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Thinopyrum intermedium showed a slower establishment phase compared to winter wheat in a controlled environment

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Abstract

Thinopyrum intermedium is currently proposed as a perennial grain crop benefiting from raising interest through its environmental performances. As a new crop, little attention was paid to the understanding of the eco-physiological regulations of its growth cycle. We conducted an experiment in growth chambers to evaluate the aboveground and belowground development of *Th. intermedium* in comparison to annual wheat during the first days of growth after sowing. The dynamic of growth was faster for wheat, in line with a strategy of rapid acquisition of resources and a quicker colonization of its environment compared to *Th. intermedium*. In contrast, the latter had a preferential investment in roots that could reflect an adaptation from nutrient-poor environments to prioritize soil resource acquisition. These insights highlighted a slow establishment phase for this new crop, which may lead to difficulties during the field establishment, such as weed competition, but could enable it to withstand stressful conditions in terms of soil resources once well established.

1 | INTRODUCTION

Thinopyrum intermedium (Host) Barkworth and D. R. Dewey, also known under the trade name Kernza, is a wheat relative (Mahelka et al., 2011), which is attracting growing interest because of its multiple roles. It produces grain for human consumption and forage for livestock, while providing various ecosystem services. Indeed, as a perennial grass, the extended belowground activity and the year-round soil cover are beneficial for soil protection, soil fertility, or water quality (Culman et al., 2013; Duchene et al., 2020). The root system of *Th. intermedium* can be as deep as 3 m (Dehaan & Ismail, 2017). The biomass of its coarse and fine roots was estimated to be 3–12 times greater than that of wheat (Sprunger et al., 2018). This leads, in the field, to 90% of soil colonized by roots within the first 60 cm of the soil compared to 60% for annual cereals (Duchene et al., 2020). In the study of Sprunger et al. (2018), *Th. intermedium* allocated 23%–50% of its total biomass to roots compared to 10% for wheat. Although great progress has been achieved through breeding (Bajgain et al., 2022), the crop is still under domestication. Its grain yield potential remains low compared to its annual counterparts, with a maximum of 1 t ha^{-1} (Fagnant et al., 2024a) as its forage production is mainly made up of the summer straw (Culman et al., 2023; Fagnant et al., 2024b).

As highlighted by Duchene et al. (2021), little attention was paid to the understanding of the eco-physiological regulation of *Th. intermedium*'s growth cycle. Measurement of plants' functional traits can help explain their individual responses to biotic and abiotic factors through a trade-off between growth and survival. This approach is useful to identify synergies and trade-offs among market and non-market services (Duru

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Abbreviations: AMF, arbuscular mycorrhizal fungi; DIY, do it yourself; GDD, growing degree days.

et al., 2015; Freschet et al., 2021). Deriving from previous theoretical and empirical works (see, for example, Mooney, 1972 or Grime, 1974), variation in plant functioning can be linked to an economics spectrum ranging from a resource "acquisitive" to a resource "conservative" strategy. These resource economics traits have consequences for plant performance across the continuum of low to high levels of resources inducing a trade-off between "slow" versus "fast" return on investment (Reich, 2014). Plant species on the fast side of the plant economics spectrum are usually characterized by greater photosynthetic activity and respiration rates, higher leaf nutrient concentration (e.g., high N content), and lower leaf mass per unit leaf area (which is the inverse of the specific leaf area). Plant species located on the slow side of the gradient, however, have the opposite strategy and build longer-lived leaves that are better defended with a lower nutrient concentration and greater leaf mass per unit area (Weigelt et al., 2021; Wright et al., 2004). In addition to leaf traits, other traits linked to seed production, fine root construction, and development and maintenance of symbiotic relationships with mycorrhiza are undoubtedly important for plant fitness (Wright et al., 2004). Contrary to leaf traits, traits related to the fine root construction are multidimensional (Kramer-Walter et al., 2016). Using global root trait data, Bergmann et al. (2020) identified two main axes of root trait variation between plant species. The first axis, referred to as the collaboration gradient, represents the trade-off between species with "do-it-yourself" (DIY) and "outsourcing" strategies. While DIY species build long but fine roots (low root diameter and high specific root length) to explore the soil and take up resources, outsourcing species outsource resource uptake to arbuscular mycorrhizal fungi (AMF) by building thicker roots with a larger cortex fraction that are better suited to host AMF. The second axis, referred to as the conservation gradient, represents a trade-off between fast and slow return on investment. While species on the fast side of the root conservation gradient are characterized by a higher-than-average root nitrogen concentration, species on the slow side of the gradient have a higher-than-average root tissue density (Bergmann et al., 2020; Weigelt et al., 2021). Together, the collaboration and the conservation gradients explain 77% of interspecific root trait variation and form the so-called root economics space (Bergmann et al., 2020; Weigelt et al., 2021).

