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*** Manuscript**

Rhizoeconomics: carbon costs of phosphorus acquisition

Running title: Rhizoeconomics

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Abstract

Plants have evolved a wide array of physiological adaptations to low soil phosphorus availability. Here we discuss metabolic and ecological costs associated with these strategies, focusing on the carbon costs of root traits related to phosphorus acquisition in crop plants. We propose that such costs are an important component of adaptation to low phosphorus soils. In common bean, genotypes with superior low phosphorus adaptation express traits that reduce the respiratory burden of root growth, including greater allocation to metabolically inexpensive root classes, such as adventitious roots, and greater formation of cortical aerenchyma, which reduces specific root respiration. Root hair formation increases phosphorus acquisition at minimal carbon cost, but may have other unknown ecological costs. Mycorrhizas and root exudates enhance phosphorus acquisition in some taxa, but at significant carbon cost. Root architectural patterns that enhance topsoil foraging enhance phosphorus acquisition but appear to incur tradeoffs for water acquisition. A better understanding of the metabolic and ecological costs associated with phosphorus acquisition strategies is needed for an intelligent deployment of such traits in crop improvement programs.

Introduction

Low phosphorus availability is a primary constraint to plant growth on earth (Lynch and Deikman 1998). Plants have evolved a diverse array of mechanisms by which to obtain adequate phosphorus under limiting conditions, including mycorrhizal symbioses, rhizosphere modification with organic acids, protons and enzymes, upregulation of phosphate translocators, and specific adaptations of root morphology and architecture (Raghothama 1999; Vance et al. 2003). Other adaptations increase efficient metabolic use of phosphorus within the plant, such as decreased growth rate, increased growth rate per unit of phosphorus uptake, remobilization of internal phosphorus, modifications in carbon metabolism and alternative respiratory pathways. While the value of these traits for phosphorus acquisition and conservation is the subject of a large and growing literature, relatively few studies have addressed the metabolic and ecological costs associated with these traits, which are an important aspect of their overall value for plant adaptation to low phosphorus soils. Our research with common bean suggests that consideration of the costs associated with specific root strategies is critical in understanding the physiological basis of adaptation to low phosphorus availability ("phosphorus efficiency"). The goals of this paper are 1) to discuss the importance of root carbon costs for plant growth under low phosphorus; and 2) to consider the idea that in addition to mechanisms for increased phosphorus uptake, adapted genotypes may also have mechanisms to reduce the carbon cost associated with phosphorus acquisition, which can result in increased phosphorus use efficiency and productivity in low phosphorus environments.

Economic analogies for phosphorus acquisition

The processes of plant growth, resource allocation, and acquisition of multiple resources have many principles analogous to optimization theory in economics (Bloom et al. 1985). When considered as economic entities with limited internal resources and constrained availability of external resources, it can be seen that plants face 'choices' in resource allocation that are likely to entail tradeoffs or opportunity costs. For example, increased carbon allocation to roots in phosphorus-limited plants bears the opportunity cost of reduced allocation to photosynthesis and reproduction. The optimization of resource allocation for growth or reproduction is well suited to economic analysis. One useful concept in this regard is that optimal allocation of internal resources should result in a situation in which no single external resource is limiting. To return to our previous example, this would result in a balance of root and shoot growth in which phosphorus and carbon were equally limiting to plant growth- a situation in which phosphorus was strongly limiting would imply that the plant had suboptimal investment in root growth, whereas a plant in which carbon was strongly limiting had suboptimal investment in shoot growth. In the plant ecology literature, this concept has been termed the Multiple Limitation Hypothesis (Bloom et al. 1985; Chapin et al. 1987; Gleeson and Tilman 1992; Van der Berg 1998). The Multiple Limitation Hypothesis appears to be valid for some, but not all mineral nutrients (Rubio et al. 2003b). The marginal rate of substitution describes the change of one quantity required to substitute for another in order to maintain the same production level, and is equal to the ratio of the marginal products for the two resources. Exchange ratios between two resources, defined as the relative amount of two resources that can be acquired for a given expenditure of reserve, depend primarily on the supply of resources, their demand and the type of reserve being expended, and may thus be a more important parameter to consider than the absolute costs. As a nutrient resource becomes increasingly limiting, economic considerations are simplified as acquisition and retention of the limiting nutrient override other concerns, and the "Law of the Minimum" holds sway (see references in Rubio et al., 2003).

These economic concepts are useful in assessing the adaptive value of traits associated with phosphorus acquisition. Traits enhancing phosphorus acquisition may actually decrease adaptation and competitiveness in low phosphorus environments, if the costs of those traits exceed the benefits of improved phosphorus uptake in that environment. This is particularly true for crop species, in which growth and reproduction, rather than mere plant survival, are valued.

Carbon as an economic currency

Economic analyses of plant resource acquisition strategies are simplified by the definition of a common currency with which to assess exchange values of diverse resources. In the case of phosphorus stress, the most direct currency is phosphorus itself, or growth parameters related to phosphorus accumulation (Koide and Elliott 1989; Koide et al. 2000). While useful insights can be gained from this approach, we will focus here on carbon as a currency for assessing plant resource allocation. Carbon has several merits in this regard, including direct involvement with the dynamics of both photosynthesis and respiration, whereas phosphorus is more static, i.e. the phosphorus content of an organ does not reveal the respiration or photosynthetic output of that organ. A related point is that the duration of resource commitment to a process is an important aspect of the metabolic cost of that investment, and carbon budgets provide a convenient metric of that investment (Lynch and Rodriguez 1994). Tissue phosphorus content is more static and thus does not readily reflect the temporal dimension of the metabolic cost of phosphorus allocation.

Respiration has often been considered in terms of a two-component functional model of growth respiration and maintenance respiration (Amthor 2000; Lambers et al.

2002). Growth respiration is usually associated with synthesis of new structural biomass, while maintenance respiration is usually associated with maintenance of tissues, enzymes, membrane potential and ion transport and is proportional to existing biomass. The respiration costs associated with ion uptake are also typically considered for roots. Carbon expended in root respiration is substantial and can amount from 8 to over 50% of daily net photosynthesis (Lambers et al. 2002). Low phosphorus availability typically increases the root to shoot ratio, and thereby increases the proportion of daily photosynthate devoted to root respiration (Nielsen et al. 1998; Nielsen et al. 2001).

Costs of phosphorus acquisition can be substantial

Root exudates

Scarcely soluble phosphorus sources in the rhizosphere can be mobilized through the action of root exudates, including protons, phosphatases, and organic acids (Hinsinger 2001). The metabolic costs of the production of phosphatases and enhanced proton efflux are unknown. The formation of additional phosphatases is likely to be a small part of overall protein synthesis and turnover. Rhizosphere acidification in response to phosphorus stress can arise by various means (Hinsinger et al. 2003), an important one being direct proton exudation, which requires ATP hydrolysis at the plasmamembrane through the action of H-ATPases (Smith 2001; Vance et al. 2003). The additional ATP cost of accelerated H pumping under phosphorus stress has not been quantified but could be significant. Root exudates in general represent about half of all belowground carbon allocation, with great variability (Nguyen 2003). The exudation of organic acids such as malate and citrate is stimulated by phosphorus stress in some species, especially nonmycorrhizal species such as Lupin and Brassicas (Hinsinger 2001; Jones 1998; Ryan et al. 2001). In nonproteoid species, exudation occurs primarily near the root apices, whereas in proteoid species, exudation derives primarily from localized cluster roots having dense lateral branching and abundant root hairs (Dinkelaker et al. 1995). Metabolic investment in these exudates can be substantial- in proteoid species, exudates can represent 5 to 25% of photosynthate production and can exceed 20% of total plant dry weight (Dinkelaker et al. 1989; Gardner et al. 1983; Johnson et al. 1996a; Johnson et al. 1996b). In lupins, phloem-translocated sugars account for about 70% of the carbon source for exudates, the remainder coming from direct root carbon fixation via PEP carboxylase (Johnson et al. 1996a; Johnson et al. 1996b). In rice, exudates induced by phosphorus stress amounted to 2-3 % of total plant biomass (Kirk et al. 1999). Plants that have been transgenically modified to increase organic acid exudation do not show growth reduction (Lopez-Bucio et al. 2000), but these studies have not typically included rigorous cost assessments.

