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Examining phosphorus use efficiency across different lettuce (*Lactuca sativa* L.) accessions

Gustavo F. Kreutz · Jehangir H. Bhadha · Germán V. Sandoya

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Abstract Most agricultural soils worldwide have limited availability of phosphorus (P); thus, crops require supplemental application of P fertilizers. Due to the economic and environmental concerns derived from the use of P fertilizers, identifying and breeding P-efficient lettuce (*Lactuca sativa* L.) cultivars is imperative for the reduction of production costs and implementation of more sustainable practices. Phosphorus use efficiency (PUE) remains unexplored in lettuce. In this research, 66 lettuce accessions of six morphological types were evaluated under the standard recommended P rate (202 kg·ha^{-1} of P_2O_5) and half-P rate (101 kg·ha^{-1} of P_2O_5). Lettuce accessions were tested in two field experiments conducted during the 2017–2018 and 2019–2020 growing seasons in the organic soils (Histosols) in the Everglades Agricultural Area of South Florida. Head weight, marketability, tissue P concentration, soil total P concentration, and soil extractable P were measured. P-efficient lettuce accessions were identified within romaine, crisphead, butterhead, Latin, and loose leaf types. Eighteen accessions were found to produce similar head weight under both half-P rate and standard-P rate conditions. Significant accession × experiment and P rate × experiment interactions were observed likely due to differences in solar radiation and weed incidence in both experiments. Marketability of loose leaf accessions was less affected by the 50% reduction in P application. Twenty-two accessions produced similar number of marketable heads under both P treatments. More comprehensive investigations must be conducted to elucidate the genetic mechanisms controlling PUE in lettuce.

Keywords Breeding · Yield · Nutrient use efficiency · Vegetables · Histosols · Everglades Agricultural Area · Muck soils

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G. F. Kreutz · G. V. Sandoya (✉)
Horticultural Sciences Department, Everglades Research and Education Center, University of Florida, 3200 East Palm Beach Road, Belle Glade, FL 33430, USA
e-mail: gsandoyamiranda@ufl.edu

J. H. Bhadha
Soil and Water Sciences Department, Everglades Research and Education Center, University of Florida, 3200 East Palm Beach Road, Belle Glade, FL 33430, USA

Introduction

Most agricultural soils worldwide present suboptimal levels of plant essential nutrients and/or are severely degraded due to intense crop cultivation and inappropriate soil management practices (Baligar and Fageria

2015). Low fertility and degradation of arable lands can negatively impact crop yield, and therefore, agricultural soils require additional fertilizer inputs to achieve adequate crop nutrition, resulting in higher production costs to farmers (Maqsood et al. 2013). Increased use of fertilizers has been associated with eutrophication of natural ecosystems (Fageria et al. 2008). These negative factors have led to a search for alternatives to minimize the utilization of fertilizers and their drawbacks (Kanter et al. 2015; Wu and Ma 2015).

Improving nutrient use efficiency is considered one of the most cost-efficient methods to reduce fertilizer expenses and environmental degradation (Ali et al. 2018). Nutrient use efficiency can be defined as higher yield production by plants per unit of applied or absorbed nutrient (Fageria et al. 2017). Mechanisms of nutrient use efficiency such as root morphology changes, induction of transporters, improved nutrient assimilation, translocation from roots to shoots, storage, recycling, and remobilization have been documented in the model plant Arabidopsis (*Arabidopsis thaliana*) and in cultivated crops including rice (*Oryza sativa* L.), maize (*Zea mays* L.), barley (*Hordeum vulgare* L.), wheat (*Triticum aestivum* L.), and coffee (*Coffea arabica* L.) (Horst et al. 1993; Walker et al. 1996; Jia et al. 2008; Kellermeier et al. 2013; Chietera and Chardon 2014; Yu et al. 2014; Moura et al. 2019). Deciphering the mechanisms of nutrient use efficiency and conducting screening experiments to identify accessions capable of producing good yield with less fertilizer inputs, allow for a better comprehension of the complex functioning of plant nutrient use efficiency and for the potential breeding of new cultivars with improved nutrient use efficiency (Reich et al. 2014).

A large fraction of nutrient use efficiency studies conducted hitherto have focused on P use efficiency (PUE) of crops. After nitrogen (N), P is the second-most essential element to plants; however, it is one of the least mobile and available nutrients in soil (Gruen et al. 2014). Phosphorus mobility and solubility in soils are influenced by plant type and macro and microenvironmental factors; among these, soil pH is the major factor to be considered when addressing the fate and transport of P in soils (Bhadha et al. 2010; Fageria et al. 2017). Phosphorus availability is reduced in soils with low pH (< 5.5) due to P sorption by iron (Fe) and aluminum (Al) ions, whereas in high pH (> 7.0) soils, P is fixed by calcium (Ca). The high fixation and low mobility of P in soils are reflected in low recovery rates of applied P fertilizers by plants; less than 25% of applied P fertilizer is recovered by crops in the year of application (Fageria et al. 2017).

Plants vary in the manner they absorb nutrients from the soil. Barley and rice accessions can uptake soil P present in the form of insoluble complexes formed with Ca and Mg (Gruen et al. 2014), including calcium phosphate and magnesium phosphate, via root exudation of organic compounds such as acid phosphatase enzymes (Gao et al. 2020; Nirubana et al. 2020). There are several screenings for PUE reported in the literature in which genotypic differences were identified in coffee (*C. arabica* and *C. canephora* Pierre; Neto et al. 2016), faba bean (*Vicia faba* L.; Daoui et al. 2011), soybean (*Glycine max* (L.) Merr.; Yan et al. 2006), rice (Vandamme et al. 2016), wheat (*T. aestivum* L. and *T. durum* L.; Ozturk et al. 2005; McDonald et al. 2010), white clover (*Trifolium repens* L.; Pereira-Carvajal et al. 2016), barley (*H. vulgare* L.; McDonald et al. 2010), and tea (*Camellia sinensis* L.; Salehi and Hajiboland 2008). Phosphorus use efficiency has been gradually incorporated as a target trait by plant breeders worldwide, especially in rice and wheat breeding programs. Reducing fertilizer application is critical for current and future sustainable practices.

In the U.S., lettuce is among the top-ten most consumed vegetables (USDA ERS 2019). California and Arizona grow approximately 94% of the total national lettuce, with Florida growing approximately 3.5% (USDA NASS 2019). The demand for lettuce in the U.S. makes it the ideal species for breeding targets such as PUE (or any nutrient use efficiency). In Florida, lettuce is primarily planted in the Everglades Agricultural Area (EAA). The EAA is an area in South Florida well-known for its high relevance to the agricultural industry in the state and for its rich organic soils (Histosols), typically referred to as "muck." Histosols in the EAA contain nearly 65% organic matter and have become shallower over time due to soil subsidence, in which organic matter is lost by decomposition, oxidation, and erosion. Soil loss helps with the incorporation of calcium carbonate from the underlying limestone bedrock into upper parts of the soil profile, increasing soil pH (Bhadha et al. 2020). In turn, the availability of some nutrients, especially P, is drastically reduced. P-efficient lettuce cultivars capable of producing higher yield with less P inputs can contribute to the reduction of fertilizer use, lower production costs and increase the sustainability of cultivation practices (Baligar et al. 2001; Ortiz-Monasterio et al. 2001; Ozturk et al. 2005; Wang et al. 2005; Ali et al. 2018).

Hence, the identification of lettuce accessions with higher PUE will allow the introgression of this trait into lettuce breeding programs for further improvement. Genetic variation for PUE has been previously identified in lettuce (Buso and Bliss 1988; Bertossi et al. 2013), and in related species including sunflower and safflower in the Asteraceae (Compositae) family (Abbadi and Gerendás 2015). However, many of the previous studies on PUE were conducted in greenhouses and not in field. Because results obtained from PUE studies under field and controlled conditions often do not correlate (Parentoni et al. 2012), it is imperative to evaluate lettuce for PUE in field, especially in unique environments as the Histosols of the EAA. It is hypothesized that lettuce can uptake P in field conditions as genetic variation for nitrogen (N) use efficiency has been reported in *L. sativa* (Macias-González et al. 2021). Additionally, lettuce reacts differently to the deprivation of P, N, or potassium (K) (Hoque et al. 2010; Simko 2020).

The objectives of this study were to: (1) identify lettuce accessions that produce a similar head weight under the standard recommended P rate and half-P rate; (2) examine the relationship between soil and tissue P concentration; and (3) understand the effects of the reduction of P application on other horticultural traits of lettuce. This study identified lettuce accessions that yielded head weights with no statistical difference under both P rates, including lines locally adapted to the EAA. These accessions may be used as sources for breeding new cultivars for PUE, which in turn may help mitigate problems associated with low soil P availability in conventional cultivation areas such as the EAA.

Materials and methods

Plant material

Sixty-six lettuce accessions of six different morphological types were used in the study. The set of accessions included 19 crisphead, 18 romaine, 12 butterhead, 12 loose leaf, four Latin, and one oilseed (Table 1). These accessions include lines/cultivars bred and adapted to Florida's conditions, obsolete commercial cultivars utilized in inland and southern production areas of California and Arizona, and heirloom cultivars and accessions named as plant introductions (PI) that were introduced to the United States Department of Agriculture (USDA)–National Plant Germplasm System/Germplasm Resources Information Network (NPGS-GRIN).

Seeds of 20 breeding lines/cultivars were previously increased from the University of Florida's Institute of Food and Agriculture Sciences (UF/IFAS) Lettuce Breeding Program. The other germplasm was requested from the NPGS-GRIN collection and from the seed company 3 Star Lettuce (Gonzales, CA).

