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Phosphorus acquisition capacity and size trait evolution in *Achillea wilhelmsii* reflect adaptation to environmental gradients

Mostafa Farajpour[1]✉, Mohsen Ebrahimi[2]✉, Mohammad Sadat-Hosseini[3], Shahab Mirinejad[4], Mahmoud-Reza Ramezanpour[5] & Sepideh Sanjari[2]

Understanding how plant traits evolve in response to environmental gradients is critical for elucidating mechanisms of local adaptation. This study investigated trait variation in *Achillea wilhelmsii* accessions from eight climatically diverse Iranian locations after cultivation under uniform conditions. Key traits—plant size, biomass, and phosphorus content—reflect adaptive divergence along an integrated environmental gradient (PCA1) derived from temperature, precipitation, and altitude. Warmer/drier, lower-altitude conditions corresponded with reduced phosphorus uptake and smaller plant size, while cooler/wetter, higher-altitude conditions favored increased phosphorus absorption and larger plant size. Principal component analyses revealed that 62.85% of observed trait variation arises from evolutionary responses via genetic divergence, driven by natural selection across environmental gradients. Populations from colder, high-altitude sites (positive PCA1 scores) evolved enhanced phosphorus uptake, likely due to selection on pre-existing genetic variation for cold tolerance, facilitating larger plant sizes. These patterns highlight how adaptation, as an inherent capacity of plants to respond to selection pressures, shapes trait divergence under environmental heterogeneity. Future studies should dissect the genetic architecture linking phosphorus metabolism, environmental gradients, and plant size evolution.

Keywords Phosphorus acquisition, Morphological traits, Genetic divergence, Temperature, Climate adaptation, Altitude

Environmental gradients, such as temperature, precipitation, and altitude, impose strong selective pressures on plant populations, driving genetic divergence and shaping locally adaptive traits over generations[1,2]. Natural selection acts on heritable variation, favoring traits that enhance survival and reproduction under specific climatic conditions[3]. For example, alpine plants often evolve cold tolerance mechanisms, while desert species prioritize water-use efficiency[4,5]. These adaptations arise through selection on standing genetic variation, enabling populations to diverge even in the face of gene flow[6].

Phosphorus (P), one of the most abundant macronutrients in plant tissues, is indispensable for energy transfer, photosynthesis, and genetic inheritance[7]. However, abiotic stresses such as low temperatures disrupt P uptake by reducing transpiration rates and altering root transporter functions, ultimately impairing growth and productivity[7]. Recent studies demonstrate that elevated P availability mitigates cold stress by enhancing photosynthesis, biomass accumulation, and antioxidant metabolism in crops such as wheat[8,9], olive trees[10], and alfalfa[11]. For instance, tobacco seedlings under low-temperature stress exhibit increased plant height and shoot biomass when supplemented with higher P levels, highlighting P's role in regulating antioxidant and

[1]Crop and Horticultural Science Research Department, Mazandaran Agricultural and Natural Resources Research and Education Center, Agricultural Research, Education and Extension Organization (AREEO), Sari, Iran. [2]Department of Agronomy and Plant Breeding, College of Abourihan, University of Tehran, Tehran, Iran. [3]Department of Horticultural Science, Faculty of Agriculture, University of Jiroft, Jiroft, Iran. [4]Forests and Rangelands Research Department, Mazandaran Agricultural and Natural Resources Research and Education Center, Agricultural Research, Education and Extension Organization (AREEO), Sari, Iran. [5]Soil and Water Research Department, Mazandaran Agricultural and Natural Resources Research and Education Center, AREEO, Sari, Iran. ✉email: m.farajpour@areeo.ac.ir; mebrahimi@ut.ac.ir

carbohydrate metabolism to bolster stress resistance[12]. These findings suggest that natural selection may favor enhanced P uptake in cold, high-altitude environments.

Temperature, precipitation, and altitude were selected as focal environmental drivers in this study due to their synergistic roles in regulating plant physiology and adaptive responses. Temperature and precipitation directly constrain metabolic rates, nutrient availability, and stress tolerance: cold temperatures limit phosphorus uptake and enzymatic activity, while aridity reduces water and nutrient accessibility[6,13,14]. Altitude, though not a direct selective agent, integrates these factors into steep bioclimatic clines, reflecting both universal geophysical trends—such as the predictable temperature decline and region-specific moisture dynamics[15]. In Iran's arid-to-subalpine ecosystems, precipitation co-varies with altitude, creating divergent selective regimes: low elevations face intensified aridity and evaporative stress, while higher elevations experience colder temperatures moderated by dampened moisture scarcity[16].

To assess adaptive responses, we focused on P uptake, plant size, and biomass—traits critical for stress tolerance and competitive success. Plant size and biomass reflect resource allocation strategies under climatic constraints[17,18].