As highlighted by Roumet et al. (2006), annuals generally occur in disturbed habitats and have functional traits enabling a rapid exploitation of resources, which is crucial to grow fast and to complete their life cycle in a short period of time. By contrast, perennial species have functional traits reflecting longer-lived tissues associated with persistence and defense, probably originating from an adaptation to survive and to monopolize space in environments where the competition is strong (Roumet et al., 2006). Some evidence of resource conservation of *Th. intermedium* was highlighted in different studies. Duchene et al. (2021) suggested that *Th. intermedium* belongs to the slow-growing and more "conservative" plants under French and Belgium temperate conditions through the higher accumulation of growing degree days (GDD) until flowering compared to earlier plants (e.g., *Lolium perenne* or *Festuca pratense*). These later flowering species are generally characterized by taller stands, longer leaf lifespan, lower specific leaf area, lower leaf nitrogen concentration, and relative growth rate. More recently, through the establishment of its nitrogen dilution curve, Fagnant et al. (2023) found out that nitrogen requirements of the crop were much lower compared to conventional annual crop such as *Triticum aestivum* L. (wheat) or *Zea mays* L. (maize). This trait is consistent with the high nitrogen use efficiency reported for this species (Sprunger et al., 2018). Furthermore, a decrease in the nitrogen amount (i.e., mass of N per hectare) of the aboveground biomass during the second phase of growth was also observed and can be related to the long-term survival strategy of the crop, with reduced resource allocation to seeds and substantial investments belowground (Fagnant et al., 2023). In this regard, Duchene et al. (2020) hypothesized that some observed root traits of *Th. intermedium* could also be linked to a resource conservative strategy, namely, the higher tissue density.

In this study, our aim was to compare early growth dynamics (i.e., the first days of growth after sowing), biomass allocation, and above- and belowground functional strategies of *Th. intermedium* with a major annual cereal crop, namely, *Triticum aestivum* L. Considering the difficulty of measuring root traits in field, this comparison was conducted under controlled environmental conditions.

Core Ideas

- *Thinopyrum intermedium* had a preferential investment in roots compared to wheat in the establishment phase.
- A slow establishment phase was observed for *Th. intermedium*.
- *Thinopyrum intermedium* exhibited traits associated with a resource conservation strategy.
- The potential competitive advantage of *Th. intermedium* in harsh field conditions can compromise its field establishment.

2 | MATERIALS AND METHODS

2.1 | Selection of species and growth conditions

The perennial grass *Th. intermedium* (Host) Barkworth & D.R. Dewey and its annual counterpart *Triticum aestivum* L. (winter wheat) were grown in a growth chamber under controlled conditions at the faculty of ULiège–Gembloux Agro-Bio Tech, Belgium. Crops were grown in adequate conditions, that is, with air temperature ranging from 20.5˚C to 22.5˚C, a mean relative humidity of 59%, and a daylength of 14 h with a light irradiance of 360 µmol m^{-2} s^{-1}.

The seeds of *Th. intermedium* originated from The Land Institute; 8th cycle of selection (TLI-C8) with an average seed mass of 13 mg. The average seed mass of wheat (Chevignon variety) was 46 mg. The experiment was conducted until seedling establishment, with plants no longer relying on seed reserves (i.e., 15 days after sowing—BBCH14 for wheat and BBCH12 for *Th. intermedium*; Meier, 2018). A completely randomized block design with eight replicates per species was used (i.e., four blocks, with two replicates per block). To facilitate root growth analyses, the two species were grown in rhizoboxes (width: 30 cm, height: 60 cm, and thickness: 2 cm). They were filled with a 5 mm-sieved substrate composed of compost (70%, v/v) and sand (30%, v/v) (Alonso-Crespo, 2021), and characterized by a density of 1.6 g cm^{-3} at the maximal water holding capacity at the beginning of the experiment. One pre-germinated seed was placed against the transparent window of each rhizobox, 2 cm below the soil surface.