Field experiments

Experiments were conducted in field to screen lettuce accessions for PUE in two different planting seasons. The experiments were planted at the UF/IFAS Everglades Research and Education Center (EREC), in Belle Glade, FL. The first set of experiments was conducted from November 2017 to March 2018, and the second set of experiments was conducted from November 2019 to January 2020 (Table 2). Experiments in both seasons were planted in Dania muck (euic, hyperthermic Lithic Haplosaprists) soil with a record of minimum P fertilization of 5 years before these experiments were conducted. Prior to each experiment, a soil test was conducted by collecting 10–15 samples across the fields and analyzed at the UF/IFAS Soil Laboratory at the EREC (Table 2).

The experiments were direct seeded on 0.15 m raised double-row beds; each 7.62 m long plot consisted of a unique accession per row. Space between rows was 0.20 m and beds were trapezoid-shaped with a bottom base width of 0.91 m and a top base width of 0.48 m. In both experiments, beds were oriented in a North–South direction. At the four-leaf stage, seedlings were thinned to a 0.30 m spacing. Pest and disease management followed the standard procedures for commercial production of lettuce listed in the Vegetable Production Handbook of Florida (Sandoya-Miranda et al. 2021). Over-head irrigation was provided throughout the crop cycle as needed. The herbicide Pursuit® was applied once post-emergence during each experiment at a rate of 0.14 $L{\cdot}ha^{-1}$ to

Table 1 Lettuce accessions utilized in the two screening experiments for phosphorus use efficiency

Accession	Type	PI number[a]	Breeder
60158	Crisphead	N/A	UF/IFAS
60162	Crisphead	N/A	UF/IFAS
60167	Crisphead	N/A	UF/IFAS
60172	Crisphead	N/A	UF/IFAS
Beacon	Crisphead	PI 604232	Nunhems B.V
Bubba	Crisphead	PI 601978	Seminis Vegetable Seeds, Inc
Chosen	Crisphead	N/A	3 Star Lettuce, LLC
Cibola	Crisphead	N/A	Paragon Seed, Inc
Cooper[c]	Crisphead	PI 661094	3 Star Lettuce, LLC
Coyote	Crisphead	PI 631465	Seminis Vegetable Seeds, Inc
Eblin[b]	Crisphead	N/A	Unknown
Flagler[c]	Crisphead	N/A	3 Star Lettuce, LLC
Green Lightning	Crisphead	PI 599597	Progeny Advanced Genetics, Inc
H1078	Crisphead	N/A	UF/IFAS
Honcho II	Crisphead	PI 601591	Seminis Vegetable Seeds, Inc
Javelina	Crisphead	PI 631464	Seminis Vegetable Seeds, Inc
Lantana	Crisphead	PI 658143	3 Star Lettuce, LLC
Reine des Glaces	Crisphead	PI 634668	Vilmorin, S.A
Sun Devil	Crisphead	PI 603974	Progeny Advanced Genetics, Inc
50098	Romaine	N/A	UF/IFAS
50100	Romaine	N/A	UF/IFAS
60182	Romaine	N/A	UF/IFAS
60183	Romaine	N/A	UF/IFAS
60184	Romaine	N/A	UF/IFAS
70096	Romaine	N/A	UF/IFAS
C1145	Romaine	N/A	UF/IFAS
Floricos 83	Romaine	N/A	UF/IFAS
Green Towers	Romaine	PI 601336	Harris Moran Seed Company
Hialeah	Romaine	N/A	3 Star Lettuce, LLC
King Henry	Romaine	PI 595620	Progeny Advanced Genetics, Inc
Manatee	Romaine	PI 641790	3 Star Lettuce, LLC
Okeechobee	Romaine	PI 658142	3 Star Lettuce, LLC
46	Romaine	PI 278108	N/A
PIC	Romaine	N/A	Unknown
Tall Guzmaine	Romaine	PI 665208	UF/IFAS
Terrapin	Romaine	PI 614861	UF/IFAS
Valmaine	Romaine	PI 543959	UF/IFAS
18076	Butterhead	N/A	UF/IFAS
50111	Butterhead	N/A	UF/IFAS
60173	Butterhead	N/A	UF/IFAS
60174	Butterhead	N/A	UF/IFAS
60176	Butterhead	N/A	UF/IFAS
60179[b]	Butterhead	N/A	UF/IFAS
70202	Butterhead	N/A	UF/IFAS
70882	Butterhead	N/A	UF/IFAS

Table 1 continued

Accession	Type	PI number[a]	Breeder
B1190	Butterhead	N/A	UF/IFAS
B1196	Butterhead	N/A	UF/IFAS
Odyssey	Butterhead	N/A	Unknown
66043	Butterhead	PI 342440	N/A
Bambino	Loose leaf	N/A	Unknown
Cordoba	Loose leaf	PI 595839	Seminis Vegetable Seeds, Inc
Galactic	Loose leaf	N/A	Johnny's Selected Seeds
North Star	Loose leaf	PI 612155	Nunhems B.V
47	Loose leaf	PI 278109	N/A
Strumicka	Loose leaf	PI 358001–1	N/A
Red Rage	Loose leaf	PI 603972	Pybas, Inc. and Douglas Peters
Revolution	Loose leaf	W6 38949	Nunhems B.V
RFX-0901	Loose leaf	N/A	Unknown
RSX743	Loose leaf	N/A	3 Star Lettuce, LLC
Tehama	Loose leaf	PI 632457	Nunhems B.V
Two Star	Loose leaf	PI 562631	Orsetti Seed Company, Inc
49530	Latin	N/A	UF/IFAS
Floribibb	Latin	N/A	UF/IFAS
Little Gem	Latin	PI 617959	Vilmorin, S.A
Pavane	Latin	PI 667705	Unknown
N/A	Oilseed	PI 251246	N/A

[a]Plant introduction number obtained from U.S. Department of Agriculture, National Plant Germplasm System (USDA-NPGS at https://npgsweb.ars-grin.gov/gringlobal/search)

[b]Lettuce accessions Eblin and 60179 were utilized only in the first experiment

[c]Lettuce accessions Flagler and Cooper were utilized only in the second experiment

Table 2 Total precipitation, average soil temperature (at − 10 cm), average aboveground temperature (at 60 cm), average solar radiation, soil pH, soil-test values, and nutrient recommendations prior to planting for each of the two experimental sites used to screen lettuce accessions for phosphorus use efficiency

Year	Total precipitation (mm)[a]	Average soil temperature (°C)	Average above-ground temperature (°C)	Average solar radiation (W/m^2)	Soil pH	Soil-test values[b]			Nutrient recommendation prior to planting (kg·ha^{-1})[c]			
						Pw[3]	K	Mg	N	P_2O_5	K_2O	Mg
2017–18	69.08	20.5	18.6	150.59	7.6	4	106	1,212	0	215	112	0
2019–20	102.36	20.9	19.3	129.08	7.1	7	173	1,202	0	187	67	0

[a]Weather data during the execution of the two experiments in the 2017–2018 and 2019–2020 seasons. Data collected from the Florida Automated Weather Network station, located in the Everglades Research and Education Center, in Belle Glade, FL

[b]Units expressed in kg·ha^{-1}, except for Pw that is expressed as water extractable P index. Nitrogen testing is not available due to the lack of reliable tests

[c]Recommendations from the UF/IFAS Soil Testing Laboratory at the Everglades Research and Education Center, in Belle Glade, FL

control grasses and broadleaf weeds at 7 days after planting. Weeds were manually removed twice during the growing season.

The difficulty associated with applying the two P treatments prevented a split-plot design, therefore, the 66 lettuce accessions used in this research were tested individually for each of the two P treatments. The total area where the experiments were planted was divided in two zones: the first zone was fertilized with the standard recommended rate (202 kg·ha^{-1} of P_2O_5) and the second zone with half of the recommended rate (101 kg·ha^{-1} of P_2O_5). Fertilizer rates were based on recommendations from the UF/IFAS Soil Testing Laboratory at the EREC (Table 2). The P fertilizer used was derived from ammonium polyphosphate 11–37-0 (Wedgworth's Inc., Clewiston, FL) and was banded during bedding at a depth of 5–10 cm below bed surface. Two post-planting split applications of 4.5 kg·ha^{-1} multipurpose 20–20–20 fertilizer (Plant Foods Inc., Vero Beach, FL) were performed in each experiment to provide supplemental nutrients as needed.

Collection of horticultural data

Accessions were evaluated at horticultural maturity, except for the accession PI 251246 (oilseed type) that was harvested along with loose leaf accessions. Horticultural maturity in loose leaf, butterhead, romaine, and crisphead is achieved, respectively, in 45–60, 60–80, 60–80, and 70–95 days after planting (Sandoya-Miranda et al. 2021). Prior to harvest, the percentage of marketable heads was estimated for each accession by dividing the number of plants that would meet market requirements (shape and size) by the total number of plants per plot. At harvest, ten heads were randomly chosen, regardless of their marketability condition, from the center of each plot to obtain the average head weight (HW), expressed in grams (g). The incidence (%) of tipburn, a lettuce disorder characterized by necrosis of newly developed leaf margins, was estimated for each plot by slicing the ten harvested heads in half.

Quantification of phosphorus in plant tissue and soil

At harvest, a sample of 10 inner leaves of the ten harvested heads from each plot were placed into individual plastic bags. Samples were then washed with deionized (DI) water to remove soil particles, placed into paper bags, and oven-dried at 65 °C for 7 days. Once dried, each sample was ground using a Wiley® mill (Model 4, Thomas Scientific, Swedesboro, NJ), and stored in 20 mL polyethylene scintillation vials (Fisherbrand™, Fisher Scientific, Suwanee, GA).

