

ORIGINAL RESEARCH

SPECIAL SECTION: BELOWGROUND PHENOTYPING

Genotypic variability in root length in pea (*Pisum sativum* L.) and lentil (*Lens culinaris* Medik.) cultivars in a semi-arid environment based on mini-rhizotron image capture

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Abstract

Physiological breeding is an approach that complements conventional breeding by providing characterizations of traits present in breeding populations. This allows breeders the ability to choose crosses based on desirable and adaptive traits, an approach that may be more reliable than selection on yield alone. In this study, we determined how much genotypic variability was present in selected lines of modern field pea (*Pisum sativum* L.) and lentil (*Lens culinaris* Medik.) cultivars from Montana, North Dakota, Washington, and Saskatchewan, Canada, and if root growth, particularly at depth, improves the fitness of lines to semi-arid environments. We conducted experiments at the Northern Agricultural Research Center of Montana State University from 2017 to 2019 inclusively to investigate root growth with mini-rhizotrons in 29 field pea lines and 25 lentil lines. Results suggest there is large genotypic variability in root length across the soil profile and the proportion of root length found below 30 cm in both crops, and these root traits appear independent of each other. In field pea, the highest yielding cultivars were intermediary in both total root length and the proportion of root length below 30 cm, suggesting large root systems and/or deeper root profiles are not necessarily beneficial in this environment. By contrast, in lentil, total root length and root length found below 30 cm was well correlated with biomass and yield. For breeders interested in improved adaptation to semi-arid environments, it may be too early to optimize root systems, and above-ground traits may still yield a better return on investment.

Abbreviations: CDC, Crop Development Center; G×E, genetics × environment interaction; HI, harvest index; PCA, principal component analyses.

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1 | INTRODUCTION

Physiological breeding is an approach that complements conventional breeding by providing characterizations of traits present in breeding populations. This allows breeders the ability to choose crosses based on desirable and adaptive traits rather than selection for yield alone (Reynolds & Langridge, 2016; Richards, 2006). In semi-arid environments, in particular, variable rainfall (in amount and timing) from year to year can lead to large genetics $\times$ environment (G $\times$ E) interactions (i.e., where cultivars do not yield consistently across environments). In such situations, it helps to understand the traits that lead to better adaptation and yield gains. Such traits are often more stably inherited and expressed in different environments (Reynolds & Langridge, 2016; Reynolds et al., 2020). This approach has been successfully used in cereal breeding in Australia and the International Center for Wheat and Maize Improvement, leading to the release of cultivars better adapted to semi-arid environments (Reynolds & Langridge, 2016; Richards, 2006).

Roots are the primary site of water and nutrient acquisition from the soil, and yet are the most under-researched organ due to the difficulty in observing them in-situ. A better understanding of root morphological and physiological traits is the new frontier in understanding adaptation to dryland cropping (Hall & Sadras, 2009), a challenge that is particularly obvious in this special issue. While the prevailing view has generally been to assume a large root system would protect against the negative impacts of drought by providing better access to soil water, Passioura (1983) suggested that the extraction of too much water too early, and excessive carbon allocation to roots might be counterproductive. This idea has recently been expanded on by suggesting the optimal size of a crop root system would depend on (a) the typical pattern of water availability during the season (Palta et al., 2011) and (b) inputs into the cropping system, with less carbon investment in the root system likely to be more efficient in high-input systems (Lynch, 2018). In support of this theory, a simulation study in wheat (*Triticum aestivum* L.) suggested that a cultivar with less root growth at the surface but more at depth could extract an additional 10 mm of soil moisture during grain filling, which led to a yield increase of over 0.5 t ha⁻¹ (Manschadi et al., 2006). Similarly, retrospective studies of the breeding programs at the International Center for Wheat and Maize Improvement for both tropical maize (*Zea mays* L.) and wheat showed that selection for high grain yield had resulted in a reduction of the root biomass in the topsoil: Bolanos et al. (1993) showed that yield improvement in maize was associated with 33% less root mass at the 0–50 cm layer with no observable differences in plant water status between old and new cultivars, whereas Pask and Reynolds (2013) showed that over time the propor-

Core Ideas

- The highest yielding field pea cultivars tended to be ranked intermediary for root length at depth.
- The proportion of deep root length was negatively correlated with biomass and yield in pea.
- Root length across depths and below 30 cm in lentil was well correlated with biomass and yield.
- Biomass and yield would be easier selection criteria in lentil despite being more variable.

tion of root biomass shifted toward deeper soil layers, which improved water use but not water use efficiency.

Field pea (*Pisum sativum* L.) and lentil (*Lens culinaris* Medik.) are pulse crops capable of forming a symbiosis with rhizobia for biological nitrogen fixation. As such, their inclusion in cropping systems is an important part of efforts to improve the sustainability of agriculture and decrease the reliance on nitrogen chemical fertilizers. Worldwide, field pea production was 10 to 16 million t between 2010 and 2019, growing over 6 to 8 million ha while lentil production was 4 to 7 million t over 4 to 7 million ha during the same period (FAOSTAT, 2020). As cool-season temperate crops, field pea and lentil are well adapted to the short growing season of the Northern Great Plains and are increasingly grown in cereal-based rotations in this region. In Montana and North Dakota, for example, the number one and two pea- and lentil-producing states in the United States, field pea was grown on approximately 190,000 and 170,000 ha, respectively, whereas lentil was grown on 270,000 and 100,000 ha, respectively, in the 2017 Census of Agriculture (USDA NASS, 2019a, 2019b). The Canadian Prairie has also become an important production center, with slightly over 1.7 million ha in field pea production in the 2016 Census of Agriculture, and over 2.2 million ha in lentil production—most of this acreage in Saskatchewan, Canada (Statistics Canada, 2017). However, because of the relatively recent interest in diversification of cropping systems, pulse breeding efforts for adaptation to semi-arid environments do not have the long history seen in cereal breeding (Siddique et al., 2013) and our understanding of adaptation mechanisms (and possible genotypic variability in such traits) is therefore not as advanced.