Each rhizobox was watered regularly to keep the substrate at water holding capacity throughout the experiment. Boxes were inclined at a 45˚ angle with the transparent window facing downward to allow the roots to grow along the transparent front window. To prevent light from reaching the roots, the transparent window was covered by an opaque plate. The experiment was stopped when roots reached the bottom of the rhizoboxes (i.e., 15 days after transplantation).

2.2 | Data collection

The root system development of each species was followed non-destructively using image analysis as described in Alonso-Crespo et al. (2023). Briefly, images of roots growing along the front window of the rhizoboxes were taken on the 9th, 10th, 11th, 12th, and 15th day after seeding. Image acquisition was done with a digital camera (i.e., Nikon D3400 with the AF-P DX NIKKOR 18–55 m lens, image resolution: 453 dpi) as shown in Figure 1. The image analysis pipeline consisted of two steps. First, a convolutional neural network was trained with the RootPainter software to detect roots in the images (Smith et al., 2022). Then, the total visible root length was estimated in each image by analyzing segmented images using the open-access software RhizoVision Explorer v2.0.3 (Seethepalli & York, 2020) using algorithms described by Seethepalli et al. (2021). At the time of image acquisition, the maximum rooting depth was manually measured and the phenological stage of each plant was rated using the BBCH scale for the two species (Meier, 2018). GDD were summed during the experiment with a mean value of 21.5˚C.

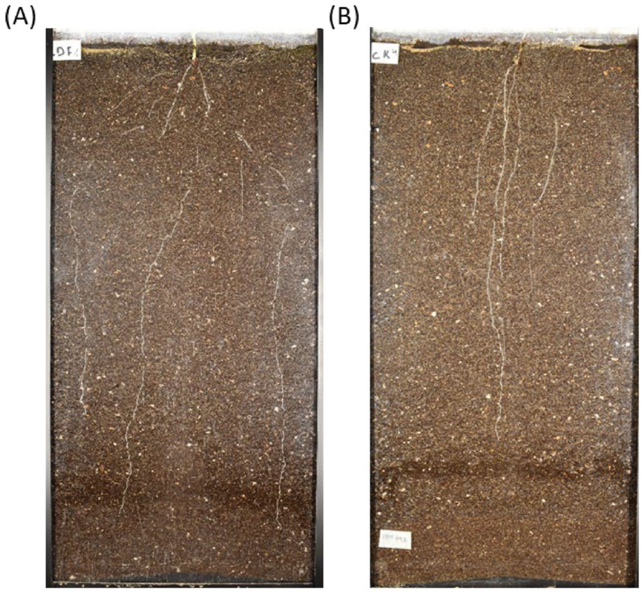

FIGURE 1 Images (scale of 5:36) of root systems at the end of the experiment (i.e., 15th day after seeding) within rhizobox for (A) wheat and (B) *Thinopyrum intermedium*.

At the end of the experiment, rhizoboxes were opened to collect the shoot and root biomass of each plant individual. Shoot and root fresh and dry (dried in an oven at 60˚C until constant weight) weights were measured right after collection. The total leaf area of each plant was obtained by scanning the lamina of fresh leaves on a flatbed scanner. The total leaf area in each image was estimated with ImageJ. The rooting system was separated in three soil layers, namely, H1 (0–20 cm), H2 (20–40 cm), and H3 (40–60 cm). Roots collected in different soil layers were scanned independently on a flatbed scanner (Epson Perfection V800 Photo; image resolution: 600 dpi) and analyzed using RhizoVision Explorer v2.0.3 (Seethepalli & York, 2020) to determine root length, root diameter, and root volume in each image.