Soil samples were collected from each field plot by collecting the rhizosphere soil around 10 plants; all samples within a plot were evenly mixed to obtain a total of approximately 400 g of soil. One sample per plot was placed into individual plastic bags and dried at 65 °C for 7 days. The dried soil was passed through a 1 mm sieve (16 mesh), collected into plastic scintillation vials, and stored for further analysis of P concentration.

Phosphorus tissue samples were extracted using a total-P (TP) protocol adapted from the UF/IFAS Extension Soil Testing Laboratory Analytical Procedures and Training Manual. Soil samples were extracted following TP and Mehlich-3 protocols (Mehlich 1984).

The TP extraction consisted of weighing 0.4 g of ground plant tissue or dried and sieved soil into a 20 mL glass scintillation vial. Samples were then placed in a muffle furnace and burnt to ashes at 550 °C for 5 h 30 min. Once samples reached room temperature, they were removed from the muffle furnace and moistened by adding five drops of deionized (DI) water. After, each sample received 2 mL of 6 M hydrochloric acid (HCl) and was maintained at room temperature for 2 h. The volume of each vial was then brought up to 20 mL, filtered with qualitative P5 filter paper (12.5 cm in diameter) and transferred to 15 mL polypropylene test tubes. Soil extractable P (M3P) was estimated following a Mehlich-3 extraction protocol (Mehlich 1984). All samples were analyzed for P concentration at the UF/IFAS Soil, Water, and Nutrient Management Laboratory using an inductively coupled plasma optical emission spectrometer (ICP-OES) (Agilent Technologies 5110 ICP-OES, Santa Clara, CA, USA).

Experimental design and data analysis

Each individual (either the standard or half of the recommended rate) experiment was arranged following a randomized complete block design (RCBD) with three replications. Each block, or replicate, was further divided into two sub blocks of 32 accessions each to account for the variation within blocks. A combined analysis of variance (ANOVA) was performed for HW, marketability, tissue TP, soil TP, and soil M3P across accessions, P rates, and experiments. For HW, the ANOVA included a covariate, consisting of residuals derived from the immediate neighboring plots, to adjust for spatial variability using the nearest neighbor analysis (NNA) (Yang and Juskiw 2011). Due to the absence of tipburn in most accessions in both experiments, tipburn data were not analyzed. The following factors were considered fixed effect: accession, P rate, experiment, and the interactions of accession × P rate, accession × experiment, P rate × experiment, and accession × P rate × experiment; the factors sub block nested within block and block nested within experiment were considered random effects. An additional partition of sum of squares was done to estimate the effects of lettuce type and respective interactions on marketability, tissue TP, soil TP, and soil M3P. This analysis did not include HW due to the differences in plant size and morphology among lettuce types.

The sums of squares were partitioned into each lettuce type. The oilseed type was represented by a single accession (PI 251246), and therefore, it was not used in the models containing the accession factor. Pairwise comparisons were performed based on Fisher's least significant difference (LSD) test ($\alpha = 0.05$) to detect non-significant differences between P rates within each accession. In this study, a lettuce accession was considered P-efficient when the HW was not statistically different ($P > 0.05$) between the two P application rate treatments. Pearson correlation coefficients were calculated between HW, marketability, tissue TP, soil TP, and soil M3P values for the P rates and experiments. All analyses were conducted using the GLIMMIX procedure in SAS® software version 9.4 (SAS Institute Inc., Cary, NC, USA).

Results

Lettuce HW under two P rates

Significant differences were identified for HW in the combined analysis for lettuce accessions ($P < 0.0001$) used in these experiments. Significant differences for HW were also observed between the two P rates ($P < 0.0001$) but no differences were detected between the two experiments ($P = 0.7331$). Only two interactions, accession × experiment (G × E) and rate × experiment (R × E) were significant in this study ($P < 0.0001$), while other interactions had no effect on the overall analysis of HW (Table 3).

As lettuce types are different in size and in morphology from one another (Fig. 1S), a separation of the square mean for HW within type indicated that butterhead ($P = 0.0251$), crisphead ($P < 0.0001$), loose leaf ($P = 0.0328$), and romaine ($P < 0.0001$) had different yields (HW) when fertilized with the standard and half-P rates (Table 3). Latin ($P = 0.0942$) and oilseed ($P = 0.1734$) accessions showed non-significant differences in yield (Table 3).

High similarity was identified in HW when lettuce was fertilized with the standard and half-P rates. Specifically, high similarity was found in the butterhead breeding lines 60176 ($P = 0.9153$) and 50111 ($P = 0.6828$) (Fig. 1); crisphead cultivars (cv.) Honcho II ($P = 0.9241$), Cibola ($P = 0.9183$), and Cooper ($P = 0.6435$) (Fig. 2); loose leaf cv. Cordoba ($P = 0.9314$), Galactic ($P = 0.6628$), Revolution ($P = 0.7435$), North Star ($P = 0.7027$), RSX743 ($P = 0.9939$), and Red Rage ($P = 0.6621$) (Fig. 3); romaine breeding lines 50098 ($P = 0.9383$), 60183 ($P = 0.9406$), and C1145 ($P = 0.7833$), cv. Tall Guzmaine ($P = 0.9630$), and PI 278108 ($P = 0.7935$) (Fig. 4); and Latin cv. Little Gem ($P = 0.8193$) and breeding line 49530 ($P = 0.7388$) (Fig. 5) (Table 4). These accessions had the lowest reduction in HW when planted with the half-P rate (Tables 4 and 1S). In this study, the above accessions were considered P-efficient because HW was not significantly affected by the half-P rate. Despite the non-significant difference ($P > 0.05$) between the two P rates, the only oilseed accession tested (PI 251246) experienced a HW reduction of 33% at half-P rate and was not considered P-efficient (Fig. 6).

A separate ANOVA was conducted to test the differences in HW among all accessions under only

Table 3 Analysis of variance of head weight (HW), marketability, tissue total-P (TP) concentration, soil total-P (TP) concentration, and soil Mehlich-3 (M3P) concentration for the 66 lettuce accessions planted under two phosphorus rates in the 2017–2018 and 2019–2020 seasons

Source of variation	Head weight		Marketability		Tissue Total-P (TP)[a]		Soil Total-P (TP)		Soil Mehlich-3 (M3P)	
	DF	*P* value	DF	*P* value	DF	*P* value	DF	*P* value	DF	*P* value
Accession (G)	65	< 0.0001	64	< 0.0001	65	< 0.0001	65	0.8828	65	0.1758
Butterhead (BH)	11	0.0003	11	0.0002	11	0.0011	11	0.6107	11	0.0484
Crisphead (CH)	18	0.0075	18	< 0.0001	18	< 0.0001	18	0.7878	18	0.7298
Latin (LA)	3	0.1573	3	0.0025	3	0.9325	3	0.3520	3	0.5533
Loose leaf (LF)	11	< 0.0001	11	< 0.0001	11	0.0015	11	0.4928	11	0.2723
Romaine (RO)	17	0.0004	17	< 0.0001	17	0.0004	17	0.9250	17	0.8900
Rate (R)	1	< 0.0001	1	< 0.0001	1	< 0.0001	1	0.0001	1	< 0.0001
BH	1	0.0251	1	0.0223	1	0.0596	1	0.0971	1	< 0.0001
CH	1	< 0.0001	1	< 0.0001	1	0.3402	1	0.0781	1	< 0.0001
LA	1	0.0942	1	0.0128	1	0.4835	1	0.5947	1	0.0403
LF	1	0.0328	1	0.1490	1	< 0.0001	1	0.0065	1	< 0.0001
Oilseed (OS)	1	0.1734	–	–	1	0.0117	1	0.6289	1	0.1885
RO	1	< 0.0001	1	< 0.0001	1	< 0.0001	1	0.0724	1	< 0.0001
G × R	65	0.7004	64	0.0009	65	0.0006	65	0.6022	65	0.3886
BH × R	11	0.9268	11	0.6014	11	0.4687	11	0.6018	11	0.0489
CH × R	18	0.6679	18	0.0124	17	0.3092	18	0.4053	18	0.6817
LA × R	3	0.0118	3	0.1230	3	0.5390	3	0.0077	3	0.0252
LF × R	11	0.8191	11	0.5418	11	0.0044	11	0.9030	11	0.8469
RO × R	17	0.7006	17	0.0365	17	0.1215	17	0.8781	17	0.5639
Experiment (E)	1	0.7331	1	0.0945	1	0.0989	1	0.2405	1	0.0107
BH	1	0.2287	1	0.4558	1	0.8817	1	0.6590	1	0.2529
CH	1	0.1608	1	0.1386	1	0.0175	1	0.1029	1	0.0352
LA	1	0.2680	1	0.1343	1	0.3973	1	0.3419	1	0.1380
LF	1	0.3434	1	0.0240	1	0.5201	1	0.4698	1	0.0308
OS	1	0.9428	–	–	1	0.0659	1	0.3622	1	0.1661
RO	1	0.2946	1	0.1399	1	0.0682	1	0.1667	1	0.0295
G × E	61	< 0.0001	60	< 0.0001	61	< 0.0001	61	0.7779	61	0.4485
BH × E	10	0.1626	10	0.1254	10	0.2458	10	0.9656	10	0.8531
CH × E	15	0.5886	15	0.0333	15	0.0788	15	0.7932	15	0.8935
LA × E	3	0.1320	3	0.1143	3	0.6868	3	0.4457	3	0.1814
LF × E	11	< 0.0001	11	< 0.0001	11	0.0005	11	0.6195	11	0.0945
RO × E	17	0.0999	17	< 0.0001	17	0.0011	17	0.7833	17	0.3574
R × E	1	< 0.0001	1	0.0064	1	0.0156	1	< 0.0001	1	< 0.0001
BH	1	0.6107	1	0.7163	1	0.1715	1	0.0021	1	0.0715
CH	1	0.0016	1	0.0217	1	0.0023	1	< 0.0001	1	< 0.0001
LA	1	0.0548	1	0.1276	1	0.2898	1	0.0457	1	0.5042
LF	1	0.4223	1	0.2888	1	< 0.0001	1	< 0.0001	1	< 0.0001
OS	1	0.3048	–	–	1	0.0658	1	0.0809	1	0.0360
RO	1	0.0004	1	0.0037	1	0.0346	1	< 0.0001	1	0.0137