We studied *Achillea wilhelmsii*, a perennial herb endemic to Iran's diverse climatic zones, ranging from arid lowlands (9.8 m elevation) to subalpine elevations (2321 m). This species' broad distribution and phenotypic plasticity make it an ideal model for disentangling genetic adaptation from environmental plasticity[19,20]. Using a common garden approach, we tested whether population-level differences in phosphorus (P) uptake, plant size, and biomass align with native environmental gradients—specifically temperature, precipitation, and altitude—to assess evidence of local adaptation. By cultivating accessions from geographically distinct sites under uniform conditions, we aimed to determine how environmental gradients influence key traits in *A. wilhelmsii*, evaluate whether trait variation reflects adaptive genetic divergence, and elucidate mechanisms underpinning climate-driven evolution in this species.

Materials and methods

Plant materials

Seeds of *A. wilhelmsii* were collected from eight accessions across Iran's elevational gradient (9.8–2321 m; Table 1). *Achillea wilhelmsii* is not listed as a threatened species under the IUCN Red List. Collection permits were granted by the Agricultural Research, Education, and Extension Organization of Iran in accordance with national biodiversity regulations. Voucher specimens are archived at the Research Institute of Forests and Rangelands Herbarium (Tehran) following taxonomic verification using *Flora Iranica*[21]. Seeds were sown in 100-cell trays (0.5 cm depth) filled with a 50:50 soil–cocopeat/perlite mixture and germinated under greenhouse conditions. At ~ 10 cm height, seedlings were transplanted to a common garden at the College of Abouraihan, University of Tehran (Pakdasht, Iran), arranged in a randomized complete block design (1 m^2 plots, sandy-loam soil). Traits were measured at flowering onset: plant height, width, length, wet/dry biomass, and phosphorus (P) content.

Phosphorus content

Fresh leaves were oven-dried (70 °C, 72 h), ground, and ashed (550 °C, 6 h). Ash residues were dissolved in 10% HCl (100 ml), and P concentration was determined spectrophotometrically (430 nm) via the ammonium molybdate method[22].

Statistical analysis

Temperature and precipitation data for this analysis were sourced from the climatology.ir dataset. As the plant grows from April to September, we calculated the average temperature and precipitation for these 6 months over the past 50 years for each location. Altitude data were obtained directly from the Herbarium of the Research Institute of Forests and Rangelands in Tehran, where the corresponding seeds were acquired.

We applied principal component analysis (PCA) separately to the environmental data and measured traits to capture underlying patterns. The PCA scores, which represent variations in the data, were calculated using the formula:

Code	Voucher no.	Province	City	Altitude
W1	8451	Isfahan	Daran	2321
W2	15,796	Lorestan	Kuhdasht	1188
W3	17,628	Qom	Dastjerd	1736
W4	19,489	Kurdistan	Baneh	1564
W5	33,976	Yazd	Tabas	687
W6	34,431	Hormozgan	Bandar-Abbas	9.8
W7	35,561	Mazandaran	Polur	2231
W8	39,346	Qazvin	Tarom Sofla	1170

Table 1. Geographical location of the eight *A. wilhelmsii* accessions.

$$PCA_i = \sum_{j=1}^{n} Z_{ij} \times e_j$$

PCA_i is the PCA score for location i. The index j iterates over the n environmental factors (or n measured traits). Z_{ij} represents the standardized values of environmental factors (or measured traits) for location i, while e_j are the coefficients from the selected eigenvector.

This yields the PCA scores for each location based on environmental factors and/or the measured characters.

We then employed linear regression to explore the relationships between the PCA scores derived from the two different datasets, using the equation:

$$PCA_{sT} = \beta_0 + \beta_1 (PCA_{sE}) + \epsilon$$

Where PCA_{sT} and PCA_{sE} represent the PCA scores for measured characters and environmental factors, respectively.

This equation illustrates the relationship between the PCA1 scores based on measured characters and those based on environmental factors, as determined by linear regression (Farajpour test).

To estimate the proportion of trait variability attributable to environmental gradients, we used the formula:

$$\textbf{Total trait variability}(\%) = \sum TVi \times Ri$$

Where: Σ = Sum of products for significantly correlated trait-environment PCA score pairs, TVi = Percentage of trait variance explained by the ith trait PCA, $Ri = R^2$ of linear regression between ith trait PCA scores and corresponding environment PCA scores.

The correlation analysis was visualized as a colored heat map using MetaboAnalyst[23]. The PCA analysis was conducted using the Statistical Analysis Software (SAS Institute, Cary, NC) for Windows version 9.1. Additionally, the graphs were created using Prism 9 (GraphPad).

Results

In this study, the measured traits exhibited relationships with environmental gradients such as temperature, precipitation, and altitude. Climate variables do not operate in isolation; rather, they interact as part of the overall climate in specific locations, making it challenging to establish causality between individual climate factors and traits.

