

Root Architecture and Nutrient Use Efficiency in Vegetable Crops

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Abstract

Nutrient use efficiency (NUE) is critical for sustainable vegetable production amid environmental and economic pressures to reduce fertilizer inputs. Root system architecture (RSA)—the three-dimensional configuration of roots in soil—fundamentally determines nutrient acquisition capacity. This review examines relationships between root architectural traits and nitrogen (N) and phosphorus (P) efficiency in vegetable crops, emphasizing Brassica species. Substantial genetic variation exists for shoot nutrient concentration and NUE measures within species. Lateral root proliferation, root hair development, and organic acid exudation correlate significantly with P efficiency, while root depth and vigorous growth enhance N capture. Quantitative trait loci on Brassica chromosomes C3 and C7 associate with P efficiency traits. Molecular mechanisms involve auxin signaling, nutrient transporters, and transcription factors regulating adaptive root responses. Arbuscular mycorrhizal fungi and nitrogen-fixing bacteria further enhance nutrient acquisition through symbiotic associations that modify RSA. Understanding and manipulating root architecture offers promising avenues for breeding nutrient-efficient vegetable cultivars that maintain yields with reduced environmental impacts.

Keywords: Root system architecture, nutrient use efficiency, phosphorus, nitrogen, Brassica, lateral roots, breeding

1. Introduction

Global vegetable production faces dual challenges: meeting increasing food demand while minimizing environmental impacts from intensive fertilizer use. Vegetables traditionally require substantial nitrogen (N) and phosphorus (P) applications, yet recovery rates are remarkably low—only 33% of applied N fertilizer is typically recovered in crops (Raun & Johnson, 1999). Excessive fertilization causes nitrate groundwater contamination, surface water eutrophication, and greenhouse gas emissions (White & Hammond, 2009). With finite P reserves potentially depleted within 100-400 years (Johnston, 2008), improving nutrient efficiency becomes imperative for agricultural sustainability.

Root system architecture (RSA) critically determines nutrient acquisition by controlling spatial root distribution

throughout soil profiles (Lynch, 1995). For mobile nitrate, deeper roots intercept leached nutrients in lower horizons, while immobile phosphate requires intensive surface soil exploration through lateral root proliferation and enhanced root hair development (Hammond *et al.*, 2009). *Brassica oleracea* species, including cabbage, cauliflower, and broccoli, exhibit substantial genetic diversity in root traits and nutrient efficiency, providing excellent models for studying these relationships. This review synthesizes current knowledge on root architecture modifications enhancing nutrient efficiency in vegetable crops, examining mechanisms, genetic control, and breeding applications.

2. Root Architectural Traits and Nitrogen Efficiency

Nitrogen availability profoundly influences root development, with distinct responses depending on N form and distribution. In agricultural soils, nitrate typically predominates at concentrations 6-10 times higher than ammonium (Garnett *et al.*, 2009). Nitrate's high mobility and leaching susceptibility favor deeper root systems with rapid soil exploration capacity. Maize genotypes with fewer but deeper crown roots demonstrate superior N uptake from low-N soils (Li *et al.*, 2016), with field trials confirming that large, deep root systems underlie high N use efficiency.

In cauliflower (*B. oleracea* var. *botrytis*), N efficiency varies substantially among cultivars. Schenk (2006) compared three F₁ hybrids, finding 'Marine' superior under limiting N supply, particularly for curd quality maintenance. This efficiency operated through enhanced N utilization rather than increased uptake capacity, with evidence suggesting cytokinin signaling involvement. Under N deficiency, reduced cytokinin export from roots triggers premature reproductive development, reducing yield and quality. This illustrates that N efficiency involves multiple mechanisms: while root architectural modifications enable enhanced capture, physiological adjustments in utilization and allocation prove equally important, particularly where quality outweighs total biomass as the primary objective.