Table 3 continued

Source of variation	Head weight		Marketability		Tissue Total-P (TP)[a]		Soil Total-P (TP)		Soil Mehlich-3 (M3P)	
	DF	*P* value	DF	*P* value	DF	*P* value	DF	*P* value	DF	*P* value
G × R × E	61	0.3015	57	0.0211	58	< 0.0001	61	0.5224	61	0.6422
BH× R × E	10	0.9758	9	0.3460	10	0.3389	10	0.8039	10	0.7469
CH × R × E	15	0.0377	15	0.7345	13	0.1423	15	0.8409	15	0.8685
LA × R × E	3	0.4216	2	0.5538	3	0.8684	3	0.2844	3	0.1756
LF × R × E	11	0.7224	11	0.9624	11	0.0011	11	0.6788	11	0.7744
RO × R × E	17	0.7051	16	< 0.0001	16	0.0082	17	0.1051	17	0.1647
Type (T)[b]	–	–	4	< 0.0001	5	< 0.0001	5	0.2211	5	0.0039
R	–	–	1	< 0.0001	1	0.2084	1	0.0705	1	< 0.0001
E	–	–	1	0.0349	1	0.2474	1	0.3462	1	0.0159
T × R	–	–	4	0.0037	5	0.0032	5	0.9175	5	0.8656
T × E	–	–	4	< 0.0001	5	< 0.0001	5	0.0096	5	0.0543
R × E	–	–	1	0.5822	1	0.4691	1	< 0.0001	1	< 0.0001
T × R × E	–	–	4	0.0377	5	0.0006	5	0.1070	5	0.1026

Covariance parameters	Estimate	Standard error	Estimate	Standard error	Estimate	Standard error	Estimate	Standard error	Estimate	Standard error
Subblock (Block)	528	672	19	15	0	–	2712	2462	3	50
Block (Year)	472	760	0	–	96,612	75,593	0	–	0	–
Residual	6035	397	361	24	793,233	56,241	117,092	7675	7054	463

[a]Tissue Total-P estimated based on dry weight

[b]As lettuce types differ in size and morphology, analysis of variance by type was not performed for head weight

the half-P rate treatment. Significant differences for HW in crisphead ($P = 0.0459$) and loose leaf ($P = < 0.0001$) were identified in this analysis (data not shown). Differences for HW were found between experiments for both the crisphead and oilseed types ($P = 0.0389$), while the G × E interaction had a significant effect on HW for the loose leaf type ($P = 0.0153$) (data not shown). In the half-P treatment, the romaine breeding lines 60183 and C1145; crisphead cv. Chosen; loose leaf cultivars RFX-0901 and North Star; butterhead breeding line 70882, cv. Odyssey, and PI 342440; and the Latin cv. Floribibb, Little Gem, and breeding line 49530 had the highest HW for each of the respective lettuce types Fig. 6.

Marketability affected by P

Our data showed a decrease in plant size, and consequently, less marketable heads in the half-P treatment. Lettuce accessions more sensitive to P deprivation were found to produce a smaller number of leaves, leading to the absence of head formation on crisphead, romaine, and butterhead types (Fig. 7). Marketability was type dependent ($P < 0.0001$; Table 3; Fig. 2S); loose leaf lettuce had the highest percentage of acceptable heads across experiments (Fig. 2S). Marketability was affected by the applied P rate, with differences being observed for butterhead ($P = 0.0223$), crisphead ($P < 0.0001$), Latin ($P = 0.0128$), and romaine ($P < 0.0001$) types, but not for loose leaf lettuce ($P = 0.1490$) (Table 3). The crisphead cv. Honcho II and the romaine cv. King

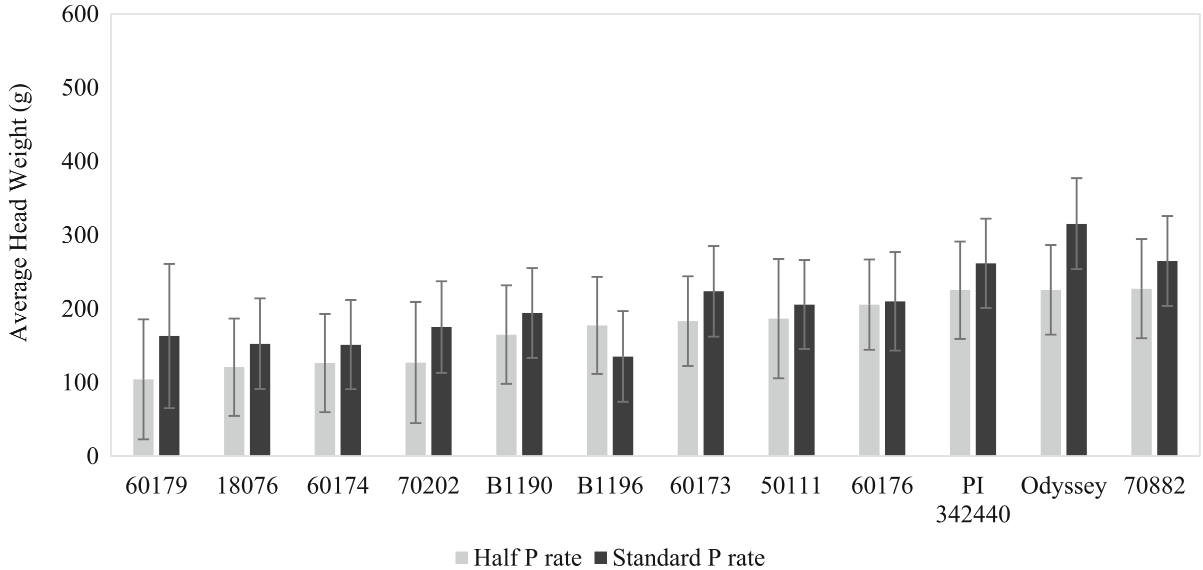

Fig. 1 Least Square Means (LSM) of head weight (g) with 95% confidence intervals of 12 butterhead accessions in experiments conducted in the 2017–2018 and 2019–2020 seasons under half-phosphorus (P) rate and standard-P rate conditions

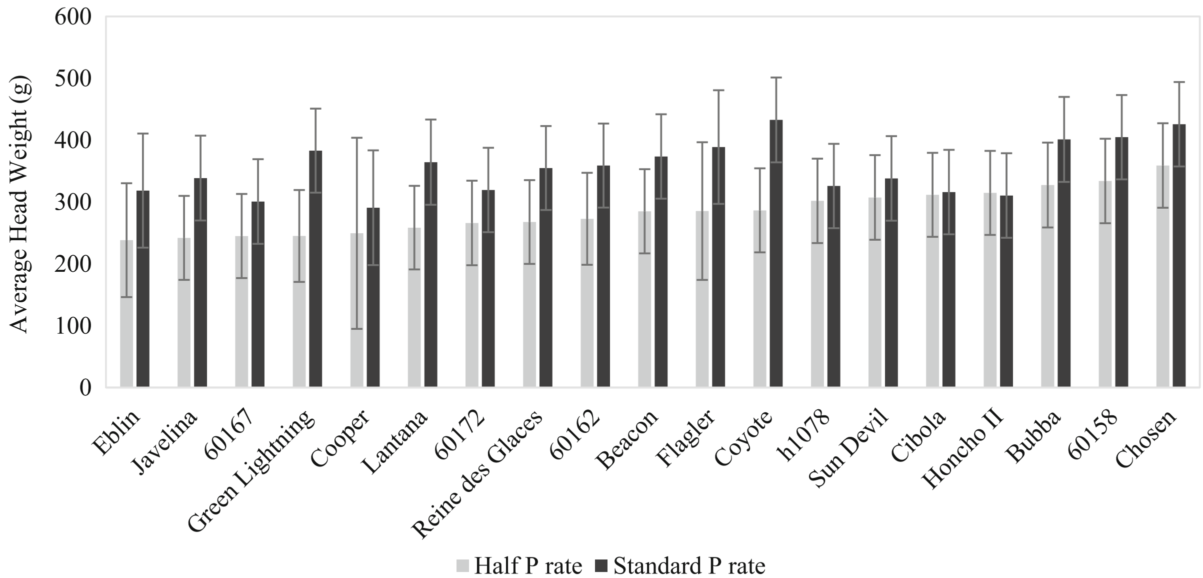

Fig. 2 LSM of head weight (g) with 95% confidence intervals of 19 crisphead accessions in experiments conducted in the 2017–2018 and 2019–2020 seasons under half-P rate and standard-P rate conditions

Henry produced a statistically higher marketability percentage when produced in the half-P treatment compared to the standard-P treatment. Similarly, twelve additional accessions had slightly higher marketability when grown at half-P rate, but the increase was not significant (*P* > *0.05*) (Table 4). Eight lettuce accessions presented a small (<10%) reduction in the percentage of marketable heads (Table 4). All interactions (G × E, G × R, R × E, and G × R × E) were found to have a significant (*P* < *0.05*) effect on the marketability of lettuce (Table 3).

