



RESEARCH ARTICLE

Adaptive architectural adjustments: Phenotypic plasticity in *Vigna radiata* seedlings under spatial constraints and nutrient variability

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Abstract

Phenotypic plasticity is the ability of a genotype to respond differently under different environmental conditions. As a result, diverse phenotypes could be produced from a single genotype. In response to the prevailing environmental conditions, phenotypic plasticity in the root architectural traits of a plant helps in efficient foraging of resources by making adaptive adjustments in the root system architecture. In the present study, fourteen root architectural traits were evaluated to assess how spatial constraints and differential nutrient availability on the seedlings of *Vigna radiata* affect their root foraging strategies during initial growth stage. We hypothesized that in response to spatial constraints and differential nutrient availability *Vigna radiata* seedlings in their early growth stage make adaptive architectural adjustments in their root traits by employing phenotypic plasticity for optimal foraging of nutrients. Out of the fourteen root architectural traits investigated in the present experiment, phenotypic plasticity index value for twelve traits were observed to be greater than 0.5 suggesting that *Vigna radiata* seedlings are capable of sensing even the slightest changes in their surrounding environment and appropriately responds to them by altering their root system architecture. We found statistically significant variations in ten traits; suggesting that rather than following a fixed developmental path like an automaton, *Vigna radiata* seedlings actively sense and respond to these environmental constraints by modifying their architectural traits to optimize the chances of survival and growth.

Keywords: Foraging strategies, nutrient availability, phenotypic plasticity, root system architecture, spatial constraints

Introduction

Phenotypic plasticity enables a plant genotype to produce different phenotypes in response to the different environmental conditions (Bradshaw 1965, Lopez *et al.* 2015). Being rooted to a place, plasticity for plants is a way of being, allowing them to grow in spatially and temporally variable environments or adapting to minute changes even in the same environment. Phenotypic plasticity is a common genetic and evolutionary concept explored for many decades; recently it has again caught attention

of the evolutionary biologists, ecophysiologists and developmental biologists, thus, emerging as a key concept to understand the development of plants in an ecological context (Parker *et al.* 2003, Wu *et al.* 2004, Sharma *et al.* 2005, Japhet *et al.* 2009, El-Serafy 2020, Alfaro and Marshall 2023). However, in spite of presence of an extensive literature on phenotypic plasticity, a clear agreement on its adaptive value is still lacking. Present study aims to fill this gap between plant developmental biology and ecology by investigating plasticity in the root architectural traits of the *Vigna radiata* seedlings during initial growth stage, in response to the spatial constraints imposed on the growing seedlings in two contrasting environments (on the basis of space and nutrient availability) for optimal foraging of resources (Alpert and Simms 2002, Givnish 2002, Chehab *et al.* 2009, Niklas 2009). *Vigna radiata* is an important pulse crop grown in arid regions of the Indian subcontinent. Tolerance and adaptability of its seedlings to low soil fertility makes it an ideal system for this experiment. Plastic responses of the roots constitute one of the major adaptive strategies to cope with the spatial constraints and nutrient heterogeneity in natural environments. Development of

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root system architecture is a dynamic process influenced by different nutritious and non-nutritious cues. Patterns of root placement are altered by diverse cues resulting in multidimensional root foraging strategies. (Hodge 2004, Cahill and McNickle 2011).

We hypothesized that *Vigna radiata* seedlings are capable of sensing spatial constraints and nutrient availability in their surrounding environment and accordingly adjust phenotypic values of its root architectural traits to efficiently forage for resources. By making plastic adjustments in their root architectural traits, roots of the growing seedlings would have to make exploration-acquisition trade-offs. We predicted comparatively longer main root lengths for the seedlings growing in the nutrient poor conditions than in the nutrient rich conditions owing to exploratory nature of the main root. Contrary to this, on encountering nutrient rich conditions, seedlings should make a trade-off between growth of main root and lateral roots i.e., instead of longer main root length it should invest more in lateral root formation for better acquisition of available resources. So, in a nutshell, we predicted that primary role of the main root is to explore resources while lateral roots work for efficient acquisition of the explored resources. But these functions of main root and lateral roots are not necessarily always fixed. We anticipated that for counter-balancing the limitations faced by main root on encountering spatial constraints lateral roots would also aid in exploratory activities of the main root. Hence, phenotypic plasticity of the root architectural traits in response to the spatial constraints and nutrient availability should help the growing *Vigna radiata* seedlings in making adaptive architectural adjustments.

