

Phenotypic plasticity of rice seedlings: case of p deficiency

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Abstract

Plant morphogenesis is subject to environmental influence. The underlying control mechanisms are of great interest for crop improvement. A phytotron study on Nippon Bare rice seedlings was conducted to analyze the effects of P deficiency on plant organogenesis (tiller and leaf appearance, root apex number) and allometric relationships (root/shoot weight ratio, specific leaf area (SLA) and specific root length (SRL), leaf blade/sheath length ratio). The results confirmed that the main effect of P deficiency is a reduction of shoot growth to the benefit of the root system. This phenomenon, apparently caused by a reduction in leaf elongation rate without changing final leaf size, explains other changes in morphogenesis, such as longer phyllochron (because leaves take longer to expand) and lower tillering rate (because tillering is largely under trophic control). Allometric parameters such as SLA, SLR, root apex number per unit length and leaf blade/sheath length ratios remained stable. Further studies on the genetic control of phenotypic plasticity are suggested.

Media summary

Environment influences plant morphology. This phenotypic plasticity was studied in young rice plants using P deficiency as “deforming” factor, in order to understand the genetic and physiological control of morphogenesis. Emphasis was on root-shoot assimilate partitioning and rate of organ appearance.

Key Words

Nippon Bare, *Oryza sativa* L., Assimilate partitioning, Phyllochron, Tillering, Root-Shoot ratio

Introduction

According to the functional balance theory, a plant optimises its strategy of biomass partitioning between roots and shoots, respectively involved in the acquisition of edaphic and aboveground resources (Brouwer, 1983). This serves to (i) allocating more biomass to organs acquiring the most limiting resource (Bloom et al., 1985) and (ii) adapting plant compartment size (and thus demand) to resource availability (Brouwer, 1983; Reich, 2001). This dynamic response to environment is an expression of the plants' phenotypic plasticity (Dingkuhn, 1996; Poorter and Nagel, 2000). Phenotypic plasticity varies among species and genotypes (Wissuwa and Ae, 2001). It is particularly crucial during vegetative stages to ensure early vigor, when plants colonize the spaces and resources and are potentially prone to weedy competitors (Caton et al., 2003; Suzuki et al., 2002). This has become a challenge for crop breeding, for example in upland rice (Dingkuhn et al., 1999).

The objective of this study is to identify morphogenetic processes that show strong phenotypic plasticity in rice at the root and shoot levels, and to describe them in terms of the underlying organogenesis and sink dynamics. As environmental factor, P deficiency was used because it is known to affect both organogenesis and biomass partitioning, generally in favor of the root system (Poorter and Nagel, 2000). Focus is on early vegetative development of Nippon Bare (*Oryza sativa* L.), the genotype sequenced by the rice genome project. The study is part of efforts to develop gene-to-phenome models of crop phenotypic plasticity, simulating plant architecture on the basis of meristem behavior.

Methods

Two experiments were carried in controlled environments at CIRAD (Montpellier, France) in 2003 on the Nippon Bare cv. (*Oryza sativa* L.). Exp1 characterized changes in morphogenesis, particularly with respect of root to shoot relationships, induced by P deficiency, and sought to relate them to tissue sugar and P concentration. With Exp2 we sought to determine whether effects on tillering of P deficiency can be explained with the generic, linear relationship between Relative Tillering Rate (RTR) and the Relative Growth Rate (RGR) that has previously been interpreted as evidence that tillering rate generally a function of assimilate supply (Dingkuhn et al., 1999).

Grains were pre-germinated (3 days at 33°C) and then seeded and grown in a phytotron (RH 70%, night/day air temperature: 23/27 °C, 9/15 h photoperiod, HQI NDL lamps providing 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR) in 1-liter pots filled with sand. Plants were irrigated daily with a complete nutrient solution. Treatments were optimal nutrition (P+) and phosphorus deficiency (P-), with P concentration reduced to 1/40 ($9\ \mu\text{mol}\cdot\text{l}^{-1}$) applied from 7 Days After Sowing (DAS) onwards. Treatments were repeated 4 times. Measurements on plants are detailed in Table 1.