To analyze these relationships, we conducted a principal component analysis (PCA) on environmental variables measured across the eight locations. The PCA extracted principal components (PCs) that represented underlying multivariate climate gradients. The first PC (PCA1) explained 80% of the total variance among locations, delineating a gradient from warmer/drier conditions at lower altitudes (negative PCA1 scores) to colder/wetter conditions at higher altitudes (positive PCA1 scores).

The measured plant traits showed significant correlations with PCA1 (Fig. 1). Linear regression analysis further explored these associations, using PCA1 scores to represent the multivariate environmental gradient. The results indicated significant relationships between PCA1 scores and various plant characteristics.

Specifically, PCA1 scores positively correlated with plant height (Fig. 2a), wet mass (Fig. 2b), length (Fig. 2c), width (Fig. 2d), and phosphorus content (Fig. 3). This suggests that as environmental conditions became cooler and wetter at higher elevations, plant traits exhibited larger or more vigorous values. Thus, the linear regression analyses supported the hypothesis that the coordinated variation in temperature, precipitation, and altitude accounts for the divergent responses observed in the measured traits across *A. wilhelmsii* populations.

Additionally, we performed a PCA on the measured traits, where Principal Component 1 (PC1) explained 64.30% of the total variance, primarily influenced by all measured variables (Table 2). Phosphorus showed the highest correlation coefficient of 0.86, followed by wet mass (0.85), plant width (0.84), plant height (0.83), and plant length (0.84). Principal Component 2 (PC2) explained 21.25% of the variance, primarily influenced by dry mass, while Principal Component 3 (PC3) explained 10.19%. Together, PC1, PC2, and PC3 explained over 95% of the total variance.

PCA1 accounted for 80% of the total environmental variance, with PCA2 explaining an additional 15%. The separate PCA of measured plant traits revealed three components, with PCA1 and PCA3 showing significant correlations with PCA1 and PCA2 scores of the environmental gradients, respectively (Fig. 4).

To test the relationships observed, we applied a generalized formula to estimate the proportion of trait variability attributable to environmental gradients (Fig. 5). The analysis revealed highly significant linear regressions between matching PCA1 and PCA3 trait scores with PCA1 and PCA2 environmental scores, yielding R^2 values of 0.86 (Fig. 6) and 0.77, respectively ($P < 0.001$).

Using the formula:

$$\text{Total Trait Variability} = (64.3\% \ \times 0.86) + (10.19\% \ \times 0.77) = 62.85\%$$

This indicates that 62.85% of the variation observed among the populations, based on measured characteristics, can be attributed to evolutionary responses driven by the three environmental gradients. Additionally, the correlation analysis (Fig. 1) found no significant relationships between soil phosphorus or pH at collection sites and the leaf phosphorus content of plants grown in the common garden.

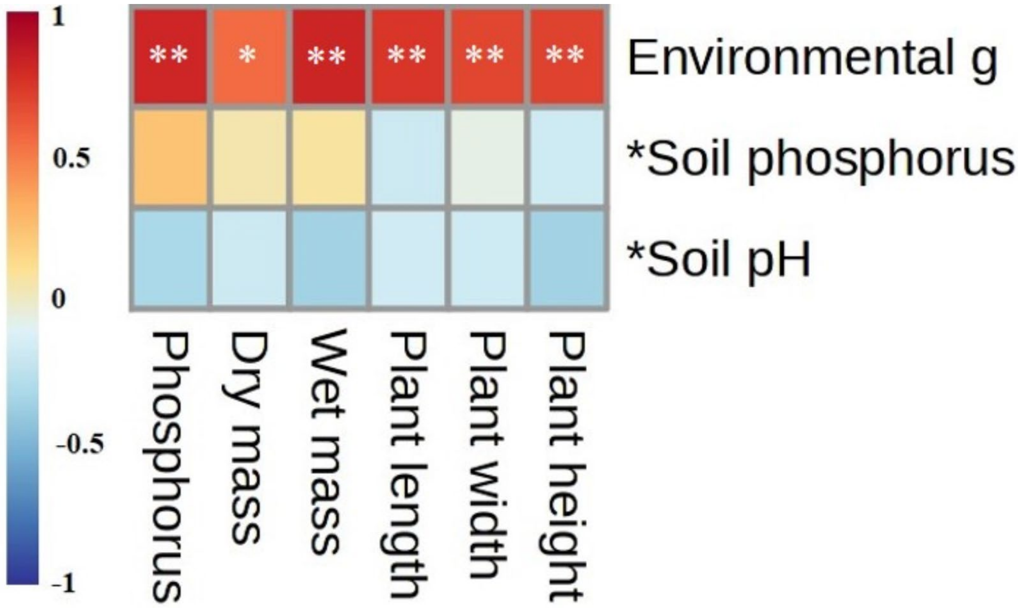

Fig. 1. Heat map showing correlation coefficients among the measured plant traits and environmental gradients (the first principal component (PCA1) scores representing integrated environmental gradients of temperature, precipitation, and altitude), for the eight *A. wilhelmsii* accessions included in the common garden study. A principal component analysis of the three environmental variables extracted PCA1 as the dominant gradient explaining 80% of total variance across sites. PCA1 scores, incorporating contributions from all three gradients based on their loadings, were then used in place of individual variables. Soil pH and soil phosphorus were additionally measured from the collection sites to assess potential relationships with leaf phosphorus content observed in plants grown in the common garden experiment. Asterisks indicate statistical significance at the 0.05 (*) and 0.01 (**) levels.