The objectives of this study were to (a) determine how much genotypic variability there is in total root length and deep rooting in selected cultivars of field pea and lentil and (b) determine if root growth, particularly at depth, improves the fitness of lines to semi-arid environments in these two crops. We used mini-rhizotrons to image root growth; these allowed for field-based and nondestructive characterization

TABLE 1 Total monthly rainfall and average maximum and minimum temperatures at Montana State University's Northern Agricultural Research Center during the field seasons in 2017–2019

Month	Rainfall			Min. temperature			Max. temperature		
	2017	2018	2019	2017	2018	2019	2017	2018	2019
	mm			°C			°C		
April	6.4	6.1	23.4	0.1	-4.1	0.5	13.7	8.5	13.5
May	11.4	27.9	38.9	4.6	7.4	3.0	20.2	22.4	16.3
June	39.9	63.5	82.3	9.8	10.6	9.0	25.8	24.2	23.7
July	3.6	4.6	16.3	13.6	12.2	11.3	32.7	29.5	28.0
August	3.0	12.7	18.5	10.5	10.6	11.6	28.7	28.6	27.6
Season total	64.3	114.8	179.4						
Season average				7.7	7.3	7.1	24.2	22.6	21.8
Historical average (1916–2020)	202.9			6.9			22.9		

of root length at four depths. Field evaluation and characterization was particularly important as plants grown in pots often become root-bound as early as the vegetative stage (Bourgault et al., 2017; Poorter et al., 2012). Rich et al. (2020) also showed that root traits at maturity are not expressed reliably in controlled-environment settings.

2 | MATERIALS AND METHODS

2.1 | Site description and management

Experiments were conducted in 2017, 2018, and 2019 at the Northern Agricultural Research Center of Montana State University (48.5° N lat, 109.8° W long), located 11 km from Havre, Montana (elevation 773 m). The plot field soil is a mix of Joplin (fine-loamy, mixed, superactive, frigid Aridic Argiustolls), Telstad (fine-loamy, mixed, superactive, frigid Aridic Argiustolls), and Scobey (fine, smectitic, frigid Aridic Argiustolls) clay loams, which have developed from glaciated plains. They are very deep, well-drained fine to fine-loamy Aridic Argiustolls with moderately slow to slow permeability according to the official soil classifications from the USDA (USDA, 1998). The plot site has been managed under no-till for over 20 yr and is managed as a rainfed crop-fallow system, with a rotation in crop types (i.e., pulses, cereals, or brassicas) to minimize disease risks. Long-term (1916–2018) average annual rainfall is 319.8 mm, with 202.9 mm falling during the growing season (April to August inclusively). Total monthly rainfall and average maximum and minimum temperatures are given in Table 1. All three years had below-average rainfall, with 2017 being a particularly challenging season due to high-velocity dry winds on 26–29 May 2017, which damaged the crops and low precipitation during the rest of the growing season.

The experiments were planted on 29 April 2017, 29 April 2018, and 23 April 2019 on different fields at the Northern Agricultural Research Center, with field pea and lentil trials planted side by side. Seeds were inoculated with peat-based Nodulator (BASF) strains for pea and lentil deposited directly in the planter cone with each seed packet. Soil phosphorus and potassium levels were acceptable (> 20 and > 150 mg kg⁻¹, respectively), so no fertilizer was applied. In 2018, a mixture of Group 2 (ammonium salt of imazamox; Raptor, BASF) and Group 6 herbicide (bentazone; Basagram, BASF) was applied on 19 June in the pea field only, while in 2019, the Group 3 herbicide ethalfluralin (Sonalan, Gowan) was applied the day before planting. Otherwise, the experiment was weeded by hand at frequent intervals to avoid weed roots confounding results. The pesticide zeta-cypermethrin (MustangMax) was also used to control the pea leaf weevil in the pea experiments at the second leaf stage.

2.2 | Experimental design

The experimental design was a partially replicated augmented design, with 48–54 plots depending on the year for each crop and replicated over 3 yr. The cultivars Aragorn and Avondale were used as check cultivars for 12 plots for pea and lentil, respectively, according to the recommendation by Cullis et al. (2006) to allocate approximately 25% of the plots to a check. Overall, 29 cultivars were evaluated for field pea and 25 for lentil (Tables 2 and 3 and following section on plant material). With some exceptions, cultivars other than the check were grown 4–6 times over the course of the 3 yr, but not all cultivars were grown every year. Plots had five rows 30 cm apart (1.5 m wide) and were 5.5 m long. In 2017, the experiment was organized in a grid of 6 rows (ranges) $\times$ 8 columns (passes) with additional passes as border plots. In 2018 and

TABLE 2 Field pea cultivars and breeding lines grown at Montana State University's Northern Agricultural Research Center from 2017 to 2019 inclusively

Cultivar names	2017 Reps	2018 Reps	2019 Reps	Total
Amigold		2	2	4
Aragorn	12 (9) ^a	12	12	33
Arvika			2 (1)	1
Carousel			2	2
CDC Amarillo	1 (0)	2	2	4
CDC Centennial	2	2	2 (1)	5
CDC Horizon	1	2	2	5
CDC Meadow	1	2	2	5
CDC Saffron	2	1	2	5
CDC Striker	1	2	1	4
Delta	2	2		4
DS Admiral	2	1	2	5
Fergie	1			1
Hampton	1	2	2	5
Jetset	2	1	1	4
Korando	1	2	1	4
LG Koda	1			1
Majoret	2	1	1	4
Mystique	1			1
Nette 2010	2 (1)	2	1	4
Pea 4010	1	1	2	4
PS077100925	2	2	1	5
PS08101022	2	2	1	5
PS0877MT076		2	2	4
PS0877MT457		2	2	4
Stirling		2	2	4
SW Arcadia	1 (0)	2	2	4
SW Midas	2	2	1	5
Viper	1	1	2	4

^aAn intense rainfall event led to some tubes floating out of their holes in 2017, and we therefore lost the root data from these plots. In 2019, two plots got mixed up at planting, leading to the loss of both root and above-ground data.

2019, the first and last ranges were used as border plots as well as the additional passes, so the experiment was organized in a grid of 4 rows × 12 or 13 columns, depending on the crop.

2.3 | Plant material

Field pea and lentil plant material evaluated (Tables 2 and 3, respectively) were primarily released cultivars from North Dakota State University, Washington State (USDA ARS), and the Crop Development Center (CDC) at the University of Saskatchewan. A few advanced breeding lines were also included in the investigation in 2018 and 2019.