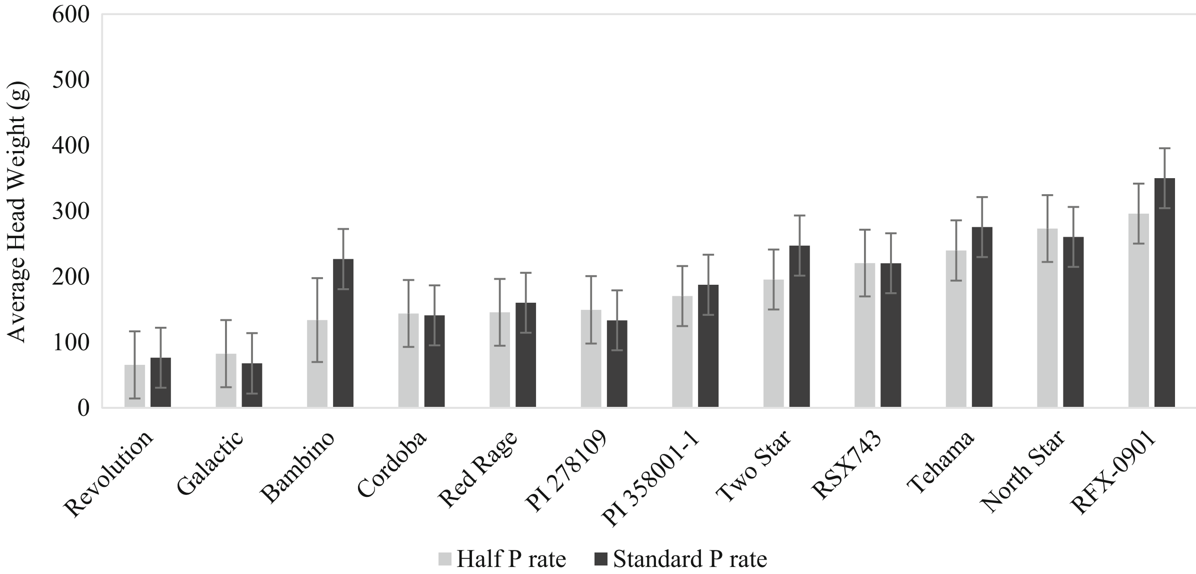

Fig. 3 LSM of head weight (g) with 95% confidence intervals of 12 loose leaf accessions in experiments conducted in the 2017–2018 and 2019–2020 seasons under half-P rate and standard-P rate conditions

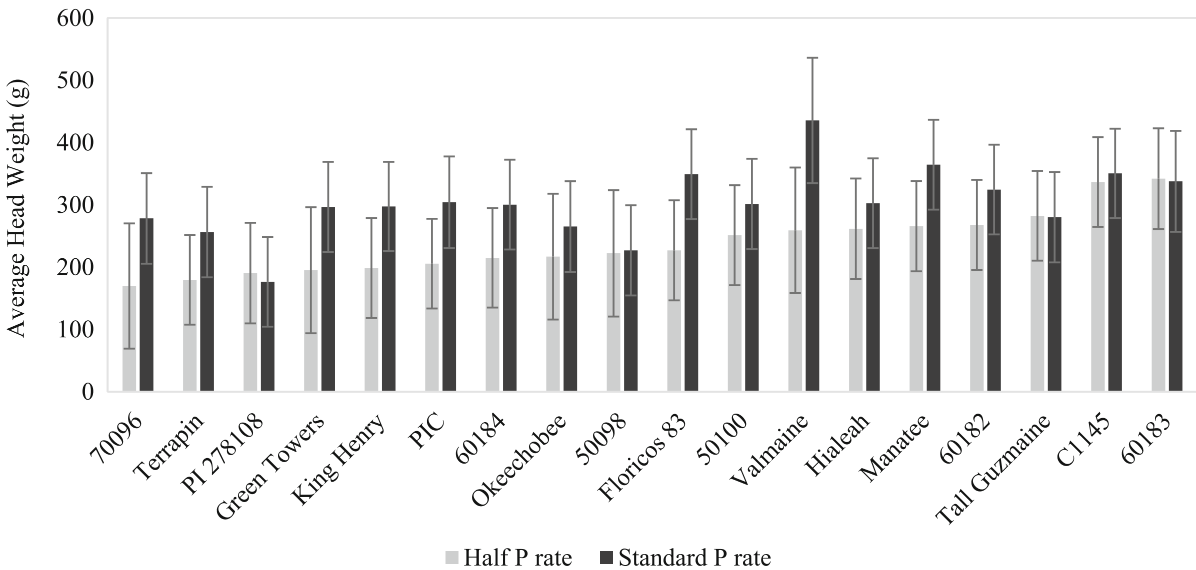

Fig. 4 LSM of head weight (g) with 95% confidence intervals of 18 romaine accessions in experiments conducted in the 2017–2018 and 2019–2020 seasons under half-P rate and standard-P rate conditions

Other unmeasured P-deficiency symptoms, such as foliage chlorosis and necrotic spotting on outer leaves, were observed in this study, especially in the half-P rate treatment (Fig. 7). Tipburn (a physiological disorder) and other biotic stresses were seldom observed in this study. In the first experiment, limited tipburn incidence was observed in the butterhead PI 342440 in both P treatments (1.7 and 2.3%, respectively). In experiment 2, the butterhead breeding line B1196 had $< 1\%$ tipburn when grown in the recommended P rate. All other accessions did not present tipburn symptoms (data not shown).

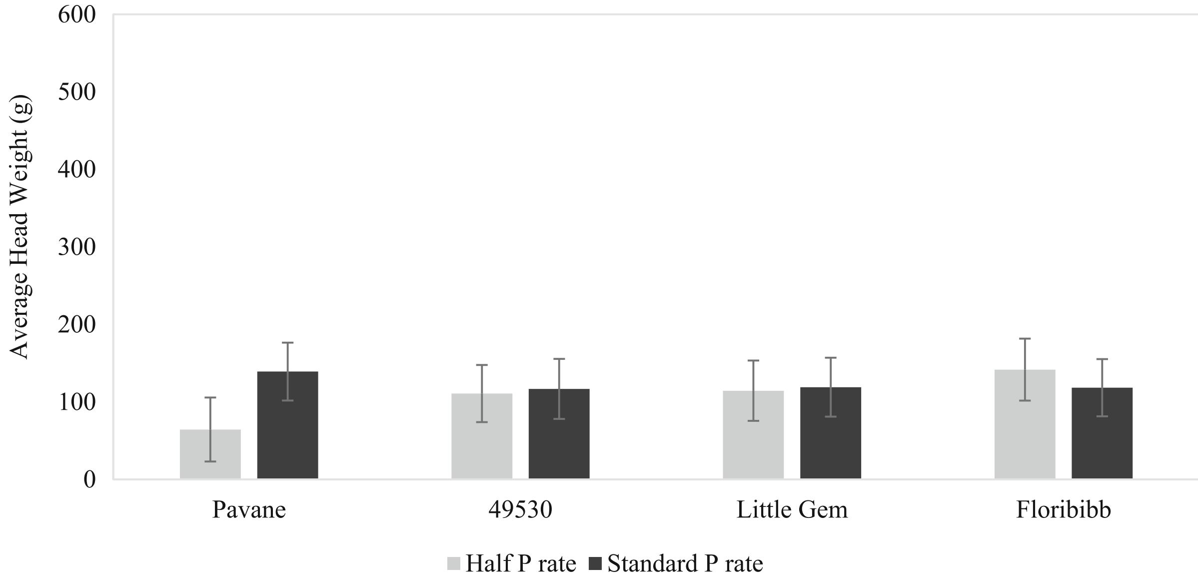

Fig. 5 LSM of head weight (g) with 95% confidence intervals of four Latin accessions in experiments conducted in the 2017–2018 and 2019–2020 seasons under half-P rate and standard-P rate conditions

Head weight and its relationship with P concentration

The TP concentration of lettuce tissue was found to be different among the lettuce types tested. The tissue TP concentration was influenced by the P rate treatments, as the type × rate (T × R), R × E, and T × E × R interactions were found to be significant ($P < 0.05$; Table 3). Romaine, butterhead, and Latin type lettuce had significantly higher tissue TP concentration than crisphead, loose leaf, and oilseed types, regardless of the P rate (data not shown).

Specific lettuce types had different concentrations of TP in tissue. In the half-P rate treatment, the average tissue TP concentration of romaine and loose leaf accessions was significantly ($P < 0.05$) higher than in the standard-P rate treatment, whereas crisphead, Latin, butterhead, and oilseed types had similar ($P > 0.05$) tissue TP concentrations under both P rates (Table 5; Fig. 3S). In addition, significant genetic variation in tissue TP concentration was observed among the loose leaf accessions in response to the reduction in the P rate ($P = 0.0044$; Table 3).

In this study, the soil TP concentration was estimated for all accessions, but no differences were observed ($P > 0.05$; Table 3). A significant effect of P rates was observed on soil TP concentration only in the overall analysis ($P = 0.0001$) and among the loose leaf accessions ($P = 0.0065$) (Table 3).

Significant differences were not observed for most lettuce morphological types in soil M3P, except for the butterhead type ($P = 0.0484$; Table 3). Variation was observed for M3P among P rates in the overall analysis and within all lettuce morphological types ($P < 0.05$), except for oilseed lettuce ($P = 0.1885$) (Table 3). The average M3P was significantly ($P < 0.05$) higher in the standard-P rate treatment than in the half-P rate treatment, indicating that the application of a lower P rate resulted in lower availability of extractable P in the soil.