Discussion

Our findings indicate that multiple traits in *A. wilhelmsii* demonstrate genetic divergence related to local adaptation along climatic gradients. Size-related traits such as height, length, width, wet mass, and dry mass show significant correlations with PCA1 scores based on temperature, precipitation, and altitude. Taller and larger plants are associated with cooler, wetter, and higher-altitude environments, while those from warmer, drier, lower-altitude areas tend to be shorter and narrower. This variation suggests divergent selection on genetic traits across different climatic conditions.

Phenotypic plasticity—the ability of organisms to modify their phenotype in response to environmental changes—can be advantageous in fluctuating environments[24]. Following Blanckenhorn's[25] criteria for demonstrating adaptive phenotypic plasticity, our study provides compelling evidence across fundamental aspects. First, we found that phenotypic variations stemming from genetic divergence confer differential fitness advantages in contrasting environments[26]. High-altitude accessions exhibit enhanced phosphorus uptake, likely improving survival in cooler climates, whereas low-altitude accessions possess traits favoring growth in warmer, drier conditions. Furthermore, phosphorus plays a critical role in photosynthetic efficiency and membrane fluidity, aiding in cold tolerance[27].

Our results suggest that *A. wilhelmsii* populations diverged genetically to adapt to the climatic conditions of their collection sites. Plants from warmer, drier, lower-altitude environments tend to be shorter and narrower, a consequence of selection on water-conservation alleles[28,29]. In contrast, populations from cooler, wetter, higher-altitude sites are taller and more robust, indicating selection favoring competitive growth alleles[30]. These patterns align with previous studies documenting intraspecific trait variation along environmental gradients in other species, suggesting that local adaptation arises from genetic divergence[31]. Additionally, our findings on wet mass correlate with climatic gradients, revealing that higher precipitation and altitude correspond to increased biomass. This is consistent with literature indicating that drought stress limits biomass production[32,33]. Broader environmental gradients significantly influence plant growth and productivity by affecting moisture and salinity levels[34,35]. Moisture and nutrient gradients are also important drivers of plant community composition, indicating their strong selective influence on traits at the intraspecific level as well[36,37].

Using a common garden design allowed us to isolate the genetic basis of trait-climate associations by ensuring all populations experienced the same abiotic conditions[38]. This minimizes environmental variance and confirms that the observed trait variation has both genetic and plastic components. While genetic capacity for plastic responses may differ between ecotypes adapted to divergent climates[39,40], our research suggests genetic divergence likely drives local adaptation in *A. wilhelmsii*. Future genetic and genomic studies could further elucidate the specific genes and alleles contributing to these locally adaptive traits.