Using the data described above, we quantified the following root traits for each species: specific root length (total root length divided by root dry weight), root mass fraction (root dry weight divided by plant dry weight), and root tissue density (ratio of the root system volume obtained and root dry weight).

2.3 | Statistical analysis

Data analysis was conducted in the R program version 4.1.2 (R Core Team, 2021).

The strength of the linear relationship between the visible root length estimated with image analysis and the root length measured after root system extraction at the end of the experiment was assessed with the *cor_test* function (Pearson's correlation coefficient) from the *rstatix* package. Measured and calculated root length were highly positively correlated, as shown in Figure S1.

The temporal evolution of total root length was modeled using a generalized linear mixed-effect model with a Gaussian distribution and an inverse-link function from the *glmer* function of the *lme4* package. The maximum rooting depth was modeled using linear mixed-effect model from the *lmer* function of the *lme4* package. The fixed effects were composed of the species treatment and the sum of GDD from sowing and their interaction. As these two parameters were measured at multiple time points in each rhizobox during the experiment, a random slope and intercept for each rhizobox was used. Blocks were also considered as a random factor (random intercept). The allometric relationship between the shoot and root biomass at the end of the experiment was tested using a linear mixed-effect model with the *lmer* function from the *lme4* package. The fixed effects were composed of the species treatment and blocks were considered as a random factor.

Leaf area, shoot and root dry weight, root mass fraction, specific root length, total root length, root tissue density, maximum rooting depth, and root diameter were analyzed using mixed-effect models, where the species treatment was considered as fixed factor, while blocks were considered as a random factor. Following analysis of variance analysis, pairwise comparisons among treatment means were evaluated with the *emmeans* function from the *emmeans* package with a Tukey adjustment for multiple comparisons. Statistical significance was set at 0.05. The *lmer* function from the *lme4* package was used for linear mixed-effect models. They were evaluated to ensure they met model assumptions using the *plotresid* function.

3 | RESULTS

3.1 | Ontogenesis

The phenological development of the two species was different, with faster development reported for wheat. The appearance of the second leaf (i.e., BBCH12) was observed at 194 GDD for wheat and at 259 GDD for *Th. intermedium*.

3.2 | Root system dynamics and development

Dynamic measurements of root front growth (maximum rooting depth) and total root length are presented in Figure 2 for the two species. Similar trends were observed for the two variables, with higher values reported for wheat throughout the experiment (Figure 2A, C). In addition, the coefficients of the temporal evolution of the root front growth were higher, and of the total root length were lower for wheat (Figure 2B, D; Table 1). Results translated a faster and denser root development of wheat compared to *Th. intermedium*.

3.3 | Biomass production, allocation, and functional traits

The shoot and root parameters measured at the end of the experiment are shown in Figure 3 for the two species. The dry weight of roots (Figure 3A) as well as their length (Figure 3B) were higher in wheat compared to *Th. intermedium*. Although we did not find any difference in specific root length between the two species (Figure 3C), the root tissue density was higher for *Th. intermedium* and the mean root diameter was higher for wheat (Figure 3D,E). Focusing on shoot parameters, *Th. intermedium* had lower shoot dry weight and leaf area than wheat (Figure 3F,G). The root mass fraction (i.e., proportion of the biomass of roots to the entire plant biomass) of *Th. intermedium* was higher than the one observed in wheat (Figure 3H).

Root proportion (i.e., root biomass within the soil layer divided by the total root biomass) within the different soil layers is shown in Figure 4. Through a slower root system establishment (Figure 2), the root proportion of *Th. intermedium* is higher (i.e., 77%) in the first cm of soil compared to wheat (i.e., 67%) as the opposed situation was observed under deeper soil layers (i.e., 20–40 cm and 40–60 cm; Figure 4).

The allometric relationship at the end of the experiment between shoot and root biomass is shown in Figure 5 for the two species. Shoot and root biomass were higher for wheat. However, the relationship between shoot and root biomass was not statistically different between species as the slopes have a wide 95% credibility interval (Figure 5).