3. Root Architectural Traits and Phosphorus Efficiency

Phosphorus acquisition presents fundamentally different challenges than nitrogen. Phosphate ions exhibit minimal mobility due to strong adsorption to clay minerals, with soil solution concentrations typically 2-10 μM (Vance *et al.*, 2003). P availability depends primarily on slow diffusion

(10-100 times slower than nitrate), making exhaustive surface soil exploration critical since most P concentrates in upper horizons where organic matter accumulates and fertilizer is applied.

Hammond *et al.* (2009) conducted comprehensive P efficiency screening in *B. oleracea*, examining 355 diversity foundation set accessions plus 74 commercial cultivars. Substantial genetic variation emerged: shoot P concentration varied 4.9-fold at low external P concentration and 2.8-fold at high P. Physiological P use efficiency ranged from -294.7 to 1268.4 g² DM g⁻¹ P. Notably, commercial cultivars showed significantly higher mean agronomic P efficiency, P uptake efficiency, and P utilization efficiency compared to the diversity set, suggesting yield selection inadvertently enriched P-efficient phenotypes.

Detailed root characterization of 18 extreme phenotype accessions revealed lateral root traits as particularly important. Lateral root number, length, and growth rate correlated positively and significantly (P<0.05) with multiple P efficiency metrics. Lateral root growth rate showed strongest correlations with agronomic P efficiency (r=0.718 at high P, r=0.659 at low P), suggesting capacity for lateral root proliferation—particularly extension rate—exceeds root system depth or angular distribution in importance for Brassica P acquisition.

Comparative studies among cabbage, carrot, and potato revealed markedly different P efficiency strategies (Schenk, 2006). Cabbage achieved 80% maximum yield with only 27 mg P kg⁻¹ soil, while carrot and potato achieved merely 4% and 16% respectively at this level. Cabbage's superior efficiency stemmed from multiple traits: root hairs 10-fold longer than carrot with 5-fold greater density, dramatic citrate exudation increases under P deficiency (absent in carrot and potato), and additional mechanisms beyond morphology. Mechanistic modeling significantly under predicted cabbage P uptake (only 40% of observed) while accurately predicting carrot and potato (80%), confirming citrate exudation's contribution to P mobilization from sparingly soluble forms.

Interestingly, genetic variation exists even within Brassica for P acquisition strategies. Ethiopian cabbage accessions (*B. carinata*) did not exude citrate but instead increased root hair length under P deficiency, demonstrating multiple evolutionary solutions to P limitation providing valuable genetic resources for breeding diverse environments.

4. Genetic Architecture and Molecular Mechanisms

QTL analysis using 90 doubled haploid *B. oleracea* lines identified significant loci on chromosomes C3 and C7 (Hammond *et al.*, 2009). On C3, QTL at approximately 30

cM showed positive effects of one parental allele for shoot biomass and P efficiency measures but negative effects for shoot P concentration, suggesting efficiency enhancement primarily through increased biomass accumulation (dilution effect). A second C3 QTL at 108 cM showed opposite effects. On C7, a QTL at 32 cM associated with lower shoot P but higher P efficiency, consistent with more efficient internal utilization. Substitution lines validated several QTL, confirming predicted allelic effects.

Analysis revealed fundamental relationships between biomass and apparent P efficiency. Within subtaxa, shoot P concentration correlated inversely with biomass (P<0.001), indicating growth dilution effects. This implies breeding for yield under P-sufficient conditions may inadvertently select lower tissue P concentrations, improving certain efficiency measures without necessarily enhancing P uptake capacity.

Molecular mechanisms regulating nutrient-responsive root development involve complex signaling networks. For nitrogen, the transporter NRT1.1 functions as sensor and transporter, participating in auxin-mediated nitrate signaling regulating lateral root development (Mounier *et al.*, 2014). High-affinity transporter NRT2.1 coordinates lateral root growth with nitrate availability (Remans *et al.*, 2006). Additional components include proton pump AHA2, CLE peptides, CLV1 receptor kinase, and micro RNAs miR167 and miR393 targeting ARF8 and AFB3 respectively (Gifford *et al.*, 2008; Vidal *et al.*, 2010).