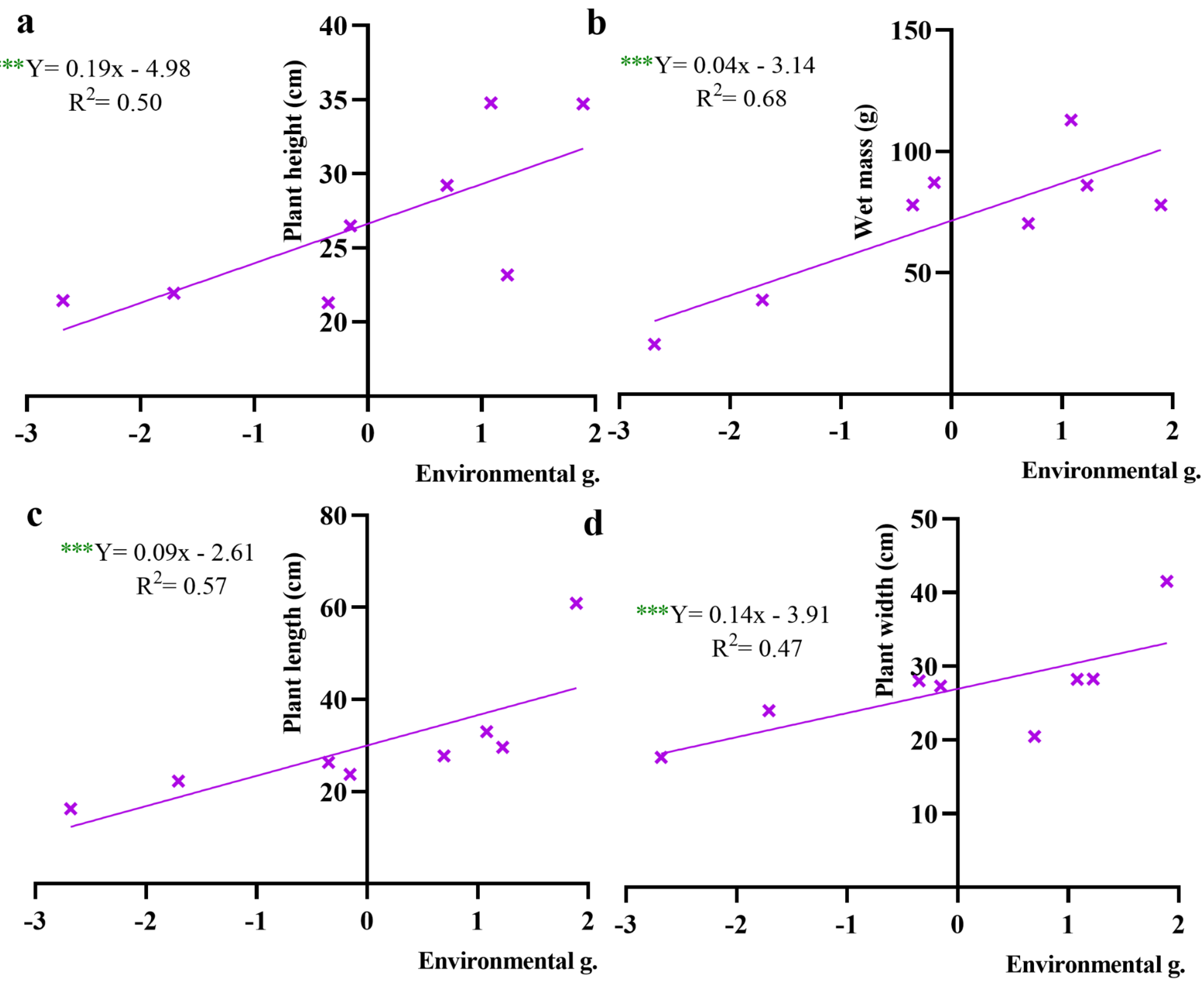

Fig. 2. Linear regression relationship between plant height, length, width, and wet mass with PCA1 scores representing integrated environmental gradients among eight *A. wilhelmsii* populations.

In examining phosphorus content in *A. wilhelmsii* leaves, our results underscore phosphorus's vital role in plant growth and development. As an essential nutrient, phosphorus influences metabolic processes and biomass production[41]. Insufficient phosphorus availability can significantly limit plant growth by restricting photosynthesis and cell division[42]. The relationship between phosphorus uptake and temperature is complex and varies among plant species and environmental conditions. Additionally, phosphorus contributes to plants' adaptability to the external environment[43] and enhances their resistance to low temperatures by being involved in the formation of phospholipids and ATP[44]. Schmidt[45] observed higher biomass phosphorus concentrations in microalgae under simulated cold region conditions, suggesting increased phosphorus uptake. Our data indicate that as temperatures decrease and precipitation and altitude increase, phosphorus absorption in *A. wilhelmsii* rises. This suggests that natural selection favors pre-existing genetic adaptations that maximize phosphorus uptake in cooler environments, leading to enhanced growth and biomass production over generations[46,47].

Previous research has demonstrated that plant genetic factors play a significant role in controlling phosphorus absorption. Matsui[46] showed that overexpression of the *AtPHR1* transcription factor in garden plants increased phosphate absorption rates. Bucher[47] highlighted the potential of genetic engineering to enhance phosphorus uptake in crop plants, and Tesfaye[48] emphasized the genomic and genetic control of phosphate stress in legumes, indicating the broad applicability of these findings. Additionally, Dissanayaka et al.[49] provided insights into the metabolic factors and utilization of phosphorus by plants, suggesting that genetic differences in absorption and transport capacities could be exploited for crop improvement.

The principal component analysis revealed that the primary source of variation among plant traits was linked to the integrated environmental gradient of temperature, precipitation, and altitude. This supports the hypothesis that natural selection acts on standing genetic variation, driving *A. wilhelmsii* populations in cooler, wetter, higher elevation areas to evolve genetic adaptations for superior phosphorus uptake, enhancing their survival under climatic stresses. While we posited that variation in phosphorus uptake could also be influenced by soil phosphorus availability and pH, our correlation analysis found no significant relationships between these