Table 1. Measurement schedule (days after sowing) and derived variables (underlined) for Exp 1 and 2.

| Measurement (instruments) and <u>estimated variables</u> | Exp1 (DAS) | Exp2 (DAS) |
|---|-------------------|-----------------------|
| Fresh & dry matter - <u>Relative Growth Rate, RGR</u> , (Tivet et al., 2001) | 7, 10, 15, 28 | 7, 15, 20, 25, 30, 35 |
| Blades elongation rate (length L & width w), <u>Leaf Area Index (LAI)+ Specific Leaf Area (SLA in cm²/g)</u> | Daily | No |
| Leaf appearance : <u>Phyllochron, ϕd^{-1}</u> | Daily | No |
| Tillering : <u>Relative tillering Rate, RTR</u> , (Tivet et al., 2001) | Daily | Daily |
| Plant height | 7, 10, 15, 28 | No |
| P content (Shoot and root) | 7, 10, 15, 28 | No |
| Sugar content (shoot and root) | 7, 10, 15, 28 | No |
| Root architecture (Winrhizo soft., pro Regent Instrument, Quebec) <u>± Specific Root Length (mm/g)</u> | 7, 19, 15, 28 | No |

Results and discussion

Aboveground growth relationships

Under P deficiency, phyllochron increased by 20 % (Figure 1a). This might be either due to slower development (plastochron) or slower leaf elongation prior to tip appearance. Final leaf length, however, was not affected (Figure 1b), whereas the post-appearance leaf elongation rate was slightly reduced for the 6th position and above on the main stem (not shown). This might indicate that final leaf length is determined at or early after leaf initiation (Tivet et al., 2001) and thus happened before P deficiency could

affect it, whereas leaf elongation rate remains responsive to the stress. The longer phyllochron in P- could thus be an effect of leaf elongation rate and the resulting time it takes for a leaf to attain its final length. Whether there is an additional effect of P- on plastochron remains open. Tillering rate was significantly reduced by P-, both when calculated on the basis of absolute time or even when normalizing the number of emerged tillers per leaves number on the main stem, as an index developmental stage (leaf appearance) (Figure 2a). Tillering is known to strongly depend on aboveground relative growth rate RGR (Dingkuhn et al., 1999), and the question is here whether the P- effect is a result of growth reduction or affects tiller initiation more directly. The classical RTR/RGR plot (Fig. 2b) indicated that the P- effect is trophic (growth and thus assimilation related), although the large experimental error provided no certain answer.

Allometric relationships

Considering roots and shoots separately, several allometric relationships remained unaltered by P- (Figure 3a: SLA, 3b: SRL). This was also the case for the dry weight ratios between leaf blades and sheaths (B/S) and roots architectural parameters such as apex number per length unit (not shown). The only allometric relationship that showed plasticity was the root/shoot dry weight ratio (R/S) which was increased very strongly in P- (e.g. in Exp 2, from 0.69 (8 DAS) to 0.50 and 0.75 (33 DAS) respectively in P+ and P-). Wissuwa and Ae (2001) reported that R/S is controlled by one or several genes induced by the environment such as P deficiency. This change in assimilate partitioning might indirectly affect tillering through an over-proportional reduction of aboveground growth under P-. This, in turn, affects a number of other root-shoot allometries, such as root apex number per tiller, which increased significantly under P-. This phenomenon resembles the development of cluster roots under P deficiency observed in other species (He et al., 2003; Shane et al., 2003).

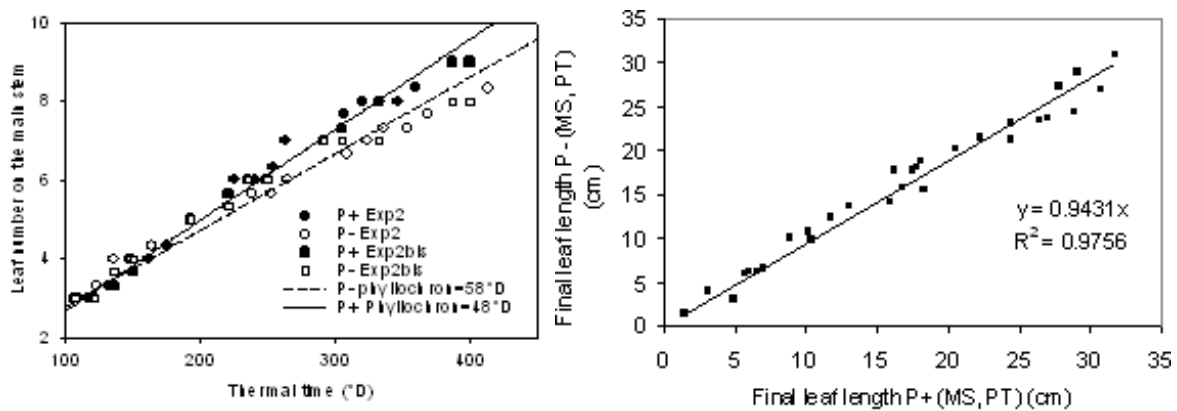


Figure 1: (a) Comparison between the phyllochron in P- and P+ (Exp1 until 28 DAS). (b) Relationship between final leaf length in P+ and P- for leaves on the main stem (MS) and primary tillers (Exp1).

