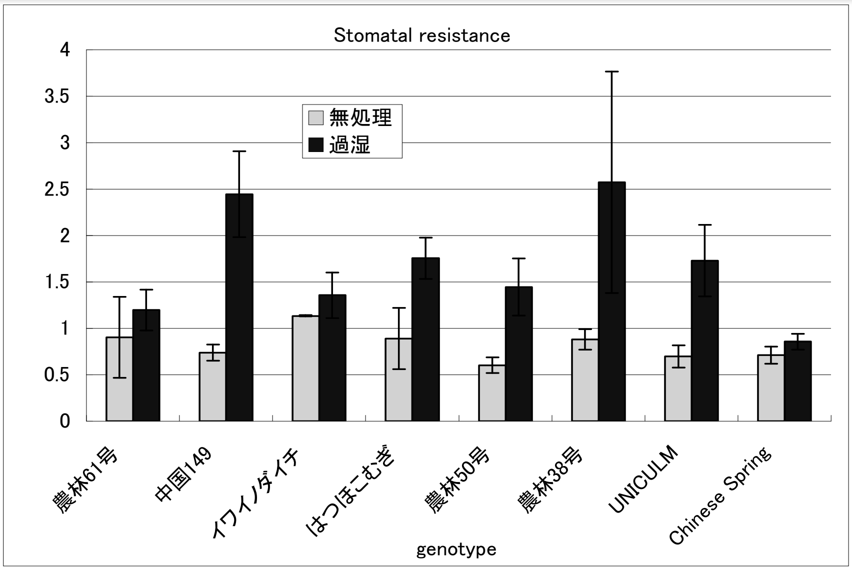
Confirmation by field experiment

Root signal

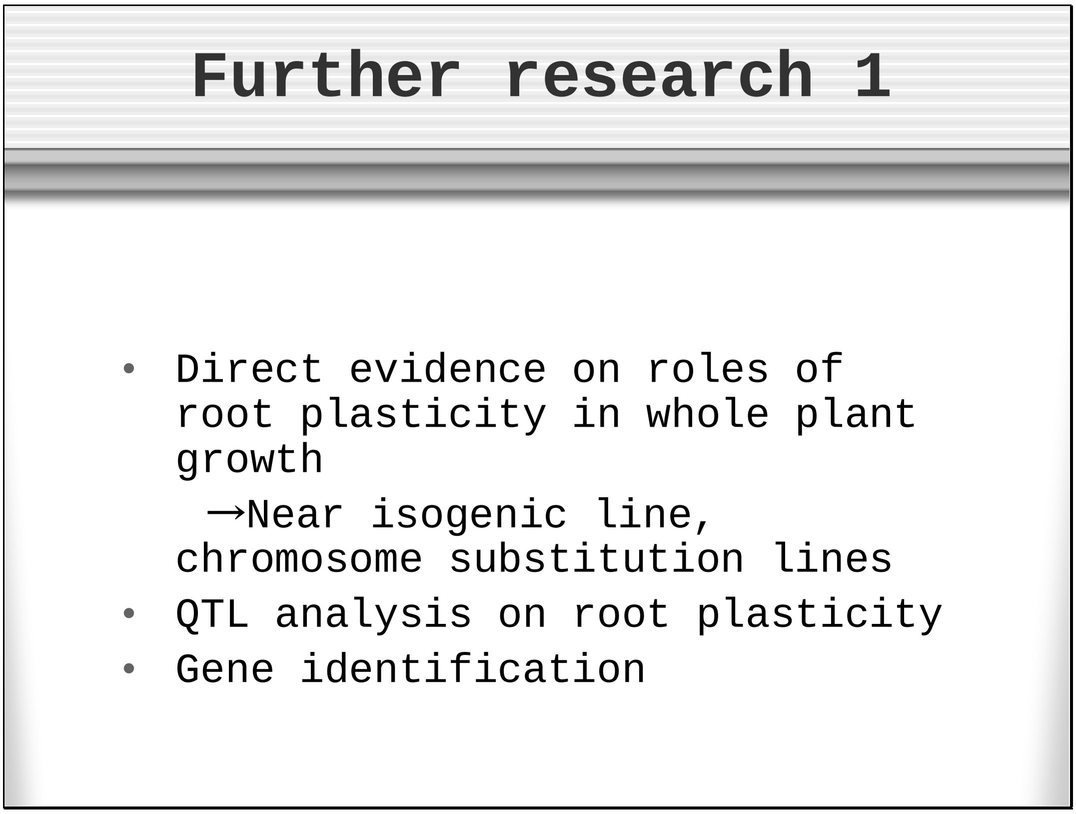


Source: Siopongco et al. 2009. Plant Prod. Sci. 12 (1): 17-28.