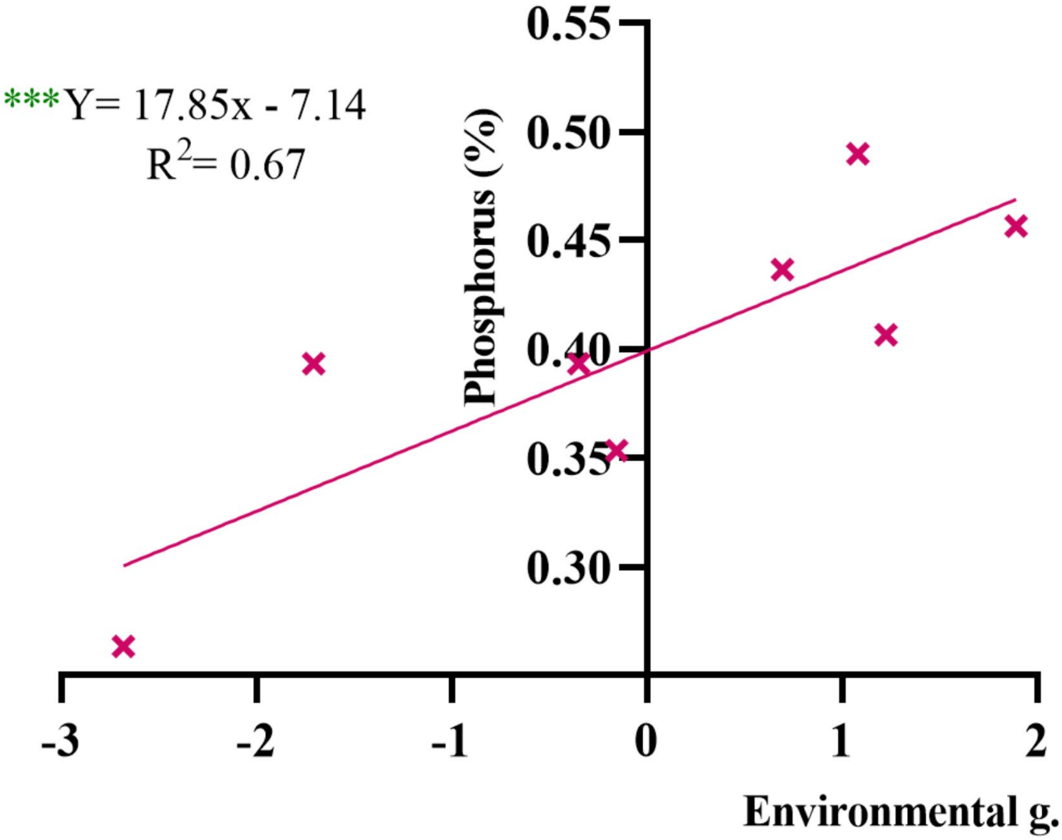

Fig. 3. Linear regression relationship between leaf phosphorus content and PCA1 scores representing integrated environmental gradients among eight *A. wilhelmsii* population locations.

Label		Principal components		
		PC1	PC2	PC3
1	Phosphorus	0.86**	−0.04	−0.36
2	Wet mass	0.85**	0.51	−0.13
3	Plant width	0.84**	−0.24	0.48
4	Dry mass	0.57*	0.79**	0.23
5	Plant height	0.83**	−0.28	−0.37
6	Plant length	0.83**	−0.50	0.23
–	Eigenvalue	3.86	1.27	0.61
–	% of variance	64.30	21.25	10.19
–	Cumulative%	64.30	85.55	95.74

Table 2. PCA based on the five character of 8 *A. wilhelmsii* accessions. Asterisks denote statistically significant correlations between traits and their PCs at the 0.05 (*) and 0.01 (**) levels.

soil factors and leaf phosphorus content in the common garden. This suggests that local soil conditions were not primary determinants of the observed phosphorus physiology divergence. Instead, environmental drivers like temperature and precipitation appear to exert a more substantial influence as selective pressures on genetic variation.

Conclusion

In conclusion, this study provides evidence that multiple plant traits in *A. wilhelmsii* are locally adapted along the multivariate environmental gradient represented by PCA1 scores derived from temperature, precipitation, and altitude data. A hypothesis emerging from these results is that phosphorus uptake by the plants increases under colder, wetter conditions at higher altitudes associated with positive PCA1 scores. We hypothesize this plays a role in the observed pattern of populations from locations with positive PCA1 scores exhibiting traits maximizing growth potential such as larger size. Increased phosphorus availability