4 | DISCUSSION

As highlighted by Freschet et al. (2021), root trait values can strongly differ between plants grown in laboratory and field experiments, as the consequence of different environmental conditions. Under our controlled conditions, on a non-resource-limited substrate and without obstacles to root growth, the dynamic of growth was faster for winter wheat

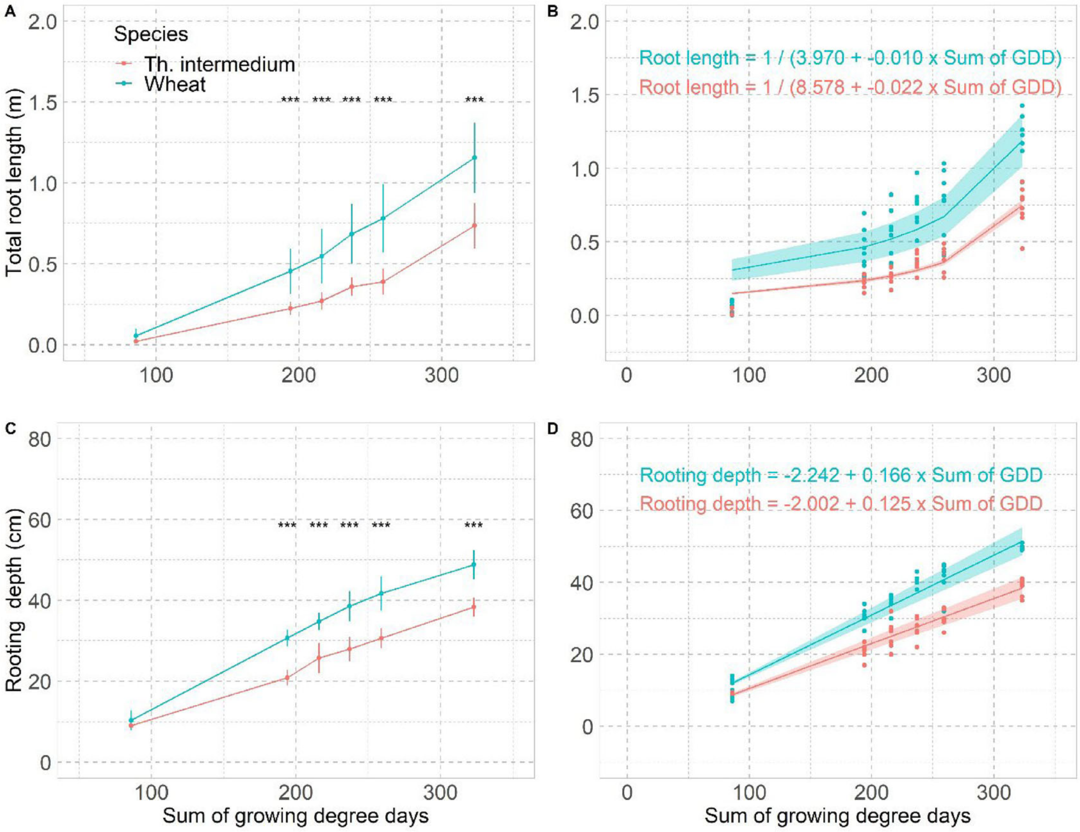

FIGURE 2 Temporal evolution of (A) total root length and of (C) maximum rooting depth for the two species. Panels B and D show generalized mixed-effect model fits describing the temporal evolution of (B) total root length and (D) maximum rooting depth. Individual observations are shown as dots. In (A) and (C), statistical differences (post hoc analysis) between species are indicated by '***' = p-value ≤ 0.001.

TABLE 1 Intercept and slope coefficients for the temporal evolution of (A) total root length and (B) maximum rooting depth for the two species.