Stomatal response to waterlogging in wheat

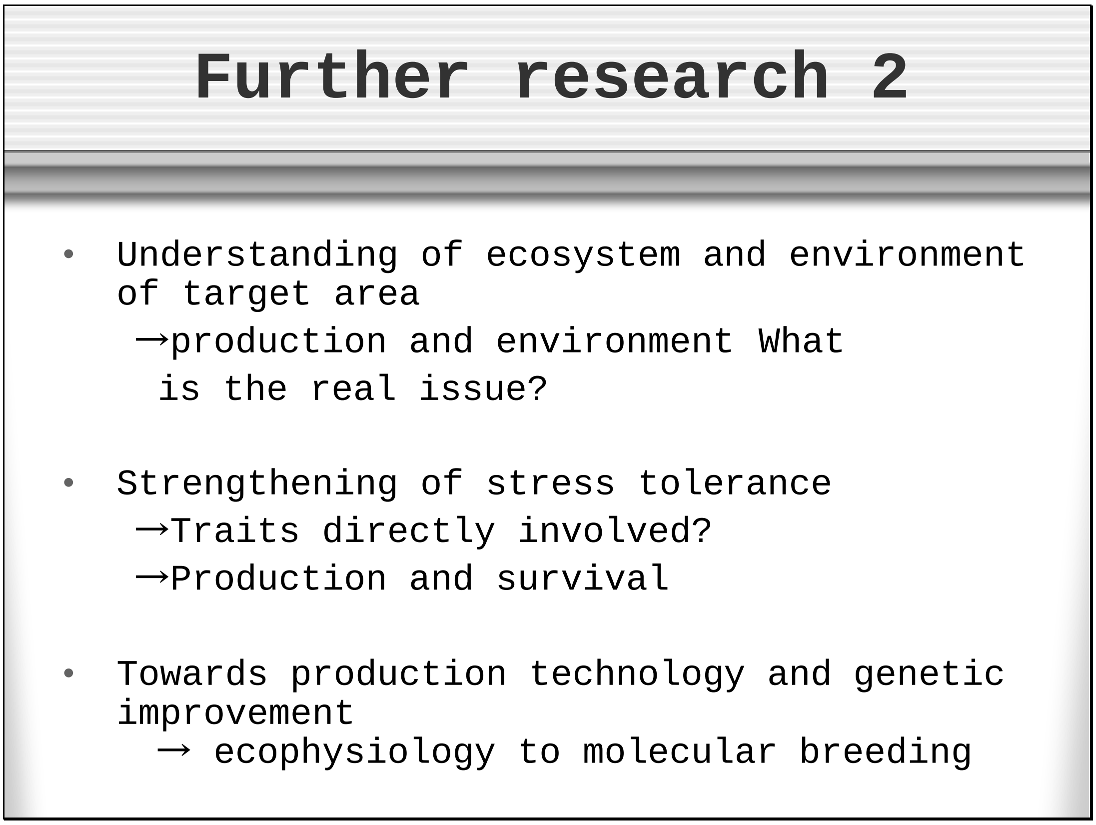


Source: Okada et al. 2007 Root Research 16(4):191



Further research 1

- Direct evidence on roles of root plasticity in whole plant growth
  →Near isogenic line, chromosome substitution lines
- QTL analysis on root plasticity
- Gene identification



Further research 2

- Understanding of ecosystem and environment of target area
  →production and environment What is the real issue?

- Strengthening of stress tolerance
  →Traits directly involved?
  →Production and survival

- Towards production technology and genetic improvement
  → ecophysiology to molecular breeding

質疑応答
Question and Answer Session

根からみた作物の水ストレス耐性
Role of Roots in Relation to Water Stress Tolerance of Crop

山内　章　Akira Yamauchi
名古屋大学農学国際教育協力研究センター
Professor, Graduate School of Bioagricultural Sciences, Nagoya University

司会：浅沼　修一　Chair person: Shuichi Asanuma
名古屋大学農学国際教育協力研究センター
Professor, ICCAE, Nagoya University

Asanuma, Chair:

Thank you very much Professor Yamauchi.　It is very fresh idea to me that not only continuous drought is important but further important is fluctuation of soil moisture condition between drought and water stress, and response of plant roots to the fluctuated moisture conditions.

Do you have any questions?