Materials and methods

Certified seeds of *Vigna radiata* (variety Shikha IPM-410-03) were obtained from the National Seeds Corporation Ltd. A simple experiment was designed to understand how spatial constraints imposed on seeds of *Vigna radiata* affect various architectural traits and plastic behaviour of the young seedlings. After surface sterilization with a 0.1% mercuric chloride solution, followed by three rinses with sterile distilled water, the seeds were randomly assigned to one of two container types: test tubes (TT) or petri plates (PP). Each container type was then subdivided into two nutritional treatments: a control group (C) using 0.8% agar gel without nutrients, and a full-strength (FS) group using Murashige and Skoog media. Further, for each nutritional group, three spatial constraint treatments were imposed based on the volume of media provided (10ml, 20ml, or 40ml). The experiment was replicated four times for each treatment combination, resulting in a total sample size of N=48.

To assess early seedling growth under the above-mentioned constraints, the seedlings were grown in growth room under controlled conditions: a light intensity

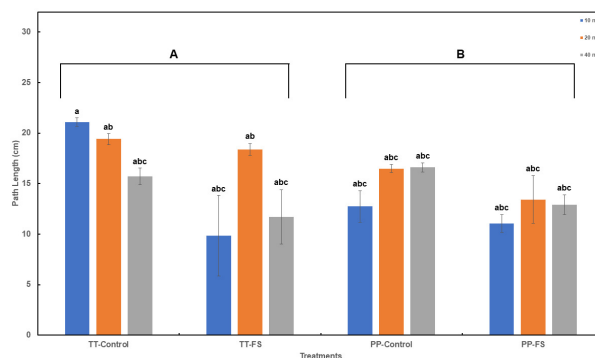


Figure 1: (Mean±SE) for Path Length of seedlings observed under different treatments.

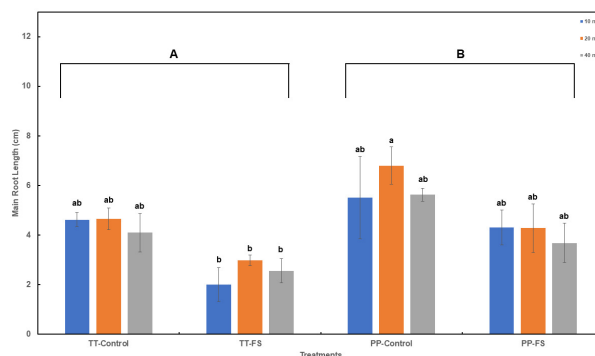


Figure 2: (Mean±SE) for Main Root Length observed under different treatments.

of $\sim 66 \mu\text{mol m}^{-2} \text{s}^{-1}$ photon flux density (PFD) with a 16-h photoperiod, a temperature of $28 \pm 2^\circ\text{C}$, and 55-60% relative humidity. Seedlings were harvested on the 10th day for measuring various architectural traits. Digital images of the harvested seedlings were captured. Prior to measuring the dry weight of harvested seedlings, they were dried in oven for 72 hours.

To measure the architectural traits from the digitized images, including Path length of seedling (PL), Main root length (MRL), Vector length of root (VL), Apical diameter of root (AD), Basal diameter of root (BD), Number of lateral roots, Pre-branching distance, Post-branching distance, Branching zone (BZ) – defined as the length of the main root where lateral roots emerge, Frequency of lateral roots on MRL, Frequency of lateral roots on BZ, and Total length of lateral roots (Kellermeier *et al.* 2014, Freschet *et al.* 2021), ImageJ software was used. After converting images into high contrast settings, Root area (RA) and Shoot area (SA) were measured with the help of wand tool in ImageJ software. Wand tool measures perimeter of an object by tracing along its edges; it is indicative of the two-dimensional space taken up by the object. Statistical analyses were performed to check significant variations in the measured traits because of different treatments using IBM-SPSS. Seedling data was subjected to the two-factor ANOVA taking container type and media-volume combinations as two main factors. For