For phosphorus, transcription factor families provide master regulation. OsPHR2 in rice and orthologs function as master P starvation regulators, binding P1BS elements in promoters of P-responsive genes (Wu & Wang, 2008). OsMYB2P-1 regulates root hair development and architecture (Dai *et al.*, 2012). WRKY75 modulates root development as a negative regulator requiring suppression for adaptive responses (Devaiah *et al.*, 2007). The rice protein kinase PSTOL1, identified through positional cloning of the Pup1 QTL, represents a major breakthrough—enhancing root growth and grain yield on P-deficient soils, with successful marker-assisted introgression into elite cultivars (Gamuyao *et al.*, 2012).

5. Root-Microbe Symbioses

Over 80% of terrestrial plants form arbuscular mycorrhizal (AM) symbioses extending effective root surface area through hyphal networks, enhancing P acquisition (Marschner & Dell, 1994). Two response patterns occur: Type I shows promoted root growth with increased lateral roots and fine roots (Gutjahr *et al.*, 2009); Type II shows inhibited growth with reduced length and surface area due to

carbon costs of symbiotic structures (Wang *et al.*, 2011). Root architecture influences colonization—larger lateral roots preferentially colonized, taprooted species showing higher rates than fibrous-rooted species (Yang *et al.*, 2015).

In legumes, nitrogen-fixing nodule symbiosis typically reduces root growth due to high carbon costs (Reich *et al.*, 2006). However, deep-rooting soybean genotypes showed better nodulation under high P than shallow-rooting types (Wang *et al.*, 2011), suggesting P acquisition-favoring traits also benefit nodule function. Several genes coordinate nodulation with root development, including LjHAR1, LATD, SUNN, and microRNAs miR160 and miR166. Recent work shows GmEXPB2 over expression produces longer roots with denser root hairs, significantly increasing rhizobial attachment and nodule number while improving plant N and P content (Li *et al.*, 2016), demonstrating potential for simultaneous improvement of P acquisition and N₂ fixation efficiency through root architecture optimization.

6. Breeding Strategies and Future Directions

Multiple approaches enable nutrient efficiency improvement: phenotypic selection under deficiency, direct root trait selection using specialized screening systems, and marker-assisted selection for major QTL. Genomic selection using genome-wide markers captures many small-effect QTL collectively contributing substantially to trait variation. While transgenic approaches face regulatory challenges, they validate gene function and demonstrate proof-of-concept for novel strategies, including PSTOL1 over expression, transcription factor modification, and organic acid exudation enhancement.

Future priorities include integrating multiple traits across nutrients, as crop performance depends on combined function under realistic conditions. Field validation remains challenging but critical, requiring non-invasive phenotyping technologies. Deeper investigation of root exudation genetics, exudation-microbial community interactions, and trade-offs with other allocations would advance understanding. Optimizing root architecture to enhance beneficial microorganism colonization represents a frontier. Research investigating nutrient interactions, balanced efficiency strategies, and climate change scenario performance would provide comprehensive understanding for developing future-adapted varieties.

7. Conclusions

Root system architecture critically determines nutrient use efficiency in vegetable crops. Substantial genetic variation exists for root traits and nutrient efficiency within species, particularly *B. oleracea*. Specific traits correlate with

efficiency: lateral root proliferation, root hair development, and citrate exudation for P; root depth and vigorous growth for N. Genetic architecture involves major QTL and multiple small-effect loci, with some conserved across species. Molecular regulation involves nutrient transporters/sensors, transcription factors, and microRNAs creating complex networks. Root-microbe symbioses both influence and are influenced by architecture, suggesting integrated improvement opportunities. Environmental context matters—optimal ideotypes vary with soil type, management, and limiting nutrients. Breeding strategies from conventional selection to genomic approaches can successfully improve efficiency, with commercial cultivars showing enrichment for efficiency traits. Developing crops with optimized root systems represents sustainable strategy for maintaining productivity while reducing environmental impacts—essential for food security and environmental stewardship amid intensifying global agricultural pressures.

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