		Intercept		**Slope**		
		Coefficient *a*	**95% Credibility interval**	**Coefficient *b***	**95% Credibility interval**	**Equation**
(A) Total root length (m)	Wheat	3.97	[3.34, 4.60]	−0.01	[−0.01, −0.01]	$y = 1/(a + b{\cdot}x)$
	Thinopyrum intermedium	8.58	[7.49, 9.67]	−0.02	[−0.03, −0.02]	
(B) Rooting depth (cm)	Wheat	−2.24	[−5.37, 0.89]	0.17	[0.15, 0.18]	$y = a + b{\cdot}x$
	Thinopyrum intermedium	−2.00	[−4.27, 0.27]	0.13	[0.12, 0.14]	

compared to *Th. intermedium*. More precisely, the higher relative growth rate of winter wheat led to higher values of total root length, rooting depth, total root dry weight, shoot dry weight, and leaf area at the end of our experiment (Figure 2 and Figure 3). These findings are in line with a strategy of rapid colonization of the environment and acquisition of resources highlighting a "fast" return on investment into tissue construction (Weigelt et al., 2021; Wright et al., 2004). In contrast, *Th. intermedium* exhibited higher root tissue density (Figure 3D), in line with what observed Duchene et al. (2020) in field experiments. Slower growth and higher root, stem and leaf tissue densities can reveal a "conservative" strategy and/or an adaptation to infertile soil conditions (Kramer-Walter et al., 2016). Therefore, studying the development of *Th. intermedium* on a resource-limited substrate could further confirm these hypotheses.

The specific root length was similar between species as a higher mean root diameter was observed for wheat (Figure 3C, E). This is in contradiction with Duchene et al. (2020) that observed a higher root diameter and a lower specific root length of *Th. intermedium* in comparison with annual wheat or rye in field. They suggested that the less efficient soil exploration of *Th. intermedium* (i.e., lower specific root length and higher root diameter) was compensated by soil resource acquisition through mycorrhizal symbionts as the AMF biomass in the soil increased