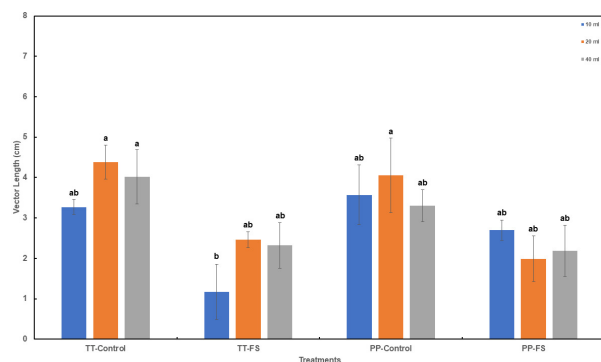


Figure 3: (Mean±SE) for Vector Length observed under different treatments.

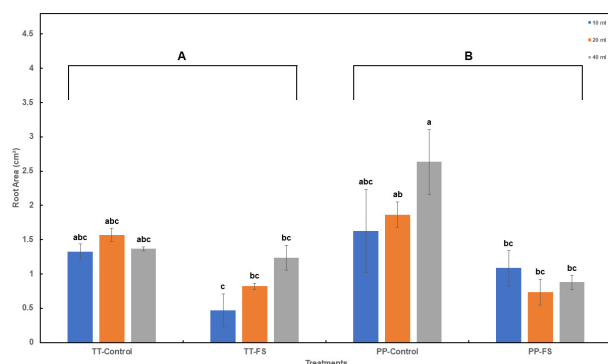


Figure 4: (Mean±SE) for Root Area observed under different treatments.

the traits with significant ANOVA results, a post-hoc Tukey test was performed to find out the treatments responsible for different patterns of the concerned trait.

Phenotypic Plasticity Index (Plv) based on the minimum and maximum mean values of each trait (Valladares *et al.* 2006, Wang and Zhou 2022) was calculated by computing the difference between maximum mean values and minimum mean values of a particular trait, and dividing this difference by its maximum mean value. Plv is a simple, robust and widely accepted plasticity index (Balaguer *et al.* 2001, Gratani *et al.* 2003, Garbelotto *et al.* 2015, Zhang *et al.* 2022). Its value ranges from 0 to 1, indicating a range from no plasticity (0) to maximum plasticity (1) for a trait.

Results

Out of the fifteen traits measured for the experiment, we found statistically significant variations in ten traits. Significant variations in PL, MRL, RA, BD, and post-branching distance were ascribed to both the factors i.e., the container type and media-volume combinations. Whereas, for AD and frequency of lateral roots on MRL, statistically significant variations were observed due to the container type only. Contrary to this, for VL, SA and, total length of lateral roots, media-volume combination caused significant variations irrespective of the container type. Variations were non-significant for number of lateral roots, pre-branching

distance, BZ, frequency of lateral roots on BZ and dry weight of seedlings.

Path Length of Seedlings

Path length of the seedlings was quantified using segmented line tool of ImageJ software, tracing total length of a seedling. Analysis of variance revealed that both the factors i.e., container type and media-volume combination caused significant variation ($p < 0.05$). The results are shown in Fig. 1, wherein capital letters over the group of bars represent comparison between different container types, and small letters over the error bars represent comparison among different media-volume combinations. Statistically significant differences are represented by different letters. Tukey test results for PL showed significant differences for both the container type and media-volume combinations, resulting in formation of two and five groups respectively. We observed the longest path length in test tube's control group containing 10 ml agar solution abbreviated as TT-Control-10 treatment (21.105 cm), and the least was in test tube's FS group containing 10 ml full strength Murashige and Skoog media i.e., TT-FS-10 (9.849 cm).