TABLE 3 Lentil cultivars and breeding lines grown at Montana State University's Northern Agricultural Research Center from 2017 to 2019 inclusively

Cultivar names	2017 Reps	2018 Reps	2019 Reps	Total
Avondale	12	12	12	36
Athena	2	2	1	5
Brewer	2	1	1	4
CDC Dazil	1	2	2	5
CDC Impala	2		2	4
CDC Impress	2		2	4
CDC Invincible	1	2	1	4
CDC Maxim	2	1	1	4
CDC Peridot	2	1	1	4
CDC Proclaim	2	2	1	5
CDC Redberry		2	2	4
CDC Richlea	2 (1) ^a	2	1	4
CDC Rosetown		2	2	4
CDC Viceroy	2		2	4
Cedar	2 (0)	2	2	4
Eston	2	2	1	5
Indianhead	2		2	4
Merrit	2	1	1	4
ND Eagle		2	2	4
NDL080187L		2	2	4
NDL120532T		2	2	4
Pardina	2	2	1	5
Pennel	2	2	1	5
Riveland	2 (1)	2	2	5
Shasta	2	2	1	5

^aAn intense rainfall event led to some tubes floating out of their holes in 2017, and we therefore lost the root data from these plots.

2.4 | Root measurements

Mini-rhizotrons consisted of clear acrylic tubes 1.05 m long × 7.5 cm in diameter, provided by CID Biosciences. These were installed at an angle of approximately 45° as soon as possible after planting. Giddings soil sampling equipment was used to remove a soil core for tube insertion. In 2017 and 2018, tubes were installed between center rows; in 2019, the tubes were installed on the row. This did not lead to more roots being captured in images in 2019 compared with 2018, but considerably less root length was observed in 2017, presumably because of the high wind episode followed by a severe drought. Root images were captured at flowering and physiological maturity with the CI-600 In Situ Root Imager (CID Biosciences), a cylindrical scanner that spanned 22 cm and was moved down the tube in four steps, separately capturing root images at depths of approximately 0–15, 15–30, 30–45, and 45–60 cm (± 5 cm). Root images were later processed

with the *RootSnap!* software (also by CID-Biosciences) to extract root length for each depth.

2.5 | Biomass, leaf area, yield, and yield component measurements

Destructive biomass samplings were collected at flowering and maturity. Plots were considered individually with 50% of plants in full bloom for first sampling. Height was recorded, then 45 cm of two central rows were cut avoiding areas near the mini-rhizotron or soil moisture access tube and brought back to the laboratory for processing. A subsample was taken and dissected into green leaves, dry leaves (if any), stems, and reproductive structures. Pea tendrils were considered as stem material. The leaf area of green leaves was measured with a LI-3100C leaf area meter (LI-COR Biosciences). The various organ subsamples and remainder of the collected sample were dried at 40 °C for at least 72 h until constant weight before dry weights were recorded.

For the maturity sampling, plots were deemed ready for harvest if more than 90% of pods were dry and grains were hard. Samples were collected on top of the mini-rhizotron after the maturity image captures, again, on 45 cm from 2 adjacent rows. Biomass samples were stored at 40 °C for 72 h. Samples were processed by first getting the full biomass dry weight, then by detaching pods and recording their number. Pods were then threshed, and grains were counted and weighed. In 2017, there were several underdeveloped grains in some lines, so grains that were green and less than 30–40% of the average size were excluded from the yield and yield component calculations. Harvest index (HI) was calculated as the ratio of yield weight to total biomass weight.

2.6 | Statistics

Cultivar means and rankings for root length data, biomass, yield, and HI were predicted from mixed model analysis procedures using the AsREML algorithm (version 4.0, VSN International) as implemented in the R language (Butler et al., 2018; R Core Team, 2020). Mixed models are appropriate here as they can handle missing data (i.e., not all cultivars grown every year), and one can specify spatial information in the error structure (Smith et al., 2005) which cannot be handled easily with a standard analysis of variance (ANOVA). However, similar to ANOVA, total variation can be partitioned between the different fixed factors by the sum of squares, and significance is assessed using the Wald test as an analog to the *F* test (Butler et al., 2018). Cultivars and years were treated as fixed factors while replicates (nested within years) were random factors. The model also specified a first-order autoregressive variance model using row and col-

umn information as spatial data in the residual term. Best linear unbiased estimates (analogous to cultivar means but taking the spatial error structure in consideration) were calculated from the mixed models and used to present cultivar rankings (Smith et al., 2005). Graphs for cultivar rankings were produced with the *ggplot2* 3.3.0 package (Wickham, 2009). Principal component analyses (PCA) were also conducted to examine relationships between traits and displayed using biplots (package *ggbiplot*, Vu et al., 2011). Biplots represent how cultivar observations related to one another, with cultivars closer together being more similar, and simultaneously show how traits, represented as vectors, related to each other, with vectors close together more closely and positively correlated, vectors at a 90° angle uncorrelated, and vectors opposite each other negative correlated (Jolliffe, 2002). Additional regression analyses were also performed with the base R package. Treatment differences and relationships were considered significant at $\alpha = 0.05$.

3 | RESULTS

3.1 | Field pea

Significant genotypic variability in total root length and root length captured below 30-cm depth were observed in pea cultivars. Cultivars with the largest root systems across depths at maturity were ‘PS0877MT457’, ‘CDC Centennial’, ‘SW Arcadia’, ‘Arvika’, and ‘Delta’ (Figure 1). Similar rankings were observed for the absolute amount of roots captured below 30 cm (Supplemental Table S4), but cultivars with the greater proportion of root length at depth at maturity were ‘Mystique’, ‘PS077100925’, ‘CDC Amarillo’, ‘Amigold’, and Arvika (Figure 2).

In addition, significant genotypic variability was also observed for grain yield, biomass at maturity, and HI (Supplemental Tables S1, S2 and S3). However, the highest grain yielding lines (‘Nette 2010’, Delta, ‘CDC Saffron’, ‘Viper’, and ‘PS08101022’) tended to be ranked intermediate for total root length, root length at depth, or the proportion of root length at depth. This was also generally true for cultivar rankings for biomass at maturity, with the top five cultivars being ‘Fergie’, ‘Majoret’, CDC Amarillo, Viper, ‘LG Koda’, except for CDC Amarillo, which ranked third for the proportion of roots below 30 cm, and third for highest biomass. The top five cultivars for HI were: PS08101022, Delta, PS077100925, SW Midas, and SW Arcadia. In addition, the cultivar Delta, which ranked second for both the highest grain yield and HI ranked in fifth place for the total root length captured at maturity.