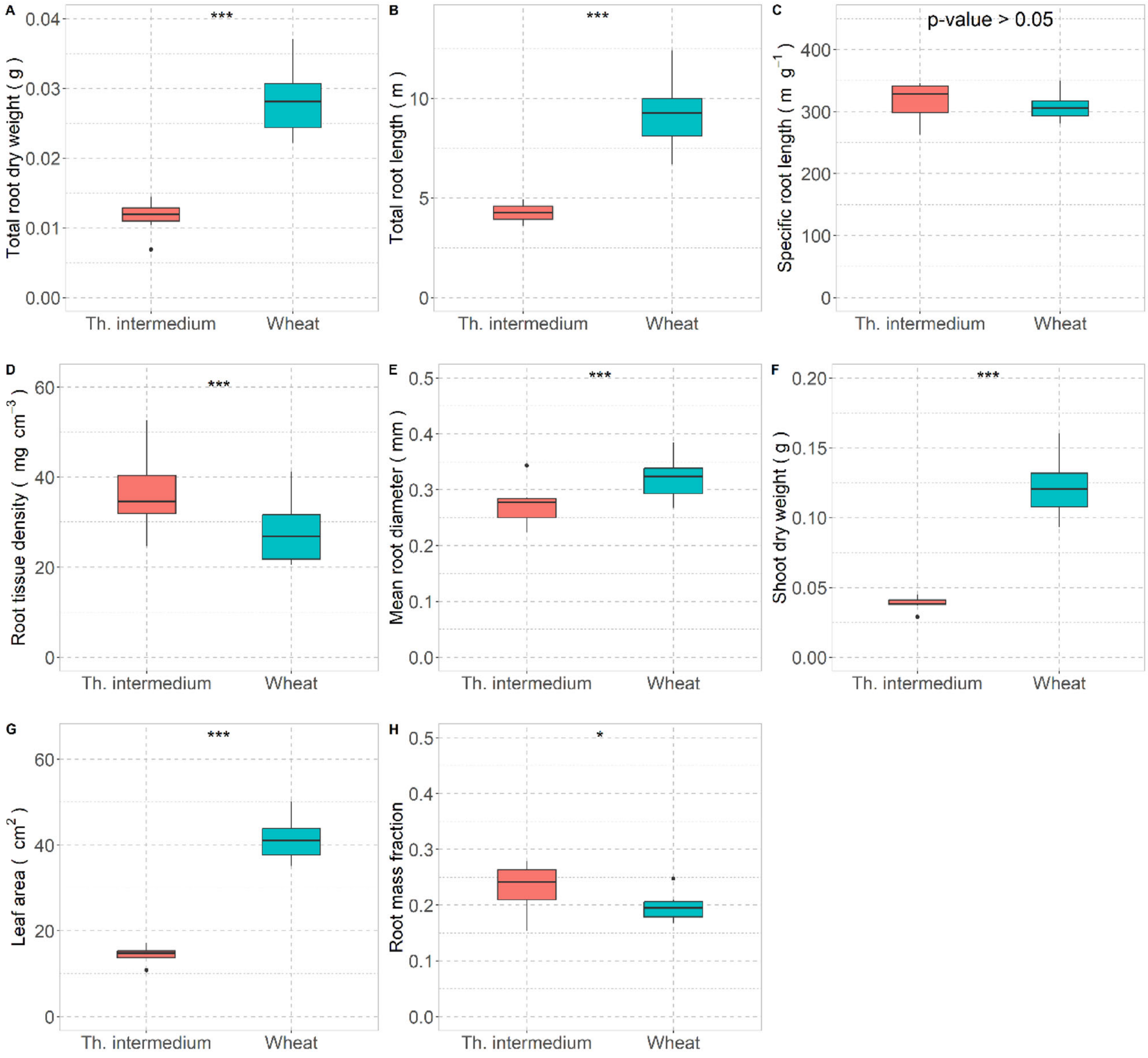

FIGURE 3 Shoot and root parameters measured at the end of the experiment: (A) total root dry weight, (B) total root length, (C) specific root length, (D) root tissue density, (E) mean root diameter, (F) shoot dry weight, (G) leaf area, and (H) root mass fraction for the two species. Statistical differences (post hoc analysis) between species are indicated by '*' = p-value ≤ 0.05, '**' = p-value ≤ 0.01, or '***' = p-value ≤ 0.001.

under *Th. intermedium*. In our study, we didn't differentiate coarse (i.e., transportive roots) and fine roots (i.e., acquisitive roots), leading to difficulties in interpreting these parameters. More dedicated work is therefore needed to conclude on the "outsourcing" strategy of these two species.

Regarding the relationship between shoot and root biomass at the end of the experiment, dynamics between species are very contrasted. Higher root biomass was translated into higher shoot biomass for wheat (Figure 5), contrarily to what was observed for *Th. intermedium*. Yet, the global partitioning of biomass toward roots was higher for *Th. intermedium* (Figure 3H). The greater proportion of biomass into roots could potentially induce a greater proportion of photosynthetically fixed carbon, which is respired and globally explain its lower relative growth rate (Poorter et al., 1990). In contrast, species with a higher amount of reserves in the seed—as it is the case for wheat—can increase the aboveground biomass partitioning of seedlings (Mašková & Herben, 2018). Thus, the fast development of wheat shoots may be highly beneficial to ensure a better light interception, as solar radiation might represent the limiting resource in nutrient-rich environments. Concerning *Th. intermedium*, its greater investment in soil exploration was also highlighted in field experiment by Sprunger et al. (2018), who found out that *Th. intermedium* allocated 23% to 50% of its total biomass to roots while it was only about 10% for wheat, leading to a root-shoot ratio two times greater for *Th. intermedium* than for wheat. In their study, Sainju et al. (2017) even reported root-shoot ratio more

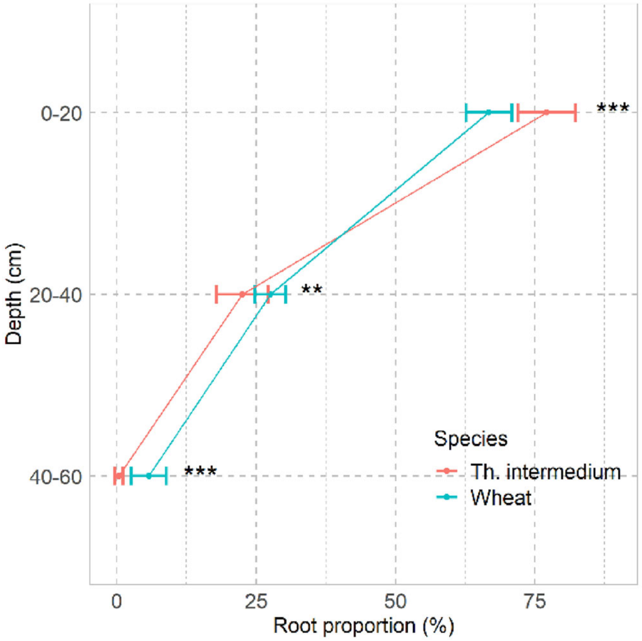

FIGURE 4 Relative proportion of roots in each soil layer for each species. Statistical differences (post hoc analysis) between species are indicated by '**' = *p*-value ≤ 0.01 or '***' = *p*-value ≤ 0.001.