Main Root Length

In the present study, for both container types longer main root lengths were observed in control treatments as

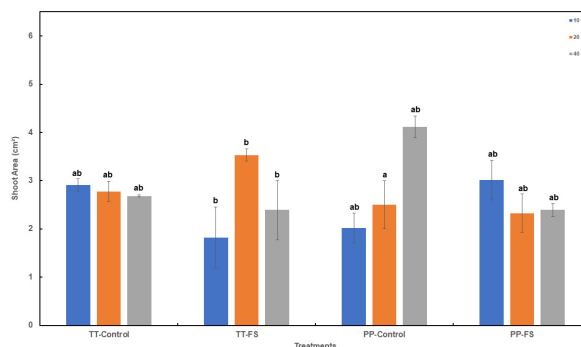


Figure 5: (Mean±SE) for Shoot Area observed under different treatments.

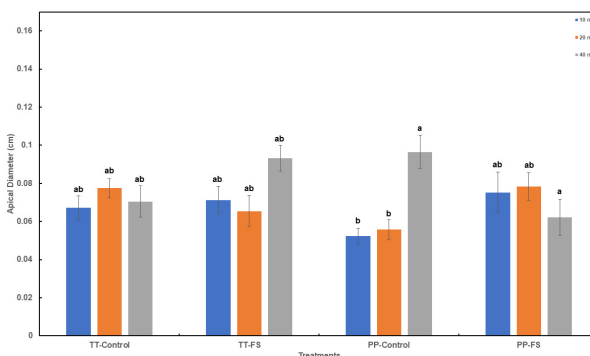


Figure 6: (Mean±SE) for Apical Diameter observed under different treatments.

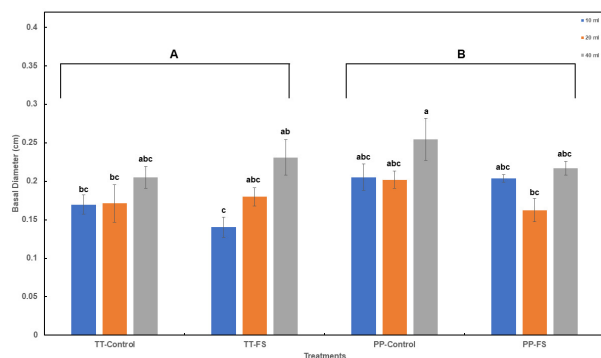


Figure 7: (Mean±SE) for Basal Diameter observed under different treatments.

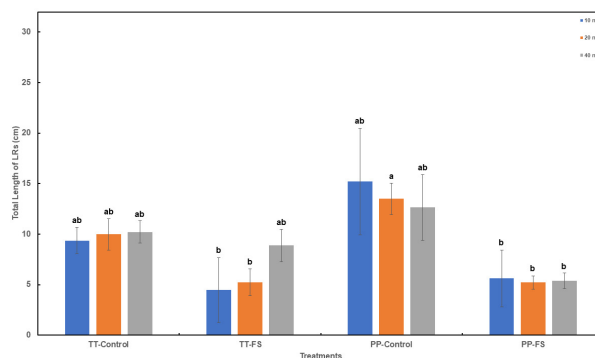


Figure 9: (Mean±SE) for Total Length of LR observed under different treatments.

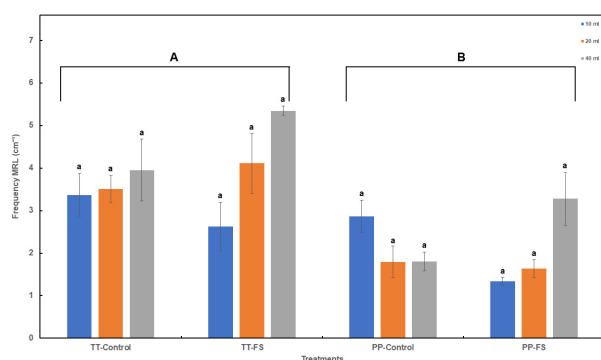


Figure 8: (Mean±SE) for Frequency MRL observed under different treatments.