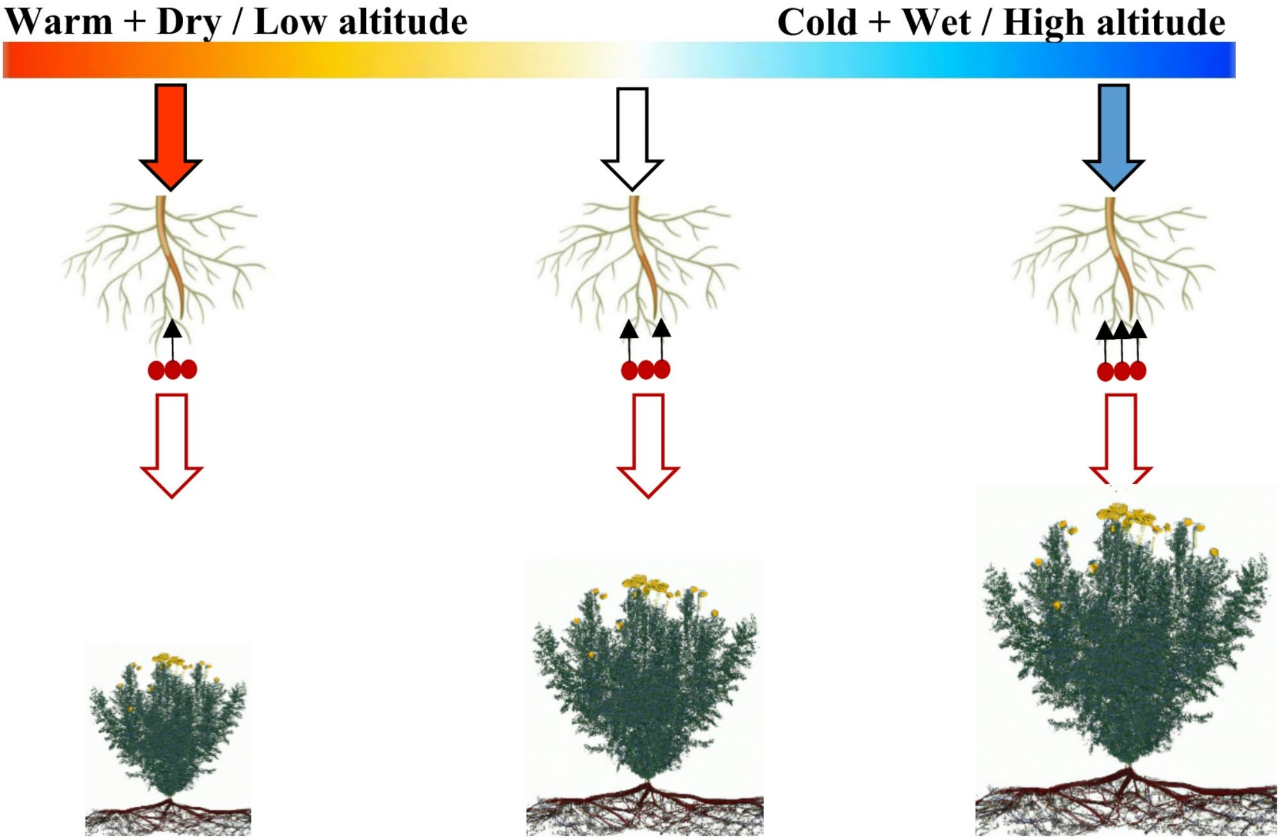

Fig. 4. Hypothesized relationships between environmental gradients, phosphorus uptake and plant size in *A. wilhelmsii*. Conditions characterized as colder, wetter and higher altitude impose selective pressures favoring plants with genetic adaptations for enhanced phosphorus uptake from soil. Over multiple generations, populations inhabiting areas associated with colder, wetter and higher altitude conditions evolve to absorb more phosphorus, allowing improved survival under stresses. Higher internal phosphorus levels optimize growth performance under colder, wetter and higher altitude conditions. In turn, increased phosphorus acquisition facilitates the evolution of larger plants through strengthened tolerance and competitive abilities, conferring adaptive advantages against populations from areas characterized as warmer, dryer and lower altitude exhibiting smaller sizes constrained by lower phosphorus absorption capacities.