The first two principal components accounted for 30.8% and 24.1% of the total variation, with the absolute number of roots below 30 cm well aligned with the first component (Figure 3). Traits related to the root system size

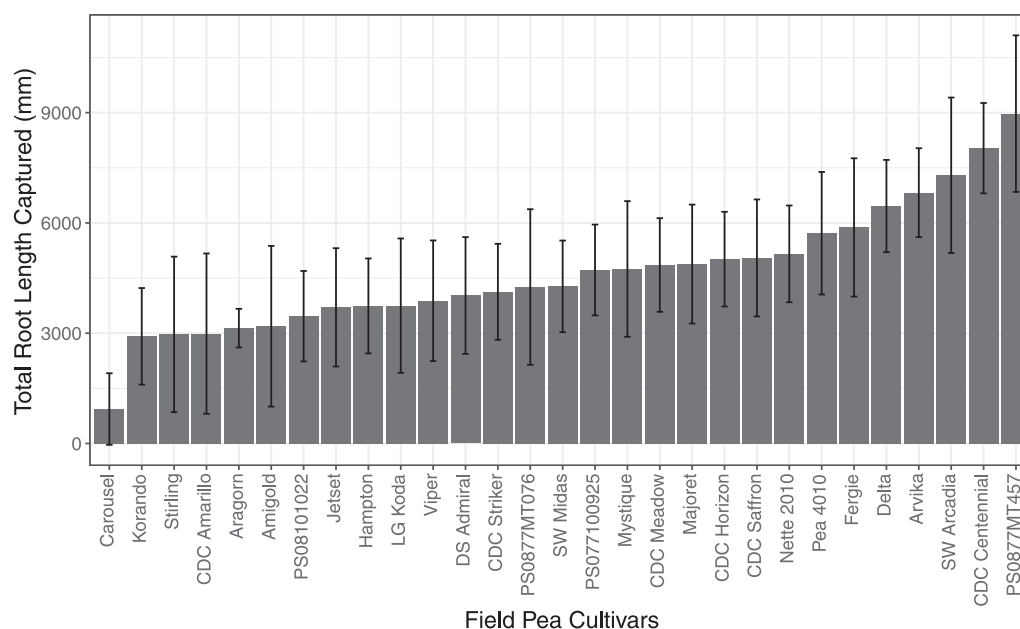


FIGURE 1 Total root length captured by mini-rhizotron in field pea cultivars grown at Montana State University's Northern Agricultural Research Center in 2017, 2018, and 2019

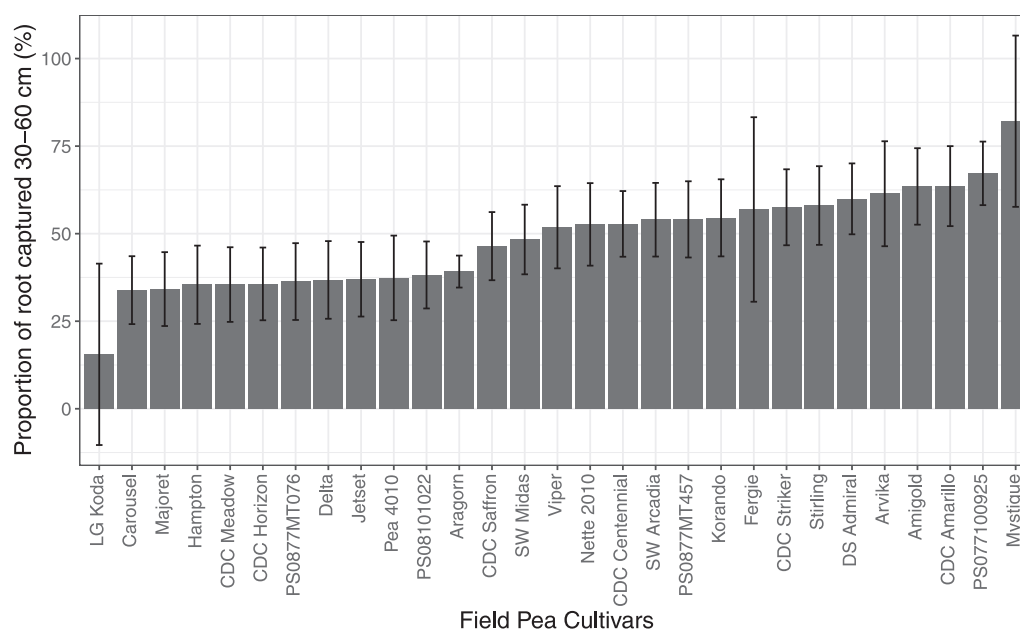


FIGURE 2 Proportion of root length captured below 30-cm depth in field pea cultivars grown at Montana State University's Northern Agricultural Research Center in 2017, 2018, and 2019

(i.e., root length at various stages of growth or depth, in absolute or proportional terms) tended to be loosely clustered in the PCA biplot. However, the difference in root growth from flowering to maturity (labeled “GrainFill”), both across the profile and at deeper layers, was relatively well correlated with the proportion of roots at depth at maturity and leaf area index at flowering but were independent of absolute values of root length at the different depths or across the profile at flowering.

In addition, the proportion of root found at depth at maturity was opposite to above-ground traits such as biomass, grain yield, and HI (Figure 3).

Looking at the sum of squares in the Wald test as the relative importance of the sources of variation showed that for yield and biomass data, a large part of the variation was attributed to the effect of different years (Table 4). By contrast, HI and the size of the root system showed cultivar differences to be more