Clearly, some species and genotypes expend substantial metabolic energy and fixed carbon resources in producing root exudates. This is most evident in the case of species that form proteoid or cluster roots. The species that form cluster roots are generally nonmycorrhizal, and inhabit soils with extremely low phosphorus availability (Neumann and Martinoia 2002). In this situation, the strategy of these species is to emphasize intensive soil mining *in situ* rather than exploring larger soil volumes for phosphorus enriched microdomains (since they are uncommon in these soils). Because of the severity of phosphorus stress, the metabolic value of phosphorus becomes substantially larger than the metabolic value of carbon, in other words, their strategy is basically to acquire phosphorus at any cost. The absence of mycorrhizas in most cluster root species could be interpreted as a means of reducing metabolic costs of phosphorus acquisition, given the cost of forming cluster roots. An interesting feature of exudates is that their value for phosphorus acquisition is ephemeral, since they have short residence times in the rhizosphere and may merely enhance phosphorus acquisition by rhizosphere microbes. The spatial localization of exudates production near the root apex, prior to the appearance of large microbial populations, may be one means of reducing such competition.

Membrane transport

The transport of inorganic phosphate across the plasma membrane is driven by cotransport with apoplastic protons generated by the H-ATPase (Smith 2001). While this represents a consumption of metabolic energy as represented in the proton motive force, it is probably small in natural soil due to the relatively small flux of phosphate across the plasma membrane in comparison with the flux of other ions. However, the net cost of phosphate uptake across the plasma membrane should take into account the fact that at realistic solution phosphate concentrations, the majority of phosphate taken up is leaked back out, due to the highly unfavorable electrochemical gradient for phosphate uptake (Elliott et al. 1984).

Mycorrhizal symbioses

The majority of higher plant species have mycorrhizal symbioses with fungi that assist nutrient acquisition (Smith and Read 1997). The VA mycorrhizas common in many annuals and hardwood species are particularly important for phosphorus acquisition, by expanding the volume of soil explored beyond the depletion zone surrounding the root itself. In exchange for phosphorus supplied to the plant, the fungal symbiont obtains reduced carbon. The carbon cost of mycorrhizal symbioses is therefore one component of the cost of phosphorus acquisition in most species. In bean, mycorrhizal colonization increased root phosphorus acquisition, but the resulting increase in shoot photosynthesis did not result in increased plant growth because of greater root respiration (Nielsen et al. 1998). At high phosphorus supply, mycorrhizal colonization reduced the growth of citrus seedlings because of greater root carbon cost (Peng et al. 1993). In general, the costs of the mycorrhizal symbiosis in various herbaceous and woody species ranges from 4 to 20% of daily net photosynthesis (Douds et al. 1988; Eissenstat et al. 1993; Harris and Paul 1987; Jakobsen and Rosendahl 1990; Koch and Johnson 1984; Nielsen et al. 1998). The greater metabolic burden of mycorrhizal roots may contribute to the nonbeneficial or even parasitic role that mycorrhizal fungi play in many agroecosystems (Ryan and Graham 2002).

Root hairs

Root hairs are subcellular extensions of the root epidermis that contribute to phosphorus acquisition by extending the zone of phosphorus depletion around roots (Foehse et al. 1991). Low phosphorus availability increases the length (Bates and Lynch 1996) and density (Ma et al. 2001a) of root hairs in a coordinated manner that is synergistic for phosphorus uptake (Ma et al. 2001b). Genetic variation among and within species for root hair length and density is associated with adaptation to low phosphorus availability (Bates and Lynch 2000a; Foehse and Jungk 1983; Gahoonia et al. 1999) and plant competitiveness in low phosphorus soil (Bates and Lynch 2001). A comparison of wild type and hairless Arabidopsis mutants showed that the presence of root hairs had no measurable effect on root respiration or plant performance at high phosphorus (Bates and Lynch 2000b), suggesting that the direct metabolic costs of root hairs are minimal. Since root hairs are extensions of epidermal cells, it is possible that they do not increase the cytoplasmic volume of the cell and so do not increase maintenance respiratory requirements *per se*, although they might increase respiration associated with ion uptake, which they facilitate. If root hairs do not incur significant metabolic costs, the large intraspecific variation observed in root hair formation is somewhat surprising- given the prevalence of low phosphorus soils we would expect that all genotypes would have abundant hairs. It is possible that long, dense root hairs have some unknown liabilities, such as increased susceptibility to soil pathogens. In bean, genetic markers associated with genotypic variation in root hair formation cosegregate with markers for organic acid exudation (X Yan and J Lynch, unpublished data). Therefore, the paucity of root hairs in some genotypes could represent a strategy to reduce carbon loss through exudates.

Increased allocation to roots

A third mechanism of increased phosphorus acquisition by plants is to emphasize root growth over shoot growth. Phosphorus deficient plants typically have higher root:shoot ratios than high-phosphorus plants, either because of allometric relationships (Niklas 1994) or because of increased biomass allocation to roots (Ciereszko et al. 1996; Gutschick 1993; Nielsen et al. 2001). Increased relative allocation to root growth is obviously beneficial for phosphorus acquisition, since phosphorus is relatively immobile in soil, but may slow overall plant growth because of the increased respiratory burden of root tissue (Hansen et al. 1998; Nielsen et al. 1998; Nielsen et al. 2001; Van der Werf et al. 1992).

Reich has recently emphasized that it is difficult to assess changes in belowground allocation from root:shoot ratios, since treatments such as low phosphorus availability result in plants of different size, which itself influences root:shoot ratio through allometry (Reich 2002). While this is true, it is also true that the actual root:shoot ratio integrated over time, rather than an allometric partitioning coefficient, determines the portion of daily photosynthate consumed by roots. In the case of bean, we have demonstrated root allocation through carbon budgets coupled with allometric analysis (Nielsen et al. 2001) as well as biomass distribution (Nielsen et al. 1998), and for the purposes of this discussion of root costs, consider both approaches to be valid.

In bean, growth reduction under phosphorus stress is associated with increased proportions of root biomass and reduced leaf appearance and expansion rates, rather than with decreased specific carbon assimilation by leaves (Ciereszko et al. 1996; Lynch et al. 1991; Nielsen et al. 2001). This pattern is consistent with the theory that carbon allocation balances tradeoffs for light and nutrient resources. Low phosphorus plants utilize a significantly larger fraction of their daytime net carbon assimilation on root respiration (c. 40%) compared to high phosphorus plants (c. 20%, Fig.1). Increased root carbon costs under phosphorus stress (because of a higher root/shoot ratio) may be an important component of reduced plant productivity.