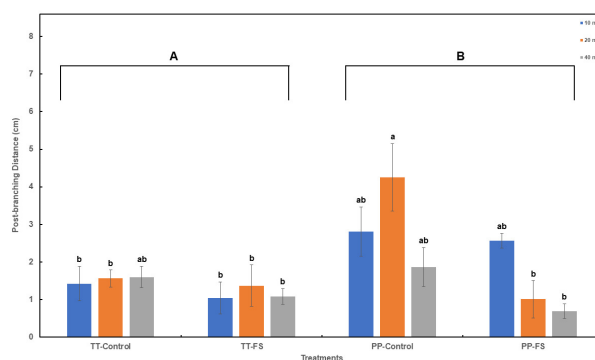


Figure 10: (Mean±SE) for Post-branching Distance observed under different treatments.

compared to FS treatments, suggesting a clear trade-off between exploration and acquisition strategies for resource foraging under contrasting nutrient conditions. Statistically significant variations ($p < 0.05$) because of container type and media-volume combinations revealed by ANOVA results strengthens the hypothesis that *Vigna radiata* seedlings are capable of altering their root architectural traits for optimal foraging of resources by sensing their surrounding environment. Tukey test results shown in Fig. 2 revealed formation of three groups on the basis of media-volume combinations. We observed the longest main root length in control group of petri plates containing 20 ml agar solution i.e., PP-Control-20 (6.803 cm) and least in TT-FS-10 (2.009 cm).

Vector Length of Root

Shortest distance between the point of origin of the main root and the root tip is defined as the vector length of the main root. According to ANOVA results, only media-volume combination caused significant variations ($p < 0.05$) in vector length, follow up Tukey test results revealed formation of three groups among twelve different treatments (Fig. 3). For all the six treatments of TT container type, MRL values were nearly similar to their corresponding VL values. But, for the six treatments of PP container type, its MRL values

were observed to be 1.5 to 2 times greater compared to their respective VL values. This indicates, *Vigna radiata* seedlings on perceiving spatial constraints, responds to these constraints by adjusting plastically their main root length even when nutrients are homogenously distributed.

Root Area

The area occupied by roots at the time of harvest is represented by root area. In the present study, minimum root area was observed in TT-FS-10 (0.469 cm²) and maximum in PP-Control-40 (2.633 cm²), which is 5.6 times greater than the least observed value of root area. Analysis of variance revealed significant variation ($p < 0.05$) because of container type and media-volume combinations. Tukey test revealed segregation of twelve treatments into five groups (Fig. 4).

Shoot Area

Shoot area is indicator of plants' responses to light availability and shade avoidance. As light conditions were controlled and kept constant throughout the experiment period, much variations were not expected in the shoot area. Analysis of variance also revealed no significant variation because of container type but different media-volume combination caused significant variations ($p < 0.05$) among different treatments. Tukey test results for shoot area presented in Fig.

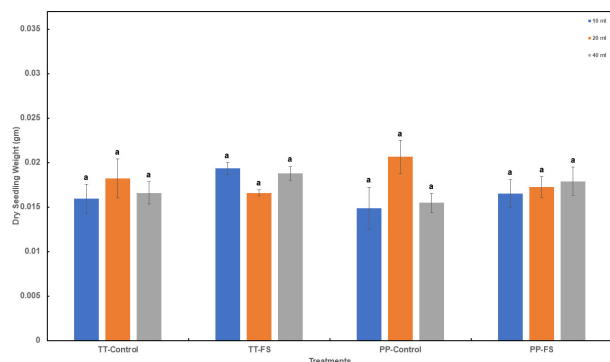


Figure 11: (Mean±SE) for Dry Seedling Weight observed under different treatments.

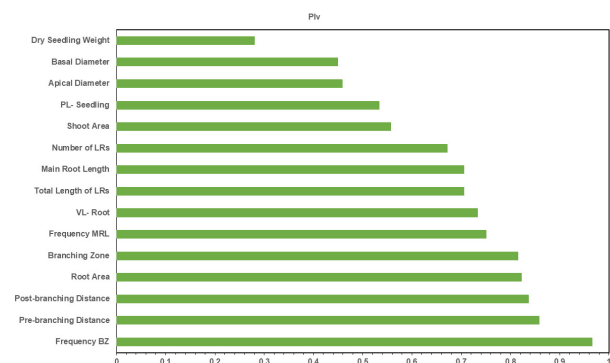


Figure 12: Phenotypic plasticity index (Plv values) for different architectural traits and dry seedling weight.