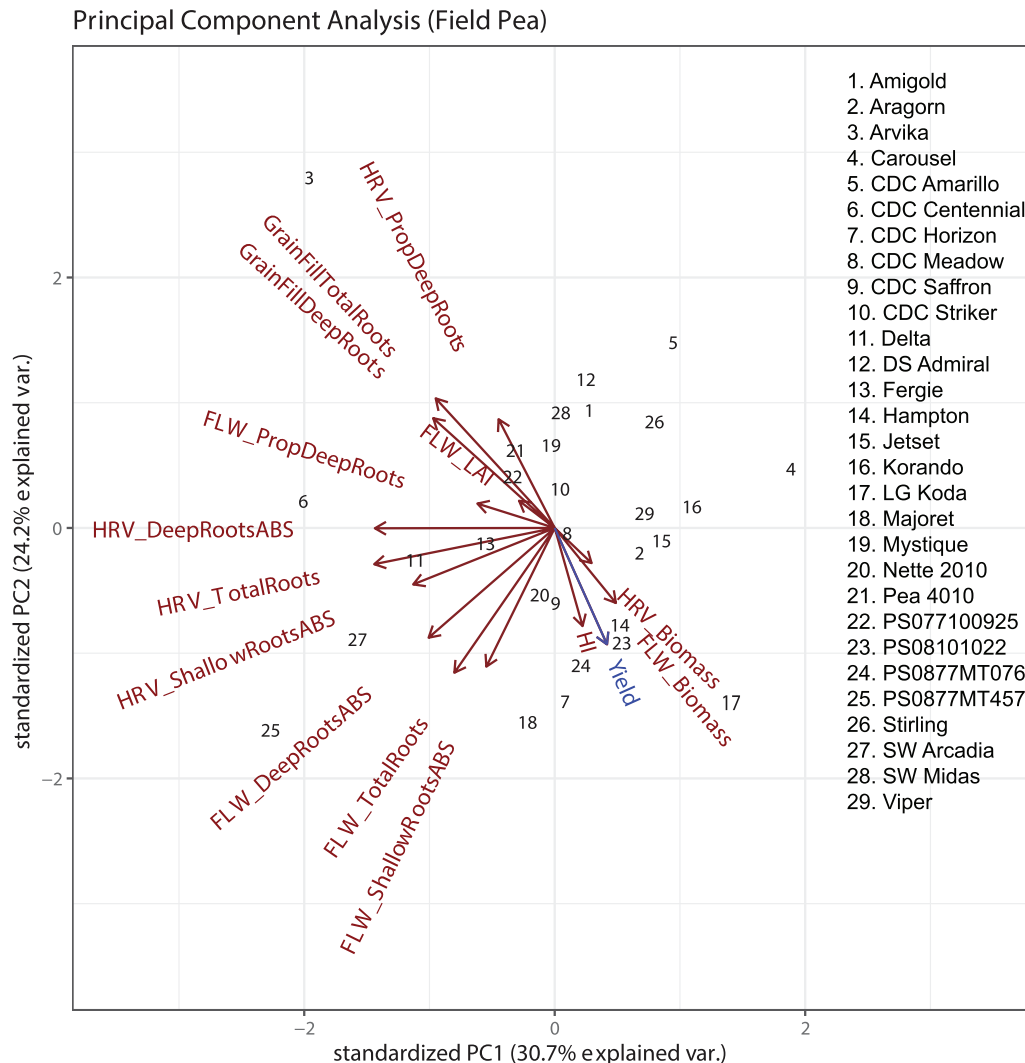


FIGURE 3 Principal Component Analysis for the field pea data collected at Montana State University's Northern Agricultural Research Center in 2017, 2018 and 2019. Directional vectors represent root and above-ground traits, while numbers refer to cultivar names

important, suggesting that these traits were not as affected by environmental conditions as grain yield and biomass. The root length captured below 30 cm and the proportion of roots below 30 cm also showed larger variation attributed to cultivars, although not as prominent as with HI or the total root length captured.

3.2 | Lentil

Significant genotypic variability in total root length captured, root length at depth, and the proportion of root length at depth was also observed in lentil cultivars. Across the 3 yr, cultivars with the largest root systems were 'Merrit', 'CDC Maxim', 'ND Eagle', 'Athena', and 'CDC Impress' (Figure 4). Merrit and ND Eagle ranked first and second for the absolute amount of root at depth but were followed by 'NDL120532T', 'CDC Rosetown', and 'Pardina' (Supplemental Table S17).

Cultivars with the largest proportion of roots at depth were 'Cedar', 'CDC Proclaim', Pardina, 'CDC Redberry', and CDC Rosetown (Figure 5).

Significant genotypic variability was observed for above-ground traits as well. The highest yielding cultivars across seasons were Pardina, 'CDC Richlea', NDL120532T, CDC Proclaim, ND Eagle (Supplemental Table S14). Interestingly, ND Eagle ranked third for the total root length captured at maturity, while 'NDL120532T' and CDC Richlea ranked in sixth and seventh place, respectively, and CDC Proclaim and Pardina ranked second and third, respectively, for the highest proportion of root below 30 cm. ND Eagle, NDL120532T, and CDC Richlea were also the top three cultivars for biomass accumulation at maturity, while Pardina had the highest HI (Supplemental Tables S15 and S16).

The first two principal components accounted for 28.5 and 23.7% of the total variation, with the root system size at flowering and maturity as well as HI relatively well aligned with

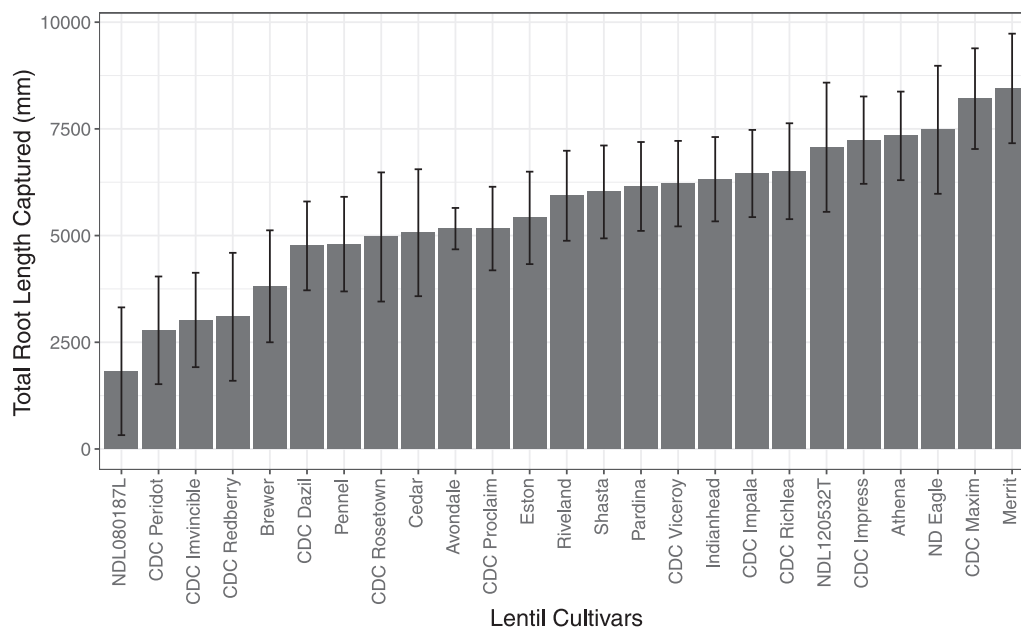


FIGURE 4 Total root length captured by mini-rhizotron in lentil cultivars grown at Montana State University's Northern Agricultural Research Center in 2017, 2018, and 2019