There is increasing evidence that root architecture, the configuration of roots in space and time, is important for adaptation to low phosphorus environments (Lynch 1995; Lynch and Brown 2001). Root architecture determines the exploration and exploitation of localized phosphorus resources by the plant, and the distribution of roots relative to their neighbors within and among root systems. Since phosphorus availability is typically greater in surface horizons than in the subsoil (Anderson 1980; Chu and Chang 1966; Enwezor and Moore 1966; Keter and Ahn 1986; Pothuluri et al. 1986), architectural traits that enhance topsoil foraging can assist phosphorus acquisition (Lynch and Brown 2001). In bean, genotypes with enhanced topsoil foraging through adventitious rooting (Miller et al. 2003), and shallower basal root development (Bonser et al. 1996) have greater low phosphorus adaptation than genotypes with deeper rooting (Liao et al. 2001; Rubio et al. 2003a). This results from the colocalization of root foraging with phosphorus availability as well as reduced competition among roots of the same (Ge et al. 2000) or neighboring (Rubio et al. 2001) plants. An optimal root architecture for phosphorus acquisition is therefore one which enhances phosphorus acquisition at minimum carbon cost, or optimizes the value of the resources required for root growth, including phosphorus itself. Shallow-rooted bean genotypes can acquire substantially more phosphorus than deep-rooted genotypes under low phosphorus conditions (Fig. 2). These genotypes have similar rates of phosphorus absorption per unit root weight and plant growth per unit of phosphorus absorbed (unpublished data). Although these genotypes had equivalent whole root system respiration costs (Fig. 1), root respiration per unit of root growth was substantially lower in superior genotypes (Fig. 3), enabling them to sustain a greater root biomass at equivalent carbon cost (Fig. 4). In this instance the minimization of whole root system carbon costs appears to be an important component of adaptation to low phosphorus environments.

Reducing root carbon costs for efficient phosphorus acquisition

Alternative respiratory pathways

Mitochondrial respiration usually proceeds via the cytochrome-mediated pathway, which results in the phosphorylation of ADP to ATP (Lambers et al. 2002). In addition to the cytochrome pathway, two nonphosphorylating pathways exist in plant mitochondria, the cyanide resistant and rotenone-insensitive pathways, which allow respiration to proceed without depleting adenylate or phosphate pools concentrations, and are induced under phosphorus stress conditions (Rychter et al. 1992; Rychter and Mikulska 1990; Theodorou and Plaxton 1993). Phosphorus stress induces other alterations in the respiration of bean roots that appear to be related to oxidative stress (Malusa et al. 2002). It is not known if genotypic differences in root respiration under phosphorus stress are related to differential induction of alternate respiratory pathways.

Shifting biomass allocation to more metabolically efficient root classes

Another potential mechanism of cost minimization in low phosphorus soil is to shift biomass allocation to more metabolically efficient root classes. In this context, metabolic efficiency refers to the carbon cost of exploring soil beyond the existing phosphorus depletion zone. In annual dicots there are several developmentally and physiologically distinct root classes, including adventitious, basal and tap roots, and their associated lateral roots (Zobel 1992). Under low phosphorus conditions, phosphorus-efficient genotypes shift root biomass allocation to favor adventitious roots (Miller et al. 2003). In bean seedlings adventitious roots have greater specific root length and less linear construction cost than basal and tap roots (Fig. 5), meaning that adventitious roots can extend into new soil at less carbon cost than basal and tap roots. Adventitious roots have other advantages for phosphorus acquisition, including shallow growth, rapid radial dispersion from the shoot, dispersed lateral branching, and abundant aerenchyma (see below) and root hairs (Miller et al. 2003). In addition to shifting biomass to adventitious roots, phosphorus-efficient genotypes have reduced specific respiration for a given root class (Fig. 6), which in this case could be due to anatomical adaptations to low phosphorus availability that reduce root costs.

Anatomical adaptations to reduce root costs

Several anatomical traits might be associated with reduced metabolic costs of root growth. As discussed above, root hairs are very important for phosphorus acquisition yet appear to incur little direct metabolic cost. Various traits contribute to specific root length (SRL), the ratio of root length and root mass. Generally, greater SRL permits more efficient soil exploration, although this relationship is complicated by the interaction of SRL with resistance to biotic stress and with root lifespan (Eissenstat 1992). Specific root length is influenced by root diameter as well as root anatomy, or “tissue mass density” (Wahl and Ryser 2000). A dramatic anatomical adaptation to reduce tissue mass density is the formation of large air spaces or aerenchyma in the root cortex. Although aerenchyma is commonly regarded as an adaptation to hypoxia (Drew et al. 2000; Jackson and Armstrong 1999), it is also induced by low nitrogen or phosphorus availability in well-aerated roots of maize (Fig. 7; Drew et al. 1989; Konings and Verschuren 1980). This response is also observed in rice (Lu *et al.* 1999) and common bean (Eshel et al. 1995; Fan et al. 2003). In maize and bean, genotypes with superior adaptation to low phosphorus soil had greater aerenchyma formation, which proportionately reduced root tissue phosphorus content, and disproportionately reduced root respiration (Fig. 8; Fan et al. 2003). The disproportionate effect of aerenchyma on root respiration may be due to the fact that aerenchyma replaces metabolically active cortical cells and therefore increases the portion of root mass occupied by nonrespiring tissues such as sclerenchyma and mature xylem. Tradeoffs for aerenchyma formation are unknown, but might include reduced niches for mycorrhizal colonization or reduced radial transport of water and nutrients.

The multiplicative effect of reduced costs on plant growth

The adaptive benefits of reduced root costs are likely to well exceed the direct benefits of conserved carbon, because of the multiplicative effects of resource conservation and acquisition on plant growth rates. Any increase in phosphorus acquisition in early growth will permit greater shoot growth, greater root growth, and therefore additional increases in phosphorus acquisition. The potential magnitude of this compounding effect was recently shown by Wissuwa (Wissuwa 2003), who used a simulation model for rice to show that increasing root fineness by 22% resulted in a three-fold increase in overall plant growth under low phosphorus conditions. In this case 90% of the additional phosphorus acquired because of this trait was an indirect benefit arising from greater photosynthesis and greater overall plant growth. Although this was a modeling exercise, it demonstrates the magnitude of potential benefits in phosphorus acquisition from relatively small reductions in root costs. Benefits would be magnified further in competitive circumstances.

Opportunity costs of root strategies for phosphorus acquisition

One component of root costs in an organismic context relates to the ability to recover resources committed to unproductive roots. Leaves generally senesce if they become unproductive due to factors such as insufficient light or suboptimal temperature, and during leaf senescence key resources including nitrogen and phosphorus are remobilized for more productive use elsewhere in the plant, such as in more illuminated regions of the canopy, or in the case of monocarpic senescence, to reproduction. A split-root study with common bean showed that resource-driven senescence does not occur in roots- i.e. roots provided with water and calcium sulfate but no other nutrients continued to survive even in plants that were severely deficient in phosphorus, occupying phosphorus and carbon resources that could have been better used by other roots (Snapp and Lynch 1996). This result was later confirmed when minirhizotron observations showed that the lifespan (survivorship) of individual roots of common bean was not affected by phosphorus availability, and in contrast to leaves, roots survived beyond grain filling (Fisher et al. 2002). These results suggest that roots, unlike leaves, retain resources committed to them regardless of their productivity for the whole plant. Commitment of resources to roots may therefore represent greater potential opportunity costs for both vegetative growth and reproduction than commitment of resources to leaves.