5 revealed formation of three groups indicating significant differences among different treatments.

Apical Diameter of Root

Analysis of variance revealed that media-volume combinations caused significant variations ($p < 0.05$) in apical diameter, while the effect of container type was non-significant. Tukey test results revealed formation of three groups (Fig. 6).

Basal Diameter of Root

ANOVA result indicated highly significant effect of both the factors i.e., container type and media-volume combinations on basal diameter. A post-hoc Tukey test resulted in segregation of all the treatments into five groups (Fig. 7).

Lateral Root Traits

Out of the seven lateral root traits observed in this study, analysis of variance showed significant variation in three traits viz. post-branching distance, frequency of lateral roots on MRL and, total length of lateral roots. For frequency of lateral roots on MRL significant variations were ascribed to only container type (Fig. 8), while for total length of lateral roots significant variations were due to media-volume combination only (Fig. 9). Contrary to this, both the factors contributed for significant variations in post-branching

distance. Post-branching distance ranged from 0.696 cm (PP-FS-40) to 3.964 cm (PP-Control-20). Tukey test for post-branching distance revealed formation of three groups as shown in Fig. 10.

For the remaining four lateral root traits i.e., number of lateral roots, pre-branching distance, branching zone and frequency of lateral roots on branching zone, ANOVA results were not significant. Least number of lateral roots (5.50) were found in TT-FS-10 and maximum (16.75) in TT-Control-20. Maximum pre-branching distance (0.448 cm) was recorded in TT-FS-10 and minimum (0.081 cm) in TT-FS-40. Maximum branching zone (3.492 cm) was found in PP-Control-40 whereas minimum (0.571 cm) in TT-FS-10. Frequency of lateral roots on branching zone ranged from 1.606 (PP-FS-20) to 61.838 (TT-FS-20).

Dry Weight of Seedlings

Dry weight of seedlings was observed to be more or less similar across all treatments. Analysis of variance also revealed no significant variations because of both the factors (Fig. 11). This suggests starting with the similar resource level, *Vigna radiata* seedlings adopt different root architectural patterns by assessing the external environment to ultimately achieve the similar final goal of optimizing fitness and survival. This altered root placement of growing seedlings in response to diverse cues by making plastic adjustments in their root architectural traits help them in efficient foraging of resources.

Phenotypic Plasticity Index

A comparison of phenotypic plasticity index of all the traits investigated for the present study is represented in the Fig. 12. Out of all the architectural traits observed for the present study, Frequency of lateral roots on BZ showed maximum plasticity (0.965) whereas minimum Plv value (0.448) was observed for BD. Dry weight of seedlings was found to be least plastic (Plv value 0.279), which implies it remained more or less similar across all treatments.

Discussion

Plants modify their foraging strategies according to the prevailing nutrient conditions to optimise resource utilisation, and maximize their chances of survival and growth (Grassein *et al.* 2010). Plant roots exhibit high exploratory activities for resource acquisition in early seedling growth phase in nutrient poor conditions, while on encountering nutrient rich patches, instead of exploring new resources roots spend more time in acquisition of the available resources (Wijeshinghe *et al.* 2001, Rajaniemi and Reynolds 2004, Rajaniemi 2007). Hence, there is a trade-off between exploration and acquisition depending on the resource availability. Maximum main root length was found in PP-Control treatments supporting our hypothesis that in nutrient poor conditions plant emphasizes on resource exploration, while comparatively shorter main