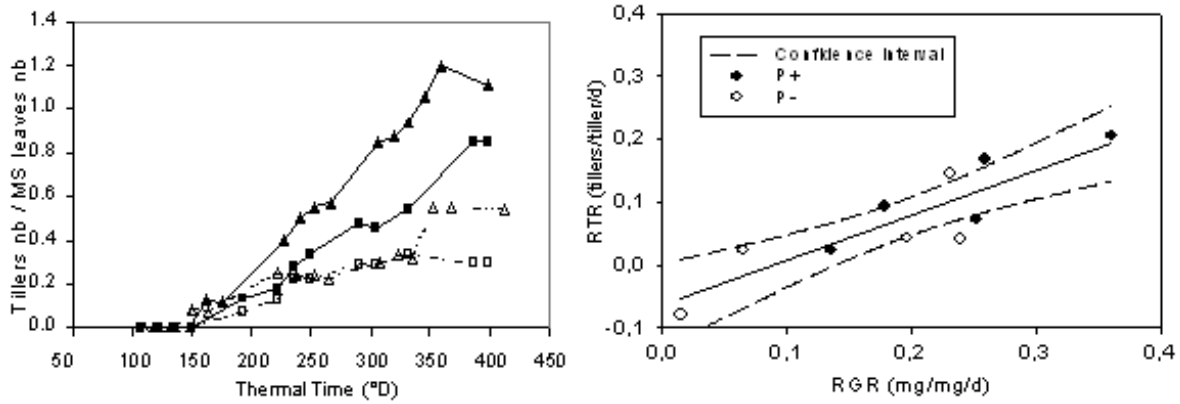


Figure 2: (a) Evolution of tillers number normalized by leaf number on the MS (Exp1). (b) Relationship between averaged RGR and RTR (Exp2; 95% confidence intervals for all data).

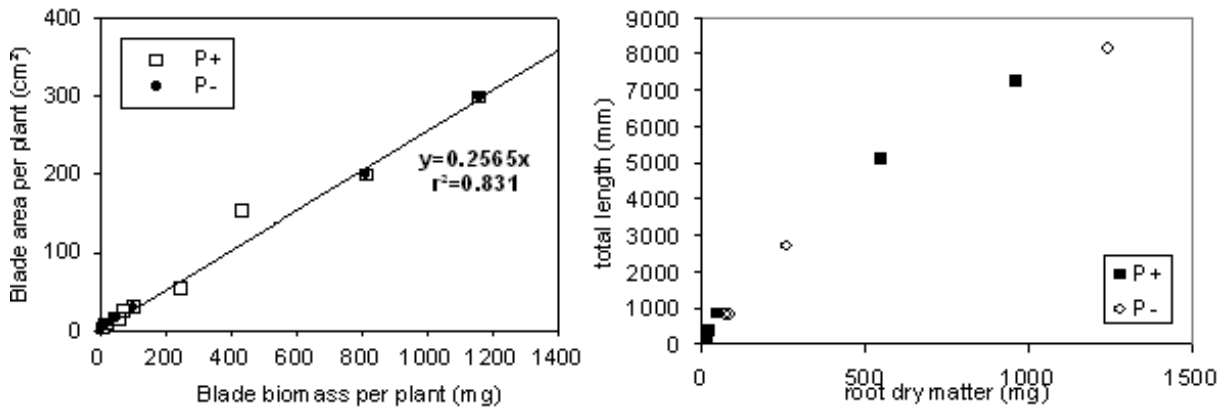


Figure 3: (a) Relationship between plant leaf area and biomass. (b) Relationship between root total length and biomass; in P+ and P- conditions (Exp1: 7, 10, 15 and 28 DAS).

Root and shoot sugar content

In both treatments shoot P concentration decreased after 10 DAS, but more rapidly in P- plants. Root P concentration responded immediately to the P- treatment (not shown). Root and shoot sucrose concentration decreased under P deficiency at 10 DAS, simultaneously with shoot P concentration. Thereafter, under P-, shoot sucrose concentration decreased gradually while roots sucrose content increases towards the values observed under P+. The resulting root/shoot sucrose concentration ratios (Figure 4) decreased for P+ and strongly increased for P-, probably indicating enhanced transport of sucrose to the sinks in the root. Shane et al. (2003) suggested that a critical shoot P concentration exists below which root growth is stimulated. Our results indicate that indeed, root growth stimulation under P- (relative to shoot) is brought about by lower assimilate demand in the shoot, and thus greater export, as opposed to increased sink activity in the root. This phenomenon seems to potentially explain all the morphological effects of P- observed in this study.