Overall, no significant correlations ($P > 0.05$) between HW and tissue TP concentration were identified in the standard and half-P rate treatments (Table 6). However, HW was significantly correlated with tissue TP at the experiment level. In the standard-P rate treatment, HW and tissue TP were negatively correlated ($r = -0.35$; $P = 0.0058$) in the first experiment and positively correlated ($r = 0.45$; $P = 0.0002$) in the second experiment (Table 2S). In addition, HW was not correlated with soil TP in either P treatment (Table 6). HW and M3P were slightly significantly correlated when lettuce was fertilized with the half-P ($r = 0.36$; $P = 0.0035$) and standard-P rate treatments ($r = 0.28$; $P = 0.0247$; Table 6). Soil TP and soil extractable P (M3P) were significantly positively

Table 4 Average head weight reduction (%), marketability reduction (%), and their respective 95% confidence intervals (C. I.) of the 66 lettuce accessions across the two experiments

Accession	Type	Head weight reduction (%)[a]	Lower C. I	Upper C. I	Marketability Reduction (%)[a]	Lower C. I	Upper C. I
B1196	Butterhead	− 30.0	− 67.7	7.7	26.0	− 62.9	115.0
Galactic	Loose leaf	− 28.0	− 65.7	9.7	23.7	− 47.7	95.2
Floribibb	Latin	− 20.0	− 57.7	17.7	19.6	− 51.8	91.1
PI 278109	Loose leaf	− 15.0	− 52.7	22.7	− 20.4	− 91.8	51.1
North Star	Loose leaf	− 10.5	− 48.2	27.2	4.3	− 67.1	75.7
Little Gem	Latin	− 6.0	− 43.7	31.7	1.4	− 63.1	66.0
PI 278108	Romaine	− 5.5	− 43.2	32.2	26.8	− 62.0	115.6
50098	Romaine	− 4.5	− 42.2	33.2	61.5	− 27.4	150.5
60176	Butterhead	− 4.0	− 41.7	33.7	33.2	− 38.3	104.6
Honcho II	Crisphead	− 3.5	− 41.2	34.2	− 172.7	− 261.6	− 83.7
Tall Guzmaine	Romaine	− 3.5	− 41.2	34.2	43.9	− 45.1	132.9
Cordoba	Loose leaf	− 2.5	− 40.2	35.2	24.4	− 47.0	95.9
C1145	Romaine	− 2.5	− 40.2	35.2	29.9	− 34.7	94.4
RSX743	Loose leaf	− 0.5	− 38.2	37.2	10.4	− 61.0	81.9
60183	Romaine	0.0	− 37.7	37.7	− 15.1	− 104.1	73.8
PI 358001–1	Loose leaf	0.5	− 37.2	38.2	− 60.6	− 149.4	28.1
Cibola	Crisphead	1.5	− 36.2	39.2	23.4	− 48.0	94.8
49530	Latin	5.0	− 32.7	42.7	11.3	− 60.1	82.8
50111	Butterhead	6.0	− 31.7	43.7	− 14.3	− 103.1	74.5
Cooper	Crisphead	7.2	− 44.3	58.8	86.2	− 65.0	237.4
Tehama	Loose leaf	8.0	− 29.7	45.7	− 17.3	− 81.8	47.3
H1078	Crisphead	8.0	− 29.7	45.7	− 15.3	− 79.9	49.2
Sun Devil	Crisphead	9.0	− 28.7	46.7	− 25.3	− 89.9	39.2
Red Rage	Loose leaf	10.0	− 27.7	47.7	− 37.6	− 109.0	33.9
70882	Butterhead	10.5	− 27.2	48.2	− 86.5	− 175.5	2.4
Hialeah	Romaine	11.0	− 26.7	48.7	47.7	− 23.7	119.2
Bubba	Crisphead	11.0	− 26.7	48.7	50.1	− 21.4	121.5
PI 342440	Butterhead	14.0	− 23.7	51.7	− 41.1	− 112.5	30.4
Chosen	Crisphead	15.0	− 22.7	52.7	3.0	− 61.5	67.6
B1190	Butterhead	15.0	− 22.7	52.7	24.0	− 47.5	95.4
RFX-0901	Loose leaf	15.5	− 22.2	53.2	21.6	− 42.9	86.2
50100	Romaine	15.5	− 22.2	53.2	24.6	− 46.9	96.0
Revolution	Loose leaf	15.5	− 22.2	53.2	31.5	− 40.0	102.9
60174	Butterhead	16.5	− 21.2	54.2	2.1	− 86.9	91.0
60172	Crisphead	17.0	− 20.7	54.7	− 40.7	− 112.2	30.7
60167	Crisphead	17.0	− 20.7	54.7	8.3	− 63.1	79.8
60158	Crisphead	17.5	− 20.2	55.2	36.7	− 34.7	108.2
60182	Romaine	17.5	− 20.2	55.2	51.6	− 12.9	116.2
Okeechobee	Romaine	18.0	− 19.7	55.7	71.9	− 17.1	160.9
60173	Butterhead	19.0	− 18.7	56.7	8.4	− 56.2	72.9
Two Star	Loose leaf	20.0	− 17.7	57.7	6.5	− 58.0	71.1
Flagler	Crisphead	20.2	− 31.3	71.8	19.0	− 88.9	127.8
18076	Butterhead	20.5	− 17.2	58.2	43.3	− 45.7	132.2

Table 4 continued

Accession	Type	Head weight reduction (%)[a]	Lower C. I	Upper C. I	Marketability Reduction (%)[a]	Lower C. I	Upper C. I
60162	Crisphead	21.0	− 16.7	58.7	72.0	0.5	143.4
Manatee	Romaine	23.0	− 14.7	60.7	34.5	− 30.0	99.1
Beacon	Crisphead	24.0	− 13.7	61.7	44.1	− 27.3	115.6
PIC	Romaine	25.5	− 12.2	63.2	22.9	− 66.1	111.9
Reine des Glaces	Crisphead	25.5	− 12.2	63.2	57.7	− 6.9	122.2
60184	Romaine	25.5	− 12.2	63.2	65.2	− 6.2	136.7
Terrapin	Romaine	26.5	− 11.2	64.2	− 19.0	− 108.0	69.9
70096	Romaine	26.5	− 11.2	64.2	61.4	− 27.6	150.4
70202	Butterhead	27.5	− 10.2	65.2	41.7	− 47.2	130.7
Javelina	Crisphead	27.5	− 10.2	65.2	55.9	− 8.7	120.4
Lantana	Crisphead	29.0	− 8.7	66.7	36.8	− 27.8	101.3
Odyssey	Butterhead	29.5	− 8.2	67.2	6.6	− 57.9	71.2
PI 251246[a]	Oilseed	29.5	− 8.2	67.2	–	–	–
Eblin[b]	Butterhead	31.8	− 19.8	83.3	–	–	–
King Henry	Romaine	32.5	− 5.2	70.2	− 156.7	− 245.4	− 67.9
Coyote	Crisphead	33.5	− 4.2	71.2	10.5	− 54.1	75.0
Green Towers	Romaine	33.5	− 4.2	71.2	63.0	− 25.7	151.8
Floricos 83	Romaine	34.5	− 3.2	72.2	64.5	− 7.0	135.9
Green Lightning	Crisphead	36.5	− 1.2	74.2	67.6	− 3.9	139.0
Bambino	Loose leaf	38.0	0.3	75.7	28.5	− 60.5	117.5
60179	Butterhead	42.8	− 8.8	94.3	25.2	− 63.6	114.0
Valmaine	Romaine	47.8	− 3.8	99.3	56.4	− 8.1	121.0
Pavane	Latin	53.5	15.8	91.2	78.1	− 10.7	166.8
LSD[d]		51.0			100.6		

[a]Negatives values indicate that marketability was higher under the half-P rate than under standard-P rate. High positive values indicate high marketability reduction when lettuce was grown under the half-P rate versus standard-P rate conditions

[b]Marketability was not estimated for the oilseed accession PI 251246

[c]Eblin did not produce marketable heads, regardless of P rate

[d]Least significant difference (LSD; $P = 0.05$)

correlated in the half-P rate ($r = 0.63$; $P < 0.0001$) and standard-P rate treatments ($r = 0.85$; $P < 0.0001$; Table 6).