Koyama:

My name is Koyama from JIRCAS.　You showed us about the water requirements.　That of rice is higher, two or three times higher, than maize.　I think it's O.K., but does that mean rice is not suitable for dry areas?　If it's not really suitable, we should not promote it in those areas.　What is the base of this calculation?　Is this based on the normal practice, or?

Yamauchi:

This value was cited from the work of the International Rice Research Institute. This one, the water requirement of rice includes the evaporation from the paddy rice field and the seepage of water to the deeper soil.　This calculation is based on the irrigated rice production with continuously flooded conditions that we normally know especially in this country, Japan.　We also have the data for maize that of course are grown under upland conditions with sufficient irrigation for comparison. Several years ago, I also tried to compare the water requirement and water use efficiency that is the dry matter production ability per unit amount of water used. And the rice was among all the cereal crops examined weakest to water shortage. It requires water most among the major cereal species examined.

There is a very serious conflict of water usage for rice in industrial sectors and agriculture, and it is now happening especially in China and other developing countries.　So, we really have to try to reduce the water use.　So, instead of continuous flooding conditions, alternative technologies that can reduce water use are being produced as we may not need continuous flooded conditions for rice production.　Results of long-time experiment show that we can not avoid yield penalty under wet-and-dry cycle conditions, which most of the water-saving technologies so far proposed contain.　So, we're trying to find mechanisms as to why the rice suffers from the yield penalty under the alternative wet-and-dry irrigation system.

Asanuma, Chair:

Any other questions?　Professor Yamauchi, do you have any data or idea about the difference in water requirements between upland rice and maize? We are now talking about continuous flooded conditions that water requirement of rice may be four or five times higher than maize.　But when water requirements are compared between upland rice and maize, which requires more?

Yamauchi:

Though I do not have data available for the comparison at the moment, I do not think they are much different if grown under the same upland field conditions. Dr. Onyango, do you have any idea which produces more dry matter and requires more water?

Asanuma, Chair:

We ICCAE invited a researcher from KARI Kibos of Kenya early this year who told us that during the drought conditions of the last year, the upland rice NERICA grew better than the maize. She said, "I would think maybe the NERICA rice is more tolerant to the fluctuation of soil moisture conditions, and of course it depends on the rainfall time of the regions".

Onyango:

I think from Professor Asanuma's statement, some information was not provided for the KARI Kibos statement on NERICA water requirement. The trial was during the short rain season and the rainfall was erratic. However, there was heavy rainfall for about one week which flooded the fields. During the floods, maize was affected more than rice and as a result the production of maize was reduced more than rice. Genotypically even upland rice will recover faster than maize from the anoxia conditions imposed by short duration of flooding. Generally rice is relatively heavy feeder in terms of water requirements.

Asanuma, Chair:

Thank you very much for your correction.　If there is no other question, let me close this session.　Thank you very much, Professor Yamauchi.

Profile

山内 章 **Akira Yamauchi**

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1987年名古屋大学大学院農学研究科博士課程満期退学。1988年名古屋大学より農学博士学位。1988年9月からテキサス工科大学農学部、続いてテキサス農工大学ブラックランド研究所にてポストドクトラルフェローとして、作物根の水吸収メカニズム、可塑性の研究に従事。1990年から名古屋大学農学部で作物学の助手、1992年から助教授、1999年から循環資源学教授、2007年から名古屋大学農学国際教育協力研究センター長に就任し、現在に至る。

この間一貫して、ストレス生理学、ならびに作物根の発育や機能を生理生態学的、さらには遺伝学的側面から明らかにする研究に従事してきた。また、レイテ州立大学（フィリピン）、国際イネ研究所などと共同研究を展開してきた。専門分野は作物生理生態学。

Academic career

Professor Yamauchi received Ph.D. in 1988 from Graduate School of Agricultural Sciences, Nagoya University.

Professional career

Professor Akira Yamauchi joined Texas Tech University as a post-doctoral research scientist, and Blackland Research Center of Texas A & M University, where he studied water uptake mechanism of plant root.

Professor Yamauchi started to work for School of Agricultural Sciences, Nagoya University as an assistant professor in 1990 and an associate professor in 1994 for crop science. His research work has been mainly on crop stress physiology and root system development and functions from physiological, ecological and genetic aspects in collaboration with other institutes such as Leyte State University (Philippines) and International Rice Research Institute. Since 1999, he has been working as Professor, the Division of Biosphere Resources Cycling, Nagoya University, and Director of International Cooperation Center for Agricultural Education, Nagoya University since 2007.