As discussed above, root architectural traits that enhance exploitation of surface horizons, or topsoil foraging, also enhance phosphorus acquisition in most soils (Lynch and Brown 2001). An important tradeoff or opportunity cost to topsoil foraging is increased sensitivity to drought stress, since in many environments, water is a deep soil resource. Indeed, a comparison of deep-rooted and shallow-rooted bean genotypes in stratified substrates showed that while the shallower genotype had superior growth when the topsoil was enriched in phosphorus, the deep rooted genotype had superior growth when the topsoil was allowed to dry (Fig. 9). Interestingly, the deeper-rooted genotype was also superior in the combination of infertile subsoil and dry topsoil, perhaps because of hydraulic lift (Horton and Hart 1998). These results are consistent with economic optimization modeling of the relationship between root architecture and multiple resource acquisition, particularly water and phosphorus. The general solution of the model is that the relative rates of change with depth in the value of the availability of resources matters most in determining the optimal basal root angle. In other words, the marginal rate of substitution of water for phosphorus is the primary determining factor for predicting the distribution of roots in the soil. Indeed, bean genotypes that are best adapted to low phosphorus environments, where phosphorus is localized in the surface soil, tend to have a more shallow basal root angle, whereas genotypes that are adapted to terminal drought environments have deeper root systems. This example illustrates the importance of considering tradeoffs in assessing the adaptive importance of specific root traits, especially in crop breeding for distinct environments.

Prospects

We have attempted to show that the metabolic and ecological costs associated with root traits for phosphorus acquisition may be important components of plant adaptation to low phosphorus soil. A number of traits can improve acquisition of phosphorus, but not all of these traits may be beneficial for overall plant growth in a given environment. Large genetic variability for these traits in crop germplasm presents an excellent opportunity to breed crops with enhanced phosphorus acquisition, an enterprise of critical importance for world food security in the 21st century given the prevalence of low phosphorus soils and the limited reserves of high-grade phosphorus ore deposits (Lynch 1998). On the other hand, the importance of costs associated with these traits is a challenge. Our ability to genetically manipulate crops has outstripped our understanding of the biology of the traits that might be manipulated. Although this problem is complex, a combination of approaches from economics, ecology, physiology, genetics, and modeling, as evidenced in research cited in this article, would be fruitful.

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Figure legends

Figure 1. Root carbon costs of common bean genotypes in late vegetative growth under high and low phosphorus availability. Each value is the mean of eight replicates. From Nielsen et al., 2001.

Figure 2. Relationship of root shallowness and phosphorus acquisition in recombinant inbred lines of common bean. Each value is the mean of eight replicates. From Liao et al., 2001.

Figure 3. Relationship of the rate of root respiration and root RGR of four common bean genotypes grown under low, medium, or high phosphorus availability at 28 and 42 days after planting. Each point is the mean of four replicates. From Nielsen et al., 2001.

Figure 4. Shoot and root biomass accumulation in two common bean genotypes grown under low or high phosphorus availability at 28 days after planting. Each value is the mean of four replicates.

Figure 5. Specific root length and linear construction cost of adventitious, basal, and tap roots of common bean at 28 days after planting. From Miller et al., 2003.

Figure 6. Specific root respiration of adventitious roots of common bean under high or low phosphorus availability at 28 days after planting.

Figure 7. Cross sections of seminal roots of maize genotype OH43 grown with high P or low phosphorus availability for 12 days. Aerenchyma are visible as large spaces in the cortex (arrow). From Fan et al., 2003.

Figure 8. Correlation between aerenchyma area and phosphorus concentration in maize roots grown at high or low phosphorus. Each data point is the mean of 4 measurements of phosphorus and 10-12 measurements of aerenchyma on comparable root segments. The analysis included roots treated with high and low phosphorus, MCP, and ethylene. From Fan et al., 2003.

Figure 9. Architectural tradeoffs between water and phosphorus acquisition in common bean. Contrasting genotypes were grown in 20 l containers divided by a mesh permitting root penetration but resistant to water flow. Water and phosphorus distribution were varied as shown. Plants were grown for 28 days.