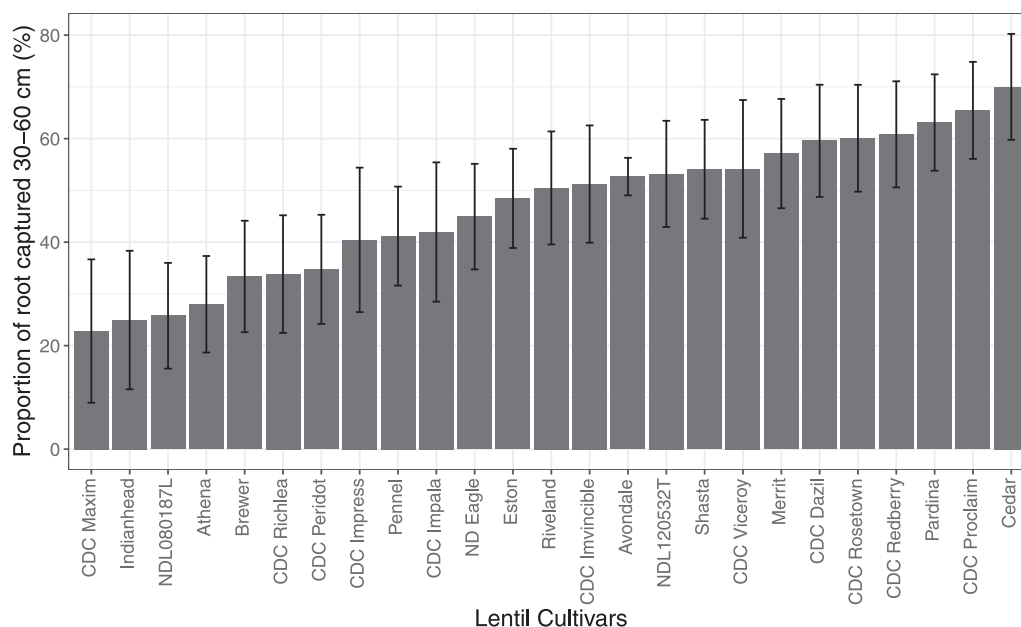


FIGURE 5 Proportion of root length captured below 30-cm depth in lentil cultivars grown at Montana State University's Northern Agricultural Research Center in 2017, 2018, and 2019

the first component (Figure 6). Trait vectors in the PCA biplot showed that absolute values of root length below 30 cm (both at flowering and maturity), and the increase in root length during grain filling, were closely correlated to yield and biomass accumulation at maturity. However, shallow root length (0–30 cm) captured at both flowering and maturity were independent of values of root length below 30 cm. Similarly, the proportion of root length below 30 cm was largely indepen-

dent of absolute values of root length at these same depths. Biomass accumulation and leaf area index at flowering, in this study, were also found to be independent of yield and HI (Figure 6).

The sum of squares in the Wald test showed similar patterns regarding the relative importance of the sources of variation than what was observed in field pea (Table 5). A large part of the variation was attributed to year effects for grain yield

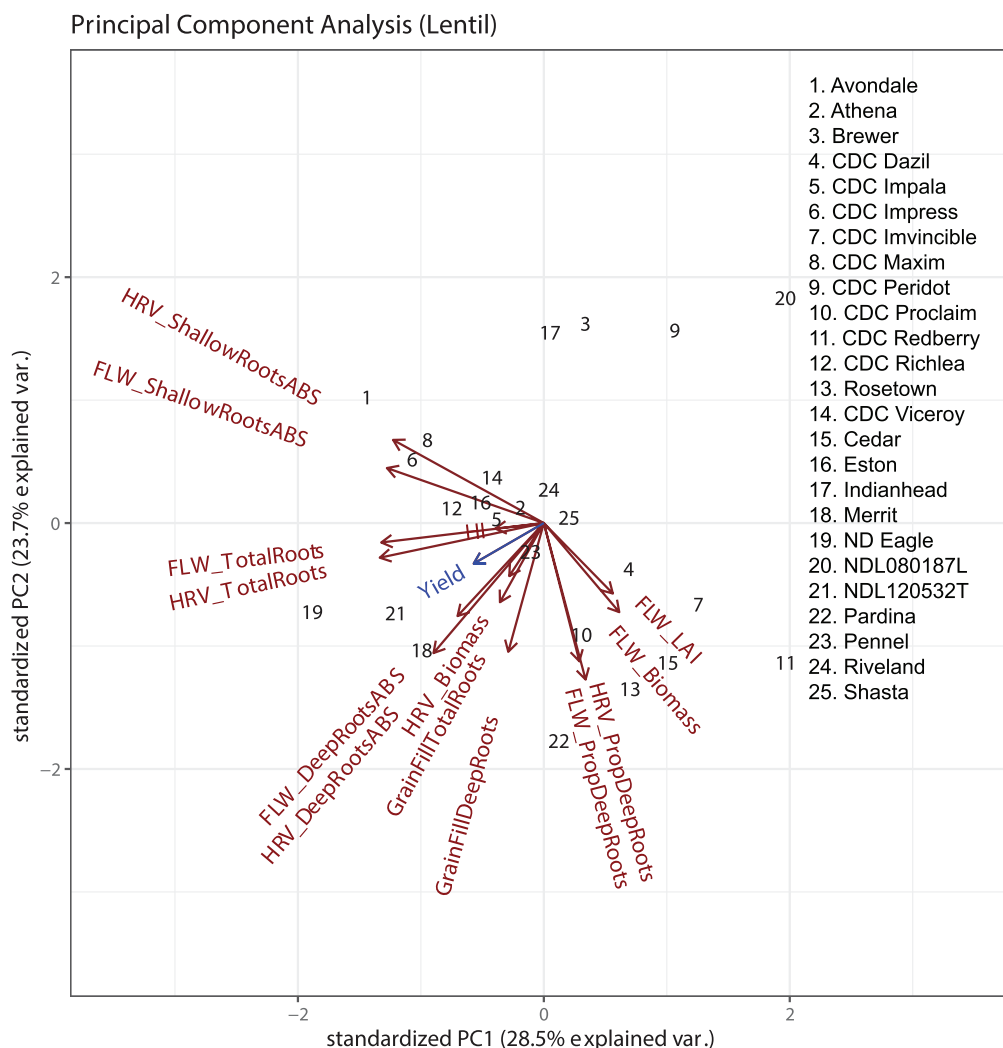


FIGURE 6 Principal Component Analysis for the lentil data collected at Montana State University's Northern Agricultural Research Center in 2017, 2018, and 2019. Directional vectors represent root and above-ground traits, while numbers refer to cultivar names

and biomass, while HI, the size of the root system, and, to a lesser extent, the proportion of root length below 30 cm, showed variation due to cultivar to be predominant. Interestingly, as opposed to field pea, variation due to years was the most important component for the root length captured below 30 cm, which suggest this trait may be more affected by the environment in lentil and under stronger genetic control in field pea.