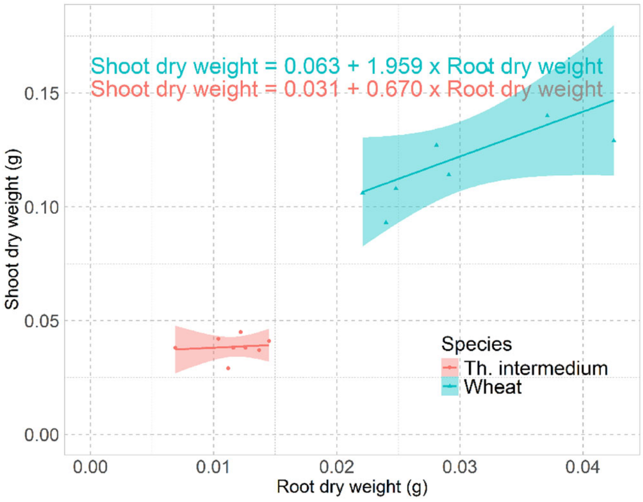

FIGURE 5 Allometric relationship between shoot and root dry weight for the two species at the end of the experiment. The slope 95% credibility interval was (0.134 and 3.807) for wheat and (−0.866 and 1.903) for *Thinopyrum intermedium*.

than eight times greater for *Th. intermedium* compared to spring wheat. A higher proportion of roots is known to be related to an adaptation to nutrient-poor environments, where belowground competition prevails, to enhance the acquisition of soil resources (Tilman, 1985). Greater root mass fraction is one of the mechanisms by which plants cope with limitations in soil resources (Poorter, 1989). Nevertheless, the poor early vigor *of Th. intermedium*, translated by low shoot biomass, can result in difficulties for its field establishment in comparison to traditional wheat varieties. In practice, this was previously observed in field conditions by Duchene et al. (2023), who reported low *Th. intermedium* biomass during the first establishment year, which resulted in important weed competition.

5 | CONCLUSION

The functional traits that were selected to allow growth in contrasted environments might reflect different conceptual strategies set up by crops to ensure their long-term survival. Results gained in this rhizobox experiment conducted during the juvenile phase of two crop species globally confirmed that winter wheat is characterized by a strategy of rapid acquisition of resources and a quicker colonization of its environment, compared to *Th. intermedium*. Such a development pattern could reflect an adaptation to nutrient-rich environments where an effective strategy would then be to maximize the capture of light through greater leaf development. In contrast, *Th. intermedium* exhibited traits associated with a resource conservation strategy. While its absolute above- and belowground growth rates were lower compared to winter wheat, *Th. intermedium* invest preferentially in its root system. This could reflect an adaptation to nutrient-poor environments, through the optimization of soil resource acquisition. While this last trait may provide a competitive advantage in harsh field conditions, it can compromise the field establishment phase of the crop. While some evidence already exists within the literature, the conclusions drawn here were obtained on juvenile plants grown in a controlled environment and on a non-resource-limited substrate and remain to be confirmed within field conditions. Yet, this study contributes to provide new evidence of a resource conversation strategy for *Th. intermedium*, which might be consistent with its well-known perenniality.

AUTHOR CONTRIBUTIONS

Laura Fagnant: Conceptualization; formal analysis; investigation; writing—original draft. **Pierre Delaplace**: Conceptualization; methodology; supervision; validation. **Benjamin M. Delory**: Conceptualization; formal analysis; investigation; methodology; supervision; validation. **Benjamin Dumont**: Conceptualization; formal analysis; supervision; validation.

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NA.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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