line figure

Figure 1

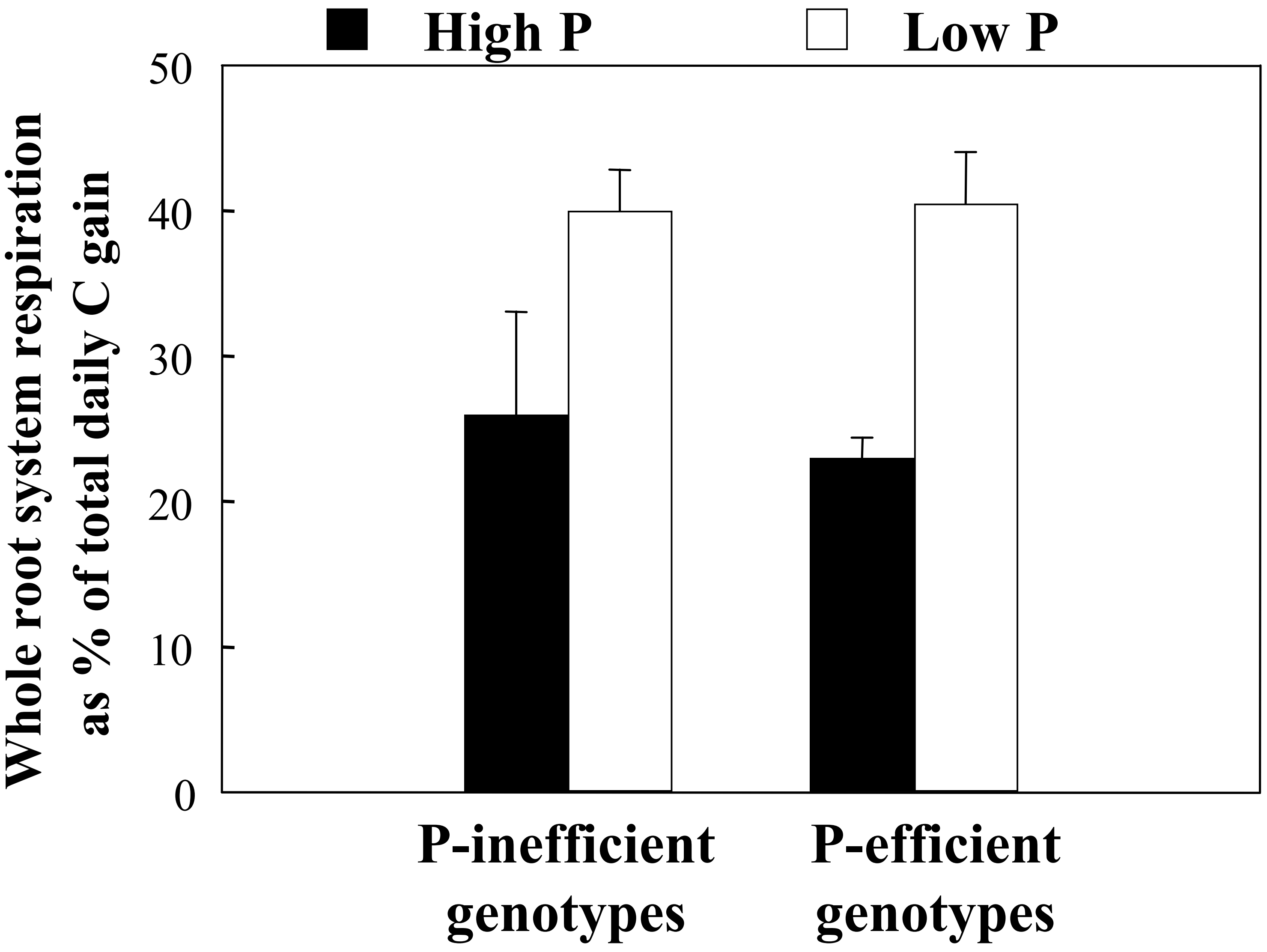
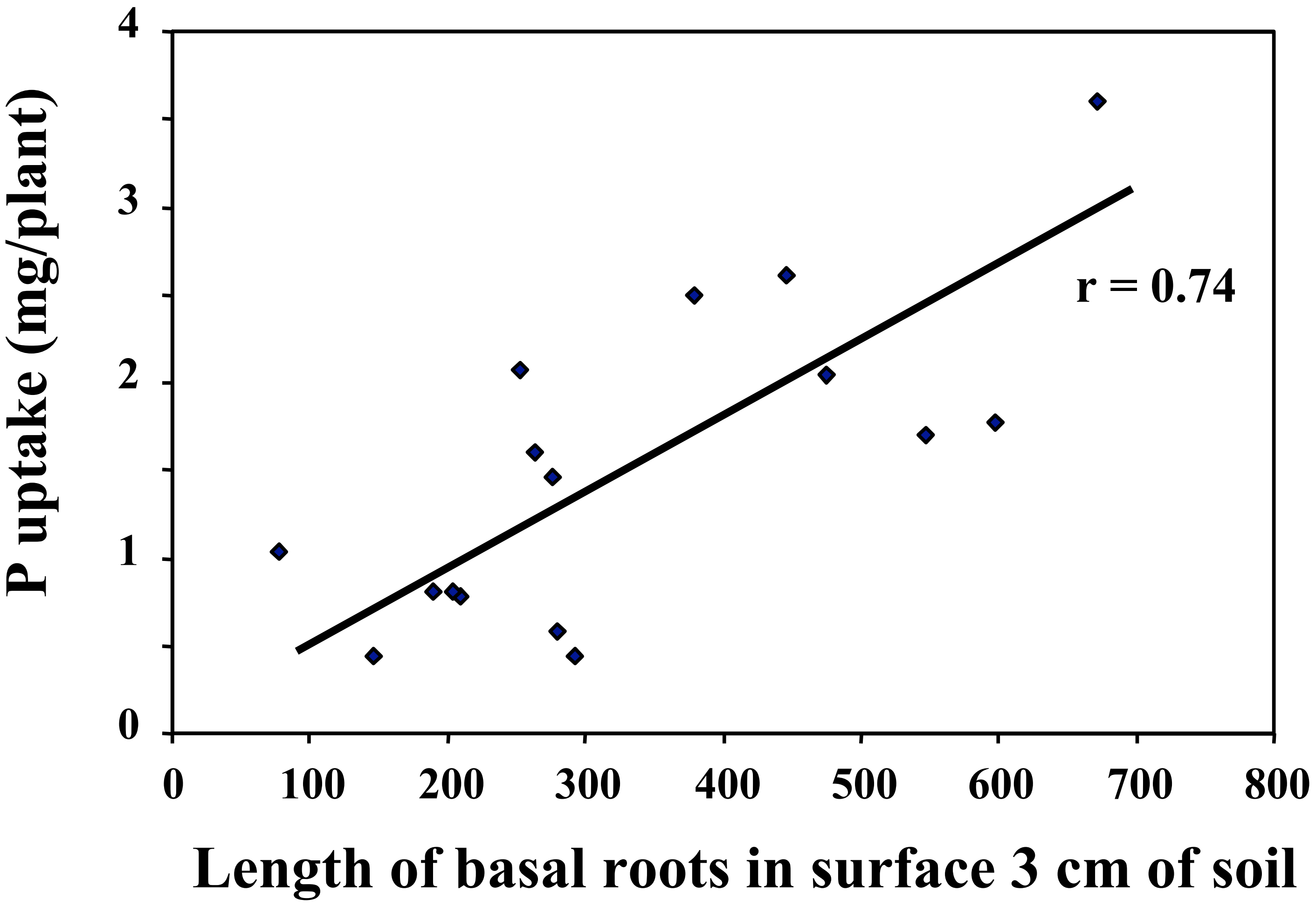
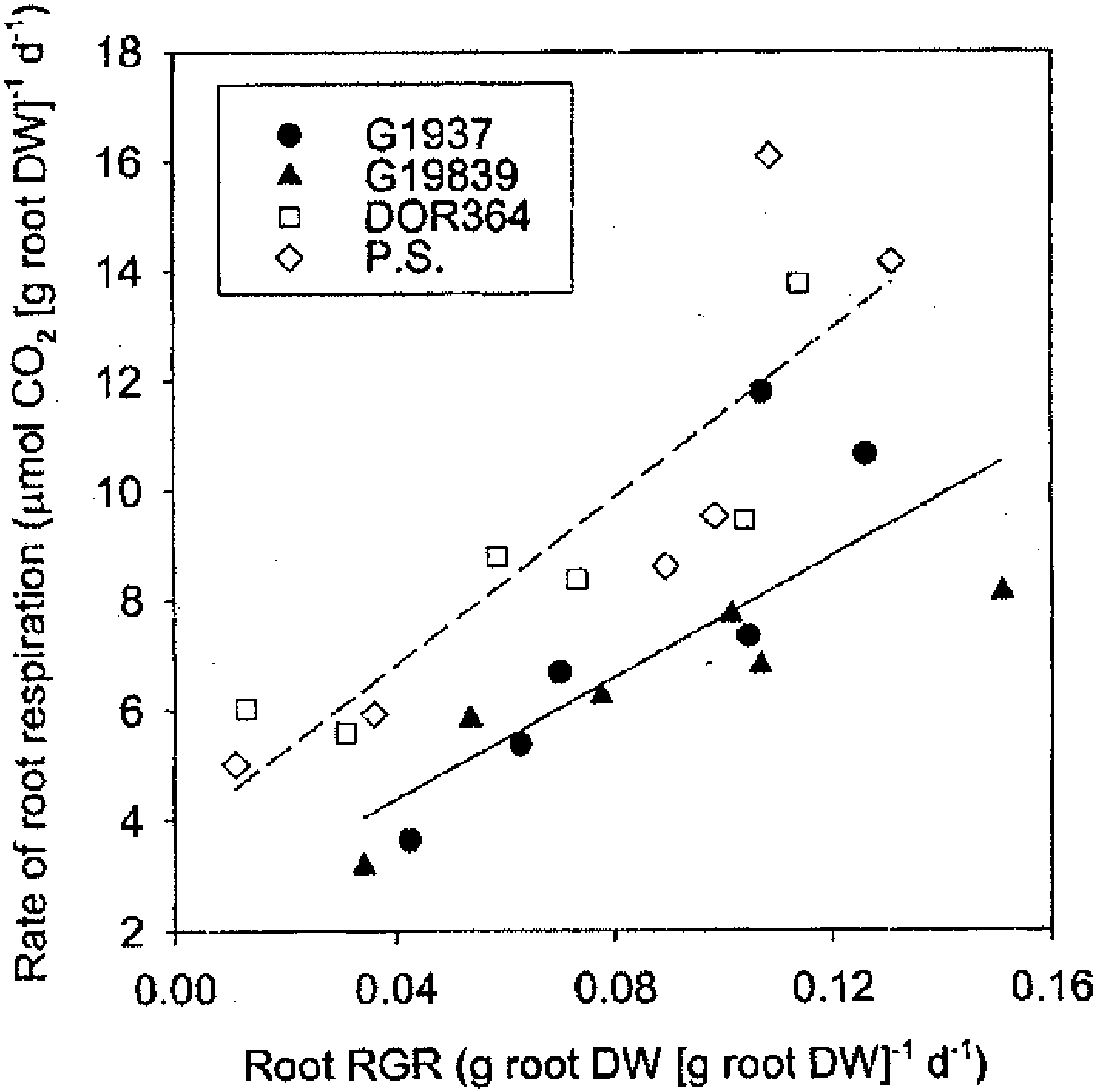