4 | DISCUSSION

Understanding the role of root systems and their contribution to yield has been deemed the “new frontier” in crop physiology (Hall & Sadras, 2009) and there are high hopes that the incorporation of root traits into breeding programs may lead to better-adapted cultivars in semi-arid growing environments (Aski et al., 2021). The large genotypic variation observed in

root system size and the proportion of root found at depth, in both pea (Figures 1 and 2) and lentil (Figures 4 and 5), and the weaker environmental impact on trait expression compared with biomass and yield (Tables 4 and 5) suggested there is a potential for selection for these two traits. Our data also indicated that these traits are independent of each other. However, it is essential to be able to correctly identify the target ideotype to be selected (Donald, 1968), and our data suggested that this may not be obvious, particularly in field pea as the highest yielding cultivars tended to rank intermediate for root length at depth or total root length (Figures 2 and 3).

Previous research suggested deep rooting and/or a higher proportion of root length at depth would be beneficial in semi-arid cropping systems (Kashiwagi et al., 2005; Palta et al., 2011; Silim et al., 1993, among others). For example, Manschadi et al. (2006), in a simulation study with wheat, showed that an additional 10 mm of water extracted at depth could lead to up to 0.5 t ha⁻¹ additional yield during a terminal drought.

TABLE 4 Sources of variation obtained with the Wald test in selected parameters in field pea data collected at Montana State University's Northern Agricultural Research Center in 2017, 2018, and 2019

Parameter	Sum of squares/Wald statistic	p-value
Yield		
Year	336.35	<.0001***
Cultivar	110.62	<.0001***
Year × cultivar	52.37	.0911 [†]
Biomass accumulation at maturity		
Year	369.28	<.0001***
Cultivar	99.40	<.0001***
Year × cultivar	92.09	<.0001***
Harvest index		
Year	7.10	.0288*
Cultivar	852.62	<.0001***
Year × cultivar	151.88	<.0001***
Total root length captured in profile		
Year	28.30	<.0001***
Cultivar	231.39	<.0001***
Year × cultivar	78.31	.0002***
Root length captured below 30 cm		
Year	27.01	<.0001***
Cultivar	70.27	<.0001***
Year × cultivar	50.38	.1048 NS
Proportion of root length below 30 cm		
Year	5.03	.0809 [†]
Cultivar	45.59	.0192*
Year × cultivar	30.34	.8381 NS

[†].10 > p > .05. *p < .05. ***p < .0001. NS, nonsignificant.

TABLE 5 Source of variation obtained with the Wald test in selected parameters in lentil data collected at Montana State University's Northern Agricultural Research Center in 2017, 2018 and 2019

Parameter	Sum of squares/Wald statistic	p-value
Yield		
Year	860.7	<.0001***
Cultivar	231.8	<.0001***
Year × cultivar	158.9	<.0001***
Biomass accumulation at maturity		
Year	127.7	<.0001***
Cultivar	98.4	<.0001***
Year × cultivar	82.1	<.0001***
Harvest index		
Year	10.5	.0052**
Cultivar	281.3	<.0001***
Year × cultivar	116.2	<.0001***
Total root length captured in profile		
Year	85.0	<.0001***
Cultivar	252.9	<.0001***
Year × cultivar	126.4	<.0001***
Root length captured below 30 cm		
Year	176.3	<.0001***
Cultivar	64.2	<.0001***
Year × cultivar	92.3	<.0001***
Proportion of root length below 30 cm		
Year	12.6	.0019**
Cultivar	45.2	.0055**
Year × cultivar	50.2	.0724

p < .01. *p < .0001. NS, nonsignificant.

Purushothaman et al. (2017) showed drought-adapted chick-pea cultivars increased root length at depth more than the susceptible cultivars. Williams et al. (unpublished data), in fields adjacent to these pea and lentil experiments (in 2018 and 2019) and using the same mini-rhizotron methodology, also showed significant correlations between grain yield and roots observed below 30 cm in barley (*Hordeum* L.) and wheat, so we could have reasonably expected to observe greater root growth (or a higher proportion of roots at depth) in high yielding cultivars of field pea and lentil. Several studies also investigated genotypic variability in the seminal root angle in seedlings (Manschadi et al., 2006, in wheat; Singh et al., 2011, in sorghum [*Sorghum bicolor* (L.) Moench]), based on the co-location of quantitative trait loci (QTL) of nodal root angle with drought adaptation (Mace et al., 2012). Our observations in field pea, however, are less clear. On one hand, CDC Amarillo stood out as a cultivar with a small root system overall

(Figure 1), but a high proportion of roots at depth (Figure 2) and relatively high biomass (Supplemental Table S2). Of the CDC lines evaluated in this study, CDC Amarillo also showed the highest yields in cultivar trials across Saskatchewan, yielding 7–10% more than 'CDC Meadow' (Raine & Cross, 2021). This does suggest that a lean but deep root system may be a useful adaptive trait in semi-arid environments. On the other hand, despite being grown on fields left fallow the previous year, and likely relying on stored soil moisture with all three growing seasons with lower rainfall than average, the highest yielding field pea cultivars did not consistently rank highly for root length captured below 30 cm, or the proportion of roots at depth. In fact, there was a negative association between root growth (both in general and at depth) from flowering to maturity, and yield and biomass traits (Figure 3), which suggested carbon allocation used for root growth during this period came at the expense of carbon allocated to yield

formation, an idea that was also proposed by Passioura (1983) and reiterated recently by Palta and Turner (2019).

In lentil, regression analyses showed significant relationships between root length captured below 30 cm as the independent variable with yield and biomass accumulation at maturity as dependent variables (adjusted $R^2 = 0.218$ and 0.328 respectively; p -values $< .001$ for both), but the total root length captured across depths showed better relationships (adjusted $R^2 = 0.488$ and 0.554 respectively; p -values $< .001$ for both). Lentil is considered source-limited and breeding directions have long included efforts to increase biomass accumulation to increase yield potential (Hamdi & Erskine, 1996; Tickoo et al., 2005). Therefore, it is not surprising that a larger leaf area may lead to greater carbon allocation to roots, which, in turn, would allow for greater water and nutrient acquisition and further allowing greater leaf area and biomass accumulation in a positive feedback loop.