Head weight performance across accessions

Regardless of P rate treatment, there were significant differences ($P < 0.05$) for HW within each lettuce morphological type among the tested accessions (Table 3). In this study, most butterhead accessions, except for 70882 and PI 342440, had significantly less HW compared to Odyssey (a commercial butterhead cultivar; Fig. 4S). Among crisphead accessions, the breeding line 60158, and cv. Bubba, Coyote, were as productive as the commercial Chosen. and Flagler; both commercial cultivars are currently used in field production in Florida (Fig. 5S). The cv. Valmaine had the highest HW among all romaine accessions, followed by breeding lines C1145 and 60183 that were as productive as cv. Hialeah or Manatee (Fig. 6S). All four Latin lettuce accessions produced statistically the same HW; Latin lettuce is not currently planted in commercial fields in Florida (Fig. 7S). The cultivar RFX-0901 had the highest HW

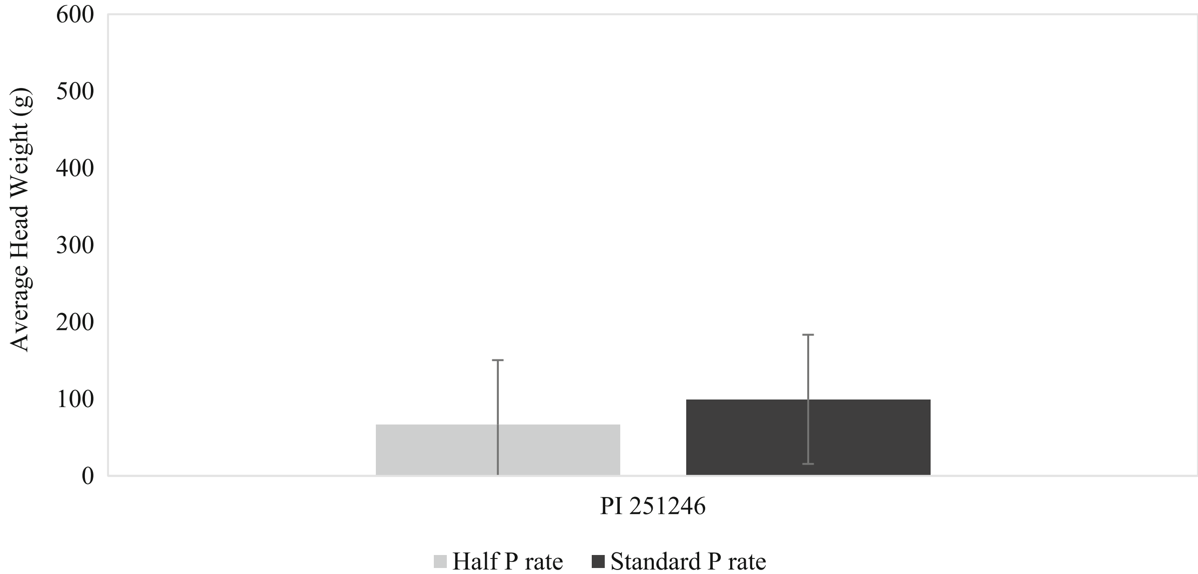

Fig. 6 LSM of head weight (g) with 95% confidence intervals of one oilseed accession in experiments conducted in the 2017–2018 and 2019–2020 seasons under half-P rate and standard-P rate conditions

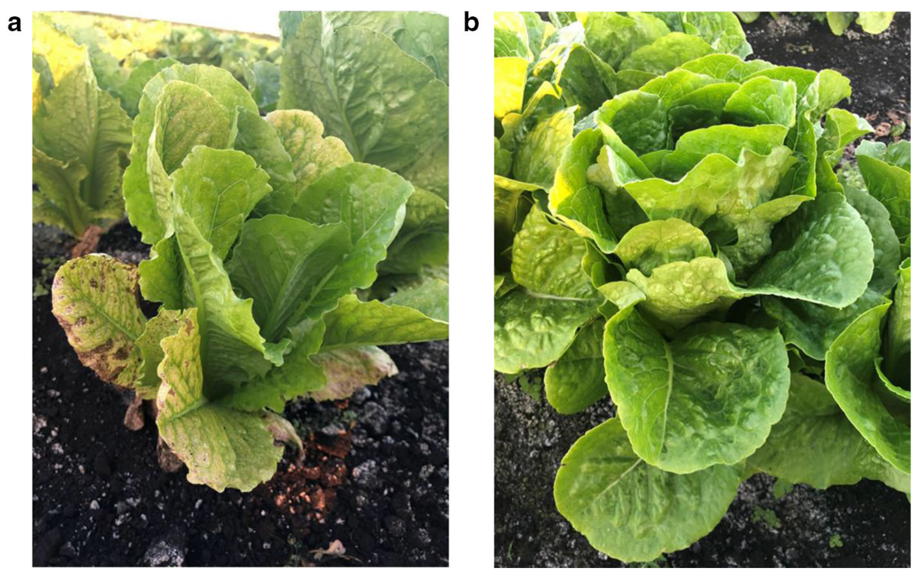

Fig. 7 Romaine lettuce grown at **a** half-P and **b** standard-P rates

of all loose leaf accessions, followed by cv. North Star and Tehama that produced statistically the same HW. Two Star, a commercial cultivar used in Florida, and cv. RSX743 had statistically less HW than cv. RFX-0901 (Fig. 8S).

Discussion

Lettuce HW under two P rates

Lettuce grown in the half-P rate treatment generally had less HW, as expected. Eighteen accessions had the same or similar HW in the half-P treatment compared with the standard P treatment on Histosols in the EAA.

Table 5 Least Square Means (LSM) of total phosphorus (P) concentration in tissue (mg g^{-1}), total P concentration in soil (mg g^{-1}), and extractable P concentration in soil (Mehlich-3; mg g^{-1}) of the 66 lettuce accessions planted under two phosphorus rates in the 2017–2018 and 2019–2020 seasons

Accession	Tissue Total-P (mg g^{-1})[d]		Soil Total-P (mg g^{-1})		Soil Mehlich-3 (mg g^{-1})	
	Half P	Standard P	Half P	Standard P	Half P	Standard P
Butterhead						
18076	6.2	5.8	1.7	2.1	0.10	0.19
50111	6.5	6.3	1.9	2.0	0.11	0.18
60173	7.1	6.8	2.0	2.0	0.18	0.20
60174	6.3	6.8	1.8	1.8	0.13	0.16
60176	7.2	6.8	2.0	1.9	0.12	0.15
60179[1]	7.1	6.9	1.8	1.9	0.10	0.19
70202	8.3	6.8	2.0	1.9	0.16	0.18
70882	6.3	6.0	1.9	2.5	0.13	0.39
B1190	6.6	7.1	1.9	2.1	0.15	0.21
B1196	5.5	5.7	2.0	2.0	0.15	0.15
Odyssey	6.8	6.1	1.9	2.0	0.12	0.16
PI 342440	9.1	7.1	1.9	1.9	0.13	0.17
Average	6.9	6.5	1.9	2.0	0.13	0.19
Crisphead						
60158	6.1	6.8	1.9	2.2	0.14	0.26
60162	5.4	5.3	2.0	1.9	0.14	0.23
60167	5.2	5.5	2.1	2.2	0.17	0.27
60172	5.9	5.9	2.0	2.1	0.15	0.19
Beacon	6.8	6.1	2.0	2.2	0.18	0.25
Bubba	6.9	6.7	2.0	2.1	0.18	0.23
Chosen	6.0	5.8	2.0	2.1	0.14	0.20
Cibola	6.6	6.6	2.0	2.4	0.17	0.29
Cooper[a]	–	7.2	2.3	2.2	0.34	0.27
Coyote	6.5	6.6	1.9	2.0	0.15	0.23
Eblin[a]	5.5	5.8	2.3	1.6	0.16	0.11
Flagler[a]	6.3	6.6	1.7	3.0	0.13	0.43
Green Lightning	6.5	7.0	1.9	1.9	0.14	0.24
H1078	5.8	7.2	1.9	1.9	0.17	0.20
Honcho II	6.7	5.8	1.9	2.1	0.16	0.16
Javelina	6.6	6.5	1.7	2.1	0.12	0.21
Lantana	6.1	6.5	2.1	2.1	0.16	0.25
Reine des Glaces	6.6	6.6	2.1	1.9	0.16	0.20
Sun Devil	5.0	5.7	2.0	1.9	0.15	0.20
Average	6.1	6.3	2.0	2.1	0.16	0.23
Latin						
49530	6.6	7.1	1.9	2.5	0.13	0.29
Floribibb	6.4	6.8	2.1	2.0	0.17	0.19
Little Gem	6.5	7.1	2.3	2.0	0.19	0.18
Pavane	7.1	6.6	1.9	2.0	0.13	0.20
Average	6.7	6.9	2.1	2.1	0.16	0.22

Table 5 continued

Accession	Tissue Total-P (mg g^{-1})[d]		Soil Total-P (mg g^{-1})		Soil Mehlich-3 (mg g^{-1})	
	Half P	Standard P	Half P	Standard P	Half P	Standard P
Loose leaf						
Bambino	7.5	5.3	1.9	2.2	0.15	0.20
Cordoba	7.0	4.8	2.0	2.1	0.13	0.20
Galactic	6.6	4.9	2.0	2.3	0.13	0.27
North Star	7.3	5.9	1.9	2.2	0.14	0.26
PI 278109	7.6	5.8	1.9	2.2	0.11	0.20
PI 358001–1	6.3	6.3	1.9	1.9	0.12	0.21
Red Rage	5.4	6.0	1.8	2.0	0.09	0.17
Revolution	6.8	5.7	1.9	1.9	0.12	0.14
RFX-0901	7.1	6.9	2.1	2.1	0.15	0.23
RSX743	6.0	6.1	2.0	2.1	0.14	0.20
Tehama	5.8	5.2	1.9	1.9	0.12	0.17
Two Star	6.8	7.5	2.0	2.0	0.12	0.16
Average	6.7	5.9	1.9	2.1	0.13	0.20
Oilseed						
PI 251246[b]	5.4	6.0	2.1	2.0	0.13	0.14
Romaine						
50098	6.1	6.3	1.9	2.0	0.14	0.18
50100	6.6	5.8	2.1	2.2	0.18	0.25
60182	7.4	6.4	2.0	2.4	0.15	0.32
60183	6.9	6.2	2.0	1.9	0.20	0.20
60184	6.6	6.6	2.1	2.0	0.21	0.21
70096	8.0	6.1	1.9	2.1	0.13	0.20
C1145	7.6	6.8	2.0	2.1	0.16	0.20
Floricos 83	7.7	7.0	2.0	1.9	0.17	0.15
Green Towers	6.7	7.3	1.8	2.2	0.17	0.24
Hialeah	7.5	6.4	2.0	2.1	0.14	0.23
King Henry	7.0	6.5	2.0	2.0	0.17	0.20
Manatee	8.3	7.4	2.0	2.0	0.15	0.22
Okeechobee	7.3	7.6	2.0	2.3	0.15	0.24
PI 278108	7.2	7.1	1.9	2.2	0.13	0.20
PIC	7.2	7.1	2.0	2.1	0.19	0.17
Tall Guzmaine	7.4	6.7	2.2	2.2	0.17	0.22
Terrapin	7.0	6.8	2.1	2.1	0.17	0.21
Valmaine[c]	5.9	5.4	2.2	2.2	0.15	0.12
Average	7.1	6.6	2.0	2.1	0.16	0.21