Figure 2



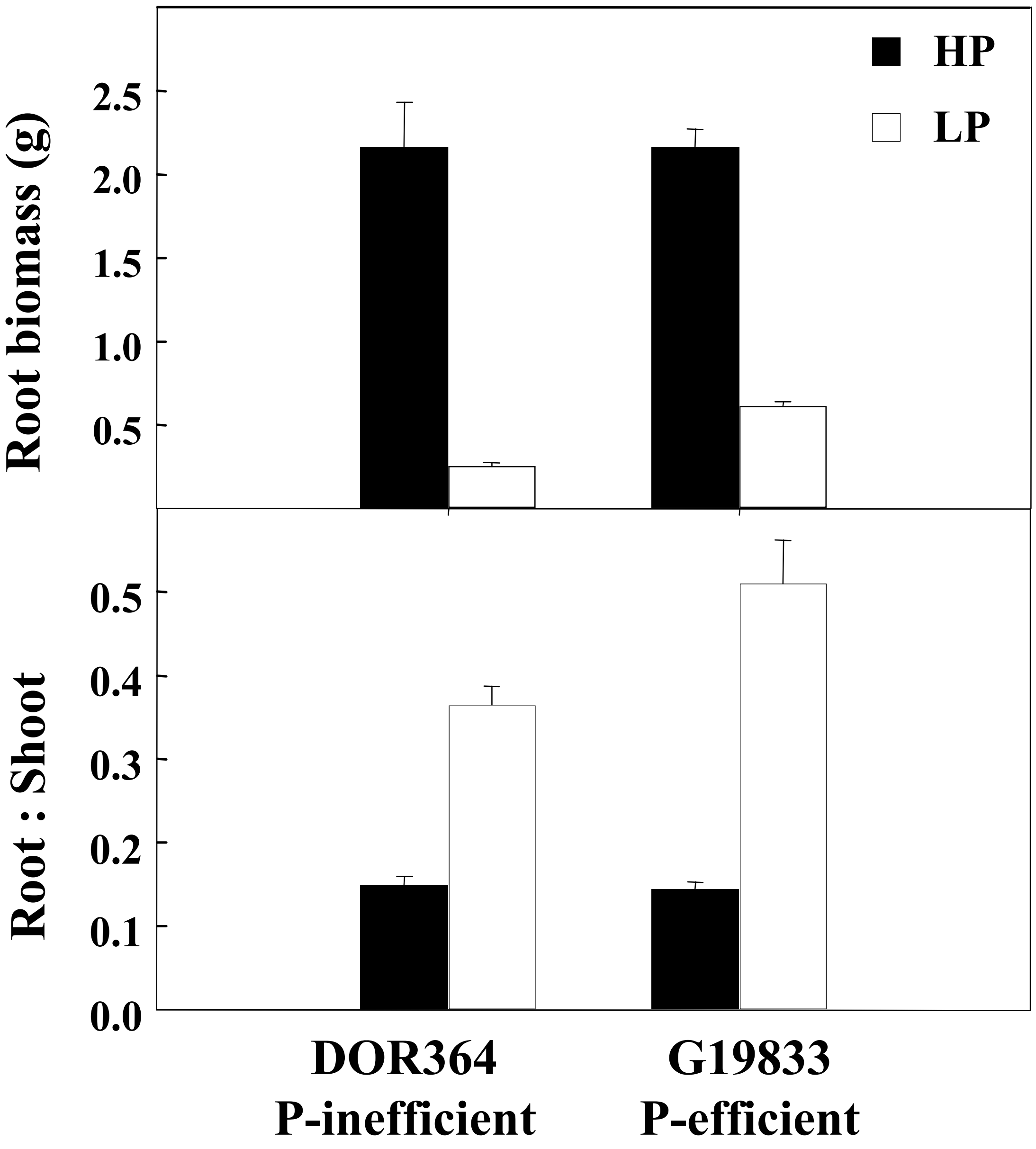
P uptake (mg/plant)
4
3
2
1
0
0
100
200
300
400
500
600
700
800
Length of basal roots in surface 3 cm of soil
r = 0.74

Figure 3



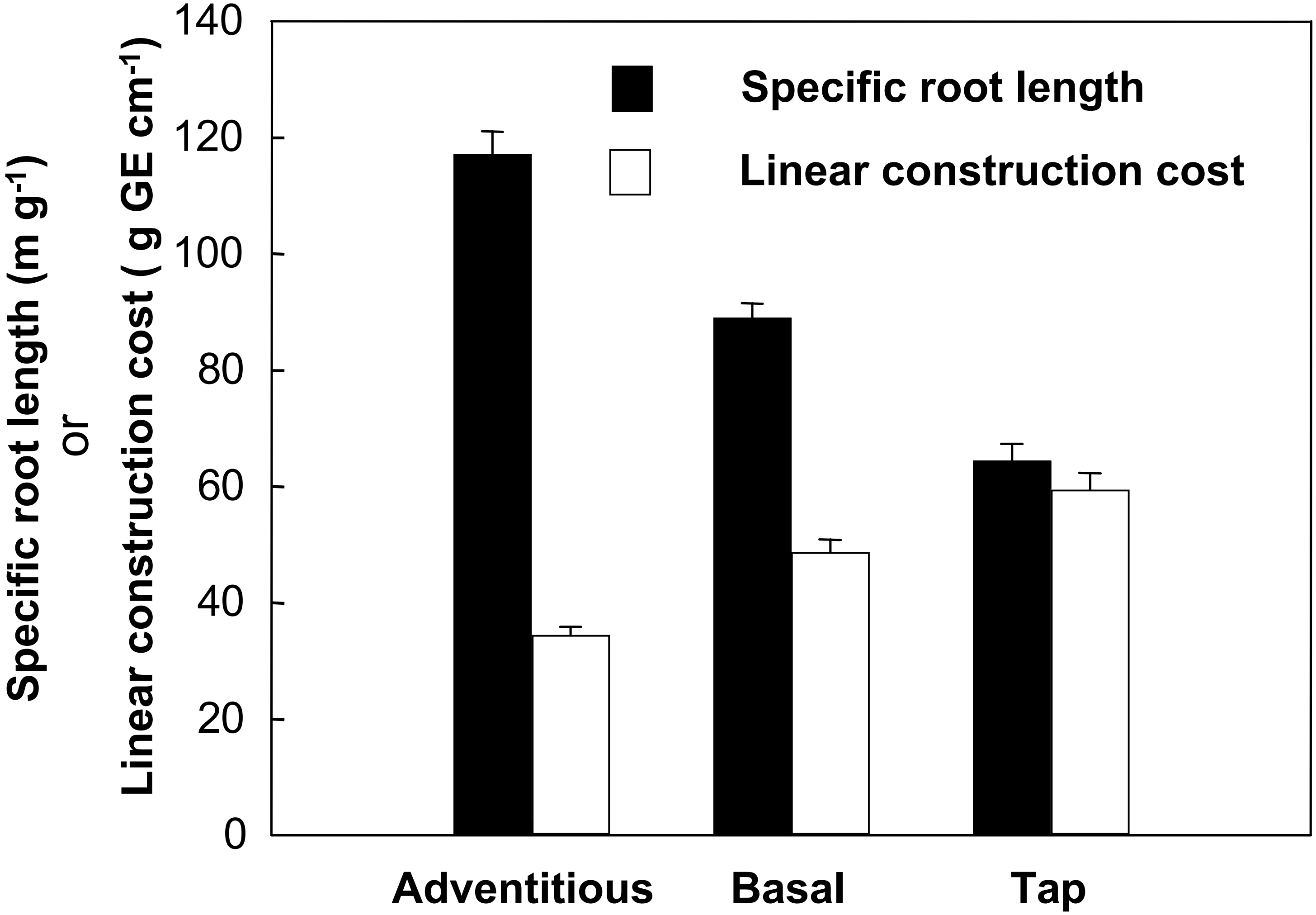
Rate of root respiration (µmol CO$_2$ [g root DW]$^{-1}$ d^{-1})
18
16
14
12
10
8
6
4
2
0.00
0.04
0.08
0.12
0.16
Root RGR (g root DW [g root DW]$^{-1}$ d^{-1})
● G1937
▲ G19839
□ DOR364
◇ P.S.