root lengths observed in FS treatments suggests that root focuses on acquisition of available resources as it spends more time in nutrient rich space by regulating its main root length. Greater the difference between main root length and vector length, greater would be the sensitivity and the plasticity of roots to their surrounding environment. Main root lengths of PP treatments, for both control as well as FS groups were observed to be almost twice of their respective vector lengths. Contrary to this, for TT treatments, differences between main root lengths and vector lengths were observed to be very less. Maximum number of lateral roots were observed in TT-Control treatments whereas maximum total length of lateral roots was found in PP-Control treatments, interestingly both of these contrasting strategies aids in fierce exploration of resources thus, achieving the similar outcome (Cahill and McNickle 2011, Gratani 2014). Greatest frequency of lateral roots on MRL was found in TT-FS-20 (4.110) and least in PP-FS-20 (1.224), whereas maximum value for total length of lateral roots was recorded in PP-Control-20 (25.24 cm) and least in TT-FS-10 (3.356 cm) suggesting a trade-off between number and length of lateral roots for better adaptations to the prevailing environmental conditions when *Vigna radiata* seedlings encounter spatial constraints. These findings align with the proposed hypothesis that roots of *Vigna radiata* seedlings make adaptive architectural adjustments in their roots in response to spatial constraints and nutrient availability.

Maximum pathlength of seedlings were observed in TT-Control-10 and PP-Control-40 indicating a trade-off for allocation of resources between root and shoot depending on the surrounding environment of the growing seedling i.e., container type, volume of media and composition of media, which eventually gives similar result for these contrasting treatments. Further, ratio of pathlength of root to pathlength of shoot was found to be 28.094% in TT-Control-10 and 51.287% in PP-Control-40, supporting the abovementioned trade-off between root and shoot. Root area is indicative of exploratory activities of roots in search of resources. When nutrients are easily available, plants would prefer acquisition of these available resources by making a trade-off with its exploratory activities. Control group always showed greater root area as compared to FS group. This suggests capability of *Vigna radiata* seedlings to make plastic adjustments in their root area as a response to the spatial constraints and availability of nutrients in their surrounding environment for maintaining the balance between resource exploration and resource acquisition activities. Non-significant difference was observed in shoot area for different container types due to controlled light conditions throughout the study period. But statistically significant differences were observed in shoot area for different media-volume combinations probably owing to the trade-off for resource allocation

between root and shoot to achieve a similar end goal (Aikio and Markkola 2002, Lopez *et al.* 2023).

Except apical and basal diameter, all other architectural traits exhibited a phenotypic plasticity index value greater than 0.5, indicating *Vigna radiata* is capable of sensing even the slightest changes in its environment and appropriately respond to these environmental stimuli by making plastic adjustments in its root system architecture (Grime and Mackey 2002, Malamy 2005, Bradshaw 2006, Morris *et al.* 2017, Hanslin *et al.* 2019, Munns and Millar 2023). Non-significant variations were observed in the dry weight of harvested seedlings across different treatments; indicating that *Vigna radiata* seedlings even after modifying their root architectural traits in response to nutritious and non-nutritious cues ultimately achieve the similar outcome of optimal foraging of resources. Phenotypic plasticity index for dry weight of seedlings was also observed to be minimum among all the traits observed in the present study. In agreement to the earlier reports of van der Weele *et al.* (2000), Liao *et al.* (2001), Correa *et al.* (2004), Fang *et al.* (2013), Zhan and Lynch (2015) and, Zhang *et al.* (2020), we observed that in the present study, twelve out of fourteen root architectural traits exhibited a great degree of phenotypic plasticity. All these evidences support and strengthen our hypothesis that by altering root system architecture in response to spatial constraints and nutrient availability, *Vigna radiata* seedlings could modify its root foraging strategies in early seedling stage to achieve the end goal of maximizing growth and survival by optimal exploration and acquisition of available resources. This study provides significant advances in our understanding of plant developmental biology, with direct implications for enhancing crop resilience to spatial and nutrient constraints.

Conclusion

Phenotypic plasticity has emerged as key concept to understand plant development through an ecological lens which is made possible by quantification of different architectural traits using image analysis. Studying plant development in an ecological context helps in seeing a holistic picture of plant phenotypic responses evoked by different stimuli. Present study is a result of amalgamation between ecology and developmental biology, which provides strong evidences to support the hypothesis that *Vigna radiata* seedlings sense the spatial constraints imposed on them as well as nutrient availability in their surrounding environments, and responds to these exogenous triggers by showing an impressive degree of phenotypic plasticity in their root system architecture for efficient foraging of resources.

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