[a]Lettuce accessions Eblin and 60179 were utilized in the 2017–2018 experiment only

Lettuce accessions Flagler and Cooper were utilized in the 2019–2020 experiment only

[b]PI 251246 is a primitive lettuce accession that does not produce marketable heads

[c]Plots of cultivar Valmaine were discarded due to seed contamination in 2019–2020

[d]Tissue Total-P estimated on a dry weight basis

Table 6 Correlations and *P* values are given in parentheses between head weight, marketability, tissue total-P, soil total-P, and soil Mehlich-3 of the 66 lettuce accessions grown in the half-P and standard-P rates conditions

Trait		Head weight		Tissue total-P[a]		Soil total-P		Soil Mehlich-3		Marketability	
		Half-P	Standard-P	Half-P	Standard-P	Half-P	Standard-P	Half-P	Standard-P	Half-P	Standard-P
Head weight	Half-P	1 (–)	0.88 (< 0.0001)	– 0.13 (0.3025)	0.08 (0.5168)	0.16 (0.1936)	0.14 (0.2615)	0.36 (0.0035)	0.27 (0.0283)	– 0.04 (0.7453)	– 0.05 (0.6935)
	Standard-P		1 (–)	– 0.02 (0.8880)	0.17 (0.1840)	0.12 (0.3425)	0.08 (0.5140)	0.36 (0.0038)	0.28 (0.0247)	– 0.16 (0.2112)	– 0.01 (0.8871)
Tissue total-P	Half-P			1 (–)	0.38 (0.0022)	– 0.02 (0.8458)	0.02 (0.8929)	0.04 (0.7702)	– 0.04 (0.7475)	0.03 (0.7804)	0.18 (0.1540)
	Standard-P				1 (–)	– 0.07 (0.5752)	– 0.01 (0.9031)	0.19 (0.1366)	0.03 (0.8029)	– 0.16 (0.2112)	– 0.06 (0.6229)
Soil total-P	Half-P					1 (–)	– 0.23 (0.0659)	0.63 (< 0.0001)	– 0.16 (0.2079)	– 0.19 (0.1277)	– 0.08 (0.5210)
	Standard-P						1 (–)	– 0.06 (0.6502)	0.85 (< 0.0001)	0.22 (0.0786)	0.11 (0.3761)
Soil Mehlich-3	Half-P							1 (–)	0.04 (0.7334)	– 0.34 (0.0059)	– 0.12 (0.3552)
	Standard-P								1 (–)	0.08 (0.5187)	0.01 (0.9033)
Marketability	Half-P									1 (–)	0.67 (< 0.0001)
	Standard-P										1 (–)

[a]Tissue total-P estimated on the basis of dry weight

It is unknown if these 18 lettuce accessions were capable of acquiring and/or utilizing P from Histosols in the EAA or whether they were able to absorb the applied P in these experiments. Further research is needed to determine whether lettuce acquired P from the soil or utilized available P.

The significant G × E and R × E interactions identified in this research warrant a deeper analysis of the environmental factors influencing PUE, despite the non-significant G × R interaction for HW. In sorghum, environmental factors such as temperature, solar radiation, rainfall, and pests and diseases are believed to affect nutrient use efficiency (Mishra and Patil 2015). In *L. sativa,* nitrogen use efficiency was found to be influenced by soil temperature (Macias-González et al. 2021). Therefore, similar environmental factors might be associated with PUE in lettuce.

Phosphorus uptake could be influenced by the soil pH, temperature, light, water availability, and biotic stressors such as weeds (Gruen et al. 2014; Reich et al. 2014; Fageria et al. 2017). The measured soil pH was 7.6 in the first experimental site, whereas it was 7.1 in the second experimental site. Although the optimum soil pH for lettuce ranges from 6.5 to 7.2 (Ryder 1999), the overall HW of most of the lettuce types was similar across the two P rates and the two experiments, indicating that a higher soil pH in the first experiment did not directly impact the lettuce HW in this study. Soil P availability in lettuce fields was found to increase by 40% when soil temperature increased from 15 to 25 °C (Johnstone et al. 2005). In this research, the average soil temperature (at − 10 cm) was 20.5 °C and 20.9 °C in the first and second experiments, respectively (Table 2). This similarity in temperature likely did not influence the G × E and R × E interactions. Solar radiation was higher in the first experiment and might have contributed to the significant G × R and R × E interactions observed in this study because higher solar radiation was found to be associated with higher yields and P uptake in soybean (Zhou et al. 2019). Despite the greater precipitation observed in the second experiment, both experiments were overhead irrigated during dry periods to provide adequate water availability to the plants. Thus, water availability was unlikely a limiting factor for P uptake in this study. Weeds in the Histosols of the EAA are a nuisance to vegetable production due to the limited number of approved herbicides and the interaction of herbicides with the high organic matter concentration in muck soils, which reduces their efficacy (Odero and Wright 2013). The unevenly high presence of weeds in these trials, especially between the weeding events, likely resulted in competition for nutrients and may have diminished P uptake in lettuce, causing these interactions to be significant. For instance, some of the same accessions used in this research produced on average 30% more yield in weed-free muck soils compared to the HW obtained under standard-P conditions (Kreutz et al. 2021).

Marketability affected by P

Overall, the reduction in the rate of P application resulted in a decrease in lettuce HW, and consequently, negatively impacted the marketability of most accessions. In lettuce, marketability is dependent on the size and shape of the leaves. In the half-P treatment, most accessions that had the lowest HW had the highest reduction in marketability. Marketability was severely affected for crisphead, romaine, butterhead, and Latin types that form heads or hearts under P-limiting conditions; this was primarily due to the stunted plant growth, reduction in the number of leaves, and lack of head/heart formation observed when P application was reduced by 50% (Fig. 7). Considering the fact that lettuce production in the EAA consists primarily of crisphead and romaine (approximately 68 and 30%, respectively), selection and breeding of P-efficient should focus on both HW and marketability.

Some accessions produced similar yield and marketability as the commercial cultivars under half-P rate conditions. Thus, lowering P rates could provide a similar lettuce crop while having less impact on crop production and the environment. Adequate reduction in P fertilization for P-efficient lettuce accessions needs to be further investigated without sacrificing HW and other characteristics important to the industry in order to become an economically feasible practice. P fertilizer reduction has been shown to be feasible for other crops. For instance, the yield of certain potato accessions was not affected by the reduction in P application from 130 to 0 kg P ha^{-1} (Sandaña 2016).

Head weight performance across accessions

In addition, some UF/IFAS breeding lines and cultivars commercially used in Western U.S. produced similar HW and marketability compared to commercial cultivars currently planted in the EAA. The UF/IFAS breeding lines have been developed under subtropical climate of Florida and, for being adapted to these environmental conditions (Kreutz et al. 2021), offer an advantage due to adaptation. Opposite, cultivars from Western U.S. were not bred for production in Florida but could be adapted to the Florida environment. These breeding lines and cultivars may be pertinent to breeding programs for the development of new locally adapted cultivars. When breeding for PUE, accessions locally adapted allow to expedite the development of new P-efficient cultivars (Parentoni et al. 2012). Though, the use of non-adapted germplasm to introgress PUE traits into an adapted cultivar was successfully conducted in common bean (*Phaseolus vulgaris* L.) breeding (Schettini et al. 1987).

Head weight and its relationship with P concentration

The significantly positive correlations detected between HW and soil M3P in the standard and half-P rates treatments indicate that higher soil P availability favors the production of higher yield in lettuce. However, no significant correlations were observed between yield and P uptake (HW and tissue TP) or soil P availability and plant P uptake (soil M3P and tissue TP). The absence of such correlations, especially between HW and tissue TP concentration, have been reported in wheat (Ozturk et al. 2005), spring barley (Römer and Schenk 1998), and in *C. arabica* and *C. canephora* cultivars (Neto et al. 2016), and might be explained by genotypic differences in P acquisition and P utilization at the cellular level in plants (Ozturk et al. 2005). More comprehensive investigations should be conducted to investigate the morphological, biochemical, and genetic features underlying PUE in lettuce to determine and quantify the mechanisms related to absorption and utilization.

The significantly positive correlations observed between soil TP and soil M3P indicate that applying P based fertilizers tends to increase soil TP of Histosols, resulting in higher P availability to lettuce. These findings are in accordance with previous studies on Histosols of the EAA, where P application increased labile P levels from 1.3 to 7.2 mg P kg^{-1} in cultivated fields and from 1.4 to 10.7 mg P kg^{-1} in pasture lands (Castillo and Wright, 2008). At half-P rate, the correlation between soil TP and soil M3P was weaker than that under the standard-P rate. This likely occurred because the standard-P application saturates P adsorption sites in the soil, favoring a higher P availability. In contrast, applying half of the recommended P rate does not allow for the saturation of P adsorption sites and more P becomes retained in the soil (Bond et al. 2006).

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Declarations

Conflicts of interest The authors declare no conflict of interest.

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