Figure 4



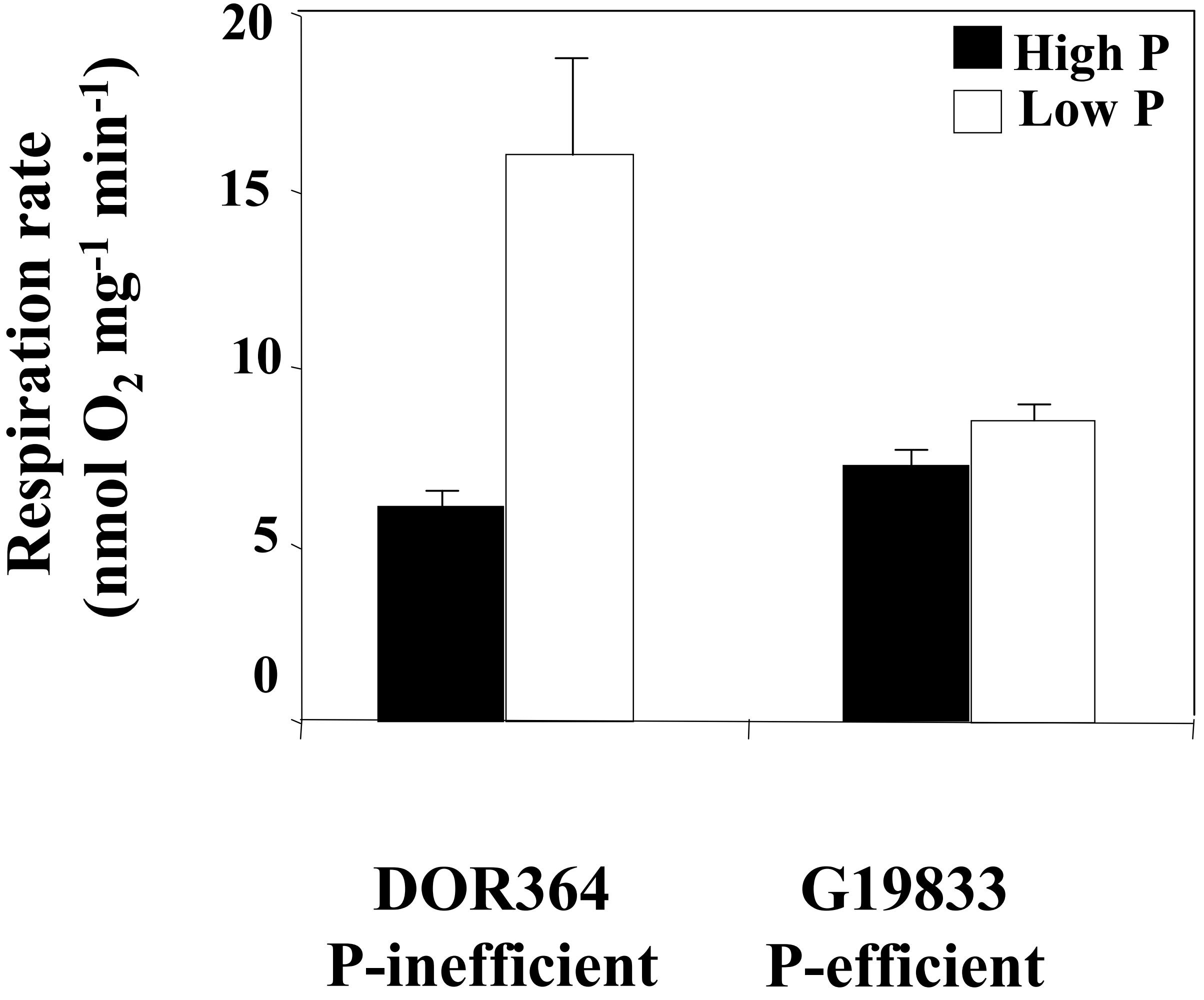
■ HP
□ LP
Root biomass (g)
2.5
2.0
1.5
1.0
0.5
Root : Shoot
0.5
0.4
0.3
0.2
0.1
0.0
DOR364
P-inefficient
G19833
P-efficient

Figure 5



Specific root length (m g^{-1})
or
Linear construction cost (g GE cm^{-1})
0
20
40
60
80
100
120
140
■ Specific root length
□ Linear construction cost
Adventitious
Basal
Tap

Figure 6



20
15
10
5
0
Respiration rate
(nmol O_2 mg^{-1} min^{-1})
■ High P
☐ Low P
DOR364
P-inefficient
G19833
P-efficient