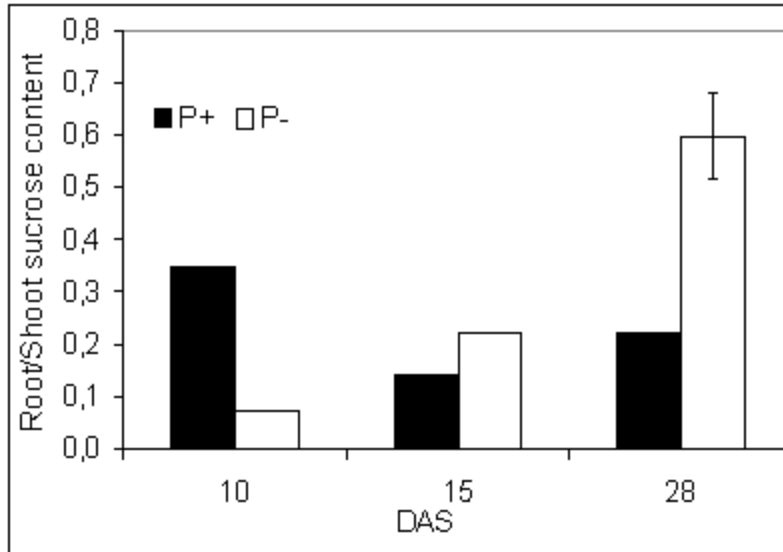


Figure 4: Sucrose contents ratio between roots and shoots, in P+ and P- treatments (Exp1 and 1bis).

Conclusion

This study aimed at analyzing the phenotypic plasticity of rice seedlings exhibited under variable P resources, a factor that is known to change plant morphology. The results confirmed that one of the main effects of P deficiency is a reduction of shoot growth to the benefit of the root system. It seems that this phenomenon, apparently brought about by a reduction in leaf elongation rate without changing final leaf size, explains all or much of the other changes in morphology and architecture, such as longer phyllochron (because leaves take longer to expand) and lower tillering rate (because tillering is largely under trophic control). Allometric parameters such as SLA, SLR, root apex number per unit length and leaf blade/sheath length ratios remained remarkably stable. However, further studies on leaf initiation rate at meristem level and observations on older plants are necessary to confirm the robustness of these results. As a next step, further studies should characterize the genetic control of the observed phenotypic plasticity, for example, whether the underlying mechanism is generic (across different stresses) or specific to P deficiency. A generic, inducible mechanism for root-shoot sink control would be of great interest for crop improvement.

References

- Brouwer, R., (1983). Functional equilibrium: sense or nonsense? *Netherlands Journal of Agricultural Science*, 31: 335-368.
- Caton, B.P., Cope, A.E. and Mortimer, M., (2003). Growth traits of diverse rice cultivars under severe competition: implications for screening for competitiveness. *Field Crop Research*, 83: 157-172.
- Dingkuhn, M., (1996). Modelling concepts for the phenotypic plasticity of dry matter and nitrogen partitioning in rice. *Agricultural Systems*, 52(2/3): 383-397.
- Dingkuhn, M., Johnson, D.E., Sow, A. and Audebert, A.Y., (1999). Relationships between upland rice canopy characteristics and weed competitiveness. *Field Crop Research*, 61(1): 79-95.
- He, Y., Liao, H. and Yan, X., (2003). Localized supply of phosphorus induces root morphological and architectural changes of rice in split and stratified soil cultures. *Plant and soil*, 248: 241-248.

Poorter, H. and Nagel, O., (2000). The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients and water: a quantitative review. *Australian Journal of Plant Physiology*, 27: 595-607.

Reich, P.B., (2001). Root-shoot relations: optimality in acclimation and adaptation or the "emperor's new clothes"? In: E.Y.a.K.U. Weisel Y (Editor), *Plant roots, the hidden half*. Marcel Dekker, New York, pp. 205-220.

Shane, M.W., Vos, M.D., Roock, S.D. and Lambers, H., (2003). Shoot P status regulates cluster-root growth and citrate exudation in *Lupinus albus* grown with a derived root system. *Plant, Cell and Environment*, 26: 265-273.

Suzuki, T., Shiraiwa, T. and Horie, T., (2002). Competitiveness of four rice cultivars against Barnyardgrass, *Echinochloa* tolerance to phosphorus deficiency in rice and the potential for its exploitation in rice improvement. *Plant Breeding*, 120: 43-48.

Tivet, F., Pinheiro, B.D.S. and Dingkuhn, M., (2001). Leaf blade dimensions of rice (*Oryza sativa* L. and *Oryza glaberrima* Steud.). Relationships between tillers and the main stem. *Annals of botany*, 88: 507-511.

Wissuwa, M. and N. Ae, (2001). Genotypic variation for tolerance to phosphorus deficiency in rice and the potential for its exploitation in rice improvement. *Plant Breeding*. 120: 43-48.