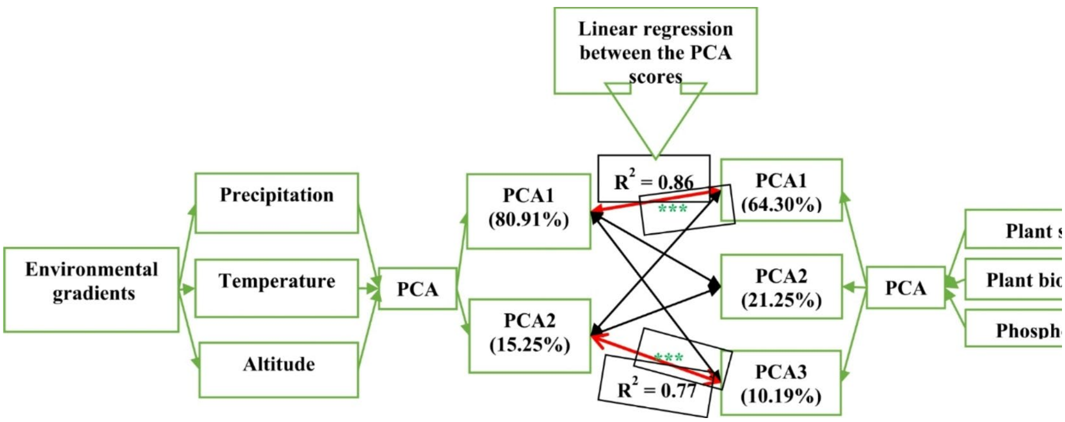

Fig. 5. Workflow diagram for quantifying the evolutionary influence of multiple environmental gradients on trait differentiation through principal component analysis, based on the Farajpour test. The red lines (***) indicate significant linear regressions observed between PCA scores of the environmental gradients and corresponding PCA scores of the measured plant traits. Application of the generalized formula incorporating percentages of variance explained (TVi) by each trait PC and R^2 values estimates the overall trait variability (62.85%) attributable to evolutionary responses along the three environmental gradients.

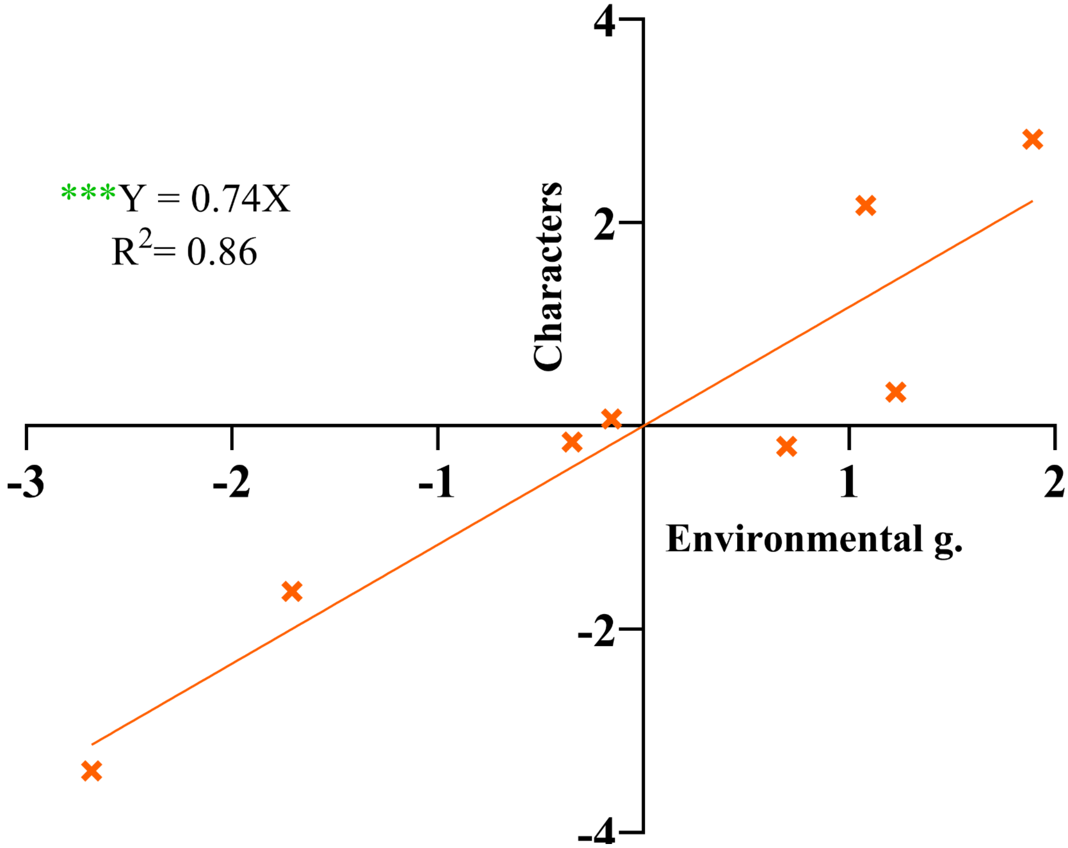

Fig. 6. The results of relating Principal Component 1 (PC1) scores from the principal component analysis of environmental variables to PCA1 scores from the principal component analysis of plant trait measurementsacross eight *A. wilhelmsii* population location.

and acquisition capacity under these environmental conditions may facilitate optimized plant growth. Size-related characteristics such as plant height, length, width, and biomass consistently correlated with shifts along the integrated environmental axis delineated by PCA1, indicative of adaptation to different abiotic conditions. Future work should aim to test the proposed relationships between phosphorus, environmental conditions and size-based traits, as well as identify the underlying genetic and genomic mechanisms. Overall, this research provides compelling evidence that natural selection has shaped locally adapted diversity in *A. wilhelmsii* via traits evolving in response to environmental variation along climatic gradients.

Data availability
All data are within the manuscript.

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MF and ME conceived and designed the research. MF conducted experiments and wrote the manuscript. MSH, SM, MRR conducted experiments. SS elaborated on the results and discussion, while doing a critical reading of

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Additional information
Correspondence and requests for materials should be addressed to M.F. or M.E.

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