Figure 7

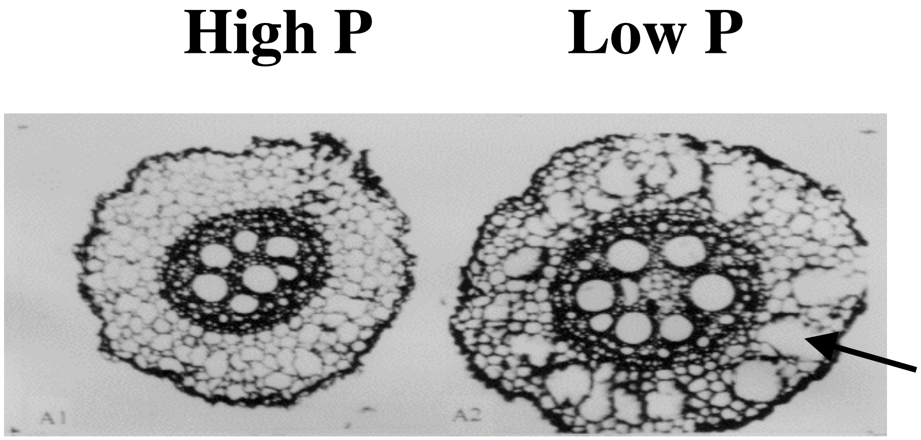
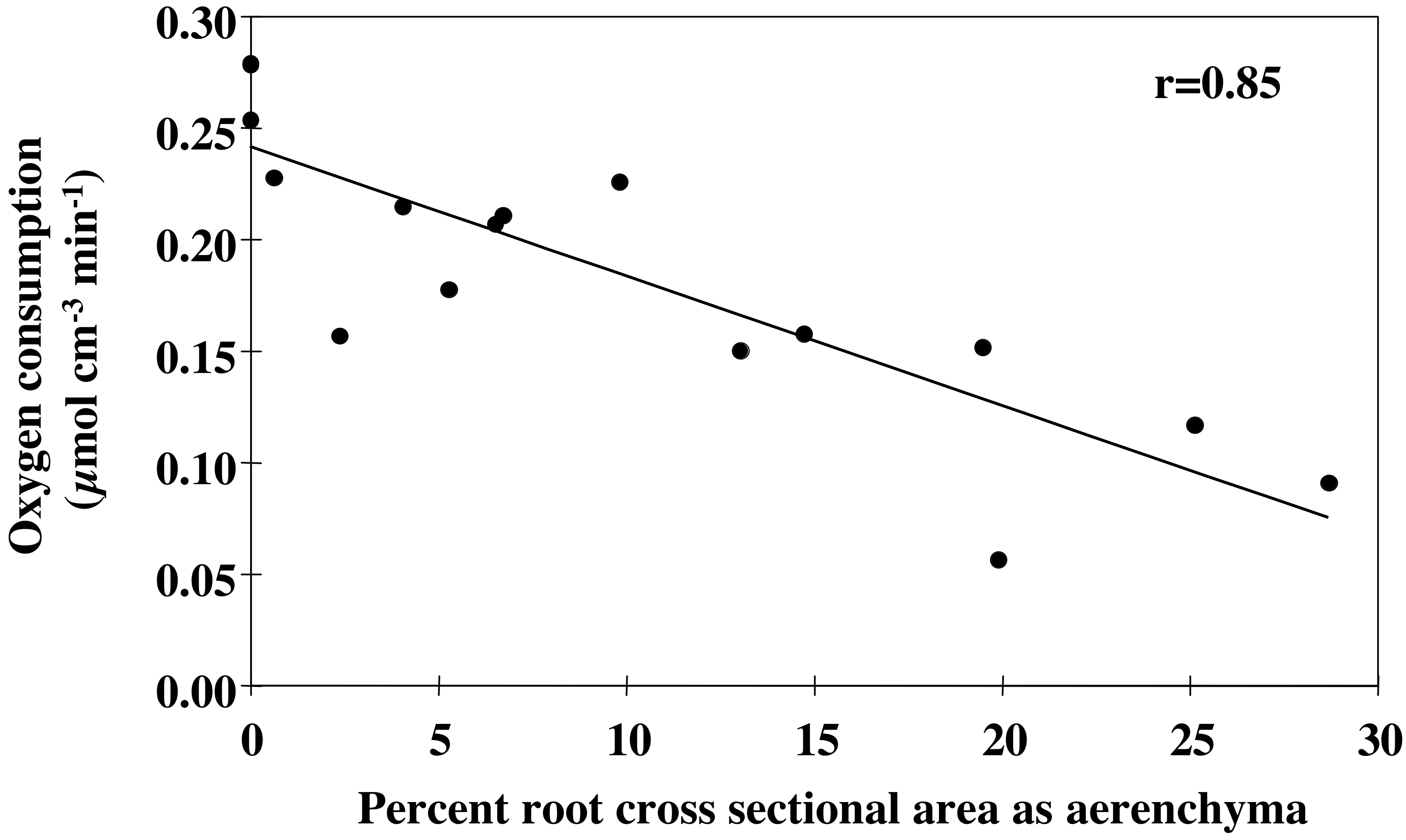
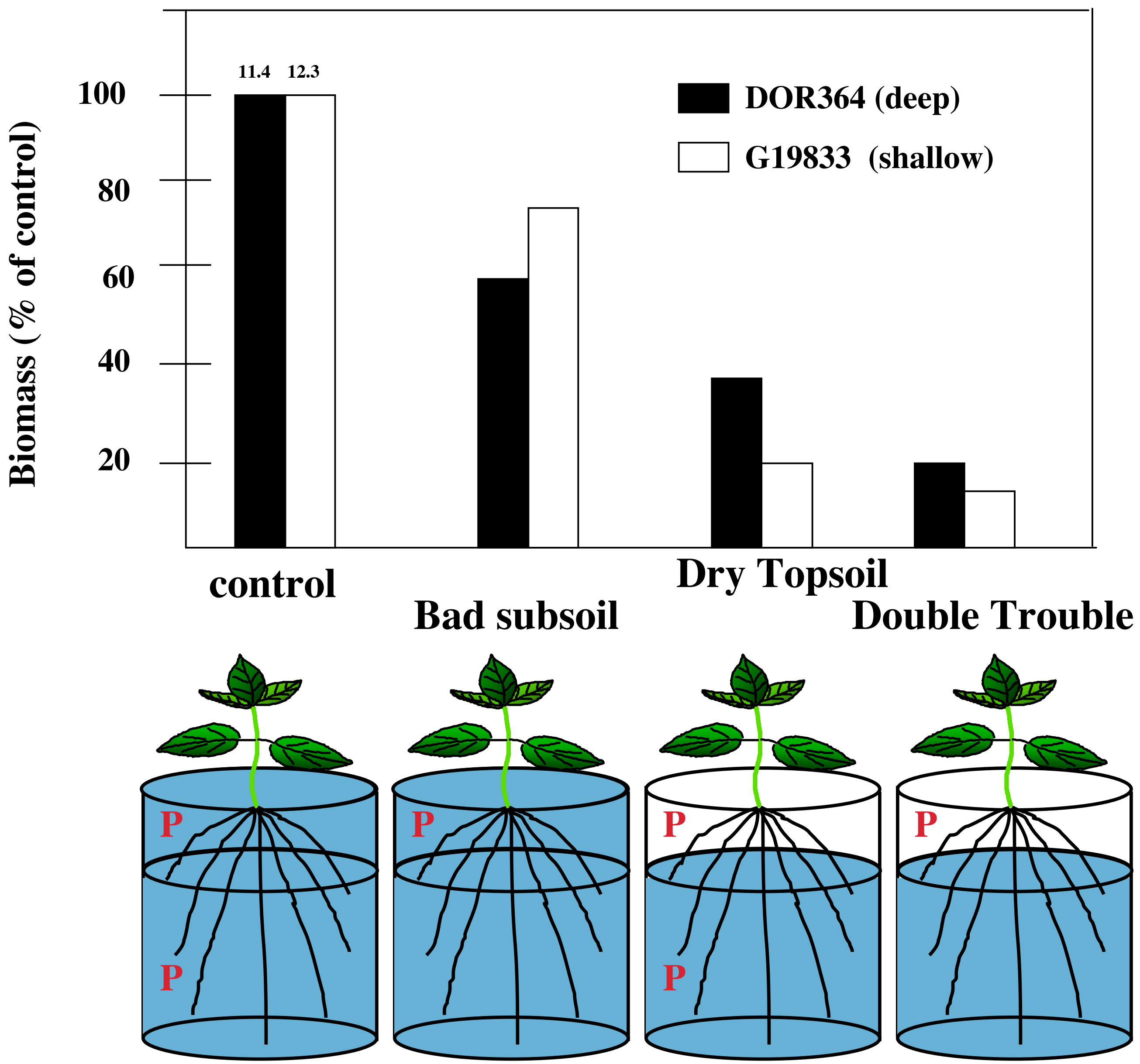


Figure 8



r=0.85
Oxygen consumption
(μmol cm^{-3} min^{-1})
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
5
10
15
20
25
30
Percent root cross sectional area as aerenchyma

Figure 9


Biomass (% of control)
100
80
60
40
20
11.4
12.3
DOR364 (deep)
G19833 (shallow)
control
Bad subsoil
Dry Topsoil
Double Trouble
P
P
P
P
P
P