Root length and root length distribution at different depths are also only two components of the function of root systems, and the assumption that root length development leads to water extraction in a direct linear relationship may be an oversimplification (Vadez, 2014). Other root system traits may also be important; the proportion of very fine and fine roots (Gorim & Vandenberg, 2019) and/or root hydraulic characteristics (Vadez, 2014) may be equally important for water extraction patterns during the growing season. While we had equipped each plot with 100-cm PR2 soil moisture probes (Delta-T Devices), the data collected did not allow the detection of plot differences in water extraction or correlations with root length data (not shown). The relative importance of root length vs. hydraulic characteristics is largely unknown in field pea and lentil and may well vary between species and between cultivars of the same species. It may even vary with environmental conditions and/or vary temporally during the growing season. Indeed, reports in chickpea (Zaman-Allah et al., 2011), pearl millet (Vadez et al., 2013), and wheat (Kirkegaard et al., 2007) have suggested that water extraction, specifically during flowering and grain filling, is responsible for improved grain yield; this may or may not be associated with greater root growth and could be associated with root hair growth if root length is already present (Vadez, 2014).

Although these experiments were side by side, and therefore not meant to be a comparison between the two crops, the different patterns observed in root traits and their relationship with above-ground traits suggested desirable root traits (Figures 3 and 6) may be different between crops, possibly needing to be pushed in opposite directions in breeding programs. The idea that lentil may benefit from a larger root system is however intriguing as we observed a similar range of values in the root length captured for both field pea and lentil (Figures 1, 2, 4, and 5), and yet, on average, lentil biomass at maturity was approximately 35% less than field pea (Supplemental Tables S2 and S15). Gan et al. (2011) also observed

larger root volumes in lentil compared with field pea and wheat under low rainfall conditions, particularly between 20 and 60 cm depths. Why lentil may require more root length for smaller biomass accumulation than field pea, for example, requires further investigation, and root hydraulic conductivity, in particular, would be worth looking into (Vadez, 2014).

While our objective was exploratory in nature, to investigate the material commonly used on the Northern Great Plains breeding programs, another limitation of this study in understanding the role of root systems in drought adaptation is the diversity in the genetic backgrounds of the cultivars investigated, a diversity that likely involved a number of other drought and/or heat adaptive traits also impacting yield (Palta & Turner, 2019), many of which may still be unknown. For example, in field pea, it is possible that CDC Amarillo was more susceptible to heat; as mentioned above, it generally yields better than CDC Meadow in Saskatchewan but yielded 20% less in 2018 (not shown). In addition to this experiment being located south of the original area of adaptation, we recorded a maximum temperature of 33.7°C on 10 June 2018, approximately 10 d before the full flowering sampling, and this might have affected different cultivars in different ways. Although CDC Amarillo was not investigated, a study by Jiang et al. (2020) identified CDC Meadow to be relatively better at tolerating heat stress based on greater retention of pods under two seeding dates in a field experiment in Arizona. Despite this, our data has suggested some interesting parents to create near-isogenic lines and investigate genetic molecular markers that may be associated with roots traits. Specifically, CDC Amarillo and PS0877MT457 in field pea were opposite for the two most important principal components, having contrasting root system sizes but with CDC Amarillo showing a large proportion of roots below 30 cm. In lentil, Athena and CDC Redberry, and 'NDL080187L' and Merrit were two pairs of cultivars that also were located opposite to each other in the PCA. Athena and CDC Redberry showed contrasting root systems in both the total root length captured and the proportion found below 30 cm, with Athena showing a relatively large but shallow root system, and CDC Redberry a relatively small but deep root system, with both lines producing very similar yields (not shown). Merrit and NDL080187L showed similar biomass accumulation but contrasting root systems, with Merrit demonstrating both a large root system and a high proportion of roots at depth compared with the relatively small and shallow root system of NDL080187L.

Sadras et al (2019) suggested “trait-based selection to improve stress adaptation can complement direct selection for yield provided the trait meets six criteria: (1) it must be genetically correlated with yield in the target environments; (2) it should be less affected by the G×E interaction than yield; (3) it should not be associated with low yield in favorable conditions; (4) it must show genetic variation; (5) it must be

genetically stable, persistent across generations and relevant in different genetic backgrounds, and (6) it must lend itself to rapid, cost-effective and reliable quantification” (p. 1. On this last point, Reynolds et al. (2020) nuanced this argument by including “precision phenotyping traits, which are generally low throughput and/or expensive, but offer the potential for high payoffs in terms of opening current bottlenecks to yield improvements” (p. 3 in phenotyping methodologies that breeders increasingly utilize. Our data demonstrated that root traits are less affected by environment and G×E interactions than yield and biomass, although year and year × cultivar interactions often remained important components of the variation observed, and these were only grown at one location. We also demonstrated genetic variation, but there is no question that the evaluation of root traits in situ with mini-rhizotrons is low throughput, labor-intensive, and expensive. Perhaps this explains why the evaluation of seedling root traits, with automated batch analysis of scanned images, has become a popular alternative. However, one should be careful to ensure that seedling root traits are indeed correlated with yields in the field (Sadras et al., 2019) or with the expected rooting behavior later in the crop’s development. Investigations in wheat and barley (Williams et al., unpublished data) suggested that this may not always be the case: stay-green barley lines with a higher proportion of roots at depth and greater root growth during reproductive stages demonstrated wider rather than narrower root angles at the seedling stage. In addition, getting realistic root growth until maturity is particularly challenging under controlled-environment conditions (Rich et al., 2020). Finally, it is crucial to understand how much, and in what growing conditions, various root traits may provide benefits before spending efforts finding proxies for root growth. This does not, at this stage, appear feasible with fast and inexpensive methods in field pea or lentil.

5 | CONCLUSION

There has been much recent interest and efforts to improve drought tolerance in crops with selection based on root traits. We conducted experiments to investigate the genotypic variability in root traits in 29 field pea cultivars and 25 lentil cultivars. While there was large genotypic variability in both root system size and the proportion of roots at depth in both crops, neither of these root traits appeared to be good selection criteria for improving yields in semi-arid growing environments. In field pea, the highest yielding cultivars tended to be ranked intermediary for the proportion of root length captured below 30 cm and in terms of total root length captured across depths. There was also a negative association between root development during grain filling (both in general and at depth), and yield and biomass traits, which suggested carbon

allocation used for root growth during this period came at the expense of carbon allocated to biomass and yield. In lentil, root length was well correlated with biomass accumulation and yield, which suggested that using biomass and yield as selection criteria would be just as effective.

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AUTHOR CONTRIBUTIONS

Maryse Bourgault: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Validation; Visualization; Writing-original draft. Peggy Lamb: Conceptualization; Investigation; Methodology; Writing-review & editing. Kevin McPhee: Conceptualization; Methodology; Writing-review & editing. Rebecca J. McGee: Conceptualization; Methodology; Writing-review & editing. Albert Vandenberg: Conceptualization; Methodology; Writing-review & editing. Tom Warkentin: Conceptualization; Methodology; Writing